UNIFYING ECOLOGY ACROSS SCALES: PROGRESS, CHALLENGES AND OPPORTUNITIES

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PUBLISHED IN: Frontiers in Ecology and Evolution

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88966-292-0
DOI 10.3389/978-2-88966-292-0

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UNIFYING ECOLOGY ACROSS SCALES: PROGRESS, CHALLENGES AND OPPORTUNITIES

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Citation: O'Connor, M. I., Barneche, D., Messier, J., Gonzalez, A. L., eds. (2020). Unifying Ecology Across Scales: Progress, Challenges and Opportunities. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88966-292-0

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frontiers in Ecology and Evolution

EDITORIAL
published: 30 October 2020
doi: 10.3389/fevo.2020.610459

Editorial: Unifying Ecology Across Scales: Progress, Challenges and Opportunities

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Keywords: ecology, global change, models, allometry, information theory, metabolic theory of ecology (MTE), population dynamics

OPEN ACCESS

Edited and reviewed by:
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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *25 September 2020*
Accepted: *09 October 2020*
Published: *30 October 2020*

Citation:
O'Connor MI, Barneche DR,
González AL and Messier J (2020)
Editorial: Unifying Ecology Across
Scales: Progress, Challenges and
Opportunities.
Front. Ecol. Evol. 8:610459.
doi: 10.3389/fevo.2020.610459

Editorial on the Research Topic

Unifying Ecology Across Scales: Progress, Challenges and Opportunities

THE NEED TO UNIFY ECOLOGY: A GRAND CHALLENGE FOR A CHANGING WORLD

Ecology is the science of how living systems grow, change, and persist. Although this is not the definition presented in most textbooks, this is the central theme of this scientific discipline as it is practiced in the current era of rapid global change. Change comes in many forms, from natural succession of communities to biological invasions affecting patterns of biodiversity to the collapse of fisheries. Understanding and forecasting natural change as well as mitigating undesirable anthropogenic change is one of the grand challenges we face in the twenty-first century.

With our collective focus on global change, the ecological sciences—from organismal, population, community, and ecosystem ecology to evolutionary ecology—are undergoing a revolution. It has become clear that although we have vast and multifaceted ecological knowledge, it has yet to solidify into a coherent body of science. For example, over decades in the latter half of the twentieth century researchers, journals and even entire academic departments focused on specific branches of ecological thinking as narrowly defined as behavioral ecology, population ecology, or community ecology. Currently though, it has become clear that to understand our changing world and our place in it, examining the ecological changes afoot from a fragmented and narrow disciplinary perspective is insufficient. Population dynamics, ecosystem functions, individual behavior, and other aspects of living systems are deeply connected, and we cannot project changes in one without understanding how they are related to other processes across scales of space and time and levels of biological organization.

CONTRIBUTIONS IN THIS SPECIAL TOPIC

In recent decades, efforts to unify ecological understanding across scales and levels of organization have flourished and disciplinary barriers have fallen (see, for example, Brown et al., 2004; Scheiner and Willig, 2008; Harte, 2011; Marquet et al., 2014). In this special topic, we highlight recent progress in the unification of ecological sciences. Papers in this issue can be organized in three groups. Some papers take a very broad view on the current state of ecology, proposing frameworks and approaches to organize understanding and guide new research (Fulton et al.; Hodapp et al.;

Kempes et al.; Martinez; O'Connor et al.). A second group provides concrete tools and approaches to unifying ecological data and models, through specific and quantitative frameworks (McCabe and Dietze; Newman et al.; Niklas and Hammond; Tekin et al.; Yen et al.). A third group provides specific analyses that reveal new insights into how dynamics in natural systems are linked across scales and levels of organization (Amarasekare; Bideault et al.; Cavan et al.; Gibert and Yeakel; Pawar et al.; Segura and Perera; Zelnik et al.; Ziv and Davidowitz). Together, this issue is full of big ideas complemented by specific analyses, providing an exciting and welcome step in our ongoing effort for a unified science of ecology.

Fulton et al. offer a sweeping view of ecology, moving through what they identify as a transitional period now to a future in which we will have developed a more coherent ecological science through better models. This paper is a must-read, providing an impressive and inspiring perspective on the successes of synthesis in ecology through models. Among the many successes they highlight is the recognition that we understand that human activities and evolutionary change both occur within ecological time scales, and "*this new reality drives home that ecology lacks a universally solid foundation from which to extend existing theories and modeling approaches to easily absorb the many interacting components and scales.*" Fulton et al. identify immediate challenges as the need to embrace new modeling approaches that span more dimensions and allow more dynamic and evolving parameterizations and structures to allow models to incorporate new sources of data. They emphasize that these advances require not only technical advances in modeling, but also coordinated advances in ecological theory and concepts, as well as multiscale data streams. To continue the ecological tradition of using models to explain and predict, now in a rapidly changing world, they argue for continued investment in an approach that unifies disparate ideas while also allowing multiple approaches to be employed to solve the problems we face.

Other contributions propose frameworks to unify concepts across scales, disciplines, and levels of organization. Consistent with Fulton et al.'s call for greater attention to a universally solid foundation for ecological science, O'Connor et al. propose strengthening the foundation by integrating concepts of information and information theory into ecology's fundamental principles. They review major concepts in information theory, and highlight how these fundamental principles of science have not been fully explored in ecological understanding. Their paper provides a set of ecological principles grounded firmly in a science that includes information processing as fundamental to living systems, along with energy flows and material cycles. Similarly, with firm grounding in these first principles, Kempes et al. provide scaffolding that explains how evolution must occur within the boundaries of the physical world, and what these physical constraints imply for all that we still do not know about evolution. Martinez extends a unifying framework further with allometric networks, and like several other proposed frameworks in this issue, Martinez includes humans and socio-ecological systems in his unifying scheme. Hodapp et al. provide additional structure through emphasizing resource use efficiency as a unifying concept across diverse living systems, which may differ in the identity and number of limiting resources, trophic levels, and ecological, temporal and spatial scales.

Inspired by the broad roadmap laid out by contributions like those described above, we might then ask, "how do we proceed and implement a unifying framework?". This is a hard question. Thoughtful and constructive answers are provided in every paper in this edition. Yen et al. identify the statistical challenge of integrating data—often collected specifically at one level of biological organization—across multiple levels of organization. They provide an approach integrating multiple data types and parameterize more complex, process-explicit models, providing a path forward to testing multi-scale theory using data spanning many organizational levels. Niklas and Hammond's contribution dives into understanding body form and function in generalized terms, and renders the allometric scaling model more biologically relevant and useful by exposing the value and meaning of the often-overlooked scaling normalization constant. Newman et al. identify and explain specific challenges that we face when trying to understand emergent patterns of complex ecological systems at landscape scales: coarse-graining, the middle number problem of the domain of data complexity, and non-stationarity issues when predicting future ecological states from models based on adjustable parameters. McCabe and Dietze offer a solution to another landscape-scale problem—scaling contagious disturbance. They provide an approach that allows modeling of such events in the context of climate change, thereby linking community-scale disturbance events with broader scale climate change and feedbacks. Cavan et al. also work with climate change models and finer scale ecological dynamics by using the metabolic theory of ecology (MTE) to link rates of carbon flux in microbial systems to global climate feedbacks.

Tekin et al.'s contribution provides an approach that could potentially also serve as an important part of a unifying framework by demonstrating that many if not all measures of pairwise interactions—present in a diverse array of complex systems across very different scientific disciplines—can be derived from and analyzed in the context of a single mathematical framework. They build upon this finding to introduce consistent measures of higher order interactions. In this way they provide a practical tool and an insightful guide to thinking about complexity that is likely to benefit unification efforts across ecological (and other scientific) disciplines.

The third set of papers in this issue dives deeper into ecological and evolutionary dynamical models. These contributions implement unifying concepts by integrating ideas from diverse areas of thought into a single framework for population dynamics, and then analyzing the models to understand possible patterns and processes in nature. Gibert and Yeakel demonstrate how evolutionary change within the context of ecological dynamics can provide unexpected links between individual traits and the structure of an emergent food web. Ziv and Davidowitz link landscape-scale features (patch size and fragmentation) to evolutionary outcomes (selection for life-history traits increasing survival) and population dynamics (likelihood of population extinction). The need for strong quantitative general predictions of fluctuations of species abundance are addressed by Segura and Perera through deriving a theoretical model that links metabolism to abundance fluctuations in ecological populations and communities. Amarasekare carefully considers how physiological effects of temperature on the rates that drive consumer resource dynamics can lead to very different consequences of warming and climate change in different thermal regimes (e.g., tropics vs. temperature). Tackling the same question from a different angle, Bideault et al. find that the way temperature dependences are distributed among the processes that determine consumer-resource interactions and outcomes can substantially affect the ultimate outcome of warming. Pawar et al. build on an immense database of consumer-resource interactions and related traits to observe that body size distributions differ for consumers foraging in two-dimensional and three-dimensional habitats. They provide a theoretical explanation for this pattern, and use their joint mathematical/empirical approach to offer new insights about how consumer resource interactions are constrained and how they flourish in different environments. Zelnik et al. provide a theoretical analysis of the effects of different spatial and temporal properties of disturbance on ecosystem stability. Their modeling approach provides insights into the tight link between temporal and spatial dimensions on ecosystem responses to disturbance. By integrating Earth System Models and satellite-derived temperature data, and using principles from MTE, Cavan et al. estimate changes in global exports of marine carbon. Their findings suggest a main role of temperature sensitivity shaping carbon outputs and call for the need of incorporating organismal temperature dependence into biogeochemical models. Each of these contributions is exciting, novel and potentially transformative to how we think about ecological dynamics and the structures they produce. These are the bricks and mortar of a unified science, providing specific and clear new ideas and observations to our body of knowledge. Many work at the intersection between population dynamics and the unifying approach of MTE, which is based on general principles of how ecological rates of energy flux and material cycling scale with body size and temperature (Brown et al., 2004).

The contributions in this issue advance current themes in unifying efforts, specifically those employing MTE (Bideault et al.; Cavan et al.) or its core allometric scaling model (Kempes et al.; Martinez; Niklas and Hammond), those integrating data and models (Fulton et al.; Newman et al.; Yen et al.), bridging between local scale dynamics and climate change models (Cavan et al.; Fulton et al.; McCabe and Dietze), and those focusing on resource use and trade-offs (Hodapp et al.; Ziv and Davidowicz). Newer themes in unifying ecological science are also emerging, in the form of emphasis on disturbance and its multi-scale consequences (McCabe and Dietze; Segura and Perera; Zelnik et al.), on trait based perspectives on consumer-resource interactions and interaction strengths (Amarasekare; Bideault et al.; Pawar et al.; Tekin et al.), eco-evolutionary feedbacks (Gilbert and Yeakel; Kempes et al.) and on information as a unifying principle for mainstream ecological thinking (O'Connor et al.). Together, the full issue opens doors and guides our steps through them in our collective efforts to better understand our changing biosphere through ecological science.

AUTHOR CONTRIBUTIONS

All authors created the vision for the special issue, served as editors, and discussed the main concept for the editorial manuscript. MO'C wrote the manuscript. All authors reviewed and edited it.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 23 October 2018
doi: 10.3389/fevo.2018.00166

General Form for Interaction Measures and Framework for Deriving Higher-Order Emergent Effects

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Interactions are ubiquitous and have been extensively studied in many ecological, evolutionary, and physiological systems. A variety of measures—ANOVA, covariance, epistatic additivity, mutual information, joint cumulants, Bliss independence—exist that compute interactions across fields. However, these are not discussed and derived within a single, general framework. This missing framework likely contributes to the confusion about proper formulations and interpretations of higher-order interactions. Intriguingly, despite higher-order interactions having received little attention, they have been recently discovered to be highly prevalent and to likely impact the dynamics of complex biological systems. Here, we introduce a single, explicit mathematical framework that simultaneously encompasses all of these measures of pairwise interactions. The generality and simplicity of this framework allows us to establish a rigorous method for deriving higher-order interaction measures based on any of the pairwise interactions listed above. These generalized higher-order interaction measures enable the exploration of emergent phenomena across systems such as multiple predator effects, gene epistasis, and environmental stressors. These results provide a mechanistic basis to better account for how interactions affect biological systems. Our theoretical advance provides a foundation for understanding multi-component interactions in complex systems such as evolving populations within ecosystems or communities.

Keywords: complex biological systems, emergent patterns, higher-order interactions, ecological interactions, biodiversity

OPEN ACCESS

Edited by:
Mary I. O'Connor,
University of British Columbia, Canada

Reviewed by:
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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *11 May 2018*
Accepted: *02 October 2018*
Published: *23 October 2018*

Citation:
Tekin E, Yeh PJ and Savage VM (2018) General Form for Interaction Measures and Framework for Deriving Higher-Order Emergent Effects. Front. Ecol. Evol. 6:166. doi: 10.3389/fevo.2018.00166

INTRODUCTION

Because of their key role in understanding the dynamics of complex biological, physical, and social systems, there is a long and rich history of studying interactions and their consequences (Wootton, 1993; Billick and Case, 1994; Darling and Côté, 2008; Mihaila et al., 2010; Hamilton, 2011; Toprak et al., 2013; Barrios-O'neill et al., 2014; Foucquier and Guedj, 2015; Palmer et al., 2015; Podgornaia and Laub, 2015; Nishikawa and Motter, 2016; Shi, 2016). These approaches have often been complemented and enhanced by network theory that has led to important advances in prediction of patterns (Segrè et al., 2005; Yeh et al., 2006; Braun and Shah, 2015). Studies of interactions and networks have heavily and almost solely focused on two-component interactions.

As a result, we have a thorough understanding of pairwise interactions and the various interaction categorization measures defined across distinct subject areas such as statistical physics, gene networks, and prey-predator systems. Yet despite this focus on interactions at the pairwise level, a general and comprehensive framework for two-way interaction categorizations has not been established. Moreover, this lack of a framework makes it particularly challenging to address and incorporate higher-order interactions that must be scaled up from any specific pairwise interaction model. This also likely contributes to the paucity of studies or higher-order interactions—defined here as interactions among three or more components—in the literature. Indeed, many studies have hypothesized or either implicitly or explicitly assumed that higher-order interactions are extremely rare and/or insignificant (May, 1972; Van Belle, 2011; Wang et al., 2015; Wootton and Stouffer, 2016). In contrast, recent studies have provided evidence that there is a large amount of higher-order interactions, suggesting a critical need to include higher-order effects to better understand complex systems and alterations of ecosystem processes (Weinreich et al., 2013; Taylor and Ehrenreich, 2015a,b; Beppler et al., 2016; Tekin et al., 2016; Levine et al., 2017; Mayfield and Stouffer, 2017).

Constructing an integrated theoretical framework that encapsulates all the pairwise interaction measures and rigorously constructs higher-order interaction measures by building up from a generalized formula for pairwise interactions would be extremely valuable for gaining insights into understanding complex systems. Here, we provide a perspicuous path to this general theory of interaction measures at pairwise and higher-order levels. We aim consequently to enhance the understanding of interactions via the comparison of different interaction measures and via the search for higher-order interactions, potentially providing profound insights into complex systems research.

In **Table 1** we give several of the most common choices for interaction measures that have been introduced and utilized in diverse fields. Diverse examples of interaction measures include (i) covariance for calculating the joint variability of multiple random variables (Rice, 2003), (ii) mutual information (MI) defined to quantify the information gained about one random variable through knowledge of the other random variable (Cover and Thomas, 2012), (iii) joint cumulants in statistical physics, also known as an n-point correlation or Ursell functions in quantum field theory (Kendall and Stuart, 1969), (iv) statistical measures of analysis of variance (ANOVA) for detecting the differences of means and variances among different groups (Cohen, 2008), (v) additive and multiplicative models introduced for quantifying the interactions among multiple predators in their ability to affect the survival of a prey population (**Figure 1**) (Sih et al., 1998), and (vi) a commonly used measure of Bliss or epistatic Independence for identification of drug-drug and gene-gene interactions (Bliss, 1939). Although these measures are all grounded on the unifying objective of quantifying the dependence or interaction between different components (referred to as objects, variables, or factors), a general theory for deriving these measures does not exist. Indeed, some of the interaction measures mentioned above are strongly associated with each other (see Similarities across different interaction measures), hence introduction of a general framework of interactions becomes much more needed.

Identifying higher-order interactions is essential because the behavior of complex systems can be unpredictable due to interactions among the pairwise subsets of system components (Case and Bender, 1981; Billick and Case, 1994). However, generalizing 2-way (pairwise) interaction measures to three or more component systems is often challenging, often done incorrectly or incompletely, and requires a heuristic process of learning the complex calculations or directly implementing software packages with implicit choices and computations. Consequently, measures for higher-order interactions are often not known or not well-defined (Tekin et al., 2017). All in all, a simplified yet rigorous approach for studying pairwise and higher-order interactions is vitally important for creating a basis to explore the patterns and consequences of emergent phenomena in a wide range of systems.

One important point to consider is that proceeding from lower-order to higher-order interaction measures requires the resolution of ambiguities concerning what exactly higher-order interactions represent (Foucquier and Guedj, 2015). In this respect, two recent studies on higher-order drug interactions with a major focus on three-way interactions—in terms of data representation and analysis—shed light by distinguishing between net and emergent higher-order interactions (Beppler et al., 2016; Tekin et al., 2016). A net interaction, which is the more commonly considered type of higher-order interaction, refers to the total interaction that results from effects at all levels. In contrast, emergent interactions arise only when *all* of the components (or objects) or some subset of components are combined. Similarly, a more comprehensive and general approach is needed to evaluate higher-order interaction effects in a wide range of fields. From an ecological perspective, when conservation management is the goal for a prey population, understanding the actual interactions among all predators can be critical. We cannot assume that more predators will increase prey risk, and similarly, without proper emergent interactions analysis, we do not know which predator removal or decrease will ultimately increase a prey's number. Therefore, a generalized approach for quantifying higher-order interactions must directly distinguish between net and emergent interactions and incorporate effects resulting from different levels of interaction [where the level corresponds to the number of components in any given subset of component, ranging from one component (level 1) up to the whole system (level *N*)]. This higher-order interaction framework would require data for responses for each subsets of components—singles, pairs, triples, etc.

In this paper, we first establish a general framework for analyzing two-way interactions and show how our framework can be used to derive the many interaction measures described above. Indeed, we show how all the measures mentioned above (such as mutual information, ANOVA, multiplicative models, etc., see **Table 1**) fit within this framework. Next, we present a conceptual and theoretical advance for building higher-order interaction measures that starts from a general framework of

TABLE 1 | Summary table of two-way interaction measures with our generalized formula $\mathfrak{I}_{XY} = \mathcal{F}(X \circ Y) - (\mathcal{F}(X \circ I) \triangle \mathcal{F}(Y \circ I))$.

Interaction measure ($\mathfrak{I}$)	$\mathcal{F}$ (Functional)	$\circ$ (Operation)	I (Identity of $\circ$)	$\triangle$ (Operation)	Applications
Covariance	Expectation (E)	Multiplication	1	Multiplication	Neuroscience Kohn and Smith, 2005; Staude et al., 2010, gene epistasis, economics Miller, 2013, signal processing Sahidullah and Kinnunen, 2016, risk analysis and management Cox L. A. Jr., 2009
Mutual information	Negative entropy ($-H$)	Addition	0	Addition	Gene epistasis Margolin et al., 2006; Moore et al., 2006, machine learning Jakulin and Bratko, 2003; Jakulin, 2005, astronomy Pandey and Sarkar, 2017
Additive model or ANOVA	Response	Addition	0	Addition	Stressor interactions Chen et al., 2008, gene epistasis Matsui and Ehrenreich, 2016, food webs O'gorman and Emmerson, 2009, political studies Sigal et al., 1988
Multiplicative model or Bliss Independence	Survival or fitness	Addition	0	Multiplication	Multiple predator studies Sih et al., 1998, drug interactions Bliss, 1939; Yeh et al., 2006, gene epistasis Segrè et al., 2005

pairwise interactions and the definition of no-interaction at the pairwise level. In doing so, we show how different interaction measures are generated by different choices of mathematical operations and functionals, potentially allowing exploration of all possible interaction measures via all possible choices of operations and associated identity elements. Importantly, our general theory of interactions facilitates the understanding of connections between different measures that are frequently used in different research areas and will thus be a useful guide for studies of interactions in many distinct fields.

Similarities Across Different Interaction Measures

Despite the fact that there are a wide range of choices for pairwise interaction metrics (see **Table 1**), interactions are defined generically based on a prediction or expectation that signifies no interaction and corresponds to each respective measure having a value of 0. Given the no-interaction expectation—equivalently referred to as additive, multiplicative, or independence expectations—the classification of interactions is evaluated based on deviations from this no-interaction case. When the combined effect is sufficiently greater or weaker than the expected effect of no-interaction, the interaction is classified as positive (synergy or cooperation) or negative (antagonism or interference), respectively (see **Figure 1** for a toy example and an ecological case study). Interpreting the magnitude of interaction often requires rescaling (normalizing), using methods such as those developed by Segrè et al. (2005) and Tekin et al. (2016), and then testing the significance by various statistical analysis methods such as t-tests, bootstrapping experiments, and Bayesian statistics (Jakulin, 2005).

Importantly, some interaction measures (as briefly overviewed in the Introduction and presented in **Table 1**) are strongly associated with each other in terms of their construction and baseline expectation of no-interaction. For instance, the underlying additive model of ANOVA is strongly linked with the additive model of Multiple Predator Effects (MPE) studies (Sih et al., 1998), where the expected effect of combination is sum of their individual effects. On the other hand, there is a correspondence between the multiplicative model of MPEs—the expected effect of combination is product of their individual effects—and the Bliss Independence model of drug interactions and epistasis (Beppler et al., 2016). These correspondences suggest that further exploration and potential applications of interaction measures to different systems could be fruitful. Our general framework uncovers these similarities and hence proves to be very useful in understanding the interaction measures and their similarities as well as their applications to different systems.

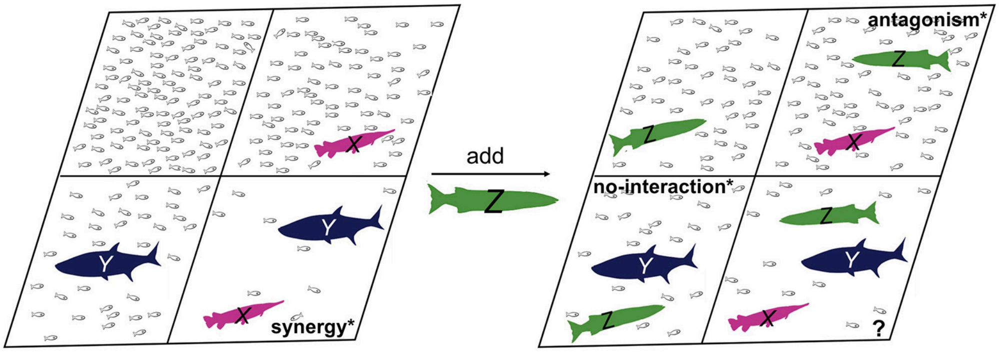
When proceeding from simpler forms of interactions (i.e., pairwise interactions) to higher-order interactions (i.e., three-way, four-way, N-way interactions), two different types of interaction classifications arise, namely net and emergent interactions (Beppler et al., 2016). Net interactions measure whether any effective interaction exists at all, whereas emergent interactions measure whether there are interactions beyond what is expected from the "sum" of the lower-order parts. Inherently, characterizing higher-order interactions necessitates data for all the system outcomes (i.e., responses) in the presence of all the subsets of components. For example, for the characterization of three-way interaction, one would need responses in the presence of each single component alone, responses under all pairwise component combinations, and responses under all three components. Overall, better understanding of how higher-order interaction measures translate into these two different types of higher-order interactions is vital to better predict dynamics of complex system cooperations.

METHODS

Generalized Form of Interaction Measures

General Theory of Two-Way Interactions

Here, we introduce a mathematical framework that generalizes and unifies interaction measure formulations for two



		interaction classification method	**Predator *X***	**Predator *Y***	**Predator *Z***	***XY***	***XZ***	***YZ***	***XYZ***
Toy example of an interaction study design	**raw data** (prey mortality)	N/A	0.09 ± 0.01	0.31 ± 0.02	0.18 ± 0.02	0.94 ± 0.03	0.20 ± 0.01	0.55 ± 0.04	0.80 ± 0.05
	interaction class	ANOVA	N/A	N/A	N/A	$p < 0.001$ (significant)	$p < 0.001$ (significant)	$p < 0.001$ (significant)	$p < 0.001$ (significant)
		multiplicative model*	N/A	N/A	N/A	$\mathfrak{I} = -0.909$ (synergy)	$\mathfrak{I} = 0.673$ (antagonism)	$\mathfrak{I} = -0.211$ (no-interaction)	*net interaction* $\mathfrak{I} = -0.611$ (synergy)
									emergent interaction $\mathfrak{I} = 2.692$ (antagonism)
		interaction classification method	**Predator *X* (*Chaoborus crystallinus*)**	**Parasite *Y* (*Pasteuria ramose*)**	**Pesticide *Z* (*Carbaryl*)**	***XY***	***XZ***	***YZ***	***XYZ***
Ecological case study*	**raw data** (*Daphnia magna* survival)	N/A	1	1	0.96	0.96	1	0.3	0.55
	interaction class	ANOVA (by original study)	N/A	N/A	N/A	0.259 (non-significant)	0.004 (significant)	0.758 (non-significant)	0.491 (non-significant)
		multiplicative model*	N/A	N/A	N/A	$\mathfrak{I} = -0.040$ (no-interaction)	$\mathfrak{I} \gg 3$ (antagonism)	$\mathfrak{I} = -0.688$ (synergy)	*net interaction* $\mathfrak{I} = -0.427$ (no-interaction)
									emergent interaction $\mathfrak{I} \gg 3$ (antagonism)

FIGURE 1 | Example representation and ecological case study of 2-way and 3-way interactions for consumer-resource systems. A toy example of an interaction study design for multiple predator effects (MPE) is given to represent 2-way and 3-way interactions, where mortality rates of prey population (small fish) are dependent on the consuming ability of certain predator or combination of predators. Schematic of no predator, single predator, pairwise combination, and triple combination of fish predator populations are illustrated in 8 different panels, where the pairwise panels of *XY, XZ, YZ* are chosen to represent the three distinct types of interactions: synergy, antagonism, and no-interaction by the multiplicative model with the rescaling introduced in Segrè et al. (2005) and Tekin et al. (2016). In particular, synergistic interaction corresponds to the case when the mortality rate with two predators is sufficiently larger than the expected mortality rate of predators based on single-predator effects. Conversely, predators can act antagonistically, meaning that the mortality rate in the presence of combined predators is sufficiently less than the expected mortality rate based on single-predator effects. In the latter scenario, predators do not interact, hence expected prey mortality is the same as actual prey mortality with both predators in the environment. Classification of interactions is typically done by evaluating the effects of the combined components relative to the effects of independent single components or lower-order combination effects. Given the raw data (see table), we employ the analysis of variance (ANOVA) as well as multiplicative model of interactions and present p-values and interaction measure calculations ($\mathfrak{I}$, see section Methods for the definition), respectively. For 3-way combinations, two distinct types of interactions are characterized by the multiplicative model, where net interaction represents the overall effect and emergent interaction represents the three-way combination effect that is beyond any pairwise interactions. The same interaction study design has been performed for an ecological case study by Coors and De Meester (2008), where stressors are a predator (*X*), parasite infection (*Y*), and pesticide exposure by carbanyl (*Z*) on a water flea *Daphnia magna* survival. A MATLAB code package that has the toy data with the implementation of the interaction measure calculations are included as part of our paper (see **Data Sheet 1**).

components (equivalently referred to as factors or objects). In a broad context, interactions are determined based on the evaluation of the combined effect relative to a null expectation of no-interaction based on the single-component effects. Hence, for defining a generalized formula for interactions, it is essential to introduce notation, properties of operations for combining components, and formulations for assessing the effects of combined or single components. Here, we define an algebraic operation $\circ$ (associative and commutative) that combines two components X and Y and that has identity element I, and a real-valued functional, $\mathcal{F}$, (a function of functions) and a second algebraic operation $\triangle$ (associative and commutative) that combines this functional with different arguments (**Figure 2**). Then, we express the definition of no-interaction as $\mathcal{F}(X^\circ Y) = (\mathcal{F}(X^\circ I) \triangle \mathcal{F}(Y^\circ I))$, and define the generalized measure for quantifying interactions between two components as

$$\mathfrak{I}_{XY} = \mathcal{F}\left(X^\circ Y\right) - \left(\mathcal{F}\left(X^\circ I\right) \triangle\ \mathcal{F}\left(Y^\circ I\right)\right) \tag{1}$$

The identity element in the functional form of the interaction measure is provided in the generalized formula to explicitly make the point that the absence of another component should yield no interaction. In other words, combining any component (X) with the identity element $(Y = I)$ should be equivalent to no interaction, corresponding to $I = 0$ for addition and to $I = 1$ for multiplication. Moreover, the arithmetic operations are restricted to either addition or multiplication to preserve the associativity and commutativity properties of combining more than two components. This preservation property is because there is no time component in our framework that corresponds to introducing different components to the system. In other words, the ordering of different components in the interaction definition does not matter, hence $\mathfrak{I}_{XY} = \mathfrak{I}_{YX}$ for two components and $\mathfrak{I}_{XYZ} = \mathfrak{I}_{YXZ} = \mathfrak{I}_{ZXY}$ for three components (see next section). By definition, $\mathfrak{I}_{XY} = 0$ generally means there is no interaction or dependence between two components, whereas deviation of $\mathfrak{I}_{XY}$ from zero suggests an interaction. Different choices of operations and functional $\mathcal{F}$ correspond to different choices of interaction measures as derived below. Furthermore, the sign and magnitude of $\mathfrak{I}_{XY}$ indicates the type and strength of interaction after proper rescaling (Segrè et al., 2005; Tekin et al., 2016). Rescaling has a firm conceptual foundation that has been proven useful in many areas and is defined relative to important baselines, such as a maximally synergistic scenario or special cases of antagonism, to appropriately reflect the strength of any interaction (Segrè et al., 2005; Sanjuán and Elena, 2006; Tekin et al., 2016). Similarly, two-way and higher-order interaction measures need a rescaling method (a normalization procedure) to distinguish different interaction categorizations.

General Theory of Higher-Order Interactions

As we proceed from two-way to higher-order interactions, there are two distinct types of interactions: (1) net interactions and (2) emergent interactions (**Figure 2**). The first form measures whether an effective or net interaction exists at all, hence defined as an effect of a combination that is different than predicted from solely the effects of non-interacting single components. On the other hand, the second form measures whether there are emergent interactions beyond what is expected from the lower-order parts of the whole combination. Below, by following a similar notation as for two-way interactions, we introduce the functional forms of generalized higher-order interaction measures. For that, we first note that the ordering of the components (or objects) does not matter as we assume the absence of a time component in our framework. Therefore, the interaction measures are symmetric with respect to each component—hence $X\left(Y^\circ Z\right)$ is equivalent to $X^\circ Y^\circ Z$ or $X^\circ Z^\circ Y$ and vice versa—because algebraic operations of $\circ$ and $\triangle$ hold commutativity and associativity properties.

Net interactions

Net interactions are measured by a direct extension of the generalized formula for two components (**Figure 2**) (Sanjuán and Elena, 2006; Staude et al., 2010; Beppler et al., 2016). For example, when three components are completely independent or do not interact at any level, then the functional with the combined components as the argument is equal to the combination of functionals of single components under the operation $\triangle$. Therefore, adding a third component (Z) into the generalized version of the two-way interaction measure (Equation 1), the generalized version of the three-way net interaction measure becomes

$$\mathfrak{I}_{XYZ,\ \mathrm{NET}} = \mathcal{F}\left(X^\circ Y^\circ Z\right) - \left(\mathcal{F}\left(X^\circ I\right) \triangle \mathcal{F}\left(Y^\circ I\right) \triangle \mathcal{F}\left(Z^\circ I\right)\right) \tag{2}$$

Next, we derive the net interaction formulation for a combination of an arbitrary number, N, of components. Representing the set of components by $X_1,\ X_2,\ \cdots,\ X_N$, and assuming there is no interaction between component X_1 and the rest of the components, we have

$$\mathcal{F}\left(X_1^\circ X_2^\circ\ \cdots\ {}^\circ X_N\right) = \mathcal{F}\left(X_1^\circ I\right) \triangle \mathcal{F}(X_2^\circ\ \cdots{}^\circ\ X_N^\circ I)$$

By induction or equivalently applying the same realization repeatedly to the right side of the above equation yields the N-way version of the generalized formula as given by

$$\mathcal{F}\left(X_1^\circ X_2^\circ\ \cdots\ {}^\circ X_N\right) = \mathcal{F}\left(X_1^\circ I\right) \triangle \mathcal{F}\left(X_2^\circ I\right) \triangle \ldots \triangle \mathcal{F}\left(X_N^\circ I\right) \tag{3}$$

Using a big $\triangle$ notation to denote the application of the operation $\triangle$ to a sequence of numbers—similar to sigma (or pi) notation for summation (or multiplication)—our generalized formula for quantifying net N-way interaction is given by

$$\mathfrak{I}_{X_1\ X_2\ \cdots\ X_N,\ NET} = \mathcal{F}\left(X_1^\circ X_2^\circ \ldots{}^\circ X_N\right) - \underset{i}{\triangle}\mathcal{F}\left(X_i^\circ I\right)$$

Emergent interactions

Emergent interactions are defined as interactions that exist even after the exclusion of all interaction effects that are due to lower-order parts and may contribute to a combined overall (net) interaction (**Figure 2**). In the drug interaction and epistasis terminology, emergent interactions are concretely defined in our recent work and clearly contrasted with the definition of net interaction (Beppler et al., 2016; Tekin et al., 2016). Specifically, an emergent interaction is an interaction that exists beyond the effects that are due to all lower-order parts, whereas a net interaction is any effect beyond only the individual component effects. In an article by Staude et al. (2010) on covariance,

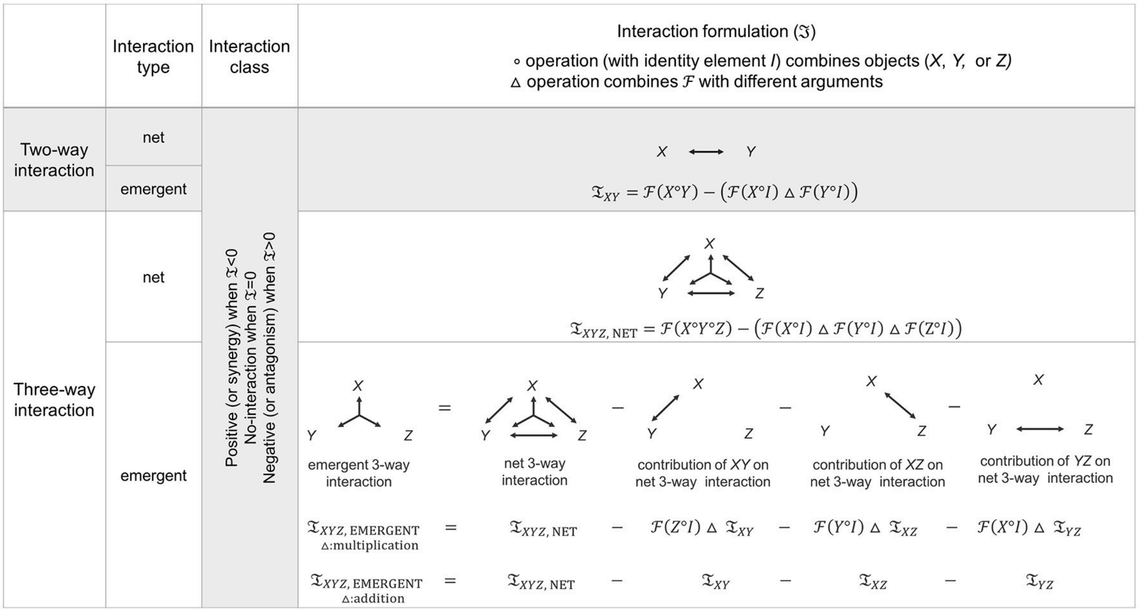


FIGURE 2 | Generalized form of interaction diagrams and measures. Two-way and three-way interaction diagrams and measures ($\mathfrak{T}$) over distinct interaction types, general functionals ($\mathcal{F}$), and operations (, △) are given. Empirically, classification of pairwise interaction requires measurements from each single component alone as well as measurements from each pairwise combination of components. On the other hand, classification of three-way interactions requires measurements from all possible subsets: measurement under each single-component alone, measurement from all pairwise subsets, and measurement from triple-component combination. Theoretically, for two-way interactions, the definitions of net and emergent interactions are identical. On the other hand, net and emergent interactions are not the same at the three-way level because the net three-way combination subsumes the pairwise combination effects of each pair (*XY*, *XZ*, *YZ*). Therefore, the emergent 3-way interaction (the diagram on the bottom far left) is expressed by subtracting all lower-order contributions from the net 3-way interaction. The interaction classification is obtained from the sign of the interaction measure, $\mathfrak{T}$, where $\mathfrak{T} = 0$ represents no-interaction, $\mathfrak{T} < 0$ represents synergy (positive interaction), and $\mathfrak{T} > 0$ represents antagonism (negative interaction). See **Figure 1** for a toy example of consumer-resource systems that depicts different interaction classes: synergy, no-interaction, and antagonism.

this concept is referred to as the dependence in the higher-order combination that is not embedded through the lower-order correlations. In information theory, Jakulin et al. (Jakulin, 2005) referred to this idea similarly and stated that interaction information among different attributes can be gained by the information that is not present in any subset. By definition, at the two-way level, an emergent interaction is identical to the net interaction because there is nothing from which to emerge except the single-component effects. On the other hand, at the next level, the emergent three-way interaction measure captures the interaction that does not originate from the pairwise parts, and hence emerges only in the presence of all three components. For more than three components, it matters what level of lower-order interactions needs to be excluded. There can be different choices based on the specific system or the main purpose of the interaction identification, as revealed in more detail below and in the **Appendix A** in Supplementary Material.

As a start, to measure the emergent three-way interaction, we calculate how much of the three-way net interaction originates from each of the isolated pairs and subtract that from the net (or total) three-way interaction. In this case, the contribution that comes solely from the pair *X*, *Y* represents the situation that only *X*, *Y* interacts within the three-way combination of *X*, *Y*, and *Z*. In other words, the remaining component *Z* within the combination does not interact with the pairwise part of *X* and *Y* or either *X* or *Y* individually. Employing the two-way interaction formula of generalized interaction measure (Equation 1) and the associative properties of operations, this is equivalent to saying that $\mathcal{F}(X^\circ Y^\circ Z) = \mathcal{F}((X^\circ Y^\circ)^\circ Z) = \mathcal{F}((X^\circ Y)^\circ I) \vartriangle \mathcal{F}(Z^\circ I)$. Hence, the two-way combination of components *X*, *Y* contributes to the entire (net) three-way interaction (Equation 2) by an amount of $\mathcal{F}((X^\circ Y)^\circ I) \vartriangle \mathcal{F}(Z^\circ I) - \mathcal{F}(X^\circ I) \vartriangle \mathcal{F}(Y^\circ I) \vartriangle \mathcal{F}(Z^\circ I)$, which is equal to $\mathcal{F}(Z^\circ I) \vartriangle \mathfrak{T}_{XY}$ when △ is multiplication and is equal to $\mathfrak{T}_{XY}$ when △ is addition. Similarly deriving the contribution coming solely from the interaction of components *Y* and *Z* and also from *X* and *Z*, the generalized formula of the emergent three-way interaction is given by disentangling the sum of the pairwise parts from the three-way interaction. Therefore, given the multiplication operation of △, the emergent 3-way interaction among components *X*, *Y*, and *Z* is

$$\mathfrak{T}_{XYZ,\ \mathrm{EMERGENT}} = \mathfrak{T}_{XYZ,\ \mathrm{NET}} - \mathcal{F}\left(X^\circ I\right) \vartriangle \mathfrak{T}_{YZ} - \mathcal{F}\left(Y^\circ I\right) \vartriangle \mathfrak{T}_{XZ} - \mathcal{F}\left(Z^\circ I\right) \vartriangle \mathfrak{T}_{XY} \qquad (4)$$

On the other hand, the weighting parameters (e.g., $\mathcal{F}(X^\circ I)$) disappear when △ is the addition operation, so an emergent interaction is given by

$$\mathfrak{T}_{XYZ,\ \mathrm{EMERGENT}} = \mathfrak{T}_{XYZ,\,\mathrm{NET}} - \mathfrak{T}_{YZ} - \mathfrak{T}_{XZ} - \mathfrak{T}_{XY} \qquad (5)$$

These expressions mean that when some interaction exists but all the pairs are independent (or not interacting), then the emergent interaction is equal to the net interaction because any interaction can only be coming from the combined effects of all three drugs for this special case. When pairwise interactions exist and do not cancel, the net and emergent interaction measures will virtually always differ. Notice also that all interaction measures are symmetric with respect to each component. Moreover, when a single component is independent (or not interacting) with the others, the emergent three-way measure vanishes, as desired.

For N components $(X_1, X_2 \ldots\ X_N)$, the emergent N-way interaction formula can be derived similarly by starting from the definition of the generalized formula for net N-way interactions and subtracting the appropriate lower-order effects. The derivation for generalized formula of emergent interactions with four components is described in detail in **Appendix A** in Supplementary Material.

RESULTS

Construction of Specific Two-Way Interaction Measures From General Theory

We will now derive how our generalized framework of two-way interactions leads to numerous interaction measures introduced in studying generic multi-component systems (**Table 1**). For this, we start by defining X and Y as random variables and will show that the generalized formula reduces to the covariance formulation and mutual information by the choice of different algebraic operations of and $\triangle$. Given that $\mathcal{F}$ is the expectation operator, and both and $\triangle$ are the operation of multiplication, $\mathfrak{I}_{XY}$ (Equation 2) becomes covariance and hence measures the joint variability between X and Y, as

$$\mathfrak{I}_{XY} = E\left(X{*}Y\right) - E\left(X{*}1\right){*}E\left(Y{*}1\right) = E\left(XY\right) - E\left(X\right)E\left(Y\right)$$

Here, we note that when X and Y are independent, their covariance is zero, i.e., $\mathfrak{I}_{XY} = 0$. Notably, the two-way covariance measure is analogous to concepts in theoretical physics such as joint cumulants or Ursell functions (Kendall and Stuart, 1969) and the Isserlis formula in statistics (Isserlis, 1918). However, the higher-order interaction formulations of these concepts differ from the higher-order covariance when there are more than three components, as derived in **Appendix A** in Supplementary Material.

Following the covariance derivation using our general theory of two-way interactions, we now show that choosing appropriate functional and algebraic operations leads to the mutual information measure of interactions. Hence, we define $\mathcal{F}$ to be negative entropy, $\triangle$ to be addition, and $\circ$ to be addition (i.e., $I = 0$). Here, the $\circ$ operation represents the combination of two components and hence defines joint entropy under the functional $\mathcal{F}$. For these choices, the generalized formula yields the mutual information

$$\mathfrak{I}_{XY} = -H\left(X, Y\right) + H\left(X\right) + H\left(Y\right)$$

Here, associating the random variables X and Y with attributes, the interaction formulation $\mathfrak{I}_{XY}$ measures the correlation between the attributes based on concepts of information theory. By definition, when X and Y have no interaction, their mutual information vanishes because no information is gained about one attribute through the other attribute (Jakulin, 2005).

Proceeding to cases for which the arguments X and Y represent experimental data rather than standard random variables, we discuss how interactions are measured by the formula $\mathfrak{I}_{XY}$ by evaluating the effects of combined components inferred from system responses ($\mathcal{F}$) such as growth, survival, or mortality rates (**Figure 1**). These experimental data types and response functions are used in many important and frequently-used measures of interactions, such as ANOVA, epistatic additivity, Bliss Independence, and multiple predator effects measures.

We begin by reviewing how ANOVA (Analysis of Variance) translates into a measure for the prediction of interactions and then deriving its correspondence with our general interaction formula. In the case of two-component systems, ANOVA interactions are quantified by a 2 by 2 factorial design with four different observations—corresponding to no components (*0*), component X alone, component Y alone, and components X and Y together. In this case, two-way ANOVA tests whether the presence of Y affects the impact of X according to a measure based on linear deviations. When the effects of observations are denoted by $\mathfrak{S}$, no interaction is described as $\mathfrak{S}\left(X\right) - \mathfrak{S}\left(0\right) = \mathfrak{S}\left(X+Y\right) - \mathfrak{S}\left(Y\right)$. Note that this equation can be re-expressed in the form $\mathfrak{S}\left(X+Y\right) - \mathfrak{S}\left(0\right) = \mathfrak{S}\left(X\right) - \mathfrak{S}\left(0\right) + \mathfrak{S}\left(Y\right) - \mathfrak{S}\left(0\right)$. Therefore, redefining the response measurement to be $\mathcal{F}\left(X\right) := \mathfrak{S}\left(X\right) - \mathfrak{S}\left(0\right)$, the interaction is quantified by the significance of deviation from the additive effects of two components, i.e., $\mathcal{F}\left(X+Y\right) - \mathcal{F}\left(X\right) - \mathcal{F}\left(Y\right)$. This corresponds to a general formula of interactions, $\mathfrak{I}_{XY}$, with $\circ$ and $\triangle$ being addition operations

$$\mathfrak{I}_{XY} = \mathcal{F}\left(X+Y\right) - \mathcal{F}\left(X\right) - \mathcal{F}\left(Y\right)$$

Regarding the use of ANOVA for interaction classifications, work by Billick and Case (1994) and Wootton (1994) demonstrate that the results of ANOVA can be misleading if the transformation of data is not carefully done or when the empirical system does not align with the assumptions of ANOVA.

Following the similar component types and response measurements, our general interaction measure produces another widely-used model of interactions, namely the multiplicative-risk model. This measure has been introduced by Soluk and Collins (1988) for quantifying multiple predator effects (MPE), and it overcomes the ambiguities of the additive prediction by ANOVA when the single components have large impacts on the response function ($\mathcal{F}$). In such cases, the additive expectation can never be achieved because the predicted combined effect is stronger than is feasible or possible for the two together (for example you cannot have a stronger effect than complete killing, see **Appendix B** in Supplementary Material for details). The multiplicative model formulates no-interaction as $\mathcal{F}\left(X+Y\right) = \mathcal{F}\left(X\right)\mathcal{F}\left(Y\right)$, based on the idea of proportional decreases in population size. It is thus much more akin to Bliss

Independence discussed below. Importantly, the multiplicative model of interaction can be written as a general interaction formula, where $\circ$ and $\triangle$ are addition and multiplication operations, respectively. Hence,

$$\begin{aligned}\mathfrak{I}_{XY} &= \mathcal{F}(X+Y) - (\mathcal{F}(X+0) * \mathcal{F}(Y+0)) \\ &= \mathcal{F}(X+Y) - \mathcal{F}(X)\,\mathcal{F}(Y)\end{aligned}$$

associates the null model of no-interaction based on the product of response measurements ($\mathcal{F}$), which is prey survival rates for the MPE system (Sih et al., 1998; Barrios-O'neill et al., 2014). The subscript notation (such as $\mathcal{F}_{XY}$) is still typically used to express response measurements under different combinations of predators, or similar component types in different settings, even though X and Y are actually being summed together in this case. Hence, the equation above takes a form $\mathfrak{I}_{XY} = \mathcal{F}_{XY} - \mathcal{F}_X\mathcal{F}_Y$. As explained in **Appendix B** in Supplementary Material, this multiplicative model is preferred over additive models that do not always yield plausible expectations of combination effects. As a further note, this multiplicative model of two-way interaction can be tested by merely applying two-way ANOVA on log-transformed data because testing for $\log\mathcal{F}(X+Y) = \log\mathcal{F}(X) + \log\mathcal{F}(Y)$ is equivalent to testing for $\mathcal{F}(X+Y) = \mathcal{F}(X)\mathcal{F}(Y)$ by properties of logarithms. However, the multiplicative model at higher-order levels is not simply equivalent to the log-transformed ANOVA as detailed below. Note that following the same logic of additive and multiplicative models, where the interaction effect signifies the deviation from the null model of additivity or multiplicativity, alternative measures to two-way ANOVA [namely Hedge's d and log response ratio (LnRR)] have been proposed to determine interactions based on the deviation from the corresponding model expectation standardized to the effect size (Gurevitch et al., 2000; Crain et al., 2008; Côté et al., 2016). Similar correction terms for the effect sizes can be added to net and emergent higher-order interaction measures for meta-analysis studies.

Intriguingly, there is a strong correspondence between the multiplicative model introduced for MPEs and the frequently used drug-interaction model of Bliss Independence. This indicates that the Bliss measure can also be expressed by utilizing the general interaction formulation we propose here, i.e., $\mathfrak{I}_{XY} = \mathcal{F}_{XY} - \mathcal{F}_X\mathcal{F}_Y$. In drug interaction studies, response measurements, $\mathcal{F}$, are given as growth rates of pathogens in the presence of single or multiple drug environments relative to the no-drug environment. Relative growth is commonly referred to as relative fitness and is indeed analogous to the survival rates of prey species in predator environments (Beppler et al., 2016). Bliss Independence categorizes interactions based on deviations from a null expectation (no-interaction case) that the percent decrease of the pathogen growth rate in the presence of drug X is not affected by the presence of the other drug Y. Analytically, the deviation from no-interaction instance is measured by $\mathcal{F}(X+Y) - \mathcal{F}(X)\,\mathcal{F}(Y)$ or $\mathcal{F}_{XY} - \mathcal{F}_X\mathcal{F}_Y$, following a subscript notation as in the multiplicative model.

Building Higher-Order Specific Interaction Measures From General Theory

In this section, we discuss the widely-used pairwise interaction measures described above and summarized in **Table 1**, and we derive the three-way interaction measures based on the corresponding no-interaction criterions and our general theory. For clarity, we follow the same order of measures as in the section on the construction of two-way interactions. Therefore, we start by reviewing the standard interaction measures when the components are random variables. In probability theory, the extensions of probabilistic measures of moments to multi-variable systems are generally referred as higher-order cross moments. For example, adapting the generalized formula of covariance (see **Table 1**) to three variables yields a 3rd-order cross moment known as co-skewness that is used as a risk management measure in finance or in social problems (Cox L. A. Jr., 2009; Miller, 2013). To be more explicit, the net interaction measure (Equation 3) is given by $\mathfrak{I}_{XYZ,\ NET} = E(XYZ) - E(X)\,E(Y)\,E(Z)$ (Stratonovich, 1967; Staude et al., 2010), which vanishes when X, Y, and Z are mutually independent with each other and each pairwise product. Next, substituting the generalized formula of two-way interactions (i.e., covariance) and the net three-way interaction, the emergent interaction (Equation 4) becomes

$$\begin{aligned}\mathfrak{I}_{XYZ,\ \text{EMERGENT}} &= E(XYZ) - E(X)\,E(YZ) - E(Y)\,E(XZ) \\ &\quad - E(Z)\,E(XY) + 2E(X)\,E(Y)\,E(Z)\end{aligned}$$

which is equivalent to the three-way covariance [i.e., $E((X - E(X))(Y - E(Y))(Z - E(Z)))$] or the non-normalized formula of co-skewness as discussed above. Notably, this three-way measure is equivalent to the Isserlis formula (Isserlis, 1918), 3-point connected correlation, or equivalently the Ursell function with three random variables (Kendall and Stuart, 1969; Staude et al., 2010). However, this does not hold true for more than three components (**Appendix A** in Supplementary Material).

Continuing with the component types as random variables, we now show that the general formula of higher-order interactions reduces to two interaction measures of paramount importance in information theory. Defining the functional $\mathcal{F}$ as the negative of entropy and following the algebraic operations that yield mutual information (see **Table 1**), the net interaction formulation coincides with the total correlation measure as given by

$$\mathfrak{I}_{XYZ,\ \text{NET}} = -H(X,Y,Z) + H(X) + H(Y) + H(Z)$$

This measures the total dependence among three attributes X, Y, and Z (Watanabe, 1960; Jakulin, 2005). By incorporating the pairwise mutual information into the emergent interaction formulation when $\triangle$ is the addition operation (Equation 5), we attain the multiple mutual information measure defined by McGill (McGill, 1954; Sun Han, 1980; Jakulin, 2005).

$$\begin{aligned}\mathfrak{I}_{XYZ,\ \text{EMERGENT}} &= -H(X,Y,Z) + H(X,Y) + H(X,Z) \\ &\quad + H(Y,Z) - H(X) - H(Y) - H(Z)\end{aligned}$$

Thus far, we have introduced the commonly used interaction and dependence measures from probability theory. Next, we move onto the standard measure of ANOVA, which analyzes the effects of multiple components via the factorial experiment design. As in the two-way interactions, we simply use the underlying additive model of three-way ANOVA and refer to it as just an additive model (**Table 1**). When the response function $\mathcal{F}$ is defined relative to the control (no component is present), the three-way net interaction formula of the additive model is given by $\mathcal{F}(X+Y+Z) - \mathcal{F}(X) - \mathcal{F}(Y) - \mathcal{F}(Z)$. Now, substituting each pairwise contribution in the generalized formula of emergent interactions (**Figure 2**), the emergent interaction measure is identical to the underlying model of three-way ANOVA.

$$\begin{aligned}\mathfrak{I}_{XYZ,\ \text{EMERGENT}} = {} & \mathcal{F}(X+Y+Z) - \mathcal{F}(X+Y) - \mathcal{F}(X+Z) \\ & - \mathcal{F}(Y+Z) + \mathcal{F}(X) + \mathcal{F}(Y) + \mathcal{F}(Z)\end{aligned}$$

This correspondence is proven explicitly in the **Appendix C** in Supplementary Material by recognizing that three-way ANOVA determines how the two-way interaction between the components X and Y is affected by an addition of a third factor Z. This in-depth derivation of the underlying model of three-way ANOVA helps to compare the statistical measure of ANOVA with other interaction classification methods.

Due to the additive model's implausible predictions under certain cases, many MPE studies have pursued the implementation of the multiplicative model (**Appendix A** in Supplementary Material). Subsequently, we now derive the definition of three-way interactions under the multiplicative model of MPE studies or equivalently the Bliss Independence formula. This derivation is very similar to the foundation of the covariance for three random variables as $\triangle$ is the multiplication operation in both concepts (**Table 1**). Defining the functional $\mathcal{F}$ as survival rate relative to the control, the net interaction measure becomes

$$\mathfrak{I}_{XYZ,\ \text{NET}} = \mathcal{F}(X+Y+Z) - \mathcal{F}(X)\,\mathcal{F}(Y)\,\mathcal{F}(Z)$$

or $\mathfrak{I}_{XYZ,\ NET} = \mathcal{F}_{XYZ} - \mathcal{F}_X\mathcal{F}_Y\mathcal{F}_Z$ using subscripts for denoting the combination of components. In this case, substituting the terms corresponding to each pairwise contribution, such as $\mathcal{F}_{XY}\mathcal{F}_Z - \mathcal{F}_X\mathcal{F}_Y\mathcal{F}_Z = \mathcal{F}_Z\mathcal{F}_{XY}$ for XY combination, the emergent interaction becomes

$$\begin{aligned}\mathfrak{I}_{XYZ,\ \text{EMERGENT}} = {} & \mathcal{F}_{XYZ} - \mathcal{F}_X\mathcal{F}_{YZ} - \mathcal{F}_Y\mathcal{F}_{XZ} - \mathcal{F}_Z\mathcal{F}_{XY} \\ & + 2\mathcal{F}_X\mathcal{F}_Y\mathcal{F}_Z\end{aligned}$$

Using a fitness definition for $\mathcal{F}$, $\mathfrak{I}_{XYZ,\ NET}$ and $\mathfrak{I}_{XYZ,\ EMERGENT}$ correspond to the net and emergent interaction formulas with three components in the fields of drug interactions and gene epistasis (Sanjuán and Elena, 2006; Beppler et al., 2016).

DISCUSSION

Multi-level interactions play an important role in explaining the characteristics of systems that arise as collective behaviors or responses among different components. As an example in conservation biology, mammalian herbivory, invertebrate herbivory, and nutrient levels all interact to affect the survival, growth rates, and fecundity of rare plant species in a forest ecosystem (McGill et al., 2006; Savage et al., 2007; Webb et al., 2010; Dávalos et al., 2014; Enquist et al., 2015). Given this importance across diverse fields, many different interaction classification methodologies have been introduced. However, a unified theory behind these choices has been lacking, and as a result, higher-order interaction measures are often incorrectly derived and interpreted and thus higher-order interactions are not well understood. Moreover, the lack of a general theory behind the pairwise interaction measures makes it difficult to establish a common understanding of higher-order interactions and to design well-defined measures that go beyond pairwise interactions. In our study, we introduce a pioneering approach to resolve these uncertainties and for studying interactions in complex systems. We further propose a general theory of interaction measures to uncover interactions at pairwise and higher-order levels. Our framework provides an advance in such a way that specific cases and measures can be derived from the definition of what an interaction means—the deviation from an expectation that there is no interaction—and what response measurements are needed to evaluate for the interactions—the functional with different arguments. From that we establish a rigorous framework for extending and generalizing these concepts and measures to higher-order levels.

In doing so, we show the utility of our general framework by deriving pairwise interaction measures across different fields—covariance, mutual information, cumulants, ANOVA, Bliss independence, and epistatic additivity (**Table 1**). Furthermore, we demonstrate that all pairwise interaction measures can be easily extended to characterize the net interaction—an overall effect resulting from all levels—and the emergent interaction—a measurement of an overall interaction effect relative to interactions at lower-order levels. We also discuss their specific representations, correspondences, and interpretations in a diverse set of study areas. Overall, our advance is of importance for studies of diverse complex systems that rely on a large number of interactions and emerge across multiple levels.

Despite a rich focus on pairwise interactions in the literature, recent studies have shown that higher-order interactions are pervasive in drug and gene systems (Taylor and Ehrenreich, 2015a,b; Tekin et al., 2016), and that the typical approach of focusing solely on pairwise interactions is most likely inadequate for successfully attaining important insights into research on complex systems (Weinreich et al., 2013; Beppler et al., 2016; Levine et al., 2017; Mayfield and Stouffer, 2017). Therefore, higher-order interactions (i.e., among any number of components) must be incorporated to fully grasp system dynamics. In this respect, our study provides a promising framework to uncover emergent phenomena in multi-component systems such as protein and gene interaction networks, multiple predator effects, food webs, interacting agents in economics, voting behaviors in political science and the cohesion dynamics of social groups.

As shown by our previous studies (Yeh et al., 2006; Tekin et al., 2016), empirical data of drug interactions separate into a trimodal distribution—clearly separating synergy, no-interaction, and antagonism—and clearly different than would arise from a random model of interactions because stochastic effects would have smoothed out this distribution and led to a more uniform distribution. Furthermore, in our previous study (Tekin et al., 2016), we assessed the statistical significance of interactions by testing against the null hypothesis of random interactions that would on average lead to a uniform distribution that ranges from −1 to 1 across the entire interaction scale. To quantify these comparisons, we used a Silverman test (Silverman, 1981) and found the higher-order emergent interactions are significantly different from random effects. These results reveal higher-order interactions are not simply due to random effects. Also worth noting is that uncertainty and error estimation due to measurements can be dealt with using bootstrapping strategies (Cruz-Loya et al., 2018).

Throughout the text, we also point out a well-founded concept of "rescaling" in physics that has been proven to enhance the categorization of pairwise and higher-order emergent effects (Segrè et al., 2005; Tekin et al., 2016). Without employing an appropriate rescaling approach, the magnitude of interactions is often not apparent and hence can lead to misleading results and erroneous insights. Therefore, appropriately understanding and rescaling the interaction formulations is an essential part of studying and understanding multi-component interactions in any system.

We further note that many systems have additional complexities besides just many interacting components or higher-order interactions. For example, in predator-prey systems, both predators and prey can evolve, and there are direct feedbacks in the interactions. Both of these effects can lead to drastic changes in multiple predator effects (MPEs) (Barrios-O'neill et al., 2014). In addition, pathogens can evolve in response to drug combinations in ways that are almost impossible to predict due to rugose fitness landscapes. To predict and understand the dynamics of pathogen populations thus requires further theory (Palmer et al., 2015). Our general framework of interactions, with additional modifications, will help address some of the important questions about complexities in biological, physical, and social systems. Overall, understanding emergent features can help us to predict the dynamical consequences of complex interactions, including in questions of crucial significance to human and global health, such as combatting the evolution of resistance to antibiotics and mitigating detrimental impacts of climate change on the diversity and stability of food webs.

AUTHOR CONTRIBUTIONS

ET, PY, and VS conceived of the project, designed the study, and wrote the manuscript. ET and VS developed new analytical tools. All authors gave final approval for publication.

FUNDING

ET, PY, and VS received funding from James S. McDonnell Complex Systems Scholar Award, US National Science Foundation (ID: 1254159, http://nsf.gov/), UCLA Faculty Career Development Award, Hellman Foundation Award, and NIH/National Center for Advancing Translational Science (NCATS) UCLA CTSI Grant Number UL1TR001881.

ACKNOWLEDGMENTS

We thank Nina Singh and Cynthia White for comments on the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00166/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 21 December 2018
doi: 10.3389/fevo.2018.00224

The Impact of Spatial and Temporal Dimensions of Disturbances on Ecosystem Stability

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Ecosystems constantly face disturbances which vary in their spatial and temporal features, yet little is known on how these features affect ecosystem recovery and persistence, i.e., ecosystem stability. We address this issue by considering three ecosystem models with different local dynamics, and ask how their stability properties depend on the spatial and temporal properties of disturbances. We measure the spatial dimension of disturbances by their spatial extent while controlling for their overall strength, and their temporal dimension by the average frequency of random disturbance events. Our models show that the return to equilibrium following a disturbance depends strongly on the disturbance's extent, due to rescue effects mediated by dispersal. We then reveal a direct relation between the temporal variability caused by repeated disturbances and the recovery from an isolated disturbance event. Although this could suggest a trivial dependency of ecosystem response on disturbance frequency, we find that this is true only up to a frequency threshold, which depends on both the disturbance spatial features and the ecosystem dynamics. Beyond this threshold the response changes qualitatively, displaying spatial clusters of disturbed regions, causing an increase in variability, and even a system-wide collapse for ecosystems with alternative stable states. Thus, spanning the spatial dimension of disturbances is a way to probe the underlying dynamics of an ecosystem. Furthermore, considering spatial and temporal dimensions of disturbances in conjunction is necessary to predict ecosystem responses with dramatic ecological consequences, such as regime shifts or population extinction.

Keywords: localized disturbance, rescue effect, bistability, return time, variability, persistence

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *29 August 2018*
Accepted: *05 December 2018*
Published: *21 December 2018*

Citation:
Zelnik YR, Arnoldi J-F and Loreau M (2018) The Impact of Spatial and Temporal Dimensions of Disturbances on Ecosystem Stability. Front. Ecol. Evol. 6:224. doi: 10.3389/fevo.2018.00224

1. INTRODUCTION

Understanding the stability of ecosystems, i.e., their ability to recover and persist in the face of natural and anthropogenic disturbances, is of fundamental importance to ecology and conservation (May, 1973; Neubert and Caswell, 1997; Loreau and de Mazancourt, 2013). Ecosystems are spatially extended, comprised of multiple interacting communities in different locations, and therefore an important factor in understanding their stability is their spatial structure (Levin, 1992; Peterson et al., 1998; Wang and Loreau, 2016). However, while the influence of space on properties such as biodiversity and food web structure has been intensely investigated (Loreau et al., 2001; Chase and Leibold, 2002; Montoya and Sol, 2002; McCann et al., 2005), basic questions regarding spatial stability remain open. In particular, despite the fact that most disturbances (e.g., fires, pest outbreak, pollution runoff) are strongly heterogeneous in space, the impact of their spatial structure on stability is largely unknown. Similarly, their temporal dimension, e.g., their timespan or the frequency of their occurrence, is critical. Taken together, these dimensions span a vast space of possible disturbances that ecosystems can face (e.g., fires and storms). This, in part, explains why reaching a clear understanding of ecosystem stability has proven to be an extremely challenging endeavor.

Research on ecosystem stability has a long history in ecology, and numerous studies have investigated how various properties of disturbances affect ecosystem responses. The importance of spatial properties of disturbances, in particular, has been assessed by a few studies of regeneration dynamics under recurrent, spatially structured disturbances (Turner et al., 1993; Moloney and Levin, 1996; Fraterrigo and Rusak, 2008). These studies introduced the concept of landscape equilibrium and demonstrated how the spatial and temporal scales of disturbances can generate different stability patterns. A point not explicitly addressed in these studies, however, is the importance of rescue dynamics occurring at a regional scale when local recovery processes are too slow or fail altogether. This can occur in sufficiently connected ecosystems, following high-intensity disturbances (Foster et al., 1998; Fraterrigo and Rusak, 2008). In fact, recovery from a disturbance is a consequence of both local and regional processes. Local processes lead to recovery due to dynamics that are internal to local communities (e.g., birth and death of individuals), while regional processes lead to recovery by bringing in individuals from neighboring communities via dispersal (Turner, 1989; Leibold et al., 2004). These two processes mediate the large-scale system response to a disturbance, and their respective parts in this response is bound to strongly depend on the spatial connectivity of the system and, importantly, on the spatial structure of disturbances.

Recent work has made this relationship more explicit, by defining three distinct regimes of recovery from a single spatially heterogenous disturbance: Isolated, Rescue and Mixing (Zelnik et al., 2018). If a system is highly connected due to strong dispersal of organisms, then it is in the Mixing Regime, and the system's behavior at large scales is essentially an extended version of a local system (Durrett and Levin, 1994). At the other extreme, if dispersal is low and hence each site acts separately with its own local dynamics, then the system is in the Isolated Regime, and its large-scale behavior is an aggregation of many independent small systems (Tilman et al., 1998; Yachi and Loreau, 1999). In between these two extremes is the Rescue Regime, where systems with intermediate connectivity show large-scale rescue dynamics due to the interaction between limited dispersal and the system's behavior at the local scale (Peterson, 2000; Dai et al., 2013; Wang et al., 2017). For instance, in the study by Dai et al. (2013), a metapopulation of yeast exhibits a front structure which emerges due to interaction of dispersal with nonlinear local behavior of the yeast. A different example is found in the work of Wang et al. (2017), where the correlations between local bird populations, mediated by dispersal, leads to a spatial scaling law of the variability of populations across North America.

While the spatial structure of both system and disturbance plays no role in the Mixing regime, for weaker dispersal it does: in both the Isolated Regime and the Rescue Regime the spatial structure of the disturbance has significant effects as it can initiate qualitatively different responses that involve both local and regional processes (Zelnik et al., 2018). This is the case in an experimental study of a predator-prey protist system, in which local extinctions are met by rescue processes, which prevent synchronization of the regional metapopulation (Fox et al., 2017). We will therefore consider systems with intermediate dispersal, and focus on the effect of the spatial structure of disturbances as well as their temporal properties.

Quantifying the impact of disturbances amounts to defining relevant stability measures. If the disturbance is an isolated event, a natural measure to consider is the return time to the unperturbed state (May, 1973; Neubert and Caswell, 1997). On the other hand, in a regime of repeated disturbances (e.g., climatic events), measures of temporal variability are commonly used (Tilman et al., 2006). In the presence of alternative stable states, those repeated disturbances can cause a regime shift from one state to another. One well-known example is that of lake eutrophication (Carpenter, 2005) due to fertilizer runoff disturbances. Here the stability measure of interest is typically persistence, i.e., the probability that a system will remain in a desired state (Holling, 1973; Pimm, 1984). Importantly, these stability measures reflect not only the spatial and temporal properties of the disturbance, but also the dynamical features of the perturbed ecosystem. Exploring this interplay is the focus of our study, which we will address by considering three spatial ecosystem models with increasing nonlinear local dynamics, ranging from logistic growth to bistability. Under various perturbation scenarios we will measure their stability using return time, variability and persistence.

We begin by looking at the ecosystem's recovery following a single disturbance, and show that changing the spatial structure of the disturbance reveals two basic recovery trajectories: isolated and rescue. Isolated recovery trajectories reflect the local resilience of the system, while rescue trajectories involve spatial processes, and their dominance signals the failure of local processes. We thus argue that the relationship between spatial structure and recovery contains substantial information about the local dynamics of the system, both close to and far from equilibrium. We continue by exploring the temporal axis of disturbances, and demonstrate a direct link between return time (following an isolated disturbance event) and temporal variability (under a regime of repeated disturbances). We find that for low disturbance frequency patterns of variability do not contain additional information in comparison to the patterns of return time. However, past a frequency threshold (which depends on the system's internal dynamics) the variability patterns change. As we will argue, this signals the onset of a new dynamical regime driven by disturbances, which can lead to a regime shift—in our case a transition from a populated to a bare state (extinction).

Our work demonstrates that the spatial dimension of disturbances can be used to reveal information on the ecosystem's internal behavior. Furthermore, our results illustrate that the conjunction of the spatial and temporal properties of disturbances may lead to unforeseen dynamical responses, with drastic ecological consequences.

2. METHODS

2.1. Models

We assume for simplicity that the local community dynamics can be described by a single state variable N that represents the ecosystem's local biomass density. We study the dynamics in multiple locations in space using partial differential equations. We define three different models that differ in their local dynamics but have identical dispersal across space with linear diffusion. In all models the local biomass may reach a carrying capacity K, so that $N = K$ (the populated state) is a stable steady state in all three models. An additional solution exists for $N = 0$ (the bare state), with its stability properties differing among models.

The first and simplest model (LG) describes local logistic growth coupled with dispersal:

$$N_t = rN(1 - N/K) + d\nabla^2 N, \tag{1}$$

where N_t is the change in time of the local biomass and $\nabla^2 N$ is the second derivative in space of N (a diffusion term). Here r is the characteristic, local dynamical rate of growth, while the rate of spread by dispersal is governed by d. In this model the bare state $N = 0$ is an unstable solution. This is the classic model of population growth (Hall, 1988), shown to appropriately depict the dynamics of various biological systems, from the growth of unicellular organisms (Gause, 1934), to human populations (Marchetti et al., 1996).

The second model (AE) describes species dynamics with a strong Allee effect (Kramer et al., 2009), so that low biomass densities are not viable. Such dynamics have been found in a variety of species, ranging from the gypsy moth to woodland caribou (Kramer et al., 2009). The model reads

$$N_t = rN(1 - N/K)(N/\alpha - 1) + d\nabla^2 N, \tag{2}$$

where α is the viability threshold, i.e. the minimal amount of biomass N that is necessary to allow positive growth. This model has two alternative stable states ($N = 0, N = K$) and a single unstable state ($N = \alpha$), and we assume that $0 < \alpha < K$. This is the simplest model for dynamics with alternative stable states, a property that has been found in many ecosystems (Scheffer, 2009), such as lakes (Carpenter, 2005) and coral reefs (Nyström et al., 2000).

Finally, our third model (SR) describes dynamics with slow recovery following intense disturbances, and stands as an intermediate between the two previous models. It will help us to clarify the distinction between strong nonlinearity and bistability. Its main feature is that while there is only one stable equilibrium at $N = K$, far from this equilibrium the return rate is very slow compared with the return rate close to equilibrium. This could model succession dynamics, for which the recovery following strong disturbances (e.g., clearcutting) is very slow, as it involves the successive colonization by different species, and not simply the regrowth of the disturbed species (Uhl, 1987), or a weak Allee effect, a prevalent feature in population dynamics (Kramer et al., 2009). The model is:

$$N_t = rN(1 - N/K)(N/K)^\gamma + d\nabla^2 N, \tag{3}$$

where γ controls the nonlinearity of the dynamics, such that at high values of γ local recovery is very slow following high-intensity disturbances.

For each model we can define a local potential (see left panels of **Figure 2**), such that its derivative with respect to N corresponds to the derivative of N with respect to time—i.e., the local dynamics. This means that the local dynamics follow the slope of this potential, so that the biomass density can be thought of as a ball moving from peaks to valleys in the landscape that the potential defines. In both the LG and SR models only one stable equilibrium exists, but the speed of return to the equilibrium may be much slower for low biomass density in the SR model. Two stable states exist in the AE model (the populated state and the bare state).

By rescaling time, space and biomass, we can effectively reduce the parameter space, and set $r = 1$, $d = 1$ and $K = 1$. Our results thus hold for any values of these three parameters. We set $\alpha = 0.4$ to make sure that the AE model recovers from a single disturbance (see next subsection), and $\gamma = 4$ to make sure the return time far from equilibrium of the SR model is sufficiently slow. We focus on one-dimensional systems as they are simpler to analyze, but the qualitative results hold for other types of spatial structure such as two-dimensional systems (see **Appendix D**). We use a system size of $L = 500$, which is large enough to allow for the spatial dynamics to manifest itself (so that the system is not in the Mixing Regime Zelnik et al., 2018), with periodic boundary conditions. For a clearer illustration, in **Figure 3** and **Figure S2** we show snapshots of a two-dimensional system of size 200×200.

2.2. The Spatial Dimension of Disturbances

We define a disturbance as a change in the state variable that is forced on the ecosystem. We consider a pulse disturbance occurring at a given time, with its full effect being applied at that time. This assumption is appropriate for the many types of disturbances that are faster than the dynamics of the ecosystem, and lends itself to mathematical analysis. We choose a disturbance that removes biomass (reduces N), so that a disturbance of strength s will reduce the overall biomass of the ecosystem by sK (but any negative values of N will be set to 0 for consistency). Once a disturbance takes place, the ecosystem may recover to its original state, or a regime shift can occur if the ecosystem is bistable. We are interested here in stability and recovery dynamics, and therefore focus on parameter values for which a single disturbance cannot lead to a regime shift.

Since a disturbance need not occur uniformly across space, we vary the spatial extent of the disturbance σ while keeping its overall strength s constant. A disturbance is performed by choosing its locus, and removing some biomass in a domain of size σ centered around the locus. We can vary the spatial extent from $\sigma = 1$ for a uniform disturbance across space, to $\sigma = s$ for a localized disturbance.

To measure recovery we use the return time T defined as the time needed for the ecosystem to recover 90% of the biomass lost to the disturbance. While the choice of a threshold is arbitrary, its specific value has no significant effect on the results as long as it is not too close to either 0% or 100% (which roughly correspond to reactivity and asymptotic resilience, respectively Arnoldi et al., 2016). By avoiding these extreme values, we simply emphasize the role played by the overall recovery dynamics, rather than by the system's initial response or final convergence.

2.3. The Temporal Dimension of Disturbances

We consider a disturbance regime by repeatedly applying disturbances with a given average frequency f, over a time period τ. For simplicity we assume no correlation in space or in time, so that the time between disturbances is drawn from an exponential distribution with some average frequency (a Poisson process, see **Appendix B** for details), while the location of the disturbance's center is drawn from a uniform distribution.

We use two measures of stability for a system that is disturbed repeatedly, i.e., variability, which measures how far the system ventures from its average value, and persistence, which measures how likely it is to move to the basin of attraction of a different equilibrium. We define variability V as the variance in time of the total biomass of the system, given a regime of repeated disturbances. In order to neglect the effect of transients, we calculate V over the last 80% of the simulations, which last for 10,000 time steps. We define the collapse probability C as the probability that the system will be in the bare state at the end of a simulation, such that $C = 0$ means no chance of a system collapse, while $C = 1$ means that a collapse is certain. We use a longer simulation time (100,000 time steps) to calculate C since we are interested in predicting a collapse before it occurs. For each of these calculations we run 100 simulations with different randomizations of the location and time of disturbances.

3. RESULTS

3.1. Spanning the Spatial Dimension of Disturbances Reveals Local Ecosystem Dynamics

We begin by looking at the response of an ecosystem to a single disturbance with varying spatial extent σ. We focus on disturbances with a fixed overall strength $s = s_0$ for simplicity and clarity, and relax this assumption in the discussion. Thus a global disturbance $\sigma = 1$ (**Figure 1**, right panels) occurs when N is decreased by $s_0 K$ in the entire system, while a localized disturbance $\sigma = s_0$ (**Figure 1**, left panels) occurs when N is set to zero in a domain of relative size s_0.

The response to a disturbance can take two possible forms: isolated recovery due to local processes, and rescue recovery due to incoming biomass from outside the disturbed region. Isolated recovery dominates the system response when each site recovers without the aid of neighboring sites (**Figure 1**, right panels). In contrast, rescue recovery occurs when the disturbed region cannot recover without the rest of the system, or when the bulk of the recovery occurs due to such spatial dynamics (**Figure 1**, left panels).

The coupling of local dynamics and dispersal results in distinct recovery processes in the three models, as shown by

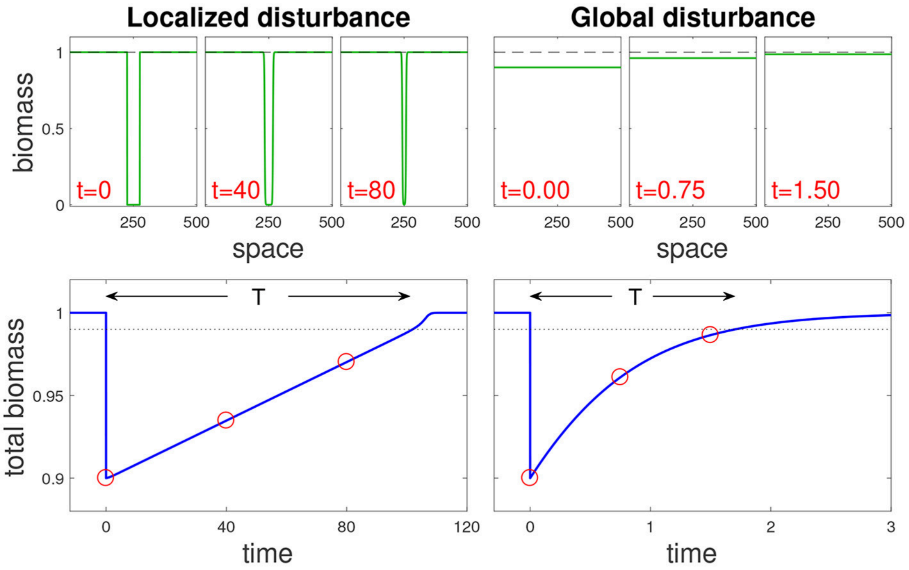

FIGURE 1 | Recovery dynamics following a localized and a global disturbance (left and right panels, respectively) for the bistable AE model (see Main text). Top panels: snapshots at different times (t) along recovery trajectories, each snapshot showing a biomass spatial profile. Bottom panels show the change in overall biomass over time following the disturbance, where the dotted line denotes the threshold beyond which the system is considered to have recovered, and red circles correspond to the snapshots. Note that the return time T from a localized disturbance is much longer than the one from a global disturbance. Disturbance parameters are $s = 0.1$, with $\sigma = 0.1$ for the localized disturbance and $\sigma = 1$ for the global one.

the trajectories in phase-space diagrams in the middle column of **Figure 2**. In these panels we unfold the recovery along two dimensions: the horizontal axis denotes the size of the disturbed region at a given time, while the vertical axis shows the biomass density in the disturbed region. Immediately after the disturbance, the system is along the dashed black curve, and it then changes over time until it enters the shaded region where it is considered to have recovered.

If a large part of the trajectory during recovery is horizontal, this means that the disturbed region is shrinking due to rescue recovery, which indicates a lack of local resilience, which would otherwise allow isolated recovery to take place. This behavior reflects the strong nonlinearity of local dynamics, which can be seen in the changing curvature of the local potential (**Figure 2**, left column). We can see that for the AE model (**Figure 2**, bottom row) the recovery is along a horizontal line for recovery scenarios with a sufficiently small spatial extent, so that regional processes bring about the recovery. In contrast, the recovery is entirely due to local processes in the LG model since the local dynamics are much faster here, while for the intermediate SR model a mixture of the two processes can be seen to take place.

These differences translate into markedly different values of the return time T (**Figure 2**, right panels). The vertical recovery trajectories that follow all disturbances in the LG model and large-sized disturbances in other models indicate isolated recovery, and hence small values of T. For the intermediate SR model localized disturbances lead to a larger contribution of rescue recovery, leading to a sigmoid shape of T as a function of disturbance extent σ. The AE model shows a similar behavior of larger T following localized disturbances, but the trend here shows a maximum for mid-sized disturbances. This occurs because in bistable systems, the most efficient way to perturb the system is to locally remove biomass just bellow the viability threshold, and then let the system collapse locally. Such a disturbance has an equivalent effect to that of a stronger disturbance that would remove all biomass over a larger region. The spatial recovery process will take longer to recover, thus giving larger return time values (see **Appendix A** for details).

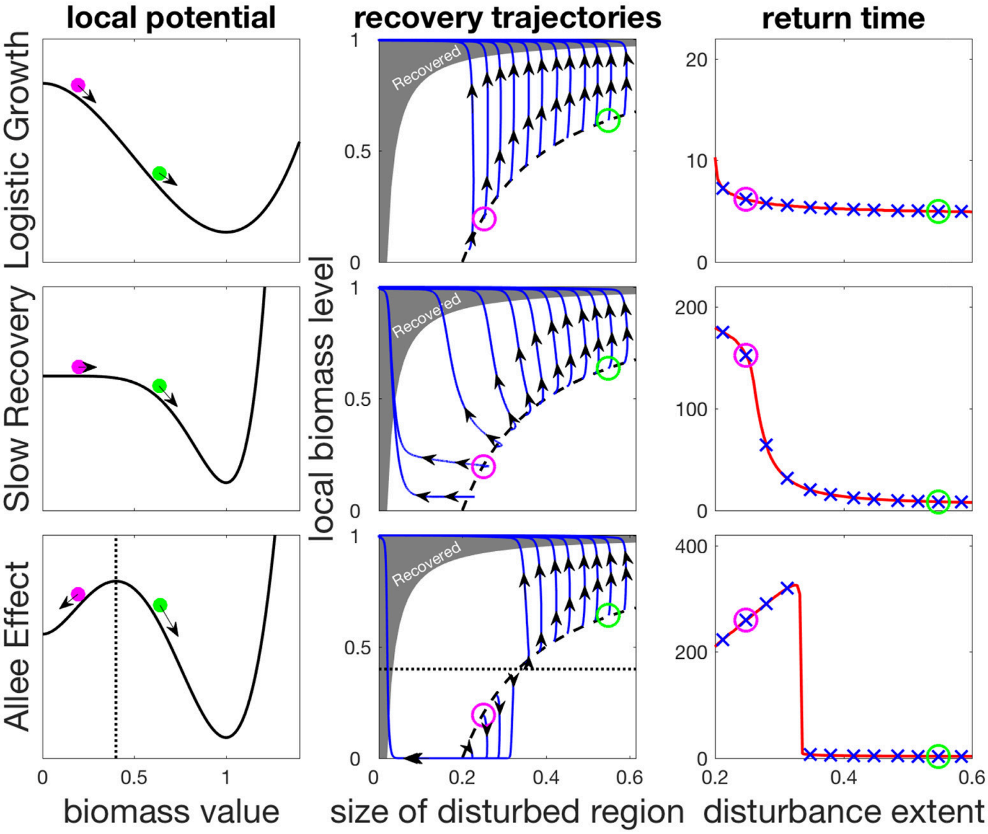

FIGURE 2 | Contribution of isolated and rescue recovery as a function of disturbance spatial extent for the three models presented in the main text. The left column shows the local potentials defining local processes. Top row: Logistic (LG) model; Middle row: the highly non-linear SR model; Bottom row: bistable AE model. Middle column: isolated recovery on the y-axis, and rescue recovery on the x-axis. Black dashed line shows the equal disturbance strength used $s = 0.2$ for different disturbance extent σ. Blue lines are recovery trajectories, where recovery is considered complete when trajectories reach the gray shaded region. For the SR and AE model, as disturbances become more localized, a shift is observed from a dominant isolated recovery (upward trajectories) to a dominant rescue recovery (leftward trajectories), impacting return times (right column). The "x" marks in blue correspond to the different trajectories shown in middle columns. The green and magenta circles show initial states following two different disturbances (left and middle columns) and their associated return times (right column). The dotted line (bottom row) shows the local tipping point of the bistable AE model, beyond which local dynamics collapse to the bare state.

This explains the humped shape of return time as a function of disturbance extent. Since bistability is a sufficient condition for a hump-shaped relationship to occur, the latter could be used as an indicator of bistability. This illustrates the more general idea that considering the spatial dimension of disturbances can allow us to probe the local dynamics of a spatially extended ecosystem.

3.2. From Variability to Collapse Under Increasing Frequency of Disturbances

Natural ecosystems are constantly perturbed, leading us to consider a temporal dimension of disturbances, namely their average frequency. We therefore translate the results of the previous section on the response to a single disturbance (**Figure 3**, top) into an understanding of temporal variability under repeated disturbances (**Figure 3**, bottom). In fact, there is a direct link between the response to a single disturbance and temporal variability in response to repeated disturbances. Indeed, biomass fluctuations are the result of past disturbances, as they integrate short- to long-term responses of the ecosystem to individual disturbances (Arnoldi et al., 2016). Variability is a statistic of those fluctuations, and is therefore a function of both the integrated response to a single disturbance and the average frequency f of disturbances. More precisely, if $g(t)$ traces the change in overall biomass through time following a pulse disturbance a time $t = 0$, then variability V can be expressed as $V = f \int_0^\infty g^2(t)dt$ (see Equation S15 in **Appendix B**). However, this identity assumes no interaction in space between the different disturbances, and therefore should not hold at high disturbance frequency.

As expected, at low frequency of disturbances the analytical approximation agrees with the numerical simulations quite well for all three models (**Figure 4**, second column). For higher frequencies (**Figure 4**, third column) where multiple disturbances often take place in the same time frame, we see a slight underestimation of the analytical approximation, although the general trend is well captured. Importantly, variability and return time show the same behavior. We see effects of regional processes on variability for more localized disturbances in both the SR and AE models, where the former shows a sigmoid shape while the latter has a hump shape, which is a consequence of the bistability in the AE model. We note that these trends hold in more general scenarios, such as disturbances with a random extent or following seasonal patterns (**Appendix D**).

At this point it would appear that the temporal dimension of disturbances f is not as informative on ecosystem behavior as the spatial dimension of disturbances σ. However, as f is increased further, a discrepancy between variability and its prediction based on recovery from a single disturbance starts to grow. This signals that the disturbances start to interact with each other, a phenomenon that is not captured by our approximation. Disturbances start to aggregate in space, which can substantially increase variability (**Appendix C**) due to large excursions toward low total biomass levels. For bistable systems such as the AE model, such excursions can lead to a collapse of the whole system. This is evident in the two last columns of **Figure 4**, in which we see, for the AE model, that the values of σ for which the discrepancy of variability is highest precisely corresponds to the values of σ for which the collapse probability is most significant. Thus, at high frequencies, disturbances of similar strength but different spatial extent lead to dramatically different responses. This example highlights the fact that the combination of spatial and temporal dimensions of disturbances can have a drastic effect on ecosystem stability.

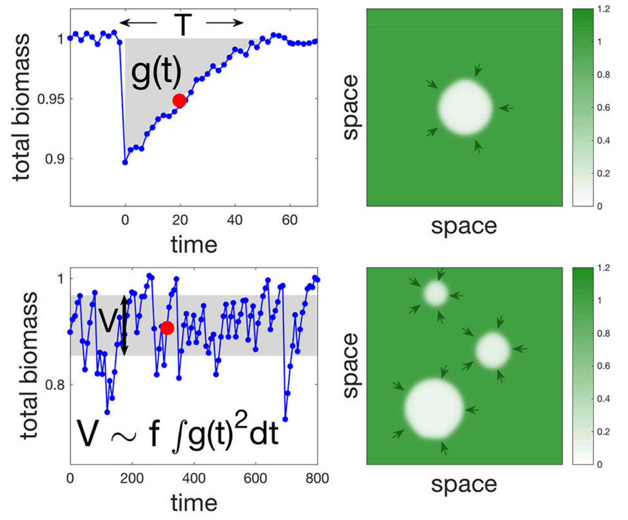

FIGURE 3 | Single and multiple disturbance regimes and the relationship between return time and variability. The left panels show time series of the overall biomass, while right panels are spatial snapshots of the corresponding time-series (red dots in the left panels). The response to a single disturbance is shown in the top left panel. We focus on two of its characteristics: return time *T*, and an integral measure of the transient *g*(*t*) (see main text). The response to multiple disturbances occurring randomly at an average frequency *f* is shown in the bottom left panel. It is summarized by its variability *V* (variance of overall biomass). In the limit of low *f* there is an inherent relationship between return time and variability in the sense that *V* can be approximated by $f \int_0^\infty g^2(t)dt$. Simulations were made using the SR model with parameters values: $s = 0.1$, $\sigma = 0.11$, $f = 0.025$, and $\gamma = 2$. Random uniform noise was added in left panels to demonstrate how realistic time series might look like.

4. DISCUSSION

Investigating the role of the spatial and temporal dimensions of disturbances in ecosystem stability, we obtained four main results: (1) In comparison with a global disturbance, a localized one of the same strength can initiate a fundamentally different, and much slower, ecosystem response, especially when local dynamics are nonlinear. (2) The return time from a single disturbance and the temporal variability caused by repeated disturbances show the same trends, even for locally intense (and therefore nonlinear) disturbances. (3) The relationship between a system's response and the spatial extent of the disturbances it experiences reveals its underlying dynamics. For instance, a hump-shaped relationship between return time and the spatial extent of the disturbances may indicate bistability. (4) The correspondence between return time and variability breaks down for high disturbance frequencies. This discrepancy signals the

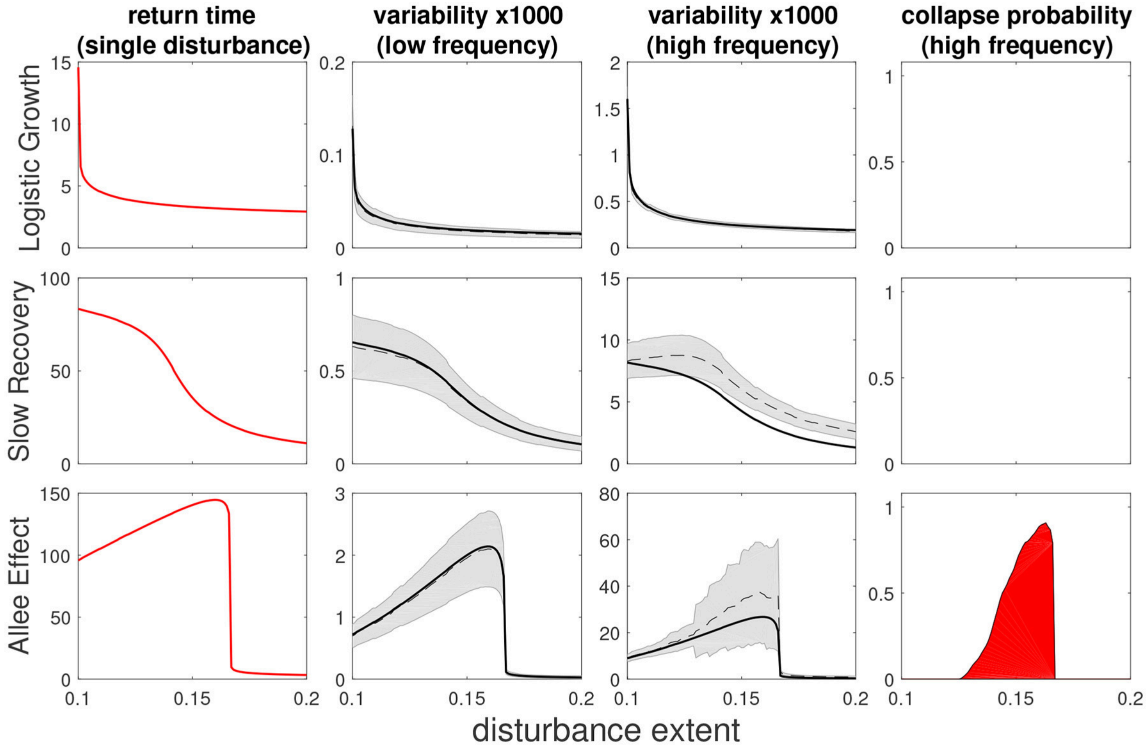

FIGURE 4 | Return time, variability and collapse probability as a function of disturbance spatial extent for three models (from top to bottom: LG, SR, AE). Left column shows return times (as in **Figure 2**) while middle columns show variability under low and high frequency of disturbances, and right column shows collapse probability. The black dashed (solid) line is a numerical (analytical prediction) value of variability, with gray shading noting error estimation. Deviation from this prediction implies some degree of interaction between disturbances. Return time and variability are qualitatively similar with low dependency of disturbance spatial extent for the LG model but a much stronger dependency when local dynamics are highly non-linear (SR and AE models). In the case of the bistable AE model we recognize a non-monotonous "hump-shaped" dependency with disturbance extent, with mid-sized disturbances causing the most severe response. Disturbance parameters were $s = 0.1$, $\sigma = 0.1$, and for low frequency: $f = 0.002$, while for high frequency: $f = 0.02$.

occurrence of spatial interactions between disturbed regions, which, in turn, may lead to a regime shift.

Although we considered simple spatially homogenous models, our results should apply to a wide range of ecosystems. Forests, savannah and shrublands might be good examples of ecosystems to which our models apply since disturbances such as fires and grazing occur frequently and are often localized, and the recovery of plant communities often follows complex succession dynamics driven by spatial processes (Adler et al., 2001; Turner, 2010; Staver and Levin, 2012). Our results, however, need not be restricted to such spatially homogeneous systems. Although we built our theory using spatially uniform models, this simplifying feature is not essential to our arguments, which only require a notion of locality. Therefore, our theory may also be relevant to less homogeneous ecosystems, such as mountain lake networks, coral reefs and riverine systems. Indeed, such ecosystems undergo different disturbances that are often strongly localized, and their dynamics may be sufficiently nonlinear (Knowlton, 1992; Campbell Grant et al., 2007; Forrest and Arnott, 2007).

Uniquely to our work, we considered systems locally pushed far from their equilibrium, and even to a different basin of attraction. In a marine ecosystem context, this could represent coral reefs (Nyström et al., 2000; Adjeroud et al., 2009) or rocky intertidal systems (Sousa, 1979; Paine and Levin, 1981), which frequently undergo intense disturbances (e.g., storm damage). These locally intense disturbances can allow rescue recovery, mediated by dispersal, to dominate the ecosystem response. In the case of the bistable (AE) model this glimpse outside the basin of attraction of the populated state is the direct cause of the hump-shaped trends of variability and return time as a function of disturbance extent. In fact, the front propagation that drives rescue recovery contains information about the ecosystem's basins of attractions, reflecting the existence of alternative stable states and the transient dynamics between them. Thus, by observing the ecosystem's response to localized disturbances, rescue recovery allows us to probe ecosystem dynamics far from equilibrium. For instance, comparing between different disturbed marine ecosystems may give further evidence that some have alternative states (e.g., coral reefs) while for others the dynamics show a succession process (e.g., rocky intertidal systems). This reasoning could be taken further by focusing on regions where rescue recovery takes place, e.g., analyzing the plant community structure at transition zones between grassland and forest in a savanna ecosystem (Augustine, 2003).

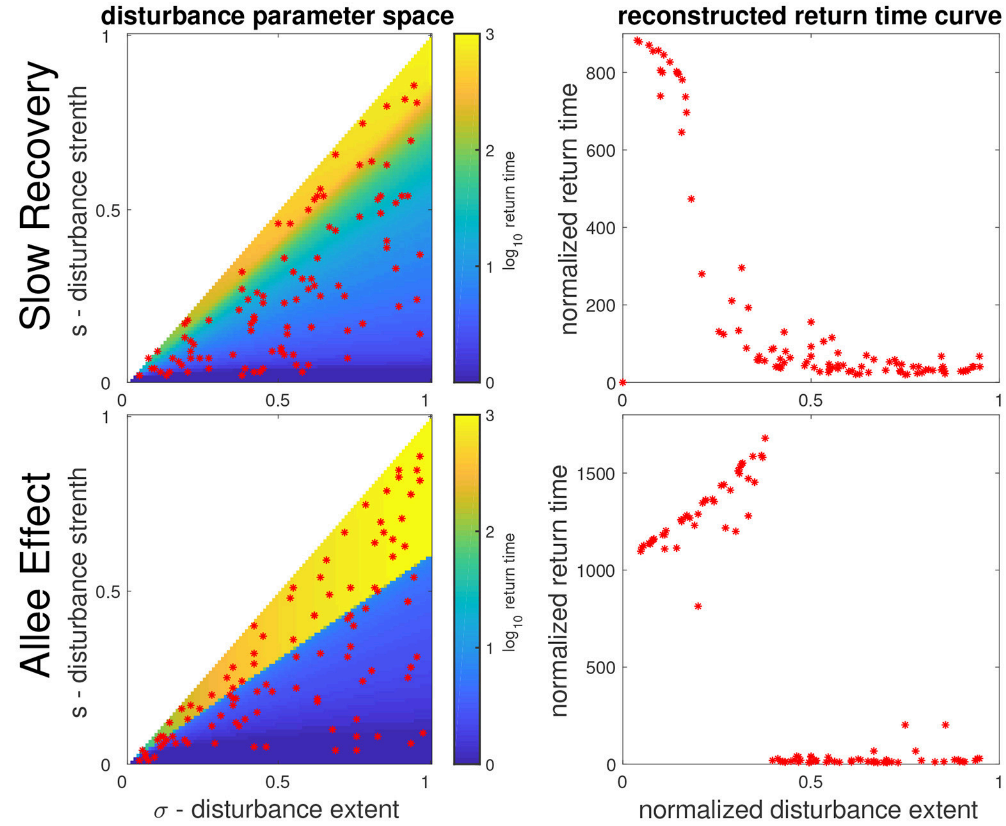

FIGURE 5 | Reconstruction of return time vs. disturbance extent curve from the more general parameter space of disturbance properties. Top (bottom) panels correspond to the SR (AE) model. Left column shows the return time over the parameter space of disturbance extent σ (x-axis) and of disturbance strength s (y-axis). Right column shows the corresponding reconstruction of the return time curve, using 100 randomly chosen points (red asterisks) in the parameter space. The return time values are normalized by the disturbance strength s, while the normalized disturbance extent is defined as $\tilde{\sigma} = 1 - s/\sigma$. Note that the hump (sigmoid) shape of the curve for the AE (SR) model are easily recognizable from these reconstructions.

Spanning the spatial dimension of disturbances could thus allow us to detect nonlinearities in ecosystem behavior, revealed by the increasing local intensity of disturbances (see **Figure 2**). One might expect that along the temporal dimension of disturbances, increasing their average frequency could also reveal nonlinear effects, since the ecosystem becomes more strongly disturbed. In fact, increasing frequency has only a trivial linear effect, as reflected by the relation we found between return time and variability (see **Figure 3**). Beyond some threshold, however, a response of a different kind emerges, due to spatial interactions between disturbed regions which aggregate in potentially large-scale clusters. This causes a higher variability than expected and can, consequently, cause a global loss of persistence or a regime shift. Taking, once again, the example of corals reefs, we could ask how the impact of both natural and anthropogenic disturbances leads to a phase-shift from hard coral to fleshy algae dominance. A regime shift due to an aggregation of unrecovered regions would occur not as a typical tipping point due to loss of resilience (e.g., due to changing temperatures), but rather due to the crossing of a threshold for disturbance frequency. Importantly, in such a scenario the two dimensions, spatial and temporal, must be considered in conjunction. The threshold beyond which aggregation occurs depends strongly on the spatial extent of disturbances and hence the associated response is not a mere superposition of responses to single disturbances. In other words, this finding highlights and explains how the interplay between the spatial and temporal dimensions of disturbances can have drastic ecological consequences, such the loss of persistence. Since our findings are purely theoretical, it would be enlightening to elucidate the prevalence of this interplay in empirical systems that have undergone regime shifts (e.g., phase-shifts in coral reefs Nyström et al., 2000 or the desertification of the once green Sahara Ortiz et al., 2000).

As previously mentioned, in bistable systems the relationship between return time (as well as variability) and the spatial extent of disturbances is hump-shaped. This relation could be used as an indicator of bistability, assessed empirically by comparing time series of the same ecosystem in different regions with estimates of the intensity of single disturbances. Its implications for ecosystem management depend on the type of disturbances considered. Anthropogenic disturbances that are largely controlled, such as logging in forests (Chazdon, 2003) or large-scale fishing (Kaiser et al., 2006), can be better planned to avoid both an unpredictable yield due to high variability and an overall collapse. For many natural disturbances control is neither possible nor desired (e.g., fires in semi-arid ecosystems necessary for plant germination Wellington and Noble, 1985), but predicting their effects and the possibility of regime shifts is paramount (Kéfi et al., 2007).

In order to focus on the role of the spatial properties of disturbances and allow a clearer presentation, we conducted our analysis assuming disturbances of constant overall strength. It is straightforward to extend the analysis to more general settings, such as a random extent of disturbances and seasonal patterns (see **Appendix D** for details). It is particularly interesting to consider the case of different values of disturbance strength s. As shown in **Figure 5**, if we randomly choose a set of points with different values of strength s and extent σ, we can use these to reconstruct a normalized version of the dependency of the different stability measures on disturbance extent. Thus we can use the different phenomena described previously, such as a hump-shape relationship as an indicator of bistability, under more general conditions, thereby making our theory more empirically accessible.

Our work is a step toward a quantitative account of spatial and temporal dimensions of disturbances, and their interplay with local and regional ecosystem dynamics. This is an important goal in the context of global change. Disturbances are of increasing frequencies and occur at different scales (which is evident, e.g., in coral reefs Jackson, 1991 and forests Turner et al., 1993), while the spatial structure of ecosystems themselves is altered by land use change, often causing fragmentation of the landscape (Harrison and Bruna, 1999). It is thus important to build a framework in which we can understand and predict the ecological impacts of this complex interplay.

DATA AVAILABILITY STATEMENT

The results shown in this study are based on Matlab code that can be found in the Github repository of https://github.com/yzelnik/stddes-scripts.

AUTHOR CONTRIBUTIONS

YZ, J-FA, and ML designed the study. YZ and J-FA performed the research. YZ, J-FA,and ML wrote the manuscript.

FUNDING

This work was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41) and by the BIOSTASES Advanced Grant, funded by the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement No 666971).

ACKNOWLEDGMENTS

We wish to thank Bart Haegeman and Matthieu Barbier for helpful discussions and comments on a previous version of the manuscript. We would also like to thank two referees for their useful comments on the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00224/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 07 January 2019
doi: 10.3389/fevo.2018.00230

The Sensitivity of Subsurface Microbes to Ocean Warming Accentuates Future Declines in Particulate Carbon Export

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Under future warming Earth System Models (ESMs) project a decrease in the magnitude of downward particulate organic carbon (POC) export, suggesting the potential for carbon storage in the deep ocean will be reduced. Projections of POC export can also be quantified using an alternative physiologically-based approach, the Metabolic Theory of Ecology (MTE). MTE employs an activation energy (E_a) describing organismal metabolic sensitivity to temperature change, but does not consider changes in ocean chemistry or physics. Many ESMs incorporate temperature dependent functions, where rates (e.g., respiration) scale with temperature. Temperature *sensitivity* describes how temperature dependence varies across metabolic rates or species. ESMs acknowledge temperature sensitivity between rates (e.g., between heterotrophic and autotropic processes), but due to a lack of empirical data cannot parameterize for variation within rates, such as differences within species or biogeochemical provinces. Here we investigate how varying temperature sensitivity affects heterotrophic microbial respiration and hence future POC export. Using satellite-derived data and ESM temperature projections we applied microbial MTE, with varying temperature sensitivity, to estimates of global POC export. In line with observations from polar regions and the deep ocean we imposed an elevated temperature sensitivity ($E_a = 1.0$ eV) to cooler regions; firstly to the Southern Ocean (south of 40°S) and secondly where temperature at 100 m depth <13°C. Elsewhere in both these scenarios E_a was set to 0.7 eV (moderate sensitivity/classic MTE). Imposing high temperature sensitivity in cool regions resulted in projected declines in export of 17 ± 1% (< 40°S) and 23 ± 1% (< 13°C) by 2100 relative to the present day. Hence varying microbial temperature sensitivity resulted in at least 2-fold greater declines in POC export than suggested by classic MTE derived in this study (12 ± 1%, $E_a = 0.7$ eV globally) or ESMs (1–12%). The sparse observational data currently available suggests metabolic temperature sensitivity of organisms likely differs depending on the oceanic province they reside in. We advocate temperature sensitivity to be incorporated in biogeochemical models to improve projections of future carbon export, which could be currently underestimating the change in future POC export.

Keywords: particulate carbon export, microbes, warming, metabolic theory, activation energy

OPEN ACCESS

Edited by:
Diego Barneche,
University of Sydney, Australia

Reviewed by:
C.-Elisa Schaum,
Universität Hamburg, Germany
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University of Exeter, United Kingdom

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *18 October 2018*
Accepted: *07 December 2018*
Published: *07 January 2019*

Citation:
Cavan EL, Henson SA and Boyd PW (2019) The Sensitivity of Subsurface Microbes to Ocean Warming Accentuates Future Declines in Particulate Carbon Export. Front. Ecol. Evol. 6:230. doi: 10.3389/fevo.2018.00230

INTRODUCTION

The biological pump exports large amounts of carbon from the surface ocean to the deep, where it can be stored on climatically-relevant timescales helping to regulate atmospheric carbon dioxide levels (Volk and Hoffert, 1985; Falkowski et al., 1998). However future ocean warming threatens to decrease the amount of particulate organic carbon (POC) reaching the deep ocean (Laufkötter et al., 2016). The magnitude of deep ocean carbon storage by the biological pump is largely dependent on 3 factors; (1) the magnitude and size-partitioning of primary production taking place in the surface mixed layer, (2) the sinking rate of the particles formed initially from particle production, and (3) the organic remineralisation rate by organisms such as zooplankton and microbes that degrade POC (Buesseler and Boyd, 2009; Turner, 2015). Each of these parameters is a function of temperature, with warming increasing all three rates if other factors, such as nutrient supply, remain unchanged (López-Urrutia et al., 2006; Taucher and Oschlies, 2011; Iversen and Ploug, 2013).

Warming is projected to increase metabolic rates (Brown et al., 2004), which will increase both primary production (more carbon available to sink to deep ocean) and the metabolic rates of heterotrophs that consume phytoplankton and sinking POC (decreasing the carbon sink) (López-Urrutia et al., 2006; Taucher and Oschlies, 2011; Cavan and Boyd, 2018). In parallel warming-induced stratification and shoaling of the mixed layer will reduce nutrient inputs to the sunlit upper ocean (Bopp et al., 2001), expanding oligotrophic waters thus likely favoring smaller phytoplankton species and ultimately reducing primary production (Bopp et al., 2005). The decrease in nutrient supply to surface waters is typically considered to have the greatest effect on the magnitude of future primary production (Marañón et al., 2014) and thus overall primary production is expected to decline, although there is some disagreement amongst models (Laufkötter et al., 2015). One feedback from warming that will increase the carbon sink is the reduction in water viscosity, allowing particles to sink through the water column faster, escaping the upper ocean where remineralisation is most intense (Bach et al., 2012).

Export production is projected to decline by 1–12% depending on the Earth System Model (ESM) model used, due to declines in the magnitude and changes in the size-partitioning of primary production, and increased remineralisation of POC due to warming (Laufkötter et al., 2016). Remineralisation occurs throughout the water column and affects both the amount of POC exported and POC attenuation through the mesopelagic zone. Export or formation of detritus can either be parameterised by simple empirical algorithms, which may include primary production and temperature terms (Dunne et al., 2005; Henson et al., 2011; Britten et al., 2017) or in ESMs by phytoplankton aggregation and remineralisation parameterisations (Aumont et al., 2015).

Currently, there are a range of approaches to parameterise temperature-dependent terms in models. For example, in the biogeochemical model REcoM2, one theoretical exponential (Arrhenius type) relationship is used to describe all temperature-dependent terms; remineralisation of particulate and dissolved organic matter, silicon uptake, zooplankton respiration, and zooplankton grazing (Schourup-Kristensen et al., 2014). However, in the PISCES-v2 model, a constant Q_{10} of 1.9 from Eppley (1972), which correlated phytoplankton growth rates with temperature, is used to describe both phytoplankton growth rates and POC degradation (Aumont et al., 2015). A Q_{10} of 1.9 implies an increase in 10°C will result in metabolic rates that are 1.9 times higher. None of the marine biogeochemical components of the ESMs account for adaptation, which may be an important response to ocean warming with knock-on effects for POC export. For example, a laboratory study has shown that after 100 generations (freshwater) phytoplankton can adapt to warming by down-regulating respiration relative to photosynthesis to maintain the carbon allocation efficiency needed for growth (Padfield et al., 2016). Although phytoplankton in nutrient-poor regions may exhibit a different adaptation response as nutrient limitation can supress the temperature dependence of phytoplankton (Marañón et al., 2014).

In some ESMs temperature dependence varies between different metabolic rates (e.g., heterotrophic processes have a higher rate of change to temperature than autotrophic processes) (López-Urrutia et al., 2006; Dunne, 2013) thus incorporating differences in temperature sensitivity are only captured at a coarse scale. At present these biogeochemical models do not acknowledge temperature sensitivity within rates i.e., differences in the response to temperature between species or between the same species living in a different biogeochemical province. However, there is unlikely to be one uniform metabolic response to warming globally.

Sensitivity to temperature can be quantified as the activation energy (E_a) of a metabolic reaction—the amount of energy needed for a chemical reaction to occur (Schoolfield et al., 1981; Clarke and Johnston, 1999; Yvon-Durocher et al., 2012). E_a can be estimated via the Metabolic Theory of Ecology (MTE), which describes how metabolic processes vary as a function of organismal mass and temperature (Brown et al., 2004):

$$\ln\left(I\,M^{-0.75}\right) = -E_a\left(\frac{1}{cT}\right) + \ln(i_0) \tag{1}$$

Where I is the metabolic rate normalized by mass (M), E_a is the activation energy, c is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), T is the temperature in Kelvin and finally i_0 is a normalization constant. The latter can be used to describe how organisms or communities are adapted to living at different temperatures (Clarke, 2006). When computed in the context of MTE using Equation 1, the E_a is the slope between mass-normalized metabolism and temperature. MTE states all organisms have an activation energy of 0.6–0.7 eV (Gillooly et al., 2001; Brown et al., 2004), thus there is little natural variation in temperature sensitivity. Activation energies higher than this range suggest organisms are more sensitive to changes in temperature, as shown in Arctic, and Antarctic zooplankton [$E_a = 1.29$ eV, (Alcaraz, 2016)], mesopelagic heterotrophs [$E_a = 0.9$ eV, (Brewer and Peltzer, 2016)] and a mixed heterotrophic microbial community from the sub-Antarctic [$E_a = 0.9$ eV, (Cavan and Boyd, 2018)]. As primary production and respiration (remineralisation) are both metabolic rates, MTE can be used to describe how they might change with future warming in the global oceans, and thus their influence on POC export. Model experiments have confirmed that temperature sensitivities of metabolic rates have an important role in ecosystem function, by regulating the magnitude of primary production and respiration (Taucher and Oschlies, 2011).

If organisms do respond differently to warming based on the environmental conditions they currently encounter, then biogeochemical models are likely to be inaccurately projecting carbon sequestration under future warming scenarios. Therefore, the objective of this study is to use empirical algorithms, including MTE, satellite data, and ESM outputs to determine the effect of temperature sensitivity on future POC export projections by 2100. We varied the activation energy in line with observations to investigate how temperature sensitivity influences POC export. MTE only accounts for changes in metabolic rates due to temperature, and thus using this framework implies that nutrients, phytoplankton community composition, and ocean physical changes, such as stratification, are unaltered in the year 2100.

METHODS

Data

Annual satellite sea surface temperature (SST) and output from the Vertically Generalized Production Model (VGPM) for primary production for 2003–2016 (Oregon State University, 2017) were used as the baseline data for the beginning of this century. Coupled-Model Intercomparison Project-Phase 5 (CMIP5) ESM outputs over 1986–2005 (historical run) and under the IPCC Representative Concentration Pathway (RCP) 8.5 (business-as-usual run) for 2081–2100 were used to estimate the change in temperature at the sea surface and at 100 m depth and the change in export and primary production by the end of this century. See **Table 1** for a list of frequently used acronyms. The 8 models used were GFDL-ESM2G and GFDL-ESM2M (Dunne et al., 2013), HadGEM2-CC and HadGEM2-ES (Bellouin et al., 2011; Collins et al., 2011), IPSL-LR and IPSL-MR (Séférian et al., 2013), MPI-LR and MPI-MR (Jungclaus et al., 2013) (see **Supplementary Table 1** and Bopp et al. (2013) for a summary of model set-ups). These models were selected as they were the ones available in the CMIP5 (at the time of our analysis) that simulated export, primary production, and temperature.

TABLE 1 | Frequently used acronyms.

Acronym	Explanation
CMIP5	Coupled model intercomparison project phase 5
E_a	Activation energy (in eV)
ESM	Earth system model
MTE	Metabolic theory of ecology
POC	Particulate organic carbon
Q_{10}	Temperature coefficient, the rate ratio at a temperature increase of 10°C
RCP	Representative concentration pathway
SST	Sea surface temperature
VGPM	Vertical generalized production model
WOA	World ocean atlas

Satellite-Derived Climatologies

Global, 9 km resolution, mean SST data for the years 2003–2016 inclusive were downloaded from the NASA ocean color database (https://oceancolor.gsfc.nasa.gov) in annual composites. The data were then averaged (mean) over the 14 years and re-gridded onto a 1 × 1° grid (**Figure 1A**). The temperature at our chosen export depth of 100 m was extracted from World Ocean Atlas (WOA) climatology (**Figure 1B**). We chose 100 m as this is typically below the sunlit mixed layer and conventionally defines the upper mesopelagic zone. Global, mean monthly primary production data (9 km resolution) for the same years (2003–2016) were downloaded from the Ocean Productivity site (Oregon State University, 2017, https://www.science.oregonstate.edu/ocean.productivity/), using the standard product of the VGPM (Behrenfeld and Falkowski, 1997). Monthly means were summed to produce a total primary production (mg C m^{-2} yr^{-1}) per year for all years, which were then converted to g C m^{-2} yr^{-1} and finally the mean over the 14 years was computed. These data were also re-gridded onto a 1 × 1° grid.

The exported POC at 100 m was calculated using the export ratio (e-ratio; export/primary production) from (Henson et al., 2011) (Equation 2):

$$e - ratio = 0.23^{*} e^{(-0.08\ ^{*}SST)} \tag{2}$$

where SST is the mean annual satellite-derived SST for 2003–2016. The e-ratio was then multiplied by primary production to give a global POC export at 100 m as in Henson et al. (2011). Primary production and exported POC were then summed globally (accounting for variability in the areal extent of the grid cells with latitude) to give production and export estimates as Gt C yr^{-1}. The input parameters (primary production and export algorithms) were varied to run a sensitivity analysis (see **Supplementary Methods**) to calculate the change in export by the year 2100 and sequentially compare the effects of each parameter on export.

ESM Projected Future Changes

Output from eight different ESMs were downloaded from the CMIP5 archive (https://esgf-node.llnl.gov/projects/esgf-llnl/) to compute the projected increase in sea temperature by 2100 (**Supplementary Table 1**). Most of the models include two phytoplankton functional groups (diatom and non-diatom) and at least one zooplankton group. The ensemble member for each model dataset was r1i1p1. Monthly historical and RCP 8.5 runs [business-as-usual (Moss et al., 2010)] were downloaded and the last 20 years of each run (1986–2005 and 2081–2100, respectively) were extracted. An annual mean, and then the mean across all years was computed for each model and time period. The desired depth levels (0 and 100 m) were extracted, temperatures converted from Kelvin to Celsius and the data re-gridded onto a

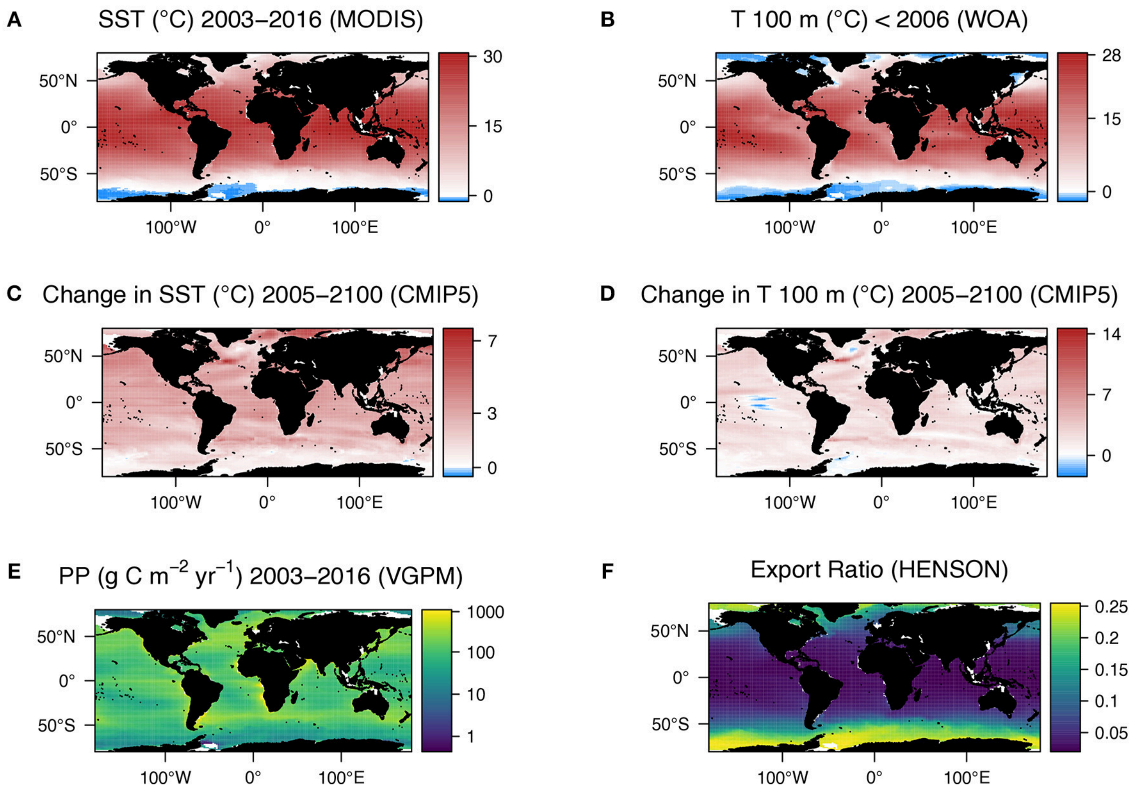

FIGURE 1 | (A) Global mean sea surface temperature climatology for 2003–2016 derived from AQUA MODIS satellite data. **(B)** Global temperature at 100 m (our chosen export depth) from WOA data collected over 1955–2012, heavily weighted toward the latter years. **(C)** Multi-model median change in sea surface temperature from 1986–2005 to 2081–2100 predicted from CMIP5 models with representative concentration pathway 8.5 applied. **(D)** Multi-model median change in sea temperature at 100 m from 1986–2005 to 2081–2100 predicted from CMIP5 models with representative concentration pathway 8.5 applied. **(E)** Mean annual primary production climatology for 2003–2016 (VGPM) and **(F)** Export ratio calculated from VGPM using algorithm of Henson et al. (2011).

$1 \times 1°$ longitude-latitude grid. Finally, a multi-model median was computed over all 8 model outputs resulting in two datasets for SST and temperature at 100 m, one for each run (historical, 1986–2005, and RCP8.5, 2081–2100). The change in temperature by the end of the century for each depth was calculated by subtracting the historical period from the end-of-century period.

The parameter "epc100" was downloaded for the same model runs and years. epc100 is the sinking mole flux of particulate organic matter expressed as carbon in seawater at 100 m. For primary production the integrated primary production "intpp" was downloaded. To make the model output comparable with the satellite-derived export estimates, the mean monthly export was summed for each year and then the mean taken for all years per model. The data were converted to a $1 \times 1°$ longitude-latitude grid and a multi-model median taken over the 8 model outputs. This was done for both the historical and RCP8.5 runs and the change in export by 2100 computed as the difference between the two datasets. The same processing steps were applied to the modeled primary production.

Applying Metabolic Theory of Ecology

To determine the change in POC export due solely to the effects of rising temperatures on microbial metabolism, the metabolic theory of ecology (MTE) was applied (Brown et al., 2004). MTE is partly based on the biomass of metabolizing organisms (Equation 1). Microbial biomass scales in the ocean with POC, such that as POC decreases with depth so does microbial biomass (Boyd et al., 1999). Bacterial biomass contributes between 20 to >100% of exported POC mass, depending on the region (Steinberg et al., 2001; Stewart et al., 2010; Collins et al., 2015), with most estimates close to 50% of POC (Ducklow et al., 1993; Boyd et al., 1999). Therefore, we normalized our estimated POC mass at 100 m to 50% to estimate heterotrophic microbial biomass, as also applied in Cavan et al. (2018). As we are computing the relative change in respiration, and the mass term is the same in all model simulations (only the temperature changes), the magnitude of the mass term has little effect on the change in respiration (see sensitivity analysis in **Supplementary Materials**).

The respiration of microbes (R_{micro}) can therefore be calculated following Equation 3:

$$R_{micro} = I * M_{HB}{}^{0.75} * e^{\frac{-Ea}{k*T}} \tag{3}$$

where I and E_a are the normalization constant and activation energy, respectively, M_{HB} is the mass of heterotrophic bacteria at 100 m, k is the Boltzmann constant (8.62×10^{-5} eV K^{-1})

and T is the temperature in Kelvin. For this global analysis I was determined as the mean of constants given for unicells ($I = 19.21$) and inverts ($I = 19.75$) in Brown et al. (2004), which was 19.48. The E_a (0.7 eV) used was also from Brown et al. (2004), which was consistent in their study over all groups of organisms tested (unicells to fish). Although deviations away from this value do exist with published E_a's ranging from 0.29 eV for primary production (López-Urrutia et al., 2006) to 1.3 eV for zooplankton respiration (Gleiber et al., 2015). For the beginning of the century, R_{micro} was calculated using the WOA temperature data at 100 m. For the end of the century we altered only the temperature term by adding the temperature change between the beginning (1986–2005) and end of the century (2081–2100) projected by the CMIP5 models at 100 m onto the WOA temperature climatology at 100 m (mean temperature 1955–2012). The change in respiration (**Figure 2A**) was computed by subtracting the beginning of the century R_{micro} from the end of the century R_{micro}.

The change in the rate of primary production (**Figure 2B**) due to increasing temperature alone was also calculated to determine the overall net decrease in POC at 100 m. For primary production the MTE constants from López-Urrutia et al. (2006) were used where in Equation (1) $I = -11.28$ and the $E_a = 0.29$ eV with M (mass) being the satellite-derived primary production (**Figure 1E**). Here though the change in SST by 2100 predicted by the difference in the beginning and end of the century runs of the CMIP5 models was used rather than the change in T at 100 m. The net change in export was calculated by subtracting the change in autotrophic primary production from the change in heterotrophic microbial respiration.

RESULTS

Using the business-as-usual representative concentration pathway (RCP8.5) the global mean projected SST increases from the beginning to the end of the century according to 8 CMIP5 ESMs (ESMs) is 2.5 ± 1.1°C (**Figure 1C**), with temperature at 100 m only increasing by 2.0 ± 1.1°C (**Figure 1D**). SST is projected to increase globally, apart from a small area in the Pacific Southern Ocean. However, whilst the temperature at 100 m is mostly predicted to increase, there are large regions where the temperature is predicted to decrease, namely in some Atlantic polar regions and the equatorial Pacific. The largest change of temperature at 100 m is in the North Atlantic. Immediately north of this warming is a region of projected cooling.

As MTE is principally based on temperature, the change in respiration, and primary production spatially reflect the change in temperature at 100 m. Using the VGPM (**Figure 1E**), Henson e-ratio (**Figure 1F**), and the change in temperature according to the CMIP5 models (**Figure 1D**), the MTE model projects an increase in the rate of microbial respiration by 2100 of 22.5% and an increase in the rate of primary production of 10.5%, resulting in a net decline in export of 12% (**Figure 2E**, **Supplementary Table 2**). Deviations from classical MTE occurred where the decline in export was large (>50%), as shown in the Arrhenius plot (**Figure 3A**, <0.5% of data points). Globally, export is projected to decrease from 3 Gt C yr^{-1} (2003–2016 climatology) to 2.6 Gt C yr^{-1} by the end of this century according to MTE, with the maximum decreasing from 100 g C m^{-2} yr^{-1} (**Figure 2C**) to 90 g C m^{-2} yr^{-1} (**Figure 2D**), found off the west coast of the US. The global total current (2003–2016 climatology) primary production is 51 Gt C yr^{-1} according to the VGPM, suggesting 6% of primary production is exported each year when applying the Henson e-ratio in present day. Under future warming, MTE projects increased primary production to 59 Gt C yr^{-1} and decreasing POC export, reducing the global mean e-ratio to 4%.

We also explored the effect of varying E_a, both globally and regionally, on projected POC export. First we increased the E_a from 0.7 to 1 eV globally resulting in 2.2 Gt C yr^{-1} of POC export in 2100, due to of an increase in respiration. Thus, the total projected reduction in POC export globally was 30%. We then explored the effect of varying E_a by latitude and temperature. Following results from a recent study in the Southern Ocean (Cavan and Boyd, 2018) we set all microbes residing below 40°S (30% of global ocean by area) to have an activation energy of 1 eV and all those northwards an E_a of 0.7 eV. This resulted in a 17% decline in POC export by 2100. Second, we imposed an E_a of 1 eV on just those regions where the temperature at 100 m is <13°C (46% of global ocean), in accordance with observational studies by Alcaraz et al. (2013, 2014) and (Cavan and Boyd, 2018), resulting in a decline in POC export of 23% by 2100.

The CMIP5 multi-model median historical (1986–2005) export was 7.6 Gt C yr^{-1} and the future (2081–2100) export is projected to be 6.4 Gt C yr^{-1}. Both these estimates are higher than our estimates made using the Henson algorithm and the MTE model. However, the net global change in POC export from our analysis of the CMIP5 model output was 16% (**Figure 2F**), the same direction of change (a decline) in export as predicted our MTE model (**Figure 2E**). The greatest effect on the change in export in the MTE model was the temperature term, which is to be expected given it forms the exponential part of the algorithm. Changing the temperature by even just a small amount (median temperature difference +0.5°C) increased the decline in export from 12 to 18% (**Supplementary Table 2**). A large temperature change (median temperature difference +3.5°C) resulted in a greater decline in export of 61%. Changing the mass term using different primary production or export algorithms did not change the total decline in export as the only change imposed between the beginning and end of the century was temperature. See **Supplementary Table 2** and supplementary text for results of the sensitivity analyses.

DISCUSSION

Satellite data can be combined with empirical algorithms and MTE to investigate the effect of future warming on the rates effecting the oceans biological pump and carbon storage. Here, we investigated the theoretical effect of warming by 2100 globally, focusing solely on temperature-driven metabolic changes to microbial respiration and primary production, and thus POC export flux. We compared our results with an analysis of CMIP5 model output projections for export production by the end of this century to put our results into context.

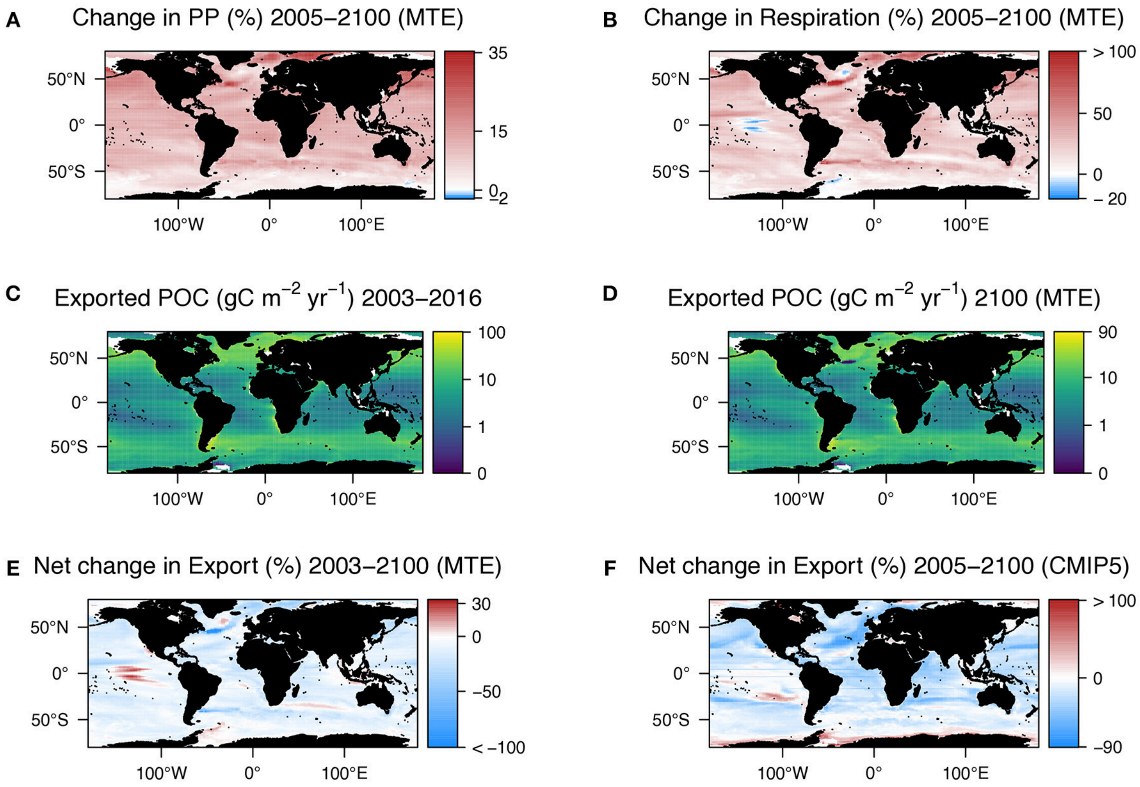

FIGURE 2 | (A) Change in primary production from current (2003–2016) data in **Figure 1E** and that estimated using the metabolic theory of ecology (MTE) and SST changes shown in **Figure 1C**. **(B)** Difference in microbial respiration of exported POC between present day (2003–2016) and 2100 estimated using MTE and the temperature changes at 100 m shown in **Figure 1D**. Notice how the patterns in both a and b match those in **Figures 1C,D**, respectively. **(C)** POC export at 100 m calculated by multiplying primary production (**Figure 1E**) by export ratio (**Figure 1F**). **(D)** POC export at 100 m in 2100 calculated by multiplying the current export **(C)** by the net change in export [**E** = change in respiration **(B)**—change in primary production **(A)**]. **(E)** Net change in export used to calculated export by 2100 in **D**. **(F)** Net change in export as determined by a suite of CMIP5 models. For both plots positive change (red) indicates an increase in export.

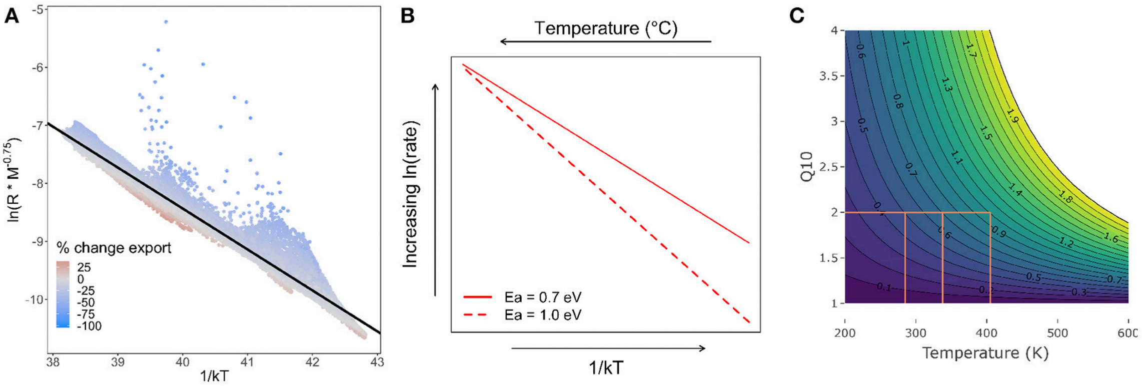

FIGURE 3 | (A) Arrhenius plot of temperature (1/kT), where k is Boltzmann's constant, and T is temperature in Kelvin against the natural log of mass-corrected (M-0.75) respiration (R). Color is the net change in export by 2100 as predicted by MTE. Black line is regression with a slope of −0.7, which is the activation energy. Where decrease in export is > ∼30% the points deviate from the line. **(B)** Change in metabolic rate. The red solid line is the change with an E_a of 0.7 eV according to metabolic theory and the red dashed line is with an E_a of 1 eV as determined by previous experimental warming studies and applied in this study. **(C)** Change in Q_{10} using Equation 4. The contours and colors are activation energies (0.1–2 eV). The orange lines show the temperature (in Kelvin) and E_a at which $Q_{10} = 2$, a commonly used parameterisation in ESMs.

Our MTE model predicted a similar decline in export (12%) as our CMIP5 model analysis (16%), which was unexpected given that our MTE model is based on a simple physiologically-based exponential equation (Equation 1) and does not include changes in physics or plankton community structure. The MTE model only accounts for two possible changes due to increasing temperature that can affect POC export (energetics of respiration and primary production), whereas the 3D CMIP5 models include future physical and chemical changes such as water circulation, stratification and nutrient availability. We expected our MTE model to potentially overestimate changes in export given it is based on an exponential relationship between temperature and metabolism and does not consider optimum temperatures for metabolism.

The lack of an optimal temperature in our MTE approach is a limitation of our model, although Cavan and Boyd (2018) found that in the Southern Ocean an optimal temperature for microbial respiration was never reached (maximum experimental temperature was 8°C above the annual maximum). In our model, metabolic rates will continue to increase exponentially with temperature, potentially over-estimating the future declines in POC export. In addition our MTE model does not account for any adaptation of microbial respiration to rising temperatures (Listmann et al., 2016), which would act to decrease the reduction in export by 2100. Nevertheless, we expect the inclusion of an adaptation term would still result in larger declines in future export when temperature sensitivity is high, which is the main aim and result of this study.

Previous studies have observed higher activation energies (E_a, 1 eV) in organisms residing at cool (polar and deeper waters) temperatures (Alcaraz, 2016; Brewer and Peltzer, 2016), suggesting these organisms are more sensitive to temperature changes when adaptation is not considered. A recent study on the effect of warming on POC export showed sub-Antarctic microbial respiration on sinking particles presents a higher E_a (0.9 eV) than predicted by typical MTE (0.7 eV and $I = 19$) (Cavan and Boyd, 2018). In our first model experiment in this study we originally set the E_a to 0.7 eV (**Figure 3A**) globally for heterotrophic respiration (Brown et al., 2004, Equation 1). Increasing the E_a from 0.7 to 1 eV (**Figure 3B**) resulted in a 30% decline in POC export globally. This is more than double our original MTE estimate of 12% when $E_a = 0.7$ eV and higher than our CMIP5 model output analysis (16%) and other ESM analyses and empirical models (Cael and Follows, 2016; Laufkötter et al., 2016).

Varying E_a by latitude and water temperature produced an intermediate response of POC export by 2100, with a 17% decline in POC export by 2100 in the Southern Ocean and 23% decline in regions where the water temperature at 100 m is <13°C. Our estimates of the spatial patters of microbial temperature sensitivity, based on a few empirical data, are likely to be over-simplifications the global sensitivity to E_a. This is because of the limited empirical data available to make more advanced simulations of the spatial variability on marine microbial E_a. As well as spatial heterogeneity in the response to temperature, there may also be variability in the organismal adaptation to warming, potentially damping the effects of variable E_a. To be able to confirm with any certainty the change in POC export associated with temperature change, observational studies need to be conducted on the response of organisms to future warming in different ocean ecosystems.

It is important to note that our MTE analysis assumes that neither the physical environment nutrient availability nor community structure change with ocean warming. Biogeochemical models do however predict shifts in phytoplankton composition, nutrient availability, magnitude of primary production, and increases in particle sinking rates (Richardson, 2008; Bach et al., 2012; Thomas et al., 2012; Dutkiewicz et al., 2013). We consider our results in the context of these predicted changes. Reduced primary production and smaller phytoplankton will produce fewer smaller, slow-sinking particles (Baker et al., 2017) where small phytoplankton dominate the community (Richardson and Jackson, 2007; Cavan et al., 2018). The reduced sinking rate due to smaller particles may be offset if viscosity decreases (due to increasing temperature) allowing particles to sink through the water column faster (Bach et al., 2012), potentially resulting in negligible changes to particle sinking rates.

Incorporating reduced primary production in our MTE model would only influence the mass term, which we have shown does not significantly influence our results (**Supplementary Table 2**). Conversely, as microbial turnover on small particles is faster than on large particles at the same temperature, likely due to the larger surface area for microbes to attach to Cavan et al. (2017), it is possible that the response of microbes to temperature will differ depending on particle size, i.e., microbes on smaller particles may exhibit a faster response to temperature change (higher E_a) than those on larger particles, but this hypothesis needs testing. Any difference in temperature sensitivity driven by the particle type/composition or size will be set principally by the mixed layer plankton composition, which could be a useful descriptor in parameterising E_a, along with biogeochemical province and/or latitude.

Accounting for the additional temperature sensitivity outlined above may alter our projections on the direction and magnitude of future carbon export, but data is currently lacking on the response of particle-attached microbes in different regions and the response of microbes residing on particles of different size and composition. Spatial variance in temperature sensitivity has been frequently observed over the past few decades, in different biomes and with different organisms, including coastal mussel populations (Gilman et al., 2006), insects (Deutsch et al., 2008), and soil microbes (Lloyd and Taylor, 1994). However, similar observations are scarce in the marine realm, hence the lack of temperature sensitivity parameterisations in marine models. The potential for a non-uniform microbial response to ocean warming across the globe has important implications for biogeochemical models, and thus ESMs. We recommend that to more accurately project the effects of climate change on carbon sequestration we need to consider that heterotrophic organisms will not necessarily respond to warming in a straightforward manner. Their response will be dependent on their ability to adapt (Visser, 2008; Thomas et al., 2012; Sal et al., 2015; Padfield et al., 2016), the species composition, and the biogeographical province and latitude they inhabit. ESMs do not currently account for a varying metabolic response such that, for example, if organisms at the Equator are exposed to a 2°C increase in temperature, current parameterizations in ESMs will elicit the same metabolic response as those at the poles exposed to the same temperature increase.

Ocean biogeochemical models that parameterize metabolic processes as a function of temperature typically use a Q_{10} approach, with some using the same value of $Q_{10} = \sim 2$ globally (Bopp et al., 2013). A Q_{10} of 2 suggests that if the temperature increases by 10°C, the rate of the reaction will double. The value of 2 is from the seminal work of Eppley (1972). There are two limitations to using the Eppley (1972) study for heterotrophic processes in biogeochemical models: (1) the study solely assessed the response of phytoplankton growth to temperature, an autotrophic process, and (2) the data were only from laboratory cultures. It is well known that autotrophic and heterotrophic processes respond differently to temperature change (López-Urrutia et al., 2006), and that organisms in laboratory conditions react differently to those in their natural environment. The Eppley Q_{10} should only be applied to phytoplankton growth and with caution given only laboratory cultures were used. Whilst the PISCES model does use higher Q_{10} for zooplankton processes, temperature dependency of POC degradation is still based on phytoplankton production rates (Buitenhuis et al., 2006) and the TOPAZ2 model uses a combination of the Eppley (1972) temperature and stoichiometry to parameterise grazing (Dunne, 2013). In the TOPAZ2 model though, export is parameterised using a temperature-dependent empirical algorithm (Dunne et al., 2005).

In the natural world, deviations away from a Q_{10} of 2 occur because Q_{10} varies depending on (1) the initial temperature, and (2) the activation energy of the reaction (which in itself varies, depending on the type of reaction being measured, **Figure 3C**). This has been highlighted in an ocean study where the bacterial degradation of dissolved organic carbon (DOC) varied ($Q_{10} = 2$–8) as different compounds of different labilities within the DOC degraded at different rates (Lønborg et al., 2018). Q_{10} can be related to activation energy using the following equation (Li and Dickie, 1987):

$$Q_{10} = e^{\left[\frac{E_a * (T_2 - T_1)}{R * T_1 * T_2}\right]} \tag{4}$$

Where E_a is the activation energy here expressed as J mol^{-1} (1 eV = 96 kJ mol^{-1}), T^1 is the initial temperature in Kelvin and $T^2 = T^1 + 10$, and R is the gas constant of 8.31 J mol^{-1} K^{-1}. For example, a Q_{10} of 2 is obtained with an activation energy of 0.5 eV and at a temperature of 285 K (12°C, **Figure 3C**). If E_a within the range found experimentally in the oceans is applied to Equation 4, then at $E_a = 0.7$ eV, T must be 338 K (65°C) to give a Q_{10} of 2. If $E_a = 1$ eV, T will be 405 K (132°C, **Figure 3C**). Only the first example here is within the normal temperature range found in the ocean (excluding proximity to deep ocean vents). At most ocean temperatures (<30°C) Q_{10} is higher (>2.5) if a typical activation energy, according to MTE, of 0.6–0.7 eV is used (**Figure 3C**). Many studies, particularly in terrestrial ecology, have shown that using a constant Q_{10} is not appropriate and variable Q_{10}, where the rate of increase is dependent on the baseline temperature, should be imposed in models (Lloyd and Taylor, 1994; Wang et al., 2014; Jian et al., 2018).

A final point to acknowledge is whether incorporating varying Q_{10} (suggested by other studies e.g., Jian et al. 2018) or E_a (suggested in our study) into ocean biogeochemical models will result in more accurate estimates of export, as these theoretical models are often deemed over-simplified. The Arrhenius equation has been continuously developed since its origins in the nineteenth Century to more closely reflect a biological system (Johnson et al., 1942), including more recently the addition of temperature-induced enzyme denaturation (Ratkowsky et al., 2005; Corkrey et al., 2012, 2016). However, these improved theoretical models have escaped the attention of many oceanographers. Whilst incorporating these more sophisticated thermodynamic models into biogeochemical models might be a step too far at present, with too many unknown parameters and certainly beyond the scope of this study, we as an oceanographic community should consider moving away from Q_{10} and the data from Eppley (1972) and start to apply process-based parameterizations founded on empirical data from natural ocean communities.

In conclusion, POC export is projected to decline by 12% by the end of the century according to fundamental metabolic theory and ESMs. The inclusion of spatially variable temperature sensitivity terms that deviate from classical MTE resulted in more pronounced projected declines in POC export; applying high sensitivity globally resulted in a decline in export of 30% and applying it just to cold regions resulted in a global decline of up to 23%. This is an important finding. Current biogeochemical models that do not account for variable temperature sensitivity are likely underestimating the change in future POC export decline, because metabolic reactions degrading POC will occur faster than currently parameterized in some regions. Where possible, metabolic functions such as respiration should be parameterized as a function of temperature as standard in models, and in turn the temperature dependence term should vary spatially. Incorporating an activation energy that varies with latitude and/or biogeochemical province would be a simple first step to assess the response of organisms to temperature change. However, we should also consider incorporating more complex thermodynamic models that can biologically explain the temperature-dependence of metabolic reactions. Future research that generates empirical data on the differing response of the same functional groups adapted to different temperature conditions is needed to elucidate these processes further and more accurately understand how carbon sequestration will change with future warming.

AUTHOR CONTRIBUTIONS

EC designed the study, collated the data with SH and did the analysis. All authors interpreted the results and EC wrote the manuscript with contributions from SH and PB.

ACKNOWLEDGMENTS

This work was funded by the Australian Research Council by a Laureate awarded to PB (FL160100131) and a European Research Council Consolidator grant to SH (GOCART, agreement number 724416). We would like to thank Joan Llort and Mike Sumner for their help in some of the early code development. We are also greatly indebted to David Ratkowsky, Ross Corkrey, and Tom Ross for discussions on thermodynamic theory and the appropriateness of using different models. The input data and the code used to build the initial MTE model is available at www.github.com/e-cavan. This study is dedicated to the memory of Dr Chris Daniels.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00230/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

REVIEW
published: 11 January 2019
doi: 10.3389/fevo.2018.00212

On the Interpretation of the Normalization Constant in the Scaling Equation

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The scaling equation, $Y_1 = \beta Y_2^{\alpha}$, has been used empirically and explored theoretically primarily to determine the numerical value and meaning of the scaling exponent, α. The mathematical interpretation of α is clear—it is the quotient of the relative rate of change of Y_1 with respect to the rate of change of Y_2. In contrast, the interpretation of the normalization constant, β, is obscure, so much so that some workers have rejected the idea that it has any biological importance. With the notable exception of Steven J. Gould's early work, Huxley's dismissal of β largely relegated the study of its biological role to that of an academic afterthought. Here, we attempt to clarify the meaning of β by using examples from plant biology to illustrate the four primary difficulties that have obscured its importance: (1) the consistency of the units of measurement and the metric being measured (e.g., meters and body length, respectively), (2) the relationship between β and α, (3) the interpretation of scaling equations, and (4) detecting if the numerical value of β has changed and if the change is biologically meaningful. Using examples, we show that β is biologically interpretable and offers a way to quantitatively consider similarities of biological form if (1) it is expressed in terms of the relative magnitudes of Y_1 or Y_2 for corresponding data points in a set of $Y_1 = \beta Y_2^{\alpha}$ equations, (2) the units of measurements are in the same scale, and (3) the corresponding dimensionless numbers are established based on the same units of measurement. We provide examples of where the numerical value of β or differences in the values of β are important, and we propose a research agenda examining the meaning of β values in terms of trait-based ecology.

Keywords: allometry, biomass allocation patterns, organic form, plant growth, plant size, scaling theory

OPEN ACCESS

Edited by:
Julie Messier,
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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 31 August 2018
Accepted: 28 November 2018
Published: 11 January 2019

Citation:
Niklas KJ and Hammond ST (2019)
On the Interpretation of the
Normalization Constant in the Scaling
Equation. Front. Ecol. Evol. 6:212.
doi: 10.3389/fevo.2018.00212

> *I'm so glad I am a Beta. Alpha children work much harder than we do because they're so frightfully clever. I am really awfully glad I'm a Beta because I don't work as hard.*
> –Aldous Huxley (Brave New World).

INTRODUCTION

A central goal of biology is the derivation of general rules that describe how organic form is achieved and how it changes, both ontogenetically and over evolutionary time, as a function of size. Scaling theory has provided a powerful over-arching perspective to achieve this goal, particularly in terms of understanding the biological nature of the scaling exponents governing families of equations taking the general form $Y_1 = \beta\ Y_2^{\alpha}$, where Y_1 and Y_2 are interdependent variables of interest, β is the normalization constant, and α is the scaling exponent. The significance of α is immediately apparent, viz. its numerical value stipulates the proportional relationship between Y_1 and Y_2 for any numerical value of β or, more precisely, it is the quotient of the relative rate of change of Y_1 with respect to the relative rate of change of Y_2 (e.g., when cast in the context of growth rates, $\alpha = \frac{1}{Y_1}\frac{dY_1}{dt}$ / $\frac{1}{Y_2}\frac{dY_2}{dt}$). It is not surprising therefore that much empirical and theoretical attention has been paid to understand how and why scaling exponents take on specific numerical values.

In contrast, with few exceptions, it is charitable to say that far less attention has been paid to the biological significance of β (see however, Enquist et al., 2007), despite the fact that differences in β values stipulate differences in the absolute size of Y_1 with respect to Y_2 for a specified α value (Niklas and Hammond, 2014). For example, if the numerical value of α is equivalent in a paired set of formulas $[Y_1 = \beta_1\ Y_2^{\alpha}][Y_3 = \beta_2\ Y_2^{\alpha}]$, it follows that $(Y_1/Y_3) = (\beta_1/\beta_2)$. Here, the numerical value of (β_1/β_2) stipulates the difference in the absolute size of Y_1 with respect to Y_3, and, since (β_1/β_2) is dimensionless, it can be used to designate shape when Y_1, Y_2, and Y_3 are in the same units and share the same metric measurements of body size (e.g., meters and body length or mass, respectively). Here, shape is defined as any dimensionless quotient constructed out of two reference dimensions, such as plant height divided by basal stem diameter. Likewise, $(\beta_1\ /\ \beta_2)$ can be used to establish differences in biomass allocation. Consider a simple example involving leaf biomass M_L allocation with respect to stem biomass M_S allocation patterns in conifers and angiosperms. Analysis of a small data shows that $M_{Lc} = 0.35{M_{Sc}}^{0.751}$ and $M_{La} = 0.13{M_{Sa}}^{0.749}$ for conifers and angiosperms, respectively (see **Figure 5**). Noting that the α values are statistically indistinguishable, we see that $M_{Lc}/M_{La} = 0.35/0.13 = 2.69$, which reveals that for any given stem mass conifers bear substantially more leaf mass than their angiosperm counterparts. It is also easy to show that β values are important even when $\alpha_1 \neq \alpha_2$ in any ordered pair of equations in a family $\{Y_1 = \beta\ Y_2^{\alpha}\}$. For example, using the previous notation and setting $\alpha_1 \neq \alpha_2$, it follows that $Y_1^{1/(\alpha 1-\alpha 2)}/Y_3 = \beta_1{}^{1/(\alpha 1-\alpha 2)}/\beta_2$. This example shows that β and α values are of equal importance, particularly because, under some circumstances, β and α values can be significantly correlated in data sets drawing on the same variables of interest (**Figure 1**).

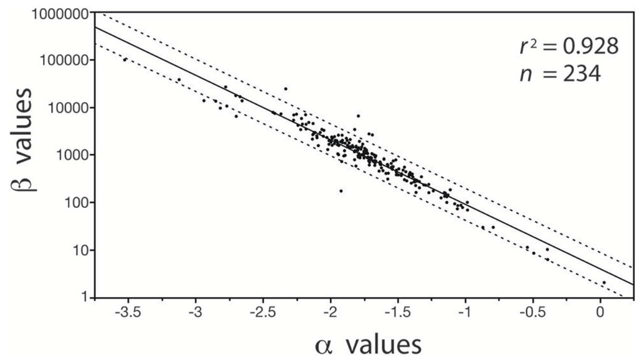

FIGURE 1 | Bivariate plot (and regression statistics of the log-log normal curve) of the inverse autocorrelation between β vs. α values for the regressions of $\log_{10}$-transformed stem diameter frequency distributions taking the general form of $N_{\{i,j\}} = \beta_j \log {D_{\{i,j\}}}^{\alpha j}$, where *N* is the number of stems in a bin size *i* and *D* is the diameter of the stems in the size bin *i* (see Niklas et al., 2003a). Dashed lines denote 95% CIs. The autocorrelation emerges because the measurement units of stem diameter is much smaller than the organisms being measured, i.e., the autocorrelation has no intrinsic biological meaning.

The goal of this paper is to explore the biological significance of β values drawing on examples from plant biology and evolution. In the following sections, we briefly review the historical background that prefaced the focus on scaling exponents to the neglect of their normalization constants. We then address the three major stumbling blocks concerning the interpretation of β values: (1) the units of β change according to the units of Y_1 and Y_2 when $\alpha \neq 1.0$, (2) β can only be computed in a size range for which the extrapolation of data is valid, and (3) β and α are often correlated (see **Figure 1**) simply because the units of measurement for Y_1 and Y_2 are much smaller than the size of the organs or organisms being measured. We show that in some cases the absolute value of β is biologically unimportant, whereas in other cases differences in β values illuminate biology. We conclude by offering suggestions for a research agenda focusing to elevate β to the equal status of α.

PREAMBLE: STATISTICS AND HISTORY

Before delving into the interpretation of β values, it is instructive to consider their "statistical" and "historical" background, i.e., why they emerge in the first place and why they are neglected in theoretical attempts to understand the biology of scaling.

Historical as well as recent studies show that researchers continue to debate the types of statistical models and the types of regression protocols that should be employed when investigating scaling relationships (Thompson, 1942; Sholl, 1950; Yates, 1950; Zuckerman, 1950; Gould, 1966; Smith, 1980; Harvey, 1982; Chappell, 1989; Packard, 2013). Nevertheless, there is consensus favoring linear regression when the error structure of a data set is multiplicative, heteroscedactic, and log normal, and the use of non-linear models when the error is additive, homoscedastic, and normal (Niklas and Hammond, 2014). The choice of model is not arbitrary therefore because (1) the error structure in a data set dictates the use of a linear or non-linear model and because (2) a data set cannot simultaneously manifest both error structures. Nevertheless, there are two philosophies regarding the implementation of a regression protocol, one that is strictly empirical and seeks the best fit to the data for the purpose of predicting trends, and another that emphasizes a mechanistic approach and seeks to test the predictions of a particular theory. In both cases, the classic scaling formula $Y_1 = \beta\ Y_2^{\alpha}$ can emerge, but the significance of its regression parameters differs according to the purpose of the analysis. When the purpose of regression analysis is *prediction*, the numerical values of β and α are strictly utilitarian. Indeed, a reviewer of Huxley's book, which arguably propelled the application of scaling analysis, noted that Huxley's methods were

> *…necessarily empirical. Of the causes of differential growth we have little knowledge; their investigation is the problem at issue. A variety of possible relations, in fact, reduce approximately to this formula. But it is not the object of the formula to establish the correctness of a particular hypothesis as the cause of differential growth; it merely expresses the observed facts with considerable accuracy in a simple way, so that many very significant features emerge which would not otherwise do so.* (Pantin, 1932)

However, the objective of the modern analysis of scaling phenomena is to uncover the *mechanisms* that drive size-dependent changes in form. The numerical values of β and α are not just numbers plugged into an equation to predict the numerical value of a dependent variable based on the numerical value of its corresponding independent variable—the values of β and α can shed light why one variable changes in value as another changes in value.

Despite the dichotomy of how regression protocols are used, the disagreement about the importance of β values dates back to the seminal publications of Julian Huxley (1887–1975) and Georges Teissier (1900–1972) (Huxley and Teissier, 1936a,b). The two differed in opinion regarding the significance of β sufficiently enough that their simultaneously published articles—in English and French—differ by only one sentence, with Teissier endorsing the biological significance of β values (Huxley and Teissier, 1936a) and Huxley, by implication, dismissing their importance (Huxley and Teissier, 1936b).

This is in marked contrast with some the earliest scaling work done in the later 19th and early twentieth centuries. Early workers, such as the German Psychiatrist Otto Snell (1859–1939) and the Dutch paleontologist, geologist, and discoverer of "Java man" (*Homo erectus*) Eugene Dubois (1858–1940), attempted to derive a quantitative means of determining how "evolved" an organism was by comparing the mass of its brain to the mass of its body (Snell, 1892; Dubois, 1897). Dubois derived the formula

$$e = cs^r, \tag{1}$$

or, when log-transformed,

$$log\, e \;=\; log\, c \;+\; r\, log\, s, \tag{2}$$

where e (for *encephalon*) is brain size, c is the "coefficient of cephalization", s is body size, and r is the "coefficient of relation" (Dubois, 1897). This same interest in correlating brain size with other traits, such as group size among primates, is a technique in practice 120 years later (Kudo and Dunbar, 2001).

Dubois' data would be combined with data on the brain sizes of various animals from diverse classes (reptilian, avis, and mammalia) by the French neuroscientist Louis Lapicque (1866–1952). Lapicque would present the data in 1907 by generating the first known log-log plot showing common slopes among allometric data (Lapicque, 1907) (**Figure 2A**). Curiously, Lapicque did not plot all of his data, perhaps because he thought of them as redundant (**Figure 2B**).

During these initial studies, it was the magnitude of difference between the different organisms–what Dubois called the "coefficient of cephalization" (c) (Dubois, 1923, 1928), and what allometrists after Huxley and Tessier call the "normalization constant" (β)—that was the object of study. As noted by Gould's review of Dubois' later work:

> *"Dubois, 1922, Dubois (1928) built his famous theory of brain evolution on a belief that evolutionary increase in b* [Gould used *b* in his notation instead of β] *occurred in steps of a geometric progression with base 2. Thus, he reasoned, the brain evolves by a doubling of neurons early in embryology;(the change is reflected only in the increase of size- independent b; the slope remains constant)"* Gould (1971)

That the scaling relationships between the mass of the brain and body seemed to have the same slope in log-log space was certainly an unusual observation, but it didn't forward the attempts to describe forms in terms of ratios of *size*, and it certainly didn't clarify how to quantify how "evolved" a given organism was.

Huxley's breakthrough, starting in 1924, was to focus on ratios of relative *growth* instead of ratios of size (Huxley, 1924). This began the shift in focus away from the differences in β, and with his joint 1936 paper with his Continental colleague, Teissier, firmly shifted the importance to α.

As a side note, we would be remiss if we failed to point out the historical timing and potential significance of the quotation with which we began this paper. Julian Huxley's younger brother, Aldous Huxley (1894–1962), published his novel *Brave New World* in 1931. This is firmly within the time period that the elder Huxley was deeply contemplating how to unify the Continental and English allometric literature, as they differed in both terminology and symbols used in equations. One can imagine the conversations between the two brothers, influencing one another in terminology and, by extension, the importance of variables (or people) as determined by the Greek letter used.

With the notable exception of Steven J. Gould's early work (White and Gould, 1965; Gould, 1966, 1967, 1971), the biological significance of β values has been largely as a side note to the more interesting α value (Newell, 1949; Huxley, 1950; Needham, 1950; Shadé, 1959). The lack of an underlying theory explaining the significance of β is strikingly similar to scaling theory before the emergence of the West, Brown, Enquist theory (West et al., 1997). This lack of attention is both a detriment to scaling theory and an immense opportunity for future research.

It would be ethically irresponsible when dealing with any historical treatment of allometry not to point out that the early application of scaling theory was often used to promote eugenics, racism, and anti-feminism (e.g., Snell, 1892). Clearly, this practice is totally unacceptable, intolerable, and scientifically invalid. As pointed out by Deacon (1990), the explicit assumption that brain size correlates in a positive linear or nonlinear way with intelligence has no valid scaling baseline for estimating differences in encephalization at different taxonomic levels. In addition, it conflates evolutionary trends in overall body and brain

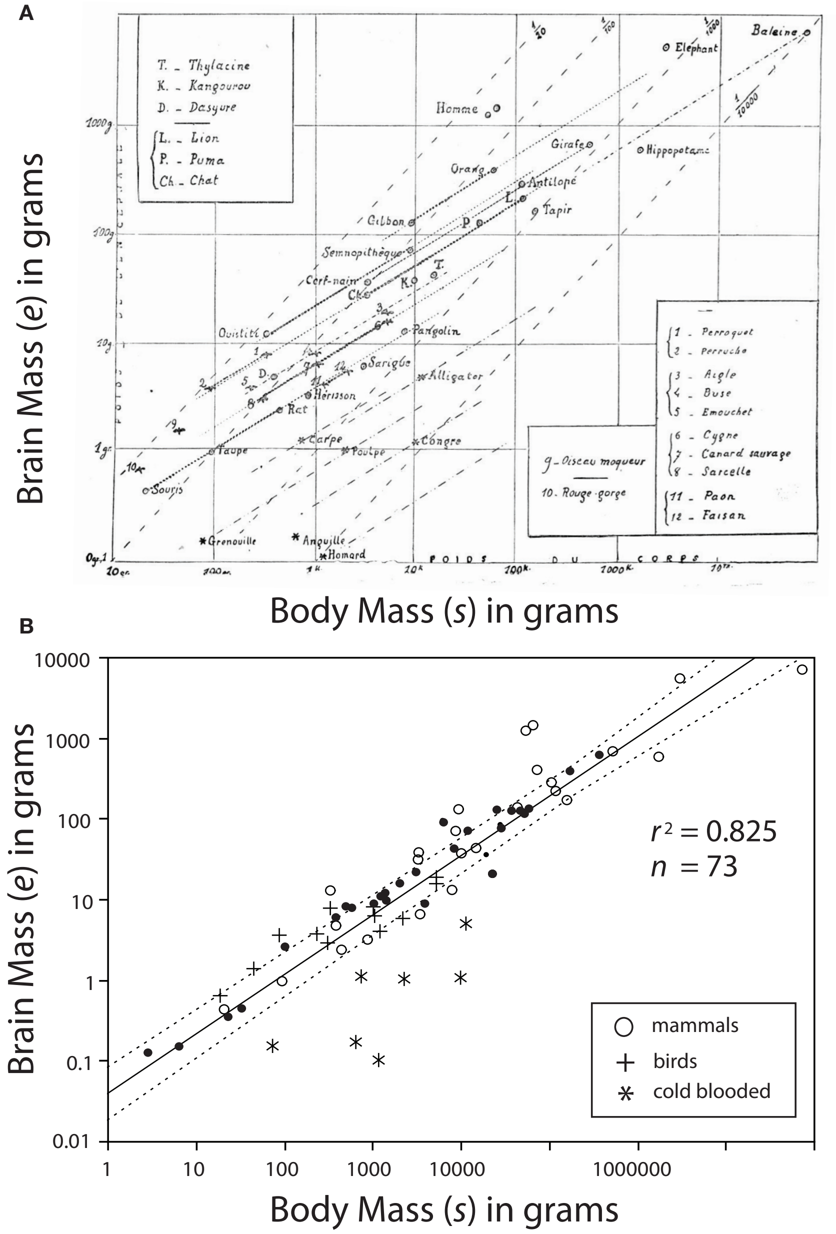

FIGURE 2 | Bivariate plot of brain mass *e* vs. body mass *s*. **(A)** A photo-copy of the first known log-log plot showing common slopes among allometric data published by Louis Lapicque (1866–1952) in 1907. Dark dashed lines represent regression curves for individual species; gray dashed lines represent boundaries of interspecific trends. **(B)** Lapicque's data replotted to include data omitted from his original diagram. Missing data indicated by black circles. Reduced major axis regression curve and 95% CIs are provided.

sizes with differences in cognitive abilities. Theories that purport to establish a correlation between brain size and intelligence are entirely incompatible with studies showing that intelligence is not intrinsically correlated with body size, but rather correlated with the degree of folding in the temporo-occiptal lobe, particularly in the outermost section of the posterior cingulate gyrus (Luders et al., 2008). And even these studies are inconclusive owing to other factors such as sexually dimorphic cranial features that conflate correlation with causation.

THE FOUR PROBLEMS WITH β

As noted in the Introduction, there are three principal difficulties that have impeded the interpretation of β values and obscured their biological significance. Here, we address these three difficulties and show that they are avoidable and surmountable.

The Problem of Dimensionality

Unlike α, which is dimensionless and thus a "pure" number, β values have dimensionality. This is easily illustrated by a dimensional analysis of any allometric relationship as for example the scaling relationship between the critical bending height H_{crit} and basal stem diameter D of trees modeled as very slender columns:

$$H_{\mathrm{crit}} = C(\frac{E}{\rho g})^{1/3} D^{2/3}, \tag{3}$$

or, when log-transformed and noting the constants in this equation,

$$logH_{\mathrm{crit}} = (1/3)log[C(\frac{E}{\rho g})] + (2/3)Log\ D, \tag{4}$$

where C is a dimensionless constant (approximately equal to 0.79 and 1.24 for an un-tapered and conical column, respectively), E is Young's elastic modulus (with units of N/m^2), ρ is bulk tissue density (with units of kg/m^3), and g is the gravitational constant (with units of m/s^2) (Greenhill, 1881). When interpreted strictly as a scaling equation with the form $Y_1 = \beta\ Y_2{}^{\alpha}$, it follows that β is $C(E/\rho g)^{1/3}$ and α is 2/3. Because N has units of kg m s^{-2}, dimensional analysis shows that β has units of m$^{1/3}$. Although this unit makes little biological sense, the importance of β cannot be rejected on dimensional grounds because any formula taking the form $Y_1 = \beta Y_2{}^{\alpha \neq 1}$ can be re-written as $Y_1 = \beta_0\ \gamma^{1-\alpha}\ Y_2{}^{\alpha}$, where γ is a dimensional conversion factor (a pacifier parameter) that has the same units as those used to measure Y_1 and Y_2. This conversion factor transforms β_0 into a dimensionless "pure" number equivalent to α regardless of the units used to measure Y_1 and Y_2. Although it is obvious, it bears repeating that Y_1 and Y_2 must be measured in the same units (e.g., m or kg) and that the units are applied to the same metric (e.g., body length or mass). Under these circumstances, comparisons are made among data sets using the same units of measurements, both β and β_0 have biological meaning. Provided that Y_1 and Y_2 are in the same units and the same metrics, we can set $\gamma = 1$ and continue to write $Y_1 = \beta\ Y_2^{\alpha}$, while recognizing that β is somewhat more complicated because it has units.

The issue of the units of measurement should not be overstated because there are mathematical tools to cope with using different units. It should be obvious that physical laws and biological phenomena cannot depend on the choice of units used to measure them. Thus, it should be equally obvious that scaling relationships between physical or biological quantities must be independent of the units in which they are measured. That this is so becomes evident by means of dimensional analysis as for example by the π-theorem. This theorem states that a physical relationship between a dimensional quantity and several parameters governing its relationship to them can be re-written as a relationship between a dimensional parameter and several dimensional products of the power of its governing parameters minus the number of governing parameters with independent dimensions. Barenblatt (2003) and Bridgman (1922) provide detailed and explicit expositions on the π-theorem and how it can be applied to scaling relationships.

To illustrate dimensional analysis, let us assume that cell growth G is some function of cell mass M and length L, and time T:

$$G = f(M, L, T) \propto M^a\ L^b\ T^c, \tag{5}$$

where the exponents a, b, and c are real numbers. The dimensional analysis of this formula proceeds by finding fixed relationships (proportionalities) between paired variables. For example, density ρ is the quotient of M and V. If cell cytosolic density is a constant, if follows that $\rho = ML^{-3}$ = a constant, and assuming that cells increase in size without changing their geometry or shape, we see that $V \propto L^3$. Because $M \propto V$, it follows that $L \propto M^{1/3}$. Thus,

$$G \propto M^{a+b/3} T^c. \tag{6}$$

Assuming that G depends on the rate at which mass is exchanged between a cell and its environment, G likely depends on overall metabolic rate, which has the dimensions of LT^{-1}. If this rate is constant on average, it follows that $T \propto L$, and because $L \propto M^{1/3}$, we find that $T^c \propto M^{c/3}$ such that

$$G \propto M^{a+b/3+c/3}. \tag{7}$$

This dimensional analysis is brought to closure when the dimensions of G are specified because the numerical values of a, b, and c depend on how Y_1 is measured. If G is measured as mass per unit time, G has the dimensions of MT^{-1}. Thus, the real numbers a, b, and c become 1, 0, and -1, respectively, such that $G \propto M^{1+0/3-1/3} \propto M^{2/3}$. If G is measured as a production rate, which has units ML^2T^{-3}, we see that $G \propto M^{1+2/3-3/3} \propto M^{0.333}$. This example shows that, for any formula $Y_1 = \beta Y_2^{\alpha}$, the units of β and the numerical value of α depend on the numerical values of the real numbers a, b, and c, which depend in turn on the dimensions of Y_1 and Y_2.

The Range of Applicability Problem

The numerical value of β and α can change over the course of ontogeny and over the course of evolution. Therefore, β and α are not "constants" even for data sets gathered across similar species. This is strikingly evident when standing leaf dry mass per plant is plotted as a function of standing stem dry mass per plant for herbaceous plants, the juveniles of woody species, and mature individuals of woody species differing in age (**Figure 3**). Inspection of the resulting bivariant plot of data shows that the numerical values of β and α change in a statistically significant way once woody plant individuals begin to manifest secondary growth and accumulate wood in their stems. Among individuals of herbaceous species, the β value is numerically smaller and the α value is numerically higher than the corresponding values manifested by juvenile and mature plants belonging to woody species. The regression curves for these two plant groupings intersect at the point where secondary growth becomes anatomically evident in representative cross-sections through stems (the gray area in **Figure 3**). [In passing, this is also the size-range predicted by computer simulations in which tree species reach reproductive maturity (Hammond and Niklas, 2009)]. Importantly, in the absence of a careful

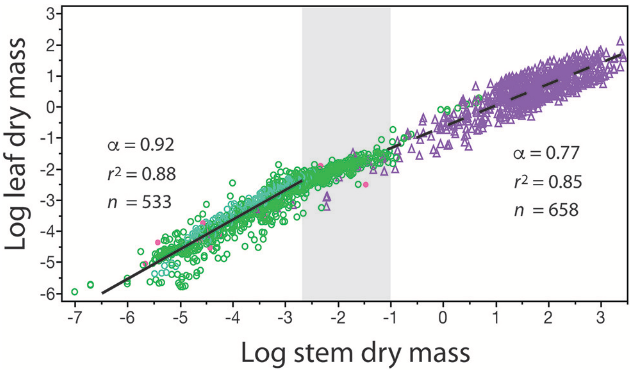

FIGURE 3 | Bivariate plot of $\log_{10}$-transformed standing leaf dry mass vs. standing stem dry mass (original units in kg) for herbaceous non-woody plants (green circles) and woody plants (purple triangles). The gray area in the middle of the plot denotes the region where the β and α values of the solid and dashed regression curves numerically change. This area also corresponds to where cross sections through representative stems manifest observable amounts of secondary tissues. Red dots indicate data from non-vascular and vascular seedless species (e.g., algae and mosses, and ferns and lycophytes). See text for scaling formulas. Data taken from the primary botanical literature.

understanding of plant anatomy and the phenomenology of secondary growth, the two regression curves would lead to significant errors in estimating standing leaf or standing stem dry mass (over estimating the former and under estimating the latter across woody plants).

This example illustrates an under-appreciated feature of any scaling analysis: it is not mathematically correct to present a formula such as $Y_1 = \beta\ Y_2^{\alpha}$ without specifying the range of Y_2 over which it holds true (i.e., $Y_i \leq Y_2 \leq Y_j$, where Y_i and Y_j are respectively the smallest and largest numerical values in a specified data set). Attempts to bypass this truism while giving β values biological meaning has resulted in meaningless mathematics, e.g., setting Y_2 equal to 1.0 at the lowest value in a data set such that $Y_1 = \beta$ across all data sets (see Lumer et al., 1942). What is important is that β values have biological meaning over their stated $Y_i \leq Y_2 \leq Y_j$ intervals even when $Y_i > 1.0$.

Extrapolating beyond the range of a data set is not necessarily a problem if the objective is to formulate predictions, or simply to graphically evaluate whether disconnected data share similar scaling exponents. Indeed, one of the efforts in science is to extend what we know to explain what we do not know. However, it is always important to know that range over which β- and α-values have been determined in scaling analyses.

The Inverse Relationship Problem

Figure 1 shows an inverse relationship between β and α values among a set $[Y_1 = \beta\ Y_2^{\alpha}]$. Similar inverse relationships have been reported by many early workers (e.g., Hersh, 1931; Hamai, 1938; Clark and Hersh, 1939; Anderson and Busch, 1941) so much so that the relationship $\beta = a\ \mathrm{e}^{-b\alpha}$ (where a and b are constants) has been held to be biologically meaningful. That this is evidently not true is easily seen by asking under what conditions would we expect to see an inverse or direct correlation between β- and α-values and under what conditions would there be no correlation? The answer to this question can be obtained by hypothesizing a set of linear regression curves taking the form $[Y_1 = \beta\ Y_2^{\alpha}]$ and by assuming that all of these curves intersect at one point (y_1, y_2), i.e., all of the curves share a common point defined by (y_1, y_2). Solving for the relationship between β and α, we obtain the formula

$$\beta = \beta'(y_2)^{\alpha' - \alpha}, \tag{8}$$

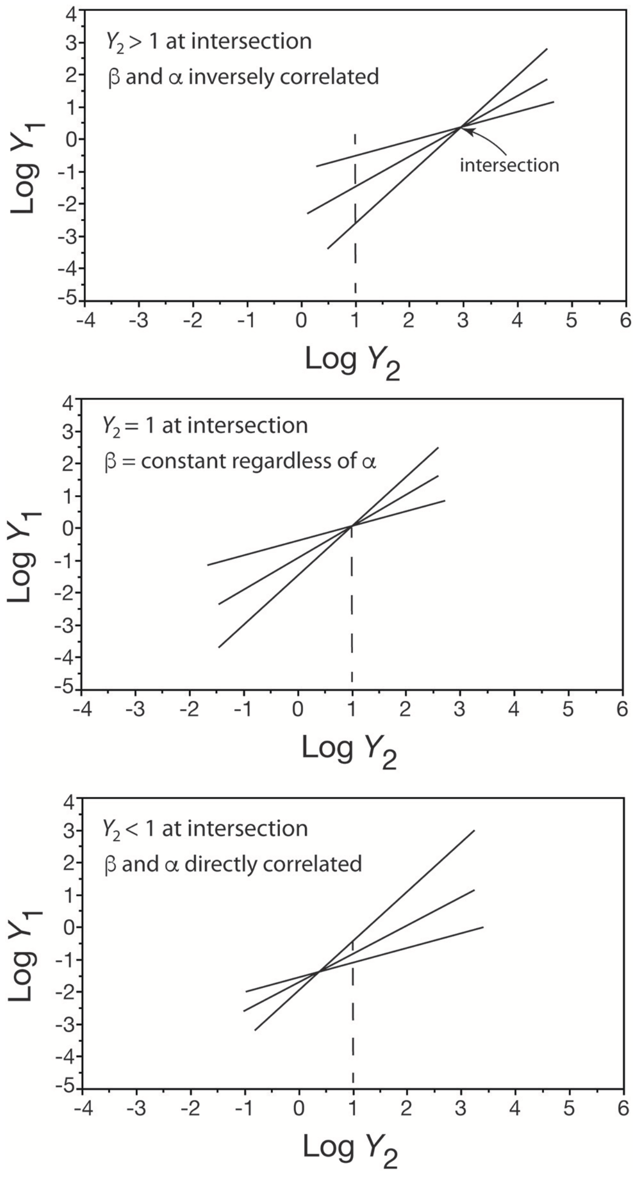

FIGURE 4 | Three bivariate plots showing how the placement of a shared point of intersection in a set of log-log linear scaling relationships (only three are shown for convenience) affects whether β and α are inversely correlated (**top**), not correlated (**middle**), or directly correlated (**bottom**). See text for details.

where y_2' is the numerical value of y_2 at the point of intersection and (β', α') is any ordered pair of the normalization constant and scaling exponent in the set of $Y_1 = \beta\ Y_2^{\alpha}$ regression curves (see White and Gould, 1965). Only three conditions exist for this formula (**Figure 4**): (1) when the point of intersection y_1' is greater than one, an inverse correlation exists between β and α because $\beta > \beta'$ if and only if $\alpha' > \alpha$, (2) when the point of intersection $y_1{}'$ equals one, $\beta = \beta'$ regardless of the value of α, and (3) when the point of intersection y_1' is less than one, a direct correlation exists between β and α because $\beta > \beta'$ if and only if $\alpha > \alpha'$.

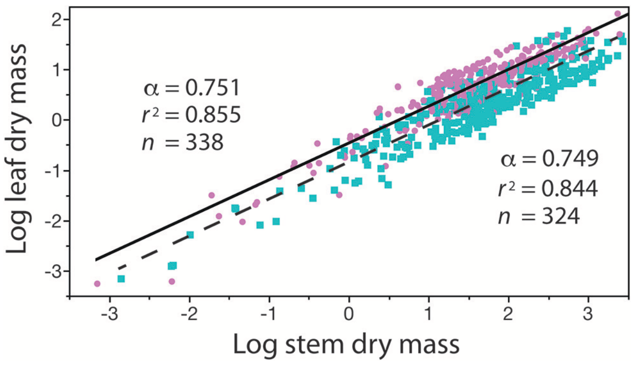

FIGURE 5 | Bivariate plot (and regression parameters) of $\log_{10}$-transformed standing leaf dry mass vs. standing stem dry mass (original units in kg) for conifers (purple circles) and angiosperms (blue squares) with corresponding solid and dashed regression curves. This example shows that differences in the numerical values of β indicate that, for any stem diameter, conifers bear more dry leaf mass than their angiosperm counterparts. See text for scaling formulas. Data taken from the Cannell (1982) worldwide compendium.

The Detection Problem

Biologists often observe deviations in the linearity of log-log linear relationships spanning many orders of magnitude as in **Figure 3** (e.g., Hammett and Hammett, 1939; Economos, 1983). In these cases, the challenge is to determine whether these deviations are statistically and biologically meaningful. From a strictly statistical perspective, determining whether the numerical value of β or α has changed can be detected using a variety of techniques as for example using segmented regression, change-point modeling, graphical inspection of regression residuals, and 95% confidence intervals (Quandt, 1958; Chow, 1960; Brown et al., 1975; Chappell, 1989). For example, Brown et al. (1975) developed the method of recursive residuals, which allows for a formal significance test. This method places considerable emphasis on graphical examination. Although a plot of residuals from a linear regression model is useful, it is not a very sensitive indicator of small changes in β. A more sensitive method was developed by Chappell (1989) that amounts to fitting a "bent line" by means of least squares regression protocols that can be validated subsequently by graphical diagnostics. Chappell's method provides a superior change-point regression model. However, it should be obvious that regardless of the technique used to determine whether the numerical value of β or α has changed presupposes that a researcher suspects that such has occurred. It is advisable, therefore, to test all scaling relationships to determine their log-log linearity.

Perhaps an even greater challenge is to determine whether a change in the numerical value of β or α is biologically meaningful. We are of the opinion that proof that a change is statistically significant is not *a priori* infallible proof that the change is biologically meaningful, and that the failure to detect a statistically significant change in a regression parameter does not necessarily mean that the change is biologically insignificant. A careful understanding of the biology of an organism or group of organisms provides the final arbitration of the challenging aspect of scaling analysis.

The Meaning of β

The four problems with β reviewed in the previous section obscure but do not diminish the biological significance of the normalization constant, which in many cases reflects an ontogenetic change in related organisms, or provides a descriptor of differences in growth or body type. **Figure 3** provides an example of where a change in ontogeny (e.g., a shift from primary to secondary growth) is attended by significant changes in the numerical values of both β and α. Consider, another example showing how β values illuminate biology (i.e., the relationship between standing leaf dry mass, M_{L}, and standing stem dry mass, M_{S}) (**Figure 5**). Reduced major axis regression analyses of these data obtains $M_{\mathrm{L}} = 0.344\ M_{\mathrm{S}}^{0.751}$ for conifers and $0.132\ M_{\mathrm{S}}^{0.749}$ for angiosperms. In this example, the numerical values of the scaling exponents are statistically indistinguishable, whereas the β values significantly differ. Consequently, for any value of standing stem mass, the standing leaf mass of conifers is on average approximately 2.6 times larger than that of the angiosperms in this data set. This computation is mathematically trivial, but it exposes a biologically meaningful fact, viz coniferous species tend to retain their leaves (which tend to have high bulk tissue densities) for 2–3 years in contrast to angiosperms, the majority of which are deciduous.

A third example in which β values take on importance is the relationship among the annual growth in stem, leaf, and root dry mass per plant: G_{S}, G_{L}, and G_{R}, respectively (**Figure 6**). Reduced major axis regression of the data shows that both G_{S} and G_{R} scale as the 1.14 power of G_{L} to yield the allometric formulas $G_{\mathrm{S}} = 1.64\ G_{\mathrm{L}}^{1.14}$ and $G_{\mathrm{R}} = 0.12\ G_{\mathrm{L}}^{1.14}$ (**Table 1**). These formulas hold across the herbaceous as well as arborescent species in the data set and indicate that on average both species groupings allocate an order of magnitude more of their total growth in body size to new stem tissues as opposed to new root tissues. This is probably a gross over-estimate because the data for root dry mass are skewed for woody roots rather than new feeder roots. Nevertheless, estimates indicate that stem growth exceeds that of total root growth.

Yet another example illustrating the importance of β values is their role in understanding plant size frequency distributions, species richness, and species-specific density. For example, across the data sets accumulated by Alwyn H. Gentry (1945–1993), stem size frequency distributions are approximated by the formula

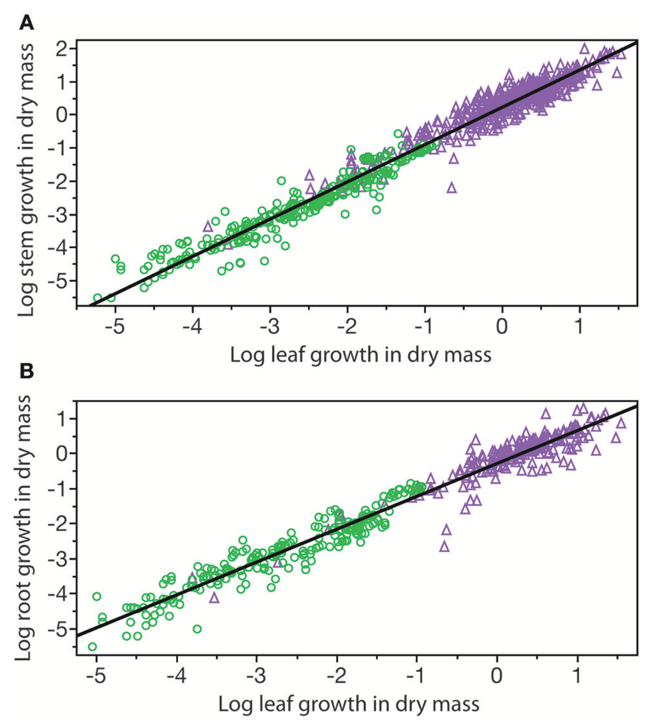

FIGURE 6 | Bivariate plots of $\log_{10}$-transformed data for stem, leaf, and root annual growth rates (original units stranding dry mass produced per year per plant) for herbaceous non-woody (green circles) and woody (purple triangles) species. Solid lines are log-log regression curves. **(A)** Stem growth vs. leaf growth. **(B)** Root growth vs. leaf growth. See text and **Table 1** for scaling formulas and regression parameters. Data for herbaceous species taken from the primary botanical literature; data for woody species taken from the Cannell (1982) worldwide compendium.

TABLE 1 | Reduced major axis regression parameters for the scaling of annual growth in stem, leaf, and root dry mass (G_S, G_L, and G_R, respectively) per plant per year ($\log_{10}$-transformed data plotted in **Figure 5**). Original units kg/yr.

Y_1 vs. Y_2	r^2	α	95% CIs	β	95% CIs
log G_S vs. log G_L	0.969	1.139	(0.664, 1.616)	0.214	(−0.493, 0.920)
log G_R vs. log G_L	0.960	1.142	(0.765, 1.519)	−0.921	(−1.480, −0.361)

$N_i = \beta \text{ Log } D_i^\alpha$, where N_i is the number of individuals within stem diameter D_i bin size (Enquist and Niklas, 2001; Niklas et al., 2003a). However, the numerical values of β and α change as a function of any change in bin size, Δx. Mathematical analyses of this variation obtains a formula predicting the total number of individuals in any size frequency distribution, N_T, approximated by the formula $N_i = \beta \log D_i^\alpha$ as a function of β, α, Δx, and maximum and minimum stem diameter (Niklas et al., 2013b):

$$N_T = \frac{\beta}{\Delta x(1-\alpha)}\left(D_{\max}^{1-\alpha} - D_{\min}^{1-\alpha}\right). \tag{9}$$

The importance of β in this context is mathematically transparent because it equals the quotient of the number of individuals in the smallest bin size Δx_{min} and $D_{min}{}^\alpha$ (i.e., $\beta = \Delta x_{min} / D_{min}{}^\alpha$), a relationship that obviates the autocorrelation between β and α (see **Figure 1**) in subsequent analyses of the biological significance of size frequency distributions (Niklas et al., 2013b).

β in Development and Evolution

The significance of β values in development and evolution can be seen in the context of how organic shape might change in an ancestor-descendent transition. Consider a log-log plot of the size of one organ-type Y_1 against another organ-type Y_2 (**Figure 7**). In the isometric condition (i.e., $Y_1 = \beta\ Y_2^{\alpha=1}$), it follows that $\beta = Y_1/Y_2$, which is dimensionless and thus can serve as a measure of shape if Y_1 and Y_2 are metrics of form (e.g., petal length and sepal length). In this example, β is invariant and the organism does not change its shape throughout its ontogeny (**Figure 7A**). If this type of organism gives rise to a descendent for which the relationship between Y_1 and Y_2 is allometric (i.e., $\alpha \neq 1$), it is evident that shape has changed and that it changes allometrically throughout the ontogeny of the descendent (i.e., $\beta = Y_1/Y_2^\alpha$). Consequently, changes in β values in the phylogeny of a lineage or clade can be used to infer evolutionary changes in shape or some other variable of interest. This hypothetical scenario is not unlike the evolutionary transition between plants capable only of primary growth into those capable of secondary growth (as reflected in **Figure 3**).

Comparisons of shape are possible even when Y_1 vs. Y_2 is allometric (i.e., $\alpha \neq 1$), provided that scaling relationships share the same exponents. Consider two regressions with the same α values: $Y_1 = \beta_1 Y_2^\alpha$ and $Y_1' = \beta_1 Y_2'^{\alpha}$ (**Figure 6B**). For any value of Y_2 within the range of both regression curves, there are two values of Y_1 (i.e., at Y_2 , $Y_1 \neq Y_1'$), such that $\beta_1/\beta_2 = (Y_1/\ Y_2^\alpha)\ /\ (Y_1'/\ Y_2^\alpha) = Y_1/\ Y_1'$. This relationship can be used to consider what appear to be stepwise (saltational) ancestor-descendent differences between related organisms (as reflected in **Figure 5**).

Finally, consider the case of two regression curves, $Y_1 = \beta_1 Y_2^\alpha$ and $Y_1' = \beta_2 Y_2^{\alpha'}$, that intersect at a single point, (Y_i, Y_j), such that $Y_1' < Y_1$ below the intersection point and $Y_1' > Y_1$ above the intersection of the two curves (**Figure 7C**). Under these conditions, it follows that $(\beta_1/\beta_2) = Y_j{}^{(\alpha'-\alpha)}$, or $Y_j = (\beta_1/\beta_2)^{1/(\alpha'-\alpha)}$. This relationship can be used to compare ancestor-descendent ontogenies as to when the form specified by the metrics (Y_i, Y_j) is achieved during growth. If the descendent achieves (Y_i, Y_j) earlier than the ancestor, the ontogenetic trajectory of the descendent has been accelerated with respect to that of the ancestor, as shown in **Figure 7C**. If the descendent achieves (Y_i, Y_j) later than the ancestor, the ontogenetic trajectory of the descendent has been retarded with respect to that of the ancestor. Note that (1) the terms "earlier," "accelerated," and "retarded" refer to rates of change, specifically the rate of change of Y_1 with respect to Y_1, i.e., $\partial Y_1/\partial Y_2 = \beta_1(\alpha)Y_2^{\alpha-1}$ and $\partial Y_1'/\partial\ Y_2' = \beta_2(\alpha')Y_2^{\alpha'-1}$, and (2) the point (Y_i, Y_j) represents some designated shared stage in the ontogeny of the ancestor and descendent (e.g., the time of germination, or sexual maturity).

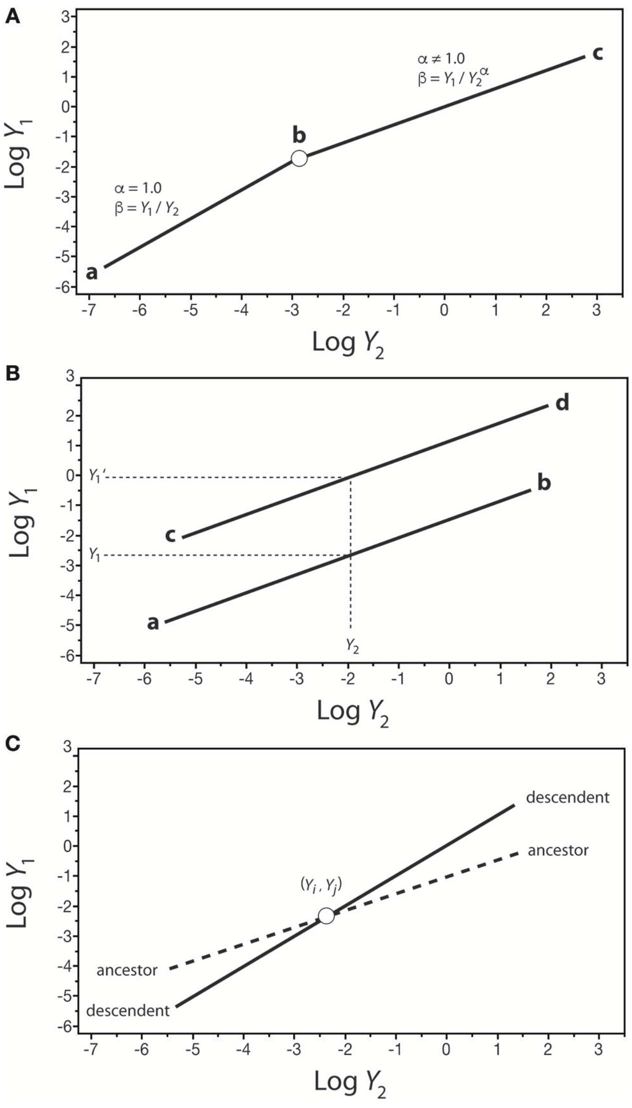

FIGURE 7 | Hypothetical scaling relationships between two body parts, Y_1 and Y_2, showing changes in β–values over the course of development or evolution. **(A)** The shift between an ancestral isometric scaling relationship between Y_1 and Y_2 (denoted by the line a-b) and an allometric relationship in the descendent (denoted by the line b-c). **(B)** Two scaling relationships sharing the scaling exponent (denoted by lines a-b and c-d) but differing in β values. For any value of Y_2, there exist two corresponding values of Y_1 (i.e., Y_1 and Y_1'). **(C)** An ancestor-descendent relationship (denoted by dashed and solid lines, respectively) in which β and α values change. If the ancestral body shape achieved at point (Y_i, Y_j) occurs earlier in the ontogeny of the descendent, development has accelerated. If the ancestral body shape achieved at point (Y_i, Y_j) occurs later in the ontogeny of the descendent, development has been retarded.

Future Directions

The purpose of this review was to show that β values are as biologically meaningful as α. That this is so becomes immediately apparent because, in general terms, β is dimensionless (i.e., a "pure" number) dependent on the scale used to measure the relationship between two variables of interest, i.e., $\beta = Y_1/Y_2$ when $\alpha = 1$ and $\beta = Y_1 / (\gamma^{1-\alpha}\ Y_2{}^{\alpha})$ when $\alpha \neq 1$ (where γ is a dimensional conversion factor). Yet, despite its obvious importance, little attention has been paid to how or why β values differ across data sets or lineages, or how it changes during the course of evolution by natural selection.

Future studies can, at the very least, document *how* β values relate to the scaling exponents governing the relationships being investigated. The greater challenge is to explain *why* β values differ and what these changes *mean*. A good way to approach this challenge is to first explore isometric scaling relationships. For example, using a large data set reporting the annual production (growth) of new leaves and stems, G_L and G_S, across conifer and angiosperm tree species (Cannell, 1982), Niklas and Enquist (2002) found an isometric scaling relationship such that $\beta = G_L/G_S$. Because G_L is the product of the number of new leaves produced per year, n_L, and leaf area, thickness, and bulk tissue density (A_L, t, and ρ_L) because G_S is the product of the number of new stems produced per year, n_S, and stem length, transverse area, and bulk tissue density (L, A_S, and ρ_L), it follows that $\beta = (n_L\ A_L\ t\ \rho_L)/(n_S\ L\ A_S\ \rho_S)$ across species. Assuming that the average values of A_L, t, L, A_S, ρ_L and ρ_S are invariant for any particular species, we see that in theory β describes the intraspecific proportional relationship between the number of new leaves and stems produced per plant per year, i.e., $\beta \propto (n_L/n_S)$. Thus, if the numerical value of β remains constant for a particular species, it follows that the number of new leaves produced per year remains proportional to the number as well as the size of new stems produced per year over the course of a plant's ontogeny. This scenario is not biologically unreasonable because the number of leaves on twigs is likely to be proportional to the size of the stems bearing them. Regardless, the hypothesis engendered by considering β to be biologically meaningful is testable empirically.

In a broader sense, what we are proposing is the examination if β in terms of trait-based ecology. Far from being a modern point of interest, trait-based ecology can be traced back to Theophrastus' *Enquiry into Plants* $(\Pi\varepsilon\rho i\ \phi\upsilon\tau\tilde{\omega}\nu\ \iota\sigma\tau o\rho i\alpha)$ written between 350 and 287 BCE, wherein he classified plants as trees, shrubs, or grasses based primarily on height and stem density (Morton, 1981) While these general traits have remained as major *de facto* classifications for terrestrial plants, ecologists have continued to propose additional trait-based criteria (for reviews, see Weiher et al., 1999; Westoby et al., 2002). The interest in conducting research in trait-based ecology is the underlying belief that understanding trait costs and benefits will provide insights into how vegetation properties differ over space (geography) and time (evolution), and explain patterns of diversity (MacArthur, 1984; Messier et al., 2010).

Part of what we have tried to illustrate in this paper is that β can often be a measure of differences in a quantitative trait among species or within a species. Real and meaningful trait-based differences between conifers and angiosperms in terms of their standing leaf mass relative to the standing stem mass can be seen when examining the numerical values of the β values (**Figure 4**). Differences in β should not be limited to what one sees among species, however: within the same species one should predict to see statistically identical α values, but differing β values depending on the natural variation of the environment. Soil quality, light intensity, water availability, and a host of other environmental factors should all contribute to intra-species variation in β that is measurable and meaningful, beyond the inter-species variations in β. Put another way, inter-species variations in β reflect different evolutionary strategies, whereas intra-species variations in β reflect the limits of the species' plasticity to environmental variation.

We are certainly not the first to propose the importance of β in terms of trait-based ecology. Work by Brian Enquist, for example, illustrated how the β for the annual biomass growth vs. whole plant leaf biomass could be derived for angiosperms and gymnosperms (Enquist et al., 2007). The paucity of published work related to β as being biologically meaningful strengthens our sense that this line of inquiry remains under-researched, and can potentially offer important insights into the questions of ecological trait-based fitness, natural plasticity, and evolutionary/biogeographical history.

AUTHOR CONTRIBUTIONS

KN and SH wrote the paper and prepared the figures.

ACKNOWLEDGMENTS

The authors thank Drs. Mary O'Connor, Angélica L. González, Diego Barneche, and Julie Messier who as editors of this special issue of Frontiers of Ecology and Evolution invited this contribution. They also thank Drs. Randy Wayne and Thomas Owens (Cornell University) and the Drs. Brummer, Michaletz, and Savage who gave generously of their time and for their constructive comments on an early draft of this paper. Funding from the College of Agriculture and Life Science (to KN) is also gratefully acknowledged.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

REVIEW
published: 14 January 2019
doi: 10.3389/fevo.2018.00233

“Unifying” the Concept of Resource Use Efficiency in Ecology

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Resource use efficiency (RUE) is an ecological concept that measures the proportion of supplied resources, which is converted into new biomass, i.e., it relates realized to potential productivity. It is also commonly perceived as one of the main mechanisms linking biodiversity to ecosystem functioning based on the assumption that higher species numbers lead to more complementary and consequently more efficient use of the available resources. While there exists a large body of literature lending theoretical and experimental support to this hypothesis, there are a number of inconsistencies regarding its application: First, empirical tests use highly divergent approaches to calculate RUE. Second, the quantification of RUE is commonly based on measures of standing stock instead of productivity rates and total pools of nutrients instead of their bioavailable fractions, which both vary across systems and therefore can introduce considerable bias. Third, conceptual studies suggest that the relationship between biodiversity, productivity and RUE involves many more mechanisms than complementary resource use, resulting in variable magnitude and direction of biodiversity effects on productivity. Moreover, RUE has mainly been applied to single elements, ignoring stoichiometric, or metabolic constraints that lead to co-limitation by multiple resources. In this review we illustrate and discuss the use of RUE within and across systems and highlight how the various drivers of RUE affect the diversity-productivity relationship with increasing temporal and spatial scales as well as under anthropogenic global change. We illustrate how resource supply, resource uptake and RUE interactively determine ecosystem productivity. In addition, we illustrate how in the context of biodiversity and ecosystem functioning, the addition of a species will only result in more efficient resource use, and consequently, higher community productivity if the species’ traits related to resource uptake and RUE are positively correlated.

Keywords: resource limitation, uptake, productivity, biodiversity, ecological stoichiometry, diminishing marginal returns, ecosystem functioning

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Edited by:
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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *31 August 2018*
Accepted: *11 December 2018*
Published: *14 January 2019*

Citation:
Hodapp D, Hillebrand H and Striebel M (2019) “Unifying” the Concept of Resource Use Efficiency in Ecology. Front. Ecol. Evol. 6:233. doi: 10.3389/fevo.2018.00233

RUE IN ECOLOGY

Resource use efficiency (RUE) is defined as the amount of biomass produced per unit of supplied resource. It is commonly applied to explain and understand ecological phenomena such as the link between potential and realized productivity or biodiversity effects on ecosystem biomass production, and therefore constitutes a concept of major interest to research questions in various ecological contexts.

The origins of the concept go back to early agricultural research. In a comprising review, de Wit (1992) summarizes how during the agricultural industrialization, the increasing use of fertilizers and the ensuing environmental consequences triggered ideas to define the optimal supply of resources so as to maximize the efficiency of agricultural production. This agricultural view on resource use efficiency dates back to the law of the minimum (Sprengel, 1826; Liebig, 1840) and Liebscher's (1895) law of the optimum, which defines the optimal supply rate and ratio of mineral nutrients to foster plant growth. Based on Liebscher's work, Mitscherlich (first in 1909) and others expressed the decelerating production of biomass with linear increases in fertilizer addition as a law of diminishing returns. Derived from this work in agricultural sciences, ecology developed similar questions, but focused on morphological or physiological mechanisms regulating the observed patterns in resource use and its efficiency (Vitousek, 1982; Chapin et al., 1997).

Its oldest and most direct conceptual application is clearly the link between potential and realized productivity within and across communities and ecosystems (for a full history of this debate, see the supplement published with Grace et al., 2016). The higher the proportion of resources turned into new biomass, the higher are the levels of realized productivity. In that respect, RUE can be understood analogously to Odum's concept of transfer efficiency (Odum, 1957) which describes the amount of energy that is transferred from one trophic level to the next measured in, e.g., joules. Similar to reductions in energy transfer due to respiration at each trophic level, the amount of resource or matter that is converted to biomass at the next higher trophic level is constrained. Reasons are manifold and include inaccessibility of resources (Soares et al., 2017), stoichiometric mismatch and the need to respire, excrete, or exudate excess resources (Andersen et al., 2004) as well as co-limitation (Danger et al., 2008). Consequently, transfer efficiency and RUE determine important emergent properties of ecosystems such as food chain length (Hessen et al., 2004) or the internal (re)cycling of nutrients (Vitousek, 1982). Also, community composition and biodiversity turnover are affected by RUE, as species differ in their ability to sequester resources and turn these into growth. Tilman's competition theory (1982) is directly based on these ideas, predicting that the outcome of resource competition will be directly linked to community-wide RUE.

The growing interest in understanding RUE as a fundamental constraint of realized productivity over the last decades has been driven by research on how species diversity affects community or ecosystem production. The central hypothesis of the biodiversity—ecosystem functioning (BEF) research is that higher levels of diversity (species richness, functional diversity) result in a more efficient use of the available resources and will therefore yield greater amounts of biomass than the same system at lower levels of diversity (Chapin et al., 1997; Loreau, 2001). In other words, species loss will result in a reduction of RUE and therefore decreased ecosystem function (Cardinale et al., 2006). In addition to ample support for this general hypothesis from theoretical work and experimental studies, there also exists an increasing number of empirical tests, especially from natural communities (Filstrup et al., 2014; Hodapp et al., 2015; Fontana et al., 2018), highlighting the importance of individual traits rather than simple diversity measures. Acknowledging this trait-dependence results in potentially different signs and strengths of BEF relationships, as different relationships between traits mediating coexistence and traits mediating RUE can exist (Hillebrand and Matthiessen, 2009). This implies potentially high degrees of context dependence in BEF relationships, which requires to shed light on RUE as a central mechanism linking composition and function in ecological systems (Nijs and Impens, 2000; Binkley et al., 2004; Forrester and Bauhus, 2016).

However, as we detail below, the way RUE has been used in ecology generally, and BEF research especially, differs broadly. This includes conceptual and mathematical differences, which come with rarely-stated specific assumptions in the way RUE is implemented. Therefore, in this review paper, we aim to unify the concept of RUE across different types of ecological systems and scales of ecological organization, as well as spatial and temporal extent to identify and describe common mechanisms and distinguish these from system- or organism-specific phenomena. Based on an overview of the existing use of the concept (section Definitions and Differences in RUE Across Systems: Interpretation and Limitations), we present the basis for a unified view on RUE (section Unifying the Concept of RUE: a Suggestion). We discuss the validity of this concept in light of recent discussions on multiple resource limitation (section RUE Under Multiple Resource Limitation) and across scales (section RUE Across Ecological, Temporal, and Spatial Scales). Finally, we specifically address the importance of RUE in the context of global change (section RUE in a Changing Environment) and BEF (Section Biodiversity Effects on RUE) research.

DEFINITIONS AND DIFFERENCES IN RUE ACROSS SYSTEMS: INTERPRETATION AND LIMITATIONS

Despite the common applicability of RUE as a concept, measurement and quantification of the relevant quantities vary considerably across ecosystems. These differences arise from distinct types of resource use, organism physiology, and ecosystem properties. **Table 1** gives an overview of examples for the definition and quantification of resource use efficiency for different types of resources, ecosystems, and organisms.

One early suggestion of how to quantify nutrient use efficiency in plants goes back to (Chapin, 1980). He stated that the resource use efficiency defined as the amount of dry matter produced per unit nutrient taken up (e.g., g biomass/g nutrient) is simply the inverse of nutrient concentration in plant tissue (e.g., expressed as % nutrient in dry mass or g nutrient/g tissue). In addition, he mentioned that future productivity could be influenced by mechanisms such as luxury consumption or accumulation of storage polysaccharides and that consequently respiration or

TABLE 1 | Examples for definitions and uses of resource use efficiency for different organism types along different ecological scales.

Limiting resource	Organism type	Definition	Measured as	Ecological scale	References	Limitation
Nutrient	Terrestrial plants	Inverse of nutrient concentration in plant tissue	Tissue nutrient concentration	Individual organism/ community	Chapin, 1980	Only valid for short-lived plants
Nutrient	Forest	Inverse of nutrient concentration in the aboveground litterfall, root turnover and organic matter increment of vegetation	Litterfall mass/ litterfall N content	Individual organism/ community	Vitousek, 1982	Assumption that litterfall is a constant proportion of ANPP
Nutrient	Microbial	Fraction of consumed organic N that is not released as ammonium	$(U_N\text{-}M_N)/U_N$ UN, gross rates of amino-acid consumption MN, gross N mineralization rate determined via stable isotope analysis	Community	Mooshammer et al., 2014	
Nutrient	Freshwater and marine plankton	Biomass production per unit of limiting nutrient	Biomass or biovolume/total phosphorus	Community	Ptacnik et al., 2008; Filstrup et al., 2014; Hodapp et al., 2015	Standing stock, not considering loss due to consumption
Nutrient	Terrestrial ecosystems	Nutrient uptake	Left over nutrient in soil	Ecosystem	Cardinale et al., 2006	
Nutrient	Marine Plankton	Amount of C or nutrient incorporated into biomass	Copepod RUE was calculated total copepod C produced per unit algal N Copepod NUE was calculated as copepod tissue N per unit algal N	Community	Plum et al., 2015	Standing stock
Water	Terrestrial, forest, peatlans, grassland	The amount of C assimilated per unit of water loss by transpiration or inverse of transpiration ratio	GPP/ transpiration	Ecosystem	Briggs and Shantz, 1913; Cowan and Farquhar, 1977, see also Brümmer et al., 2012	
Water	Temperate steppe	Photosynthesis per unit of water loss due to respiration	Leaf photosynthesis/ leaf transpiration	Leaf	Niu et al., 2011	
Water	Temperate steppe	Gross ecosystem productivity per unit water transpired	GEP/ transpiration	Canopy	Niu et al., 2011	
Water	Temperate steppe	Productivity per unit water transpired	GEP/ canopy transpiration, net ecosystem CO_2 exchange/ evapotranspiration, leaf photosynthesis/ leaf transpiration	Leaf, canopy and ecosystem	Niu et al., 2011	
Radiation	Forest ecosystems	GPP per unit radiation intercepted by terrestrial vegetation	Net ecosystem exchange fluxes of CO_2/absorbed photosynthetically active radiation (PAR)	Ecosystem	Garbulsky et al., 2010	
Carbon	Microbial	Biomass C produced per unit organic carbon resource C consumed	Growth rate/(growth rate + respiration rate)	Community	Keiblinger et al., 2010	

The limiting resources used for the examples as well as possible limitations of the respective measurements are given.

rates of photosynthesis and assimilation might be more adequate measures of the efficiency of nutrient use. Vitousek (1982) further pointed out that the definition of inverse concentrations in plant tissue can only be applied to short-lived plants, because in perennial plant species seasonal processes, such as withdrawal of nutrients from senescing leaves, allow within-individual recycling of nutrients. He suggested quantifying resource use efficiency as the inverse of the nutrient concentration of the aboveground litterfall, root turnover, and the organic matter increment. However, this approach only works when litterfall mass is a constant proportion of ecosystem production, which is usually not the case since higher proportions of nutrients are allocated to wood production than leaf production across gradients of forest productivity (Binkley et al., 2004).

Water use efficiency (WUE) in plant communities is usually quantified as ratios of gross primary production over transpiration, i.e., unit of water loss (Garbulsky et al., 2010; Niu et al., 2011; Brümmer et al., 2012). In aquatic systems, RUE usually refers to biomass production per unit of nitrogen or phosphorus. Here, biomass production is commonly quantified as some measure of standing stock (particulate carbon, biovolume, or other proxies, such as chlorophyll a concentration for phytoplankton) and divided by values of total pools of the limiting nutrient (Ptacnik et al., 2008) or similar quantities representing the degree of nutrient limitation (Breton et al., 2017). Another example is the approach by Hood et al. (2018) who used the ratio of net primary production, calculated as the difference between gross primary production (GPP) and autotrophic respiration divided by nutrient uptake as a measure for RUE of the autotroph community. Rates of GPP are generally laborious or even infeasible to obtain, especially in the field. Hence, the above definitions all use measures of standing stock as proxies for productivity. However, few studies report actual rates, such as photosynthetic capacity per leaf nitrogen content (Field and Mooney, 1983) and ratios of productivity rates over nutrient supply (Lehtinen et al., 2017).

Thus, the major divide between different applications of RUE is the difference between using gross and net production, and replacing the latter with estimates of standing stock. This is crucial as it has strong implications for interpretation. Gross production is an estimate of realized productivity including losses (exudation, excretion, or mortality through senescence and consumption), whereas especially in aquatic systems, realized productivity is often only weakly related to standing stock at all. Hence, a major drawback of using estimates of standing stock instead of productivity rates is that it is impossible to determine biomass losses due to consumption, which is a bias that will differ strongly between ecosystems.

For example, one general difference between aquatic and terrestrial systems is that aquatic systems are characterized by rapidly growing primary producers, which are more efficiently consumed by herbivores (Shurin et al., 2006). In part, this originates from better palatability of phytoplankton compared to terrestrial plants due to lower proportions of low-quality structural components, such as lignin or cellulose (Hessen et al., 2004). Consequently, aquatic systems have higher energy transfer efficiency compared to terrestrial ecosystems (Cebrian, 1999).

However, other system-specific caveats in using gross or net productivity or standing stocks also apply. In forests, nitrogen use efficiency (NUE) depends on resource resorption from senescing leaves and should therefore be integrated over the whole year, which is hardly feasible in most studies (Birk and Vitousek, 1986). Thus, any resource use efficiency determined based on standing stock values is confounded by system-specific conditions, which complicates the interpretation of observed differences between systems.

Similar issues are debated regarding differing ways to quantify the amount of limiting resource in a system. Using total resource pools such as soil N or P, or total N and P in water, ignores the fact that not all of this pool may be available to organisms. Additionally, bioavailability of resources differs considerably between nutrient types (Soares et al., 2017). Thus, any RUE calculated based on "total nutrient pool" measurements will inevitably deviate from the real ratio. Similar issues arise when using remaining resource concentrations in the ecosystem as a proxy since these do not reflect the available, but only the left-over resource pool.

A third line of differences between RUE approaches captures the identity of the potentially limiting resources (**Table 1**), which reflects different physiological processes and their distinct resource requirements, as well as system-specific constraints on availability. For example, contrary to aquatic systems, water availability is one of the most crucial and limiting factors to plant growth and photosynthesis in terrestrial systems (Farooq et al., 2012). Therefore, water use efficiency (WUE) is only relevant in a terrestrial setting. Several approaches to RUE in autotroph organisms focus on photosynthesis, i.e., relate to the efficiency of using light energy and water to transform atmospheric CO_2 into biomass. Thereby, water use efficiency (WUE) and light use efficiency (LUE) in plants mainly reflect processes of carbon fixation and thus differ from nitrogen use efficiency, which is the result of carbon fixation AND protein synthesis. Heterotrophic organisms, in contrast to autotrophs, rely on organic carbon as their main energy source and their growth is majorly constrained by the nutrient content of their diet (Hessen et al., 2004). Therefore, the energy and the matter related aspects of RUE are rather tightly coupled. In heterotrophic microbes, however, the balance between metabolic processes is highly regulated and therefore resource use of carbon as well as nitrogen and other nutrients is rather flexible (Keiblinger et al., 2010; Mooshammer et al., 2014). Thus, although RUE definitions for different types of resource or organism might resemble each other, the observed patterns will likely vary as RUE is regulated by different mechanisms.

UNIFYING THE CONCEPT OF RUE: A SUGGESTION

Given the plethora of alternative definitions and proxies for variables in numerator and denominator of the ratio quantifying RUE, it might be worthwhile taking a step back to reconsider what exactly RUE is supposed to represent and under what circumstances the common assumptions hold. According to its general definition, RUE is the ratio of the amount of biomass produced (i.e., productivity) per unit resource. However, regardless of the difficulties in choosing the most adequate or representative variables for its quantification, the relationship between resource availability and productivity is far from trivial as it involves essentially two processes, the uptake and the conversion of resources into biomass. This aspect is illustrated by the "production ecology equation" (Monteith and Moss, 1977; Binkley et al., 2004, Eqn. 1), where the realized gross productivity of a system is determined by the amount of resource supplied, the proportion of resource taken up, and the efficiency of converting the ingested resource into new biomass.

$$\text{GPP} = \text{resource supply x resource uptake x resource use efficiency} \tag{1}$$

Depending on the relative increase or decrease of each of the three components in the equation and the position along the resource supply axis, productivity can show correlations of either direction with RUE. Hence, interpretation of empirical patterns becomes less straightforward. However, the knowledge of potential feed-back mechanisms and interactions between these three components offers the opportunity to understand diverging patterns across environmental conditions and systems.

For example, the common assumption originating from the concept of "diminishing marginal returns" (de Wit, 1992) describes a decelerating increase of biomass accumulation with an increasing supply of resource (**Figure 1**). This implies decreasing levels of RUE with increasing resource supply (Niu et al., 2011), but this assumption does not hold in general (Binkley et al., 2004). An addition of resources can lead to both, enhanced or reduced, RUE in the resource that was manipulated (Han et al., 2016, see also sections RUE Under Multiple Resource Limitation and RUE Across Ecological, Temporal, and Spatial Scales). Binkley et al. (2004) show that higher water supply increased the amount of light captured by a clonal eucalyptus stand, but these increased levels of light capture were lower than the increase of GPP, which indicates an increase in RUE of light. Similarly, water uptake increased in response to elevated water availability, but again the differences were smaller than the relative changes in GPP, indicating higher levels of WUE (Binkley et al., 2004).

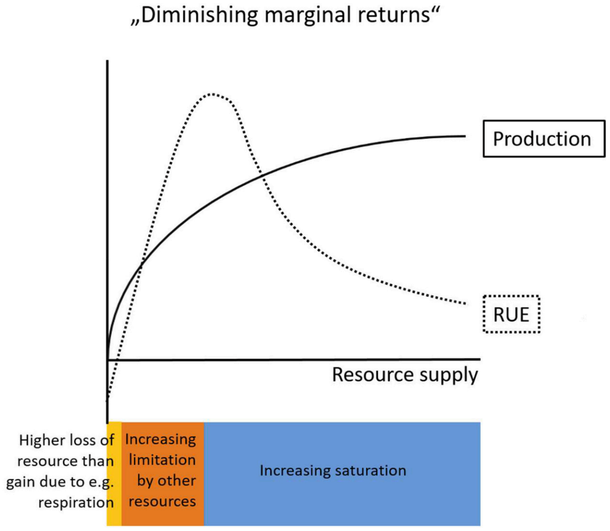

FIGURE 1 | Conceptual graph describing the relationship of resource use efficiency (RUE) and production with increasing levels of resource supply. The law of "Diminishing marginal returns" predicts decelerating rates of production with increasing resource supply. RUE on the other hand is usually negative at very low resource supply rates (yellow) due to resource losses as a consequence of general maintenance mechanisms (e.g., respiration). With increasing resource supply RUE increases until limitation by other resources constrains resource needs (orange). Finally, at very high resource supply levels saturation sets in (blue) which gradually decreases the amount of a particular resource that can be incorporated into new biomass.

In fact, the effect of increased resource supply on productivity depends on the scale of operation (leaf vs. canopy) and the type of resource (light vs. nutrients) (see section RUE Across Ecological, Temporal, and Spatial Scales). In terrestrial ecosystems, the assumption of decreasing RUE as resource supply increases at least partly holds at the leaf level. Physiological constraints lead to negative net gains of resource (i.e., higher losses due to for example respiration than gains in resource) and accordingly negative RUE values at very low levels of resource supply. As a consequence, RUE must increase at the lower end of resource supply until it is increasingly constrained by limitation from other resources and finally decreases as the saturation point for a particular resource is reached (**Figure 1**). However, the RUE patterns at the leaf scale can vary substantially from patterns at higher organismal or ecological level (see section RUE Across Ecological, Temporal, and Spatial Scales). The difference between these observed patterns arise from the variable forms of relations between resource uptake and somatic (or numerical) growth. Growth directly depends on external resource supply only if there is no storage involved, otherwise growth depends on the internally available resource stocks (e.g., cell quotas, i.e., intracellular level of the limiting nutrient) (Monod, 1950; Droop, 1983). In phytoplankton, the ratio between minimal cell quota (reflecting demand) and maximal cell quota (reflecting storage) can give information on the degree of luxury consumption possible, i.e., to what extent an organism is able to take up and store surplus resources. The potential decoupling of supply and production through luxury uptake and storage differs between resource types and organisms leading to different relationships between resource-supply and RUE at the individual scale and above. Moreover, it allows for preemption effects, where RUE is not driven by the potentially most productive species but by species able to monopolize resources through rapid uptake (Schmidtke et al., 2010; Kardol et al., 2013).

Most established ways of calculating RUE do not consider uptake explicitly, as in many empirical situations disentangling uptake and conversion efficiency is not trivial. Still, we recommend the use of the ecology production equation in order to explicitly state the assumptions underlying the calculations (**Figure 2**). This also implies to acknowledge different roles for both functional response (i.e., intake rate of a consumer as a function of resource density) and numerical responses (i.e., consumer population density as a function of resource density) to resource gradients, which has strong implications for altering the supply to RUE relationship at different levels of organization (see section RUE Across Ecological, Temporal and Spatial Scales).

RUE UNDER MULTIPLE RESOURCE LIMITATION

For decades, primary production in communities was considered to be limited by the least available nutrient, reflecting the classical law of the minimum postulated by Sprengel (1826) and popularized by Liebig (1840). However, more recent evidence suggests that primary production in multispecies communities is

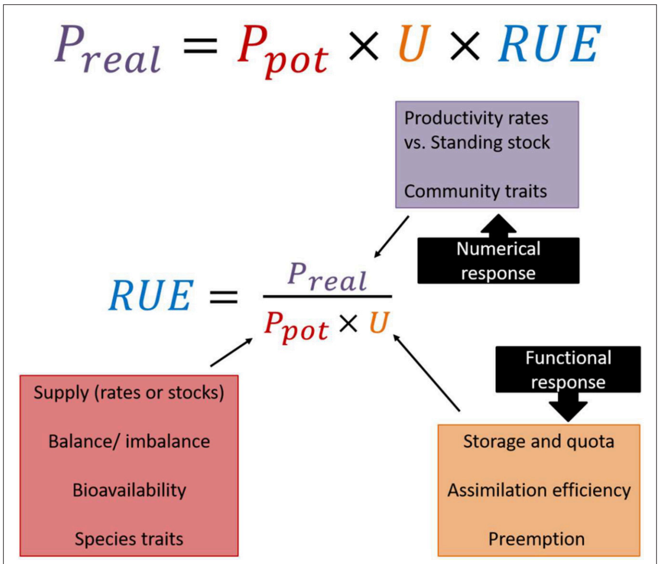

FIGURE 2 | Based on the production ecology equation, realized productivity (P_{real}) is a product of potential productivity (P_{tot}), resource uptake (U), and resource use efficiency (RUE). Rearranging the equation gives the common definition for RUE as the realized productivity divided by the amount of assimilated resources, which is influenced by resource availability and uptake. Thus, several ecological mechanisms have to be taken into account when quantifying and interpreting RUE patterns.

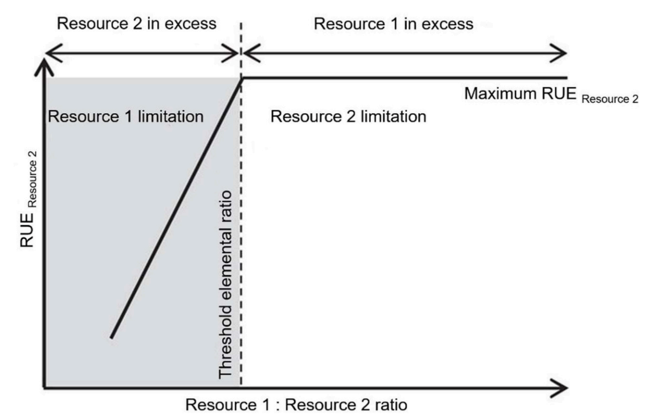

FIGURE 3 | Conceptual figure modified after (Mooshammer et al., 2014). The relation between threshold elemental ratio (TER) and resource use efficiency (RUE) depending on the available resource ratio. The TER is defined as the optimal resource elemental ratio for consumer growth (Urabe and Watanabe, 1992). The TER marks the ratio of two resources above which a maximal RUE for one resource is reached (here resource 2) as this resource becomes limiting. While the limiting resource is expected to be used for growth, the resource in excess must be disposed of.

frequently limited by multiple nutrients (Arrigo, 2005; Elser et al., 2007; Harpole et al., 2011). At the organism level, biochemical processes can be actively and passively co-limited by nutrients substituting each other, regulating each other's uptake rate or being equally essential (Saito et al., 2008; Bonachela et al., 2015; Sperfeld et al., 2016). At the community level, co-limitation additionally occurs as the result of individual populations being limited by different resources (Danger et al., 2008).

The predominance of co-limitation has also direct consequences for the definition of RUE, which in most cases is defined as biomass production (realized productivity) per single, limiting resource reflecting potential productivity. Until now, co-limitation of resources has been little considered when using RUE (but see Lehtinen et al., 2017, who include resource availability and resource ratios in their (phytoplankton) model; Hirose and Bazzaz, 1998; Tarvainen et al., 2015; Han et al., 2016). Here, we discuss the importance of acknowledging resource ratios when addressing RUE (section Stoichiometry and RUE) and use this discussion to address RUE across multiple trophic levels (section Multiple Trophic Levels).

Stoichiometry and RUE

Multiple resource limitation can be considered in different ways when assessing RUE. One way is to explicitly mark the transition between limitation by one resource to limitation by another, e.g., by using the concept of threshold elemental ratio (TER) (**Figure 3**). Here, one resource is limiting at any time but the identity of the limiting resource can switch depending on the supply ratio. TER was introduced in the framework of Ecological Stoichiometry (ES) (Sterner and Elser, 2002). ES is used to describe and understand the relation between organisms and populations and their surrounding environment based on the availability of and demand for multiple resources. The TER concept has been developed to understand the interactions between trophic levels (Urabe and Watanabe, 1992; Sterner, 1997; Sterner et al., 1997), especially to distinguish between energy-limited and nutrient-limited growth. Further, this approach was used to investigate consumer-resource interactions (Andersen et al., 2004) and fluxes of energy and materials (Allen and Gillooly, 2009). When consumers ingest food of different chemical composition, they can be limited by energy if the C:nutrient ratio in their food is very low. With increasing C:nutrient ratio, however, the nutrient becomes so dilute in the ingested particles that growth rate decreases even if ingestion rates are maximal (Urabe and Sterner, 1996).

The threshold elemental ratio is the food C:nutrient ratio at which this switch between C- and nutrient limitation occurs, and can differ between consumer species by an order of magnitude, depending on nutrient requirements (Frost et al., 2006). TER thus reflects that organisms require elements for metabolism in ratios which are often different from what is available in their environment. While primary producers mainly obtain the same nutrient ratios as their environment (Elser and Urabe, 1999; Güsewell, 2004), higher trophic levels, such as zooplankton consumers or invertebrate and vertebrate taxa, keep a relatively fixed elemental body ratio, independent from the available food sources (Andersen and Hessen, 1991; DeMott et al., 1998; Elser et al., 2000; Jaenike and Markow, 2003). Therefore, consumers demand for essential nutrients and the relatively plastic balance of these nutrients in their prey can create elemental mismatches.

Keeping such a fixed elemental body ratio and thus facing a mismatch compared to the ratios mostly manifested by producers, requires physiological mechanisms (by regulating their cellular nutrient content via excretion or respiration) and implies some costs (Elser et al., 2001; Kooijman et al., 2004; Vrede et al., 2004). Some consumers adjust their food intake by increasing the individual grazing rate with increasing mismatch between their own requirements and their food as demonstrated in a meta-analysis, pointing toward compensatory feeding responses (Hillebrand et al., 2009). Others select their food dependent on its nutritional content (Mayntz et al., 2005) or digest and retain elements in ratios different from that in the food in order to minimize the imbalances between the available food and their requirements. Below, we show that stoichiometry and stoichiometric mismatches are affected by changing environmental conditions (section RUE in a Changing Environment) and subject to adaptation on micro- and macroevolutionary time scales (section Resource Use Efficiency Across Temporal and Spatial Scales).

While TER has mainly been used to characterize the resource need of heterotrophic consumers, the concept also applies to autotrophs or mixotrophs, where the limitation between two elements switches at optimal ratios between these resources (**Figure 3**). This has been described as a mechanism to enhance nutrient supply under nutrient-limited conditions for phytoplankton (Rothhaupt, 1996; Klausmeier et al., 2004a,b; Hillebrand et al., 2013) as well as terrestrial plants (Wakefield et al., 2005; Farnsworth and Ellison, 2008). Recent evidence suggests that mixotrophs (i.e., organisms that are able to use different sources of energy and carbon) may buffer stoichiometric constraints for herbivores and thus stabilize secondary production compared to systems dominated by phototrophs (Moorthi et al., 2017).

A second approach to consider multiple resource limitation when assessing RUE (**Figure 4**) is to distinguish between balanced and imbalanced resource supply (Cardinale et al., 2009). Nutrient uptake, and therefore RUE, also depend on the balance or imbalance of resource ratios, the heterogeneity of their spatial distribution and the identity of the most limiting resource. Cardinale et al. (2009) separated between the amount of resources and the ratios of these resources by standardizing (rescaling) all resource concentrations and then using Euclidian geometry for distinguishing between resource balance and imbalance. Balanced resource supply means that all resources are equally abundant with all of them equally rare or abundant. Imbalanced resource supply indicates that some resources are available in excess while others are limiting. Studies using this approach showed that more balanced supply of resources leads to more efficient resource use and thus higher overall RUE as less resources remain unconsumed (Gross and Cardinale, 2007; Cardinale et al., 2009; Hodapp et al., 2016). This could reflect the low RUE for the overly abundant resources or the inability to access resources if uptake of multiple resources is co-dependent.

Recently, Han et al. (2016) extended a model based on the production ecology equation considering one resource (Binkley et al., 2004) to integrate multiple resource use efficiency. A test of their algorithm on a water-availability gradient in semi-arid grasslands showed that water availability affected the resource absorption rates, resource use efficiencies and resource availabilities of all three resources in their model, water, light and nitrogen, and that their interaction jointly regulated ecosystem productivity.

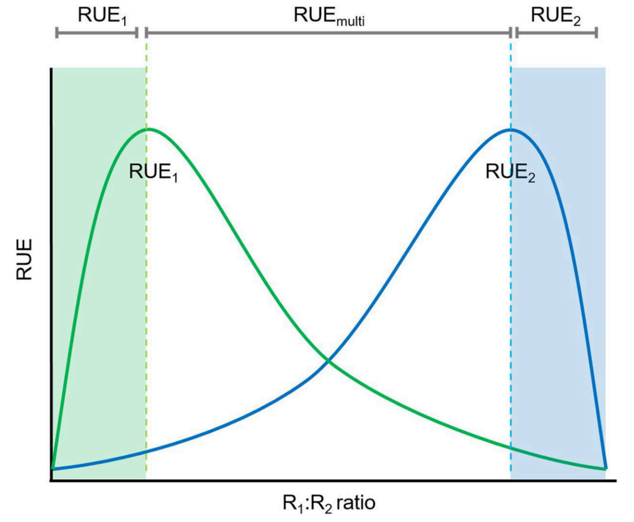

FIGURE 4 | Relationships between resource ratio and RUE under multiple resource limitation. Under conditions when one resource is limiting (either high or low R_1:R_2 ratio) RUE can be determine based on a single resource (either R_1, green shaded area, or R_2, blue shaded area) whereas multiple resource limitations need to be considered for the determination of RUE if both resources are in higher supply (more balanced).

Multiple Trophic Levels

Approaches considering multiple resources have major appeal when addressing RUE across more than one trophic transfer. The community structure of a food web depends on the efficiency of energy transfer between different trophic levels (Hutchinson, 1959; Hairston et al., 1960). Hessen et al. (2004) argued that while energy is given in joules, carbon units are more suitable to describe both energy and matter flows. However, the efficiency of C transfer depends also on the cell quotas of N and P relative to C (Hessen et al., 2004). Moreover, the ratios in which consumers digest and retain elements depend on organism-specific resource limitations and might differ from that in the food material. Another example for multiple nutrient interactions across trophic levels are organisms with an intermediate role in the food web, that “repack” small food compounds by ingesting and assimilating them and thus serve as more complex food sources for higher trophic levels. In general, uptake and utilization efficiency of nutrients differ among organisms on different trophic levels and lead to differences in the release of resources, which is greater for the resource in excess. This leads to the suggestion to consider not only one but multiple resources when defining RUE among multiple trophic levels.

RUE ACROSS ECOLOGICAL, TEMPORAL AND SPATIAL SCALES

The constraints on resource use efficiency are likely to be different at different scales of organization from individuals to ecosystems (section Resource Use Efficiency Across Scales of Organization) and also when including more environmental heterogeneity when increasing the temporal and spatial scale of inference (section Resource Use Efficiency Across Temporal and Spatial Scales).

Resource Use Efficiency Across Scales of Organization

The cellular and individual RUE are mainly characterized by the functional response of resource uptake to resource supply, reflecting the concentration—dependent on an increase in uptake as well as luxury consumption and storage. The RUE at the level of populations, communities or ecosystems involve resource use in the form of somatic growth or numerical responses (**Figure 5**). Moreover, the processes affecting resource demand and (co)limitation are highly different between these different scales (Danger et al., 2008; Saito et al., 2008). At the scales of cells, organs or organisms, limitation is mainly based on biochemical processes. Co-limitation occurs when the resource uptake and incorporation of one element depend on the availability of another. Within populations, genetic, and phenotypic variation between individuals creates differences in demand for—and thus limitation by—different resources. This variability will increase when considering different species or species interactions (competitive or mutualistic), as the community-level resource use differs from the one exhibited by single species (**Figure 5**). Thus, the role of stoichiometry of resource supply will also increase with levels of ecological complexity, especially if it includes interactions between species (Kay et al., 2005). For example, mycorrhiza-plant associations can be described as a trade-balance between the abundant access of plants to carbon and the access of the fungal partner to soil nutrients (Schwartz and Hoeksema, 1998; Johnson, 2010). Here, the shared use efficiency for the different resources is higher than predicted from each partner's specific RUE. Similar mutualistic increases in effective RUE can be found in endosymbiont bearing animals (Fenchel and Finlay, 1991), but also in ecosystem-wide facultative mutualisms (Bradley and Kenneth, 2001). In any of these cases, RUE is predicted to change when extending the scope from single individuals to species to the community level, where the directionality of change depends on the type of interaction between organisms. Mutualistic interactions and complementarity can be predicted to increase shared resource use efficiency, whereas interference competition or predation might reduce overall RUE.

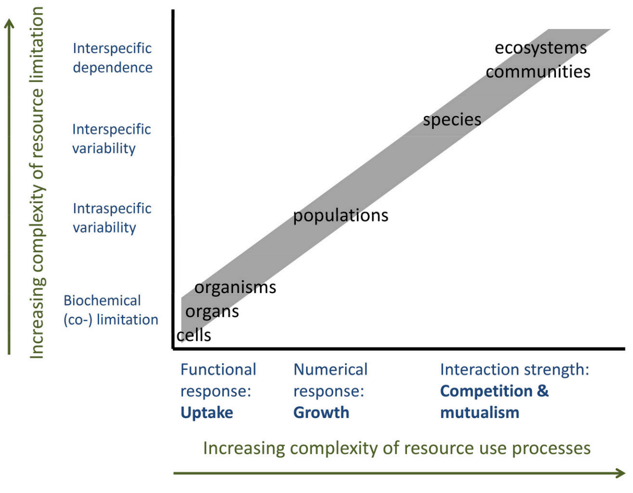

FIGURE 5 | Resource use and resource demand depending on organizational levels from single cells to ecosystems. Increasing complexity of resource use processes and types of resource limitation decrease the predictability of RUE by up or downscaling across levels of organization.

Much empirical evidence supports the idea that the relationship between resource supply and RUE depends on the scale of organization. Increased precipitation decreases the efficiency of water use at the level of single leaves, but increases it at the canopy and ecosystem level (Niu et al., 2011). Likewise, leaf-scale resource use efficiency for light in trees declines with increasing irradiance, but increases at the scale of entire forests (Binkley et al., 2004). In these examples, the efficiency of the functional response decreases with supply (lower marginal gains), but the interactions between individuals and species as well as the inclusion of growth responses can lead to different relationships at the community scale. This is true beyond autotrophs. For herbivores, decreasing food quality (increasing stoichiometric mismatch between consumer and plant) leads to increased ingestion rates at the level of individuals, but decreased population or community biomass (Hillebrand et al., 2009). The latter example reflects that individuals tend to overcome shortage by compensatory functional responses, whereas poor growth efficiency leads to reduced resource use efficiency at higher levels of organization.

Resource Use Efficiency Across Temporal and Spatial Scales

Examining patterns of RUE at larger spatial and temporal scales will, in most cases, lead to an increase in the heterogeneity of resource supply rates and ratios and thereby alter RUE. The consequences of spatial heterogeneity of resource supply for RUE have been well developed in models and experiments conducted in the framework of metacommunity (Leibold and Miller, 2004) or metaecosystem (Gounand et al., 2018) ecology. In both theories, resource use in local habitats (patches) is explained from local community dynamics as well as regional processes (dispersal, mobility). Regional scale RUE will be affected by three major factors, (i) the relative difference in the resource supply between patches, (ii) the spatial connectivity between patches, and (iii) the spatial arrangement of the heterogeneity in resource supply. Theory and empirical evidence give predictions for changes in RUE across all pairwise combination of these axes (**Figure 6**). With respect to resource supply, models,

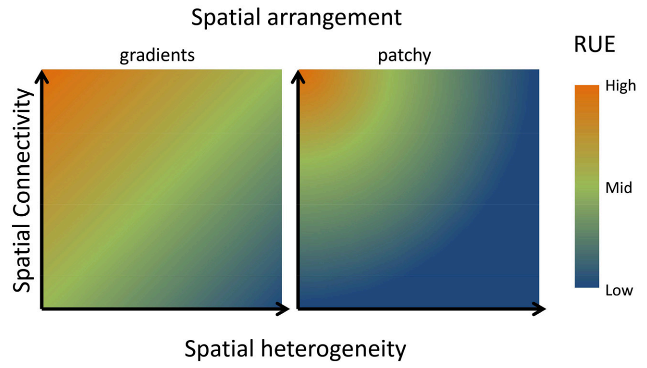

FIGURE 6 | Conceptual graph describing consequences of scaling up in space for RUE. If multiple resources are more heterogeneously distributed in space, RUE will decline unless high spatial connectivity (high rate of dispersal or active movement of consumer) allows efficient capture of multiple resources across the resource landscape (Hodapp et al., 2016). Thus, RUE will be minimal if resources are heterogeneously distributed, but low connectivity prevents consuming resources in different patches. The positive effect of dispersal or mobility decreases however, when neighboring patches differ strongly in their resource supply, reflected by the difference between a more gradual heterogeneity in the left panel compared to a more patchy difference in resource supply in the right panel. As detailed in the text, similar arguments can be made for temporal fluctuations in resource supply.

and experiments converge on the conclusion that a more heterogeneous landscape of resource supply leads to overall lower RUE at the landscape scale. On the one hand, the heterogeneity affects how well resource uptake traits match the local environment. On the other hand heterogeneity in multiple resources likely leads to stoichiometric imbalances, leading to higher amounts of resources left over and lowered multi-element RUE (Gross and Cardinale, 2007; Hodapp et al., 2016; Gülzow et al., 2019). Consequently, the RUE at larger spatial scales becomes more dependent on the variability and complementarity of resource traits between species (Cardinale et al., 2004; Hodapp et al., 2016). Regarding spatial connectivity, spatial connectivity alters the spatial imprint on RUE if diffusive processes homogenize resource differences (Gülzow et al., 2019) or organisms are able to move between patches (Marleau et al., 2015). In both cases, resource supply will be experienced as less heterogeneous and regional RUE will not decrease as much as in a low connectivity system (**Figure 6**). Extending these predictions, stoichiometric distribution models have been developed to address how the RUE of a spatially foraging consumer will eventually lead to spatial patterns in resource stoichiometry (Leroux et al., 2017).

Both axes will be altered by the spatial distribution of resources (Hodapp et al., 2016). In a landscape characterized by smooth resource gradients, neighboring patches are similar in their resource supply, and a short-distance disperser is likely to find similar resource conditions as in its original patch, increasing RUE (**Figure 6**). By contrast, in a landscape where resources are much more randomly distributed, a species performing well in one patch and producing a lot of offspring might disperse into neighboring patches with highly different resource supply, where its RUE will be low. Depending on the relative strength of dispersal compared to local responses of population growth to resource availability, a very patchy distribution of resources will be detrimental to overall resource use.

In contrast to the large number of studies examining RUE in space, there is a much smaller body of literature on the effect of larger temporal scales on RUE. However, in principle the same arguments prevail: RUE will decrease when measured over longer time scales if different resources are supplied asynchronously, leading to temporal imbalance in supply stoichiometry, analogous to the spatial supply imbalance (**Figure 6**). This effect will be less prominent if long-lived species can integrate over the fluctuations in supply, analogous to the effect of connectivity in space. RUE will also be higher if changes in temporal supply are gradual, whereas pulsed, abrupt changes will decrease the match between resource use traits and resource availability (**Figure 6**). A nice support for this analogy is a study on Norwegian spruce stands, showing that RUE peaks for different resources occurred in different seasons (Tarvainen et al., 2015).

On evolutionary time scales, the stoichiometric match between resource requirements and supply ultimately determines the trade-off between the material and energetic costs of a particular trait or strategy and its fitness benefits (Kay et al., 2005). For instance, resources that are allocated to structural components as opposed to fast growth can be valuable investments if they are beneficial in terms of reproductive success. Thus, flexibility in elemental ratios and therefore mechanisms driving RUE are subject to selective pressure.

In general, responses to spatial and temporal gradients of resource supply might differ (Paruelo et al., 1999), thus, more research joining both perspectives might be needed to assess the full scale dependency of RUE.

RUE IN A CHANGING ENVIRONMENT

Given the central role that has been ascribed to RUE in explaining biodiversity effects on ecosystem processes, it is mandatory to understand how RUE will directly be affected by anthropogenic drivers of environmental change. These drivers can be separated in two categories: those altering RUE through altering resource supply, and those altering RUE by altering the demand.

Anthropogenic changes in supply include eutrophication (or in later years also re-oligotrophication), fossil fuel burning increasing e.g., carbon dioxide availability in the atmosphere, changes in precipitation or changes in light climate, e.g., through increased turbidity. The effect of altering the availability of any of these resources will alter the RUE for this resource, where the sign depends on the non-linear relationship between supply and RUE (see section Unifying the Concept of RUE: a Suggestion, **Figure 1**). Additionally, changes in the supply of any resource can indirectly influence RUE for another resource, a phenomenon often observed in agricultural studies, which aim to increase productivity and RUE with minimal effort in irrigation and fertilization. Examples include increasing water use efficiency over gradients of CO_2 availability (Policy et al., 1993; Keenan et al., 2013) and light (Aranda et al., 2007). Likewise, enhancing CO_2 increased light and nutrient use efficiency (Hirose and Bazzaz, 1998).

Global warming is an example for an anthropogenic driver of global change affecting the demand rather than the supply. It has only recently been fully accepted that one of the consequences of global warming is that the inevitable increase in base metabolic rates and growth rates alters the absolute and relative demands for nutrients. One of the most elegant examples is the model by Thomas et al. (2017) that shows how the minimal requirements for a nutrient increase with temperature, whereas simultaneously an increase in nutrient supply allows for a thermal optimum shifted to higher temperatures. While others have argued that the increase in demand might be alleviated by higher efficiency in resource use (Toseland et al., 2013), there is evidence from studies on phytoplankton showing that half saturation constants for nutrients increase with temperature (Bestion et al., 2018) or that internal algal stoichiometry reflects higher relative nutrient limitation (Yvon-Durocher et al., 2015). A recent study investigating combined temperature and supply level effects on phytoplankton community growth (Verbeek et al., 2018) showed that whereas single treatments of temperature increase or oligotrophication led to increases in RUE, the combined treatment resulted in non-linear responses, reflecting the mismatch between increasing demand and decreasing supply. Similarly, shifts in biochemical composition of zooplankton species with increasing temperature were shown, where the sign of the effect was dependent on resource availability (Bullejos et al., 2014). In addition to effects of increasing mean temperature, species responses to changes in temperature variance are also governed by asymmetric thermal performance curves. In most cases, performance declines faster at superoptimal temperatures than it increases at suboptimal temperatures. Consequently, the effect of temperature fluctuations on growth rate (and thus resource demand) in the short term can be net positive or net negative depending on the degree of asymmetry in the thermal performance curve (Bernhardt et al., 2018). On longer time scales different adaptive response were shown to evolve under different timescales depending on the frequency of the environmental fluctuation (Botero et al., 2015). Thus, the changes in demand and supply of resources that interactively shape responses of RUE are influenced by the magnitude and fluctuation of environmental properties.

BIODIVERSITY EFFECTS ON RUE

A common perception among ecologists is that higher levels of diversity (richness and evenness) generally result in higher levels of depletion of the supplied resources, i.e., resource use efficiency, which then leads to an increase in biomass production (**Figure 7**). While there is plenty of theoretical and empirical support for this assumption for mainly terrestrial ecosystems (Cardinale et al., 2006), the general patterns show quite a variability across systems (Balvanera et al., 2006). In fact, study outcomes from natural systems suggest a considerable flexibility of diversity effects on RUE and production (Filstrup et al., 2014; Gagic et al., 2015; Hodapp et al., 2015; Fontana et al., 2018).

As illustrated by the production ecology equation, system productivity is determined by more than just RUE. In fact, the common diversity effects, such as complementarity, selection, and facilitation are, strictly speaking, associated with resource uptake rather than resource use efficiency itself (Nijs and Impens, 2000). As illustrated earlier, resource uptake is intricately related to and regulated by RUE through resource demand, depending on environmental conditions, species interactions, and metabolic constraints.

However, whether increased species richness yields higher biomass depends on the resource use efficiency traits of the species that is added to the system. Given a system with a certain number of species and the associated RUE, increasing community richness by just a single species will result in the re-distribution of resources within the species community and any resource re-distributed from a species with high RUE to a new species with lower RUE will result in a reduction of community productivity (Nijs and Impens, 2000). An appropriate example is phytoplankton communities, where the potential for complementarity effects is lower due to the rather homogeneous aquatic environment and the fact that plankton are floating freely in the water column, i.e., they have similar access to nutrients. Schmidtke et al. (2010) showed experimentally that instead of increasing biomass, all of their tested algal communities declined in biomass when adding further functional groups to the species assemblage. They ascribe this pattern to a trade-off between growth rate and the ability to build larger amounts of biomass as slow-growing species produced higher biovolumes in monoculture, but were outcompeted by fast-growing, less productive species in the species mixtures. Hence, positive effects of diversity on RUE and production will only occur in case of a positive correlation between resource uptake and resource use efficiency traits of the additional species. This is not contradictory to the huge body of biodiversity-ecosystem functioning (BEF) literature, which, in the vast majority, reports positive diversity effects. Classic BEF experiments tend to influence their outcomes, because in these highly controlled environments the only reason why species coexist is usually resource complementarity. In natural systems, however, coexistence is affected by many more mechanisms, e.g., dispersal rate, (selective) grazing pressure, and environmental fluctuations.

Here, adding more species might not or even negatively affect total RUE when traits mediating coexistence are not or are negatively related to traits mediating resource use (Mouquet et al., 2002).

Additional variability in natural systems originates from the distribution of resource supply. Resource supply can be more or less heterogeneous in space, time, and the range of resource options provided, e.g., variability in nutrient ratios. In this context, more heterogeneous resource supply requires high trait diversity in uptake and/or resource use in order to achieve complementarity and high proportions of realized biomass production. On the contrary, in uniform resource environments (i.e., low heterogeneity in resource supply), resources will most

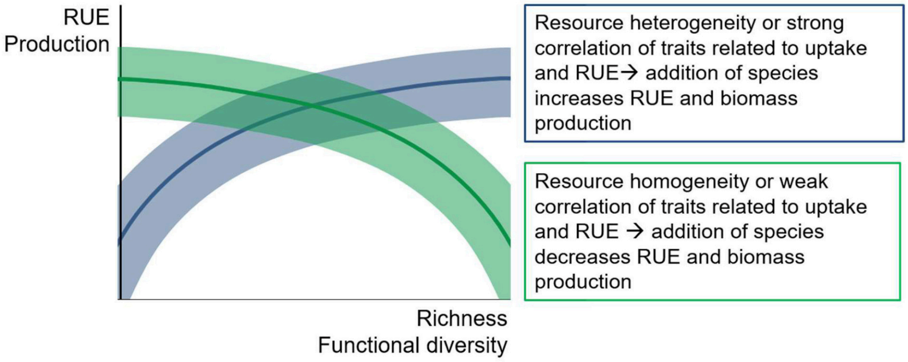

FIGURE 7 | Conceptual figure of possible relationships between diversity measures and resource use efficiency (RUE) or productivity. Positive, neutral or negative correlations are possible, depending on the match between resource supply and species assemblage. Shaded areas indicate potential variation around the general trend.

effectively be turned into new biomass when the local community consists of one or a few species that are well adapted to the given resource conditions (Hodapp et al., 2016). However, natural environments are seldom static or uniform. Therefore, in the more common case of patchy environments and fluctuating resource conditions over time, large regional species pools, and sufficient connectivity between patches will always serve as insurance for sustaining high levels of RUE, and therefore, ecosystem functioning through time (Danger et al., 2008). These considerations also hold with regard to other environmental factors. For instance, Norberg et al. (2001) use a theoretical framework to illustrate how the phenotypic diversity effects on functioning are affected by changing environmental conditions. Empirically, this can be shown by the effect of temporal or spatial heterogeneity on BEF relationships (Allan et al., 2011; Isbell et al., 2011). More species are needed to maintain a certain fraction of the productivity in systems varying more in space or time, as the species-specific RUE decreases if there are times or places where the performance of specific species is not maximal. In other words, environmental dimensionality has to match the dimensionality of species traits in the local assemblage in order to guarantee efficient use of the given resources (Ptacnik et al., 2010), and consequently, higher productivity.

CONCLUSIONS

As discussed in the previous sections, RUE and its role in governing BEF relationships does not only vary due to organism-specific physiological properties, but also between levels of biological organization and in response to heterogeneity in environmental conditions. Thus, while the ultimate aim of studies on RUE should be to relate rates of productivity to the amount of available resource, it might not be feasible to define a general concept for the quantification and mechanisms driving RUE that is valid across types of ecosystem, organism, and resource. Albeit, any deviation from the original concept that might be necessary needs to be acknowledged and discussed when making inferential statements. New insights could be generated by testing the extension of the concept to more than one nutrient and investigating how anthropogenic alteration of environmental conditions will affect long-term changes in RUE.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

ACKNOWLEDGMENTS

The authors would like to acknowledge the organizers of the 2018 Unifying Ecology Across Scales Gordon Research Conference, Mary O'Connor and Angelica L. Gonzalez, for discussion.

DH acknowledges funding by the Helmholtz Association at the Institute for Functional Marine Biodiversity (HIFMB) Oldenburg, MS and HH acknowledge funding by the German Research Foundation (DFG: STR 1383/1-1, STR 1383/6-1, HI 848/15-1, HI 848/24-1) within the priority program DynaTrait (SPP 1704).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 07 February 2019
doi: 10.3389/fevo.2019.00015

Eco-Evolutionary Origins of Diverse Abundance, Biomass, and Trophic Structures in Food Webs

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Organismal traits and their evolution can strongly influence food web structure and dynamics. To what extent the evolution of such traits impacts food web structure, however, is poorly understood. Here, we investigate a simple three-species omnivory food web module where the attack rates of all predators evolve as ecological dynamics unfold, such that predator trophic levels are themselves dynamic. We assume a timescale where other vital rates that govern population dynamics are constant and incorporate a well-known tradeoff between attack rates and the conversion of prey into predator biomass. We show that this eco-evolutionary model yields a surprisingly rich array of dynamics. Moreover, even small amounts of selection lead to important differences in the abundance, trophic, and biomass structure of the food web. Systems in which intermediate predators are strongly constrained by tradeoffs lead to hourglass-shaped food webs, where basal resources and top predators have large abundances, but intermediate predators are rare, like those observed in some marine ecosystems. Such food webs are also characterized by a relatively low maximum trophic level. Systems in which intermediate predators have weaker tradeoffs lead to pyramid-shaped food webs, where basal resources are more abundant than intermediate and top predators, such as those observed in some terrestrial system. These food webs also supported a relatively higher maximum trophic level. Overall, our results suggest that eco-evolutionary dynamics can strongly influence the abundance-, trophic-, and biomass-structure of food webs, even in the presence of small levels of selection, thus stressing the importance of taking traits and trait evolution into account to further understand community-level patterns and processes.

Keywords: consumer-resource interactions, eco-evo dynamics, omnivory, biomass, metabolic costs, trophic levels

OPEN ACCESS

Edited by:
Diego Barneche,
University of Exeter, United Kingdom

Reviewed by:
Jian Yen,
The University of Melbourne, Australia
Asta Audzijonyte,
University of Tasmania, Australia

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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *28 June 2018*
Accepted: *18 January 2019*
Published: *07 February 2019*

Citation:
Gibert JP and Yeakel JD (2019)
Eco-Evolutionary Origins of Diverse
Abundance, Biomass, and Trophic
Structures in Food Webs.
Front. Ecol. Evol. 7:15.
doi: 10.3389/fevo.2019.00015

INTRODUCTION

Food webs often share structural similarities across ecosystems, such as the relationship between the number of species and the number of feeding interactions (Martinez, 1992; Williams and Martinez, 2004; Gravel et al., 2013), the existence of an upper limit to the number of trophic levels (Pimm et al., 1991; Williams and Martinez, 2004), and the prevalence of highly repeated structural modules (McCann et al., 1998; Milo et al., 2002; Williams et al., 2002; Paulau et al., 2015). Surprisingly, these characteristics are relatively conserved over both space and time (Lafferty et al., 2008; Dunne et al., 2014; Yeakel et al., 2014), although some of these structural patterns might have simple statistical underpinnings (Williams, 2010). Understanding the factors that determine these structural similarities, despite large differences in the identity of species and environments that give rise to these food webs has long been a central issue in ecology (May, 1973; Cohen and Newman, 1985; Pimm, 1991; Dunne, 2006; Dunne et al., 2008; Lafferty et al., 2008; McCann, 2011; Allesina and Tang, 2012; Gravel et al., 2013, 2016).

Multiple biotic and abiotic factors have been shown to influence food web structure. For example, the transfer of energy and matter across trophic levels is highly inefficient, which limits the number of trophic levels (Schoener, 1989; Arim et al., 2016). The quality of energy also changes across trophic levels: arthropods are richer in protein than in lipids as their trophic level increases (Wilder et al., 2013) which is why adaptive foraging (Kratina et al., 2012) and/or prey switching (Abrams and Matsuda, 2004) can lead to omnivory in food webs (Thompson et al., 2007). In addition, environmental variables often determine food web structure. For example, temperature may decrease the number of trophic levels (Petchey et al., 1999; Brose et al., 2012), influence the biomass distribution and body-size structure of food webs (Yvon-Durocher et al., 2011; Gibert and DeLong, 2014; Binzer et al., 2016), and alter the energetic structure and function of soil food webs (Schwarz et al., 2017) as well as the number of interactions between species in mountain communities (Lurgi et al., 2012).

Phenotypic traits, such as body size, have long been known to play an important role in determining food web structure through gape limitation in aquatic food webs (Arim et al., 2010, 2016) and thus, predator-prey interactions (Vucic-Pestic et al., 2010; DeLong and Vasseur, 2012; Schneider et al., 2012; Kalinkat et al., 2013; DeLong et al., 2014). In fact, larger body sizes often result in consumers that feed at higher trophic levels (Riede et al., 2011), thus playing a central role in determining food web trophic structure (Petchey et al., 2008; Iles and Novak, 2016; Barneche and Allen, 2018). The effect of traits other than body size, however, has long been overlooked, despite evidence that such traits can impact both vulnerability to predation (Black and Dodson, 1990; Hammill et al., 2010; Yin et al., 2011), as well as foraging rates (Gibert et al., 2017). Trait variation has been shown to strongly influence predator-prey dynamics (Bolnick et al., 2011; Schreiber et al., 2011; Vasseur et al., 2011; Gibert and Brassil, 2014; Gibert and DeLong, 2015; Gibert et al., 2015), which could in turn impact food web structure and dynamics. For example, genetic variation on host plants determines which herbivores feed on them (Barbour et al., 2016) through trait matching (Dehling et al., 2016), which determines food web structure from the bottom up. Phenotypic variation in predator traits, on the other hand, increases predator connectivity and reduces trophic level (Gibert and DeLong, 2017), which structures food webs from the top down. Together, these results suggest that evolutionary changes in traits controlling predator-prey interactions can have important but poorly understood impacts on food web structure and dynamics.

Indeed, ecological and evolutionary processes are increasingly recognized to operate at largely overlapping timescales (Thompson, 1998; Yoshida et al., 2003; Hairston et al., 2005; Jones et al., 2009; Cortez and Ellner, 2010; Vasseur et al., 2011; DeLong and Gibert, 2016; DeLong et al., 2016; Yeakel et al., 2018a), and the combined effects of these eco-evolutionary dynamics may have a large influence on food web structure (Allhoff et al., 2015). Given that genotypes and phenotypes as well as genetic and phenotypic variation, can all influence patterns of species interactions, evolutionary change occurring on ecological time-scales has the potential to impact ecological dynamics within food webs, thus leading to changes in abundances across trophic levels, which we refer to as *abundance structure*. Considering that biomass is the product of a species average mass and its abundance, changes in food web abundance structure may also lead to changes in the distribution of biomass across the food web, which we refer to as *biomass structure*. Last, because trophic levels also change as ecological dynamics unfold (Gibert and DeLong, 2017), how such changes in abundance and biomass structure impact the distribution of trophic levels throughout the food web, which we refer to as *trophic structure,* is largely unknown.

Here we assess the effects that low levels of evolutionary change in traits controlling predator-prey interactions can have on the abundance, biomass, and trophic structure of a simple food web. To do so, we investigate the steady state behavior of the omnivory trophic module (a resource, an intermediate consumer that eats the resource, and a top predator that eats both; **Figure 1A**) where the abundances and the parameters controlling each predator-prey interaction are subject to selection, and thus, change over time. We show that even small amounts of evolutionary change can lead to important differences in abundance and biomass structure, as well as maximum trophic level, underlining the potential importance of eco-evolutionary dynamics in shaping the structure of food webs.

METHODS

The Model

We model the eco-evolutionary dynamics of a three species omnivory module (**Figure 1A**) as it is the simplest system where the trophic level of the top predator can change over time. The underlying ecological model tracks the abundances of the top predator (T), the intermediate consumer (C), and the basal resource (R). We assume that all predator-prey interactions are controlled by a type-II functional response, determined by the attack rate (α), and the handling time (η) of the predator. Resources grow logistically, hence experience density-dependence, and predators die at constant per-capita rates (d_C and d_T). Together, our ecological dynamics are defined by the following system of differential equations:

$$\frac{dR}{dt} = rR\left(1-\frac{R}{K}\right) - \frac{\alpha_{RC}RC}{1+\alpha_{RC}\eta_{RC}R} - \frac{\alpha_{RT}RT}{1+\alpha_{RT}\eta_{RT}R} \quad (1)$$

$$\frac{dC}{dt} = \varepsilon_{RC}\frac{\alpha_{RC}RC}{1+\alpha_{RC}\eta_{RC}R} - \frac{\alpha_{CT}CT}{1+\alpha_{CT}\eta_{CT}C} - d_C C \quad (2)$$

$$\frac{dT}{dt} = \varepsilon_{RT}\frac{\alpha_{RT}RT}{1+\alpha_{RT}\eta_{RT}R} + \varepsilon_{CT}\frac{\alpha_{CT}CT}{1+\alpha_{CT}\eta_{CT}C} - d_T T, \quad (3)$$

were K is the carrying capacity of the resource, r is the maximal per-capita growth rate of the resource, ε_{RC} is the efficiency of resource biomass conversion into consumer biomass, ε_{RT} is the

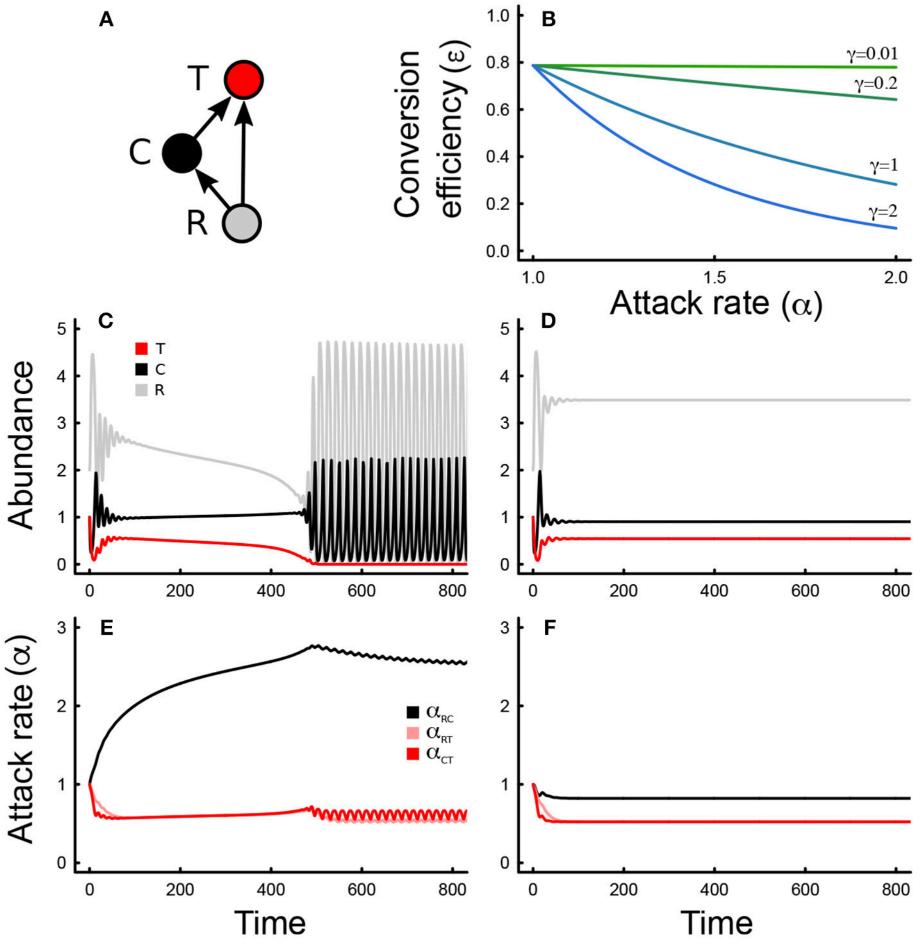

FIGURE 1 | (A) Depiction of the omnivory food web module, where T is the top predator (red), C is the intermediate consumer (black), and R is the basal resource (gray). Colors are consistent across all figures. **(B)** Tradeoff between conversion efficiency (ε) and attack rate (α) for different levels of the tradeoff magnitude (γ). **(C)** Changes in abundance over time for all three species, and all evolving attack rates **(E)**, for a low consumer tradeoff ($\gamma_{RC} = 0.01$). **(D,F)** Same as in **(C,E)** but for a large consumer tradeoff ($\gamma_{RC} = 2$). Parameter values in **Table 1**.

efficiency of resource conversion into top predator biomass, and ε_{CT} is the efficiency of consumer biomass conversion into top predator biomass.

To model the evolutionary component of the full eco-evolutionary omnivory module, we assume that only the traits controlling the attack rates of both predators can evolve over time. If large changes in important underlying traits, such as body size, were to occur over time, we would expect sweeping changes across all parameters (DeLong et al., 2014; DeLong and Gibert, 2016). Instead, we are implicitly assuming that the timescale is relatively short and selection by the environment is relatively weak such that the other vital rates in the model remain constant. Under these assumptions, we model the evolution of predator attack rates using the standard formulation (Lande, 1976; Kondoh, 2003; Ellner and Becks, 2010; Schreiber et al., 2011), where the rate of evolutionary change of the focal trait (here, the attack rates) is determined by the total amount of heritable genetic variation for that trait (or the product of the genetic variance, σ^2, with the heritability of the trait, h^2), and the adaptive landscape, defined as the rate of change of the per-capita growth rate of the focal predator (i.e., its absolute fitness, $W_i = \frac{1}{N_i}\frac{dN_i}{dt}$) with respect to a change in the evolving trait:

$$\frac{d\alpha_i}{dt} = \sigma_i^2 h_i^2 \frac{\partial W_i}{\partial \alpha_i}. \tag{4}$$

We also assume the existence of a tradeoff between predator conversion efficiencies and attack rates following previous work (Mougi and Iwasa, 2010; Van Velzen and Gaedke, 2017), which leads to reduced conversion efficiencies with increased attack rates (**Figure 1B**):

$$\varepsilon_i = \varepsilon_{i_0} e^{-\gamma_i(\alpha_0 - \alpha_i)}, \tag{5}$$

where ε_{i_0} is the maximum conversion efficiency, α_0 is the initial attack rate (at $t = 0$), and γ_i is the strength of the tradeoff. When the strength of the tradeoff, or tradeoff magnitude, is low, the attack rate and conversion efficiency of the consumer are relatively independent; when the tradeoff magnitude is

TABLE 1 | Model parameters and variables descriptions and values.

Parameter or variable	Name	Values
R, C, T	Resource, consumer, and top predator abundances, respectively	Initial values: $R_0 = 2$, $C_0 = 1$, $T_0 = 1$
r	Maximum per-capita growth rate	1.5
K	Carrying capacity	5
α_{RC},α_{RT},α_{CT}	Consumer-resource, top predator-resource and top predator-consumer attack rates, respectively	$\alpha_{RC} = \alpha_{RT} = \alpha_{CT} = 1$, at $t = 0$
η_{RC},η_{RT},η_{CT}	Handling times, for all three pairwise interactions	$\eta_{RC} = \eta_{RT} = \eta_{CT} = 0.1$
d_C,d_T	Consumer and top predator death rates	$d_C = d_T = 0.8$
ε_{RC_0},ε_{RT_0},ε_{CT_0}	Conversion efficiencies when the tradeoff magnitude is zero for all three pairwise interactions	$\varepsilon_{RC} = \varepsilon_{CT} = 0.8$, $\varepsilon_{RT} = 0.2$
γ_{RC},γ_{RT},γ_{CT}	Tradeoff magnitude for all three pairwise interactions	Specified in each figure
$\sigma_i^2 h_i^2$	Product of the genetic variance σ_i^2, and the trait heritability h_i^2, for each species i (heritable genetic variation)	$\sigma_i^2 h_i^2 = 0.5$ for all i unless otherwise specified

high, low attack rates lead to high conversion efficiencies and vice versa (**Figure 1B**). The tradeoff magnitude can lead to differences in transient and steady state dynamics in abundance (**Figures 1C,D**), as well as trait evolution (**Figures 1E,F**). Different assumptions regarding this tradeoff are possible for different ecological contexts, though a thorough exploration of how these would play out is beyond the scope of the present paper [but see (Gounand et al., 2016) for examples of variation in such assumptions in a different context]. The starting parameter values of the model were chosen to allow species coexistence in the absence of evolution.

Food Web Structure

To address how eco-evolutionary dynamics may affect food web structure, we tracked equilibrium abundances for all three species across different combinations of the tradeoff magnitude associated with the attack rate of the intermediate consumer preying on the basal resource (γ_{CR}) and that of the tradeoff magnitude associated with the attack rate of the top predator preying on the consumer. The tradeoff magnitude associated with the attack rate of the top predator preying on the basal resource (γ_{TR}) was kept constant and equal to unity. Thus, we were able to examine how species abundances changed across trophic levels. The model can lead to oscillations in abundance in certain regions of parameter space, in which case we used a geometric mean over time as our measure of average species abundance.

To assess how trophic structure changed over time, we measured the maximum trophic level in the food web module over time, which has been shown to change dynamically with species abundance in the omnivory module (Gibert and DeLong, 2017). Using the standard definition of trophic level, $TL_i = 1 + \sum_{j=1}^{n} p_{ij} TL_j$, where TL_i is the trophic level of species i, and p_{ij} is the fractional contribution of species j to the diet of species i, it is possible to rewrite the p_{ij} as a function of predator foraging rates. The trophic level of the top predator, T, then becomes:

$$TL_T = 1 + \frac{1}{\varepsilon_{RT}\frac{\alpha_{RT}RT}{1+\alpha_{RT}\eta_{RT}R} + \varepsilon_{CT}\frac{\alpha_{CT}CT}{1+\alpha_{CT}\eta_{CT}C}} \times \left(TL_R \varepsilon_{RT} \frac{\alpha_{RT}RT}{1+\alpha_{RT}\eta_{RT}R} + TL_C \varepsilon_{CT} \frac{\alpha_{CT}CT}{1+\alpha_{CT}\eta_{CT}C} \right), \qquad (6)$$

where $TL_R = 1$ and $TL_C = 2$. Because the foraging rates are functions of time, the trophic level of the top predator, TL_T (i.e., the maximum trophic level of the omnivory module) will also be a function of time. The trophic level will approach a stable steady state as the abundances approach a stable steady state.

Last, we converted steady state abundances into biomass by multiplying steady state abundances by species body mass. We defined the mass of the basal resource to be equal to 1 unit of mass, and used well-known predator-prey body size scaling relationships (Layman et al., 2005; Brose et al., 2006; Riede et al., 2011) to obtain the mass of the intermediate consumer and that of the top predator. The scaling exponent between prey and predator mass varies widely in nature but has a mean of 1.16 (Brose et al., 2006). We examined three different scaling exponents to observe its influence on equilibrium biomass structure: 0.85, 1.16, and 1.5, while keeping the intercept constant and equal to 1.80 (Brose et al., 2006). These three scenarios impose different constraints on the biomass structure of the food web. A larger scaling exponent means that predators tend to be much larger than their prey compared to a scenario where the exponent is smaller. All analyses were performed in Julia v0.62 (Bezanson et al., 2014) using the *DifferentialEquations* package (Rackauckas and Nie, 2017). Julia code is available to download from https://github.com/JPGibert/Eco_evo_food_webs

RESULTS

General Dynamics

The eco-evolutionary dynamics of the omnivory food web module are quite sensitive to changes in the tradeoff magnitude that controls the relationship between conversion efficiencies and attack rates when only one attack rate is allowed to evolve at any given time (**Figures 1C–F**, **2**). We find that the tradeoff magnitude associated with the attack rate of the intermediate consumer on the resource mediates coexistence (red arrow, **Figure 2A**) in the parameter range that was analyzed. When the tradeoff magnitude is small, the consumer attack rate evolves to very large values, which leads to competitive exclusion of the top predator, and unstable consumer-resource dynamics. Intermediate values lead to stable coexistence (**Figure 2A**), whereas too large of a tradeoff magnitude leads to instability and fluctuations in both abundances and traits (**Figure 2A**). Steady state attack rates decrease with increasing tradeoff magnitudes throughout, although trait fluctuations are observed only at very large values of the consumer tradeoff magnitude (**Figure 2B**).

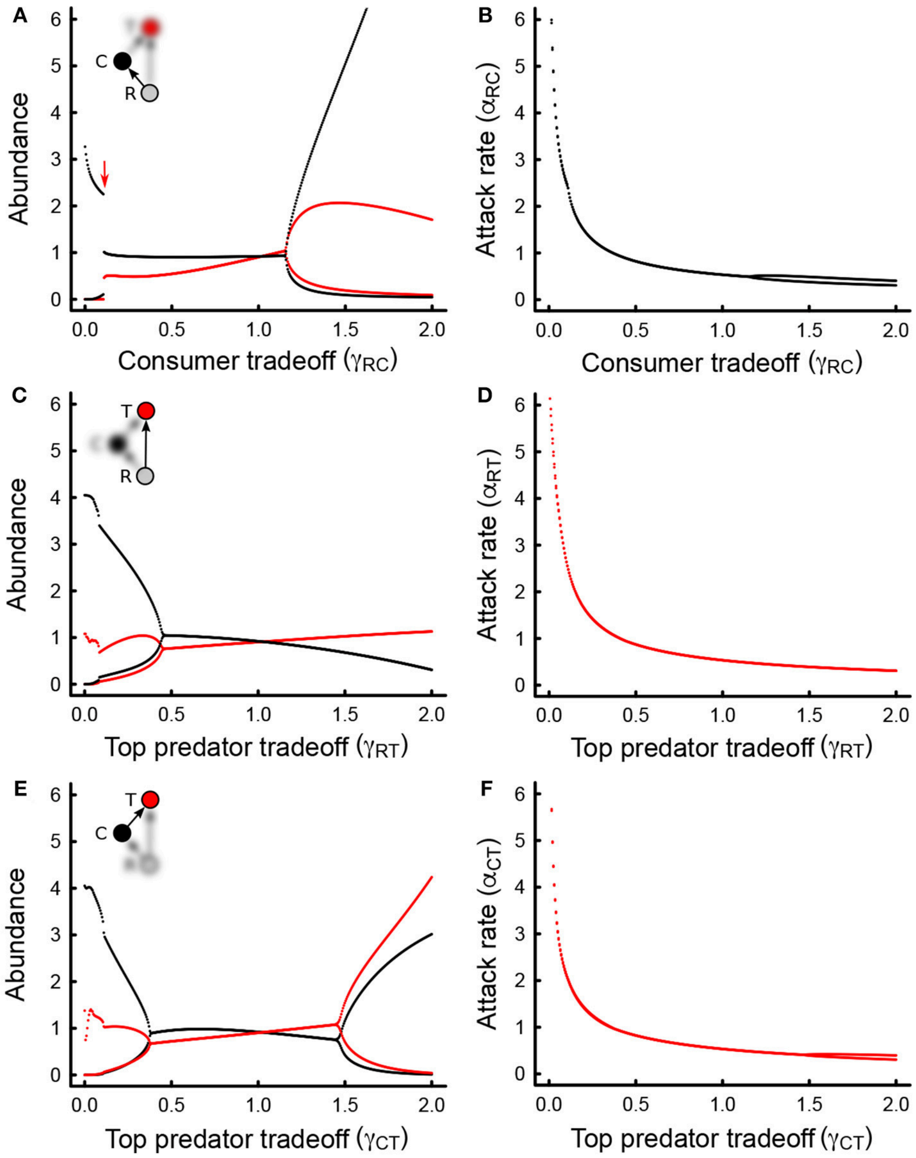

FIGURE 2 | (A) Bifurcation plots (abundance minima and maxima at equilibrium) for the top predator (red) and intermediate consumer (black), across increasing levels of the consumer tradeoff (γ_{RC}). Only the attack rate between the consumer and the basal resource is allowed to evolve. Oscillatory behavior (instability) occurs whenever maxima and minima are not equal (there are two curves rather than one). The red arrow indicates the tradeoff value below which top predators cannot persist. **(B)** Same as in **(A)** but for the consumer attack rate instead of the abundance. **(C)** As in **(A)** but for the tradeoff associated with the attack rate between the top predator and the basal resource (γ_{RT}). **(D)** As in **(B)** but for the interaction depicted in **(C)**. **(E)** As in **(A,C)**, but for the cost associated with the attack rate between the top predator and the intermediate consumer (γ_{CT}). **(F)** As in **(B,D)** but for the interaction depicted in **(E)**. In all cases, only the focal attack rate is allowed to evolve, and all other parameter values are as in **Table 1**.

Tradeoff magnitudes also impact steady state abundances, with intermediate consumer abundances being larger than top predator consumer abundances for low to moderate values of the tradeoff magnitude, and smaller for larger values (**Figure 2A**).

These results largely hold for the tradeoff magnitude associated with the other interactions: the tradeoff magnitude of the top predator consuming the resource, and that of the top predator consuming the intermediate consumer (**Figures 2C–F**). However, neither the tradeoff magnitude of the top predator consuming the basal resource, or the intermediate consumer appear to affect persistence (**Figures 2C,E**), although both can impact stability: an increase in the tradeoff magnitude of the top predator-resource interaction leads to more stable dynamics (**Figure 2C**), and an increase in the tradeoff magnitude of the top predator-intermediate consumer interaction first stabilizes the system at lower values, and then destabilizes the system at larger values (**Figure 2E**). In all cases, steady state attack rates decline as the tradeoff magnitudes increase (**Figures 2D,F**).

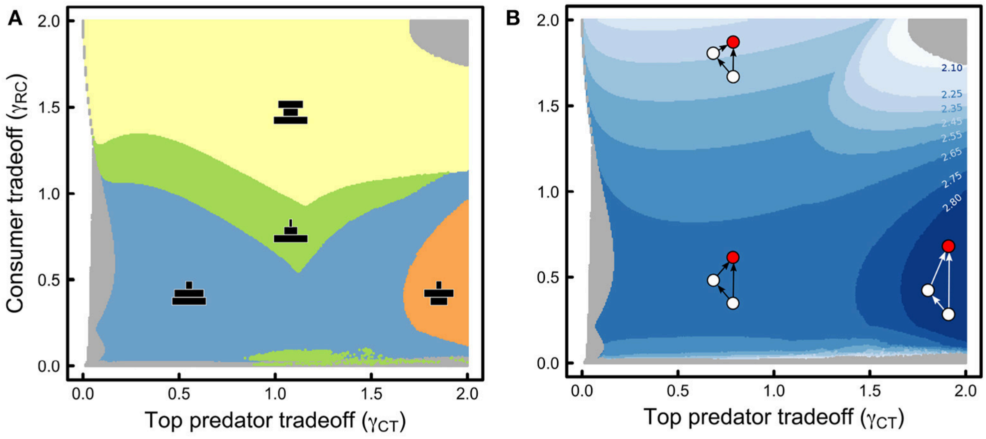

FIGURE 3 | (A) Plot of discretized changes in the abundance structure of the omnivory food web module assessed across all combinations of the consumer tradeoff (γ_{RC}), and the top predator tradeoff (γ_{CT}). A qualitative depiction of the abundance structure appears in black within each discrete region. **(B)** Discretized plot of the continuous changes in maximum trophic level (trophic level of the top predator, depicted in red), as the top predator and consumer tradeoffs change. Numbers indicate the trophic level of the top predator at each boundary. Gray areas indicate regions where coexistence is not feasible in **(A,B)**. Parameter values as in **Table 1**.

An increase in tradeoff magnitudes also leads to larger top predator abundance than intermediate consumer abundance (**Figures 2C,E**). Together, these results suggest that dynamically rich behaviors emerge from the eco-evolutionary dynamics of omnivory, even when selection is weak.

Impacts on Food Web Structure

Changes in steady state abundances with tradeoff magnitudes result in differences in the abundance structure of the food web (**Figure 3A**). The omnivory food web module can take on different shapes depending on which species (resource, intermediate consumer, top predator) has higher or lower abundances. Indeed, observed abundance structures in our model range from a top-heavy hour-glass food-web, when the intermediate consumer has a large tradeoff magnitude (**Figure 3A**, yellow), to a bottom-heavy pyramid when the intermediate consumer has a smaller tradeoff magnitude (**Figure 3A**, blue, green). When the intermediate consumer has a small to moderate tradeoff magnitude, several scenarios are possible. If the top predator has a smaller tradeoff magnitude, the abundance structure becomes a "bent pyramid": consumer abundances are more similar to resource abundances than they are to top predator abundances, giving the pyramid a convex curvature (**Figure 3A**, blue). If the top predator has a moderate tradeoff magnitude, a pyramidal abundance structure is also possible, but consumer abundances are smaller and more similar to top predator abundances than they are to resource abundances, giving the pyramid a concave curvature (**Figure 3A**, green). Last, if the top-predator has a large tradeoff magnitude, the abundance structure of the food web is diamond-shaped, where intermediate consumers are the most abundant of all species (**Figure 3A**, orange).

Interestingly, all changes in abundance structure are accompanied by changes in the maximum trophic level of the food web: maximum trophic level ranges from low for the hourglass abundance structure to high for the diamond abundance structure (**Figure 3B**). In other words, as eco-evolutionary dynamics unfold, hourglass food webs result in top consumers and intermediate consumers with similar trophic levels, and overall greater amounts of omnivory as the top predator relies more heavily on the basal resource (**Figure 3B**). On the other hand, diamond abundance structures result in top predators with a greater dietary reliance on intermediate consumers than on resources, resulting in a higher trophic level, which in turn leads to a more chain-like food web trophic structure (**Figure 3B**).

Taking into account three different scaling exponents for the predator-prey mass relationship (**Figure 4A**), the equilibrium biomass structure of the food web remains qualitatively similar to that of the abundance structure, but with some important quantitative differences (**Figures 4B–D**). First as the exponent increases such that predators are increasingly larger than their prey, the hourglass biomass structure becomes more prevalent (**Figures 4B–D**). Second, the size of parameter space that leads to diamond biomass structure appears to be unaffected by an increase in the steepness of the body size relationship, which suggests that other factors influence its occurrence (**Figures 4B–D**, orange). Third, bent pyramid biomass structures (**Figure 4**, blue) become more rare as the scaling exponent increases, while concave-pyramid biomass structure (**Figure 4**, green) becomes more common across the range of parameter values that we consider.

DISCUSSION

The results of our model show that ecological and evolutionary processes can jointly determine food web abundance, trophic, and biomass structure. By modeling a simple tri-trophic system with omnivory, in which the maximum trophic level of the food webs can be accounted for explicitly, we have shown that most

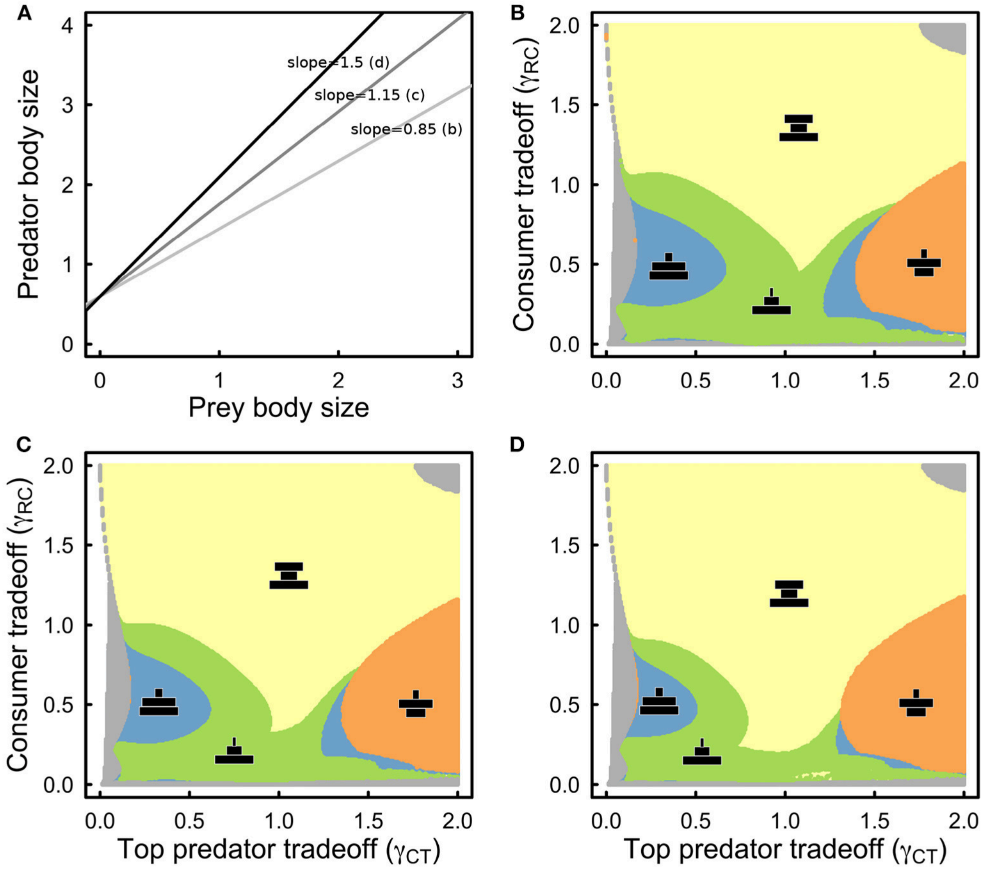

FIGURE 4 | (A) Plot of the assumed predator-prey body-size scalings where only the scaling exponent was allowed to change. The middle line is the average taken across taxa (Brose et al., 2006). **(B)** Same as in **Figure 3A**, but with respect to biomass structure and assuming 0.85 as the slope of the predator-prey body size scaling. **(C)** As in **(B)** but for a slope of 1.15. **(D)** As in **(B,C)** but for a slope of 1.5. Color coding and qualitative biomass depictions (black) as in **Figure 3**. All other parameter values as in **Table 1**.

types of abundance and biomass food-web structures, namely, pyramid, hourglass, and diamond, can occur as the result of eco-evolutionary dynamics, even when selection is weak. As omnivorous interactions are ubiquitous in nature (Thompson et al., 2007), our theoretical predictions may be relevant for larger and more complex food webs. Together, our findings suggest that the dynamical and evolutionary constraints on food web structure are perhaps much greater than previously thought.

Evolutionary changes in attack rates, as ecological dynamics unfold, can impact species persistence (**Figure 2**), as well as steady state abundances and their stability (**Figures 1**, **2**). Such impacts are mediated by the tradeoff between conversion efficiency and attack rates. This tradeoff is common in nature (Kiørboe, 2011). Increasing attack rates typically are the consequence of greater velocities for cursorial predators (Aljetlawi, 2004; Pawar et al., 2012). These greater velocities can in turn result in a higher metabolic cost (Carbone et al., 2007), which leads to lower net assimilation rates and, thus, conversion efficiency. Because of this, we posit that larger tradeoff magnitudes would be typically associated with increased metabolic costs and lower conversion efficiencies. We point out that larger tradeoff magnitudes could also be driven by concomitant changes in assimilation rates as attack rates evolve, provided that other physiological traits are also evolving. While we explicitly assume that this does not occur in our framework, we acknowledge that our results could be interpreted from this perspective, and the sensitivity of our model results to differences in the attack rate-conversion efficiency relationship suggests that this may be a fruitful area for additional empirical and theoretical work.

The magnitude of the metabolic costs associated with predation can strongly impact food web richness and stability, emphasizing the important role that this tradeoff plays in trophic interactions. Lower costs typically lead to less speciose, unstable systems (**Figure 2A**), intermediate costs lead to speciose, stable systems, and large costs lead to speciose, but unstable dynamics (**Figure 2**). Metabolic costs can in turn scale with phenotypic traits such as body size (Brown et al., 2004; DeLong et al., 2010; Barneche and Allen, 2018; Yeakel et al., 2018b) or depend on external environmental factors such as temperature (Gillooly et al., 2001; Savage et al., 2004). Larger organisms, or organisms that experience elevated temperatures, may thus have increased metabolic costs than do smaller species or species that live in colder climates. Ecosystems where intermediate predators are too small or live in colder climates may thus be less speciose and unstable, as is the case in high-latitude predator-prey systems involving rodents and raptors (Hanski et al., 1991, 1993; Brommer et al., 2010), while speciose but more stable systems may be more common in warmer climates (Ims et al., 2008).

The relationship between metabolic costs and steady state abundances and instability has consequences for different aspects of food web structure, as different abundance, and biomass distributions are possible for different values of the metabolic costs (**Figures 2**, **3**). Indeed, as unstable dynamics typically occur at low and high values of the metabolic costs, we expect food webs occurring in those value ranges to experience fluctuations in predator-prey dynamics. If we further consider that large fluctuations can increase the chance of stochastic extinctions (May, 1973; Chesson, 1981; Fox and Kendall, 2002), then our results suggest that food-web structures that are composed of species with very low or very high metabolic costs may be prone to stochastic extinction. For example, it is possible that diamond food-web structures may be rare in nature, and perhaps more often exist in a transient state, as such structures appear to be associated with very large metabolic costs for the top predator, and hence, large fluctuations in abundance.

Albeit a minimal food web module, our model retains key features of large, complex food webs, such as the occurrence of omnivory and more than two trophic levels, features that are generally not included in models exploring eco-evolutionary dynamics [e.g., (Schreiber et al., 2011; Vasseur et al., 2011; DeLong and Gibert, 2016; Yeakel et al., 2018a)]. Interestingly, such a simple model yields a surprisingly rich array of possible food-web abundance and biomass structures and reveals important differences in the maximum trophic level as a function of metabolic costs. While there is variation in the types of biomass structures observed within different ecosystem types (Hatton et al., 2015), fully inverted or hourglass food webs may be more typical of marine ecosystems (Fath and Killian, 2007; Woodson et al., 2018) but see (Trebilco et al., 2013) for an alternative standpoint), pyramid food webs tend to be terrestrial (Hatton et al., 2015), while diamond food webs may be more common in ponds, lakes or other systems with very abundant intermediate consumers, and less common top predators (Polis, 1999).

Our model offers key insights into how differences in food-web structure across ecosystems may be influenced by the eco-evolutionary dynamics of attack rates and their associated metabolic costs. For example, our results suggest that marine ecosystems (hourglass-structured food webs) should have higher metabolic costs associated with intermediate predators, while top predators should generally have lower costs (**Figures 3**, **4**). This may indeed be true: larger organisms suffer lower energetic penalties when swimming because of reduced drag, while smaller organisms spend more energy to overcome drag (Batchelor, 2000). Our results also suggest that terrestrial ecosystems (pyramid-structured food webs) occur whenever intermediate predators have lower metabolic costs, while top predators can be variable (**Figures 3**, **4**). This prediction also appears to be supported by observations: energy expenditures associated with terrestrial cursorial locomotion scales with body size (Carbone et al., 2007), such that smaller organisms, typically occupying lower trophic levels [e.g., (Riede et al., 2011)], have lower costs than larger, higher trophic, organisms.

While direct empirical tests of these predictions may be challenging, it may be possible to assess the validity of some of these ideas using *Daphnia* sp. as a top predator. Daphnia can prey upon both meso and micro zooplankton (Wickham, 1998), and as such, can prey upon bacteria as well as their protist consumers. This would lead to an omnivory module with Daphnia as the top predator and omnivore, a bacterivore protist species as the intermediate consumer, and bacteria as the resource. Microcosms can be inoculated with clonal Daphnia, in which evolution is not possible because of the absence of variation, or non-clonal Daphnia, which will allow for eco-evolutionary dynamics to ensue (Fussmann et al., 2003). Over time, it would be possible to assess whether there are differences in abundance or biomass accumulation between the two treatments, and also assess whether parameters of the Daphnia functional response, such as attack rates or handling times, are diverging between the clonal and non-clonal lines. It would then be possible to examine whether changes in metabolic costs could lead to similar abundance and biomass accumulations by running the same experiment at two different temperatures. While these results would not be exactly replicating the assumptions of our toy model, they could shed light on whether eco-evolutionary dynamics can influence food web abundance and biomass structure.

Taking individual-level and trait variation into account has recently been shown to be important to fully understand population and community-level patterns (Bolnick et al., 2011; Violle et al., 2012; Gibert et al., 2015). Indeed, genetic variation in basal resources strongly determines which organisms can prey upon them, thus influencing food web structure from the bottom up (Barbour et al., 2016), while phenotypic variation in predator traits determines species-level connectivity (Gibert and DeLong, 2017), trophic level (Svanbäck et al., 2015; Gibert and DeLong, 2017), and can be used to predict multiple structural features in food webs (Gibert and DeLong, 2017). Our model only follows mean attack rates and disregards how joint changes in mean and variance could potentially influence food web structure through eco-evolutionary dynamics. Because both genetic and phenotypic variation can directly impact food web structure and the pace of evolutionary change, an extension of our initial exploration that includes the dynamics of trait variance as well as that of mean trait values may further illuminate how evolving traits may impact food web structure.

We show that even small amounts of evolutionary change for traits that determine the strength of predator-prey interactions may lead to dramatic differences in food web structure. We therefore anticipate that additional complexity, such as the simultaneous evolution of multiple traits [e.g., through ecological pleiotropic traits (Strauss and Irwin, 2004; DeLong and Gibert, 2016)], a larger number of species with highly heterogeneous interactions such as those observed in empirical food webs, the inclusion of changes in variation as well as mean trait values, as well as a broader exploration of parameter space, will provide additional insight into the fundamental eco-evolutionary drivers of the different types of large-scale structural attributes observed in food webs. As a case in point, differences in the functional form of imposed tradeoffs can lead to quantitative differences in model output in a model that tracks trait selection in food webs (Gounand et al., 2016). Moreover, in a tri-trophic model with explicit life-history stages tracking juvenile and adult biomass, differences in energy transfer leads to differential biomass accumulation across stages, including overcompensation (De Roos et al., 2007). In some cases, biomass accumulation is more likely for juveniles than for adults, and vice versa, which is analogous to our results that show the emergence of different abundance and biomass food web structures.

Despite the inherent simplicity of our approach, we show that an impressively diverse array of food web abundance, biomass, and trophic structures are possible when trait evolution is incorporated into a three-species omnivory model. Changes in metabolic costs (or assimilation rates) mediating trait evolution and energy transfers across species are partly responsible for resulting patterns of abundance and biomass accumulation across trophic levels, which leads to differences in trophic structure and trophic position. Our model reproduces most known types of abundance and biomass structure, i.e., concave and convex pyramidal structures, diamonds, and hourglasses, which suggests that even small levels of evolutionary changes in one trait can have important consequences on these large-scale structural characterizations of food webs.

AUTHOR CONTRIBUTIONS

JPG conceived the study, JPG and JDY designed the analyses, and JPG implemented the modeling. JPG and JDY analyzed the results and wrote the manuscript.

FUNDING

JPG was funded by a James S. McDonnell Foundation Postdoctoral Fellowship in Complex Systems. JDY was supported by startup funds from the University of California, Merced.

ACKNOWLEDGMENTS

We thank Uttam Bhat, Ritwika VPS, and Taran Rallings for helpful discussions and comments, and we are indebted to two reviewers for their suggestions on a previous version of this manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 25 February 2019
doi: 10.3389/fevo.2019.00045

Temperature Modifies Consumer-Resource Interaction Strength Through Its Effects on Biological Rates and Body Mass

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Temperature is the most significant environmental gradient at the global scale, impacting the distributions of species and their ecological interactions. It is now established that temperature affects several biological rates and body mass, and can, in turn, alter interaction strength. Latitudinal variation in the strength of interactions has been observed for trophic and competitive interactions and many studies support that biotic interactions are more intense at low latitudes. Nevertheless, the mechanisms underlying the temperature dependence of trophic regulation, the effect of consumers on their preys, remain unclear. The aim of our study is to get better insights on the effects of temperature on trophic regulation. We used a consumer-resource model and considered that organisms' biological rates present a unimodal thermal response and that body mass decreases with temperature. We compared three measures of interaction strength: per capita, per population and net interaction strength. Our results demonstrate that the effect of temperature on interaction strength is contingent upon which species' biological rates are temperature dependent. When all biological rates are temperature dependent, the thermal response of interaction strength is hump-shaped following the scaling of search rate, whilst it is monotonically decreasing when only mortality rates vary with temperature. Finally, we show that temperature can indirectly impact trophic interaction strength through the temperature-size rule. A decrease in organisms' body size due to temperature induces a decrease in per capita and per population interaction strength and tend to decrease net interaction strength, depending on which trophic level follows the temperature-size rule. Our analysis gives an overview of how temperature, through various effects, may impact different measures of interaction strength.

Keywords: consumer-resource, interaction strength, temperature, metabolic theory, body mass, temperature-size rule

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *31 August 2018*
Accepted: *06 February 2019*
Published: *25 February 2019*

Citation:
Bideault A, Loreau M and Gravel D (2019) Temperature Modifies Consumer-Resource Interaction Strength Through Its Effects on Biological Rates and Body Mass. Front. Ecol. Evol. 7:45. doi: 10.3389/fevo.2019.00045

1. INTRODUCTION

Temperature can strongly affect food-web structure and interaction strength (Beveridge et al., 2010; Rodríguez-Castañeda, 2013). Understanding its impact on trophic regulation is vital for predicting the consequences of climate change on communities and ecosystems stability. The strength of consumer–resource interactions is expected to vary along large-scale latitudinal and climatic gradients (Schemske et al., 2009), with recent evidence suggesting that these interactions are stronger toward lower latitudes and in warmer regions. Several studies have indeed shown that changes in temperature can induce shifts in the magnitudes of top-down and bottom-up forces. For instance, it can strengthen the effect of fishes on primary producers in aquatic systems (Kratina et al., 2012; Shurin et al., 2012), of spiders and vertebrate predators on plants in terrestrial systems (Barton et al., 2009) and of large mammalian herbivores on primary producers (Gibert and Delong, 2014). Within the Arctic, predation tends to decrease with latitude whilst herbivory tends to increase (Legagneux et al., 2014). Indirect effects (cascading effects through trophic levels) may thus increase the complexity of the impact of temperature by inducing antagonistic effects between trophic levels (Beveridge et al., 2010). Moreover, the short- to long-term responses of interacting species may diverge. Warming may induce accelerated feeding rates, resulting in stronger top-down control over short time-scales, whereas, in the longer term, food-web reorganization could lead to weaker top-down control (Brose et al., 2012). Some interactions are then magnified with warming while others are weakened depending on the study system and the duration of the study. This diversity of empirical observations suggests that the response of trophic regulation to warming could be context-dependent (Gilbert et al., 2014; Sentis et al., 2014; Amarasekare, 2015). Discrepancies among studies about the impact of temperature on trophic regulation can arise for two reasons, among others: (1) increased temperatures induce various changes on individual metabolism and body mass that can in turn impact interaction strength in multiple ways, and (2) different measures of interaction strength are typically used from one study to another and thus lead to different interpretations.

Temperature affects individuals' life-history (reproduction, development and survival) and foraging traits (search rates and handling times) (Savage et al., 2004; Englund et al., 2011). It has long been established that, in addition to body mass, temperature affects biochemical reaction rates, metabolic rates, and nearly all other biological activities (Gillooly et al., 2001; Brown et al., 2004; Savage et al., 2004). However, the temperature dependence of some biological rates may vary from one species to another. For instance, the temperature dependence of search rates varies according to foraging strategies. For sit-and-wait predators, it may not be dependent upon temperature (Sentis et al., 2017b), while it can be temperature dependent for predators that actively search for prey. Temperature changes can also induce reductions in body mass for many organisms, including diatoms (Montagnes and Franklin, 2001), phyto- and zooplankton, and fishes (Daufresne et al., 2009; Gardner et al., 2011). Within the range of physiologically tolerable temperatures for ectothermic organisms, individual body mass is expected to decrease with warming according to the temperature-size rule (TSR) (Atkinson, 1994). This phenotypically plastic response can be explained by the fact that adult size is a combination of individual growth rate (increase in weight per time) and development rate (increase in life stage per time). Because development rates are more sensitive to temperature (i.e., increase faster with warming) than are growth rates (Forster et al., 2011; Gardner et al., 2011; Zuo et al., 2012), individuals reared at warmer temperatures typically reach a maturity at a smaller size than those reared at colder temperatures (Atkinson, 1994; Zuo et al., 2012). Reduced body mass has been considered as the third universal ecological response to global warming (Daufresne et al., 2009). Body mass is a key aspect of community structure as it strongly determines life history rates and the strength of interaction between species (Pawar et al., 2016). As body mass affects biological rates and foraging traits, temperature can, through the TSR, indirectly impact consumer-resource dynamics (Osmond et al., 2017; Sentis et al., 2017a). Integrating these different effects of temperature into a general framework is thus essential to predict its effect on interaction strength (Osmond et al., 2017; Sentis et al., 2017a).

Even though many theoretical studies analyze the effect of temperature on the dynamics of food chains, most of them focus on how temperature impacts stability (oscillations and predator persistence) (Vasseur and McCann, 2005; Gilbert et al., 2014; Amarasekare, 2015) via its effect on biological rates only. These studies neglect indirect effects of temperature on food webs via the TSR and do not explicitly consider interaction strength. Sentis et al. (2017a) and Osmond et al. (2017), in contrast, study the effect of warming on interaction strength through its effects on biological rates and body mass. However, they consider conditions under which organisms remain below their optimal and only one interaction strength measure [the dynamic index (Berlow et al., 1999) or net interaction strength, called B_{CR} in Osmond et al. (2017)]. Yet it is known that some tropical ectotherm species already experience stressful body temperatures impacting their physical performance (Huey et al., 2009). Understanding the dynamics of species interaction under a sufficiently consequent temperature range is essential to tackle the effects of climate change on communities. To bridge these gaps we consider temperatures above optima but also different interaction strength measures.

Although the concept of interaction strength seems intuitive, many definitions have been used (Laska and Wootton, 1998; Berlow et al., 2004). Generally speaking, interaction strength is a measure of the magnitude of the effect of a species on the growth rate of another (Laska and Wootton, 1998). However, theoreticians and empiricists measure interaction strength in different ways (Laska and Wootton, 1998); and, even within theoretical and empirical studies, there are discrepancies in the way it is quantified. Berlow et al. (2004) enumerated a set of interaction strength measures that include for instance elements of the community matrix, biomass flux, maximum consumption rate or perturbation effects on population abundance. Field experiments have shown that the removal of species from ecosystems can highly impact species communities (Paine, 1980, 1992). Various indices of net interaction strength have thus been derived from removal experiments and describe how a focal species impacts the abundance of other species in the community. These experiments are however limited because their results can vary with experimental duration, with the density of the focal species and with the species composition of the community (Wootton and Emmerson, 2005). Several indices have also been used for the analysis of theoretical models. Many studies use per capita effect of a species on the growth rate of another one because it is defined without reference to the equilibrium state, explicit in many models and because many other measures can be derived from it (Laska and Wootton, 1998; Wootton and Emmerson, 2005; Novak and Wootton, 2010). Commonly used interaction strength indices relate to various food web properties and dynamics therefore may lead to misleading conclusions (Berlow et al., 2004). For instance, a strong interaction strength measured from the community matrix does not always coincide with a strong effect of species removal (Berlow et al., 2004). There is then a need to clarify the haziness around how temperature impacts different interaction strength measures, to help bridge the gap between theory and experiments.

Hence, while most studies focus on one interaction strength measure at a time, we investigate here, how temperature affects three aspects of interaction strength. We aim at decomposing the different mechanisms that may influence the effect of temperature on trophic regulation in a linear food chain. We develop a nutrient explicit tri-trophic model of consumers and resources to tackle the joint effects of temperature on interaction strength and compared three different commonly used theoretical and experimental measures of interaction strength: per capita, per population and net (i.e., log response ratio) interaction strength. We derive predictions of how the temperature dependence of species' biological rates impacts the relationship between temperature and theses measures of interaction strength. Finally, we examine how temperature indirectly affects interaction strength through decreasing organisms' body mass.

2. MODELING FRAMEWORK

2.1. Consumer-Resource Model

The model is nutrient explicit and describes the dynamics of a three level linear food chain (see **Figure 1**). The nutrient (N) is assimilated by an autotrophic primary producer (P), itself eaten by a herbivore (H) which is consumed by a carnivorous top-predator (C). The dynamics are given by:

$$\begin{aligned}\frac{d\mathrm{N}}{dt} &= I - d\mathrm{N} - \mu\mathrm{NP} \qquad (1)\\ \frac{d\mathrm{P}}{dt} &= q\mu\mathrm{NP} - a_{\mathrm{PH}}\mathrm{PH} - (z_{\mathrm{P}} + b_{\mathrm{P}})\mathrm{P}\\ \frac{d\mathrm{H}}{dt} &= e_{\mathrm{PH}}a_{\mathrm{PH}}\mathrm{PH} - a_{\mathrm{HC}}\mathrm{HC} - (z_{\mathrm{H}} + b_{\mathrm{H}})\mathrm{H}\\ \frac{d\mathrm{C}}{dt} &= e_{\mathrm{HC}}a_{\mathrm{HC}}\mathrm{HC} - (z_{\mathrm{C}} + b_{\mathrm{C}})\mathrm{C}\end{aligned}$$

where N is the nutrient concentration and P, H and C the total biomasses of primary producer, herbivore and carnivore, respectively. Temperature and body mass dependencies of parameters are omitted for clarity of the representation. Nutrients are continuously added and leached out of the system at rates I and d, respectively. μ is the primary producer growth rate and q the carbon-to-nitrogen ratio. Some biomass is lost due to respiration and mortality at rates z_i and b_i, respectively, for the different compartments i. a_{ij} is the mass-specific search rate and e_{ij} is the conversion efficiency of resource i to consumer j biomass. We consider a Type-I functional response as a first approximation in order to track equilibrium densities. b_i is a constant mortality rate to account for various processes that do not depend upon temperature, such as dilution, sedimentation or natural disturbances. Similarly, e_{ij} does not vary with body mass and temperature (O'Connor et al., 2011; Dell et al., 2014; Pawar, 2015). Conversely, biomass production rate μ, biomass loss rate z_i and search rate a_{ij} may all vary with body mass and temperature.

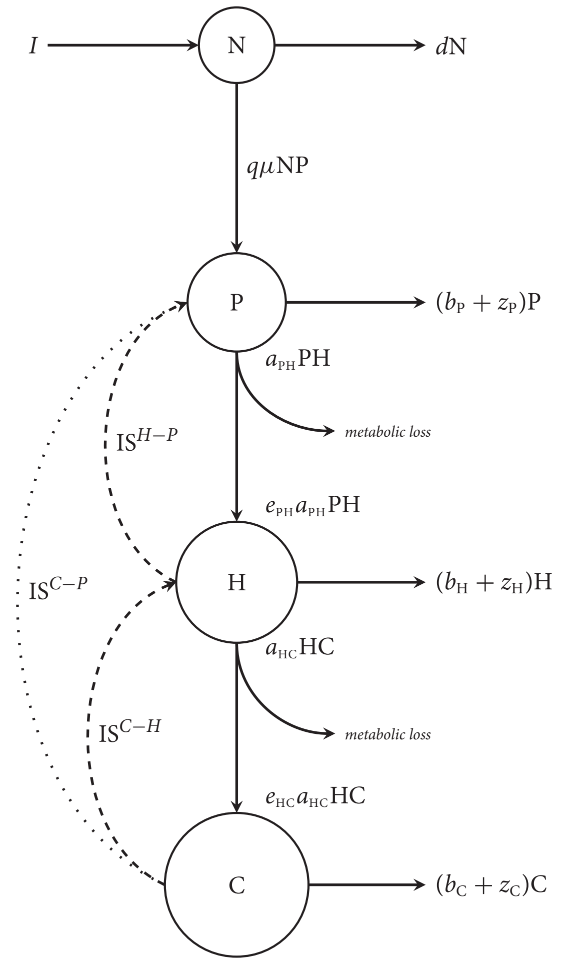

FIGURE 1 | Conceptual diagram of the model. N, P, H and C respectively represent the nutrient, primary producer, herbivore and carnivore variables. Complete arrows stand for fluxes between variables and metabolic losses and dashed arrows correspond to the effects of consumers on resources. IS stands for interaction strength. IS^{H-P} and IS^{C-H} represent the direct interaction between herbivores and primary producers and between carnivores and herbivores, respectively; while IS^{C-P} represents the indirect interaction between carnivores and primary producers.

2.2. Body Mass and Thermal Dependence of Biological Rates

Following the "Metabolic Theory of Ecology," we used the Boltzmann-Arrhenius model from chemical reaction kinetics to describe the rise of several biological rates with temperature (Gillooly et al., 2001; Brown et al., 2004; Savage et al., 2004). Many biological rates also decline at high temperatures, often due to changes in enzyme kinetics (Johnson and Lewin, 1946), and therefore we also consider the Johnson-Lewin function. Hence, according to the Boltzmann-Arrhenius-Johnson-Lewin model (BAJL model here after), the scaling of a metabolic (or a biological) rate, r_i, with average adult body mass m_i and body temperature T, in Kelvin, is given by:

$$r_i(T, m_i) = r_0 m_i^{\beta} e^{-\dfrac{E}{kT}} l(T) \tag{2}$$

with,

$$l(T) = \frac{1}{1 + e^{\dfrac{-1}{kT}\left(E_D - \left(\dfrac{E_D}{T_{opt_r}} + k\ln\left(\dfrac{E}{E_D - E}\right)\right)T\right)}} \tag{3}$$

where r_0 is a rate-dependent constant and β the allometric scaling exponent. E is the activation energy in eV (electronvolts) of the rising response and E_D the average energy constant at which proteins denature, therefore controlling the rate of decline beyond T_{opt_r}, the temperature at which rate r is maximal. Finally, k is the Boltzmann constant ($8.617 \times 10^{-5}\ eV.K^{-1}$). The thermal response of biological rates according to Equation 2 is illustrated in **Figure 2**. We take the average values of activation energy E from Dell et al. (2011) for a given trophic level and a given biological rate. As few data are available for the de-activation energy E_D, we consider the average value across all trophic levels and biological rates (Dell et al., 2011). The growth rate μ and the search rate a_{ij} vary with temperature and body mass according to Equation 2. However, the biomass loss rate z_i follows an exponential increase with temperature, as described by the first part of Equation 2 when $l(T) = 1$. Biological rates and body temperature are assumed to be uniform within species. Parameters are summarized in **Table 1**.

2.3. Temperature-Size Rule

We use the estimates of temperature-size response slopes from Forster and Hirst (2012) (see also Sentis et al., 2017a) to simulate the temperature dependence of body mass according to the following equation:

$$m_i = c m_{i_{293}} e^{s(T - 293.15)} \tag{4}$$

where c is the conversion of dry mass into wet mass, $m_{i_{293}}$ is the dry mass of species i at 293.15 K and T is temperature. s quantifies the sign and magnitude of the TS response and is determined by the percentage change in body mass per degree (originally in Celsius in Forster and Hirst (2012), we converted from Kelvin) : $PCM = (e^s - 1) \times 100$. TS response slopes vary between ecosystem types but we consider only the mean TS response for aquatic organisms (the average response for freshwater and marine metazoa), which is negative. The reference body masses are measured at 293.15 K, in our case body masses therefore decrease for temperatures above 293.15 K (Forster and Hirst, 2012):

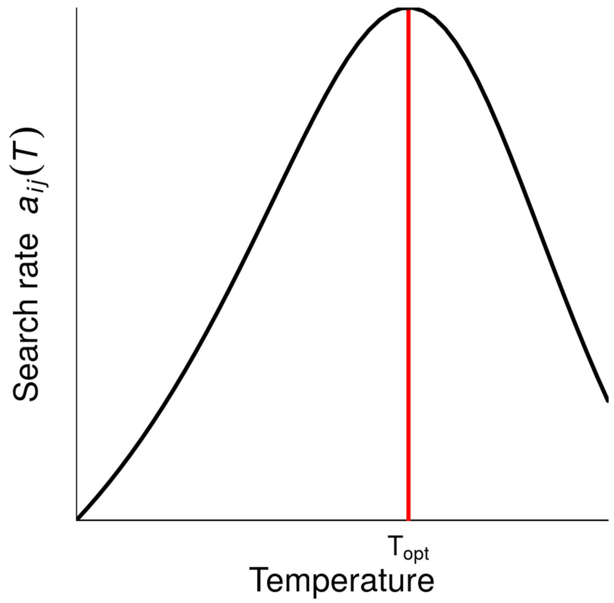

FIGURE 2 | Effect of temperature on the search rate a_{ij} which is equal to per capita interaction strength, IS_{pc}, as described by Equation 2. T_{opt} is the temperature at which the rate value is maximal. Below T_{opt}, the individual stands within its PTR ("Physiological Temperature Range"), where the trait performance increases with temperature, whilst above T_{opt} the trait performance decreases. Note that growth rate μ also follows this equation, but mortality rates z_i monotonically increase with temperature.

$$PCM = -3.90 - 0.53\log_{10}(m_{i_{293}}) \tag{5}$$

From this TS response slope, we investigate three possible scenarios where either (1) only the carnivores, (2) herbivores and carnivores and (3) all species follow a TS response, in addition to the case with no TSR at all. We chose these scenarios because, according to Forster and Hirst (2012), in aquatic environments, increases in species' sizes cause the temperature-size response to become increasingly negative.

2.4. Measuring Interaction Strength

The strength of ecological interactions can be assessed through several ways. We consider here three different interaction strength (IS hereafter) measures (Berlow et al., 2004). Per capita IS, IS_{pc}, measures the direct and instantaneous effect of a consumer individual j on the growth rate of a resource individual i; it equals search rate, a_{ij}, in our model (**Figure 2**, Equation 2). This measure is commonly used in theoretical studies because it is defined without reference to the equilibrium state (Laska and Wootton, 1998; Wootton and Emmerson, 2005; Novak and Wootton, 2010), contrary to other measures, which typically include equilibrium densities. The second IS measure we consider is per population IS, IS_{pp}, which is the direct long term effect of the population of consumer j on the growth rate of the resource i at equilibrium and is equal to $IS_{pc}J^* = a_{ij}J^*$,

TABLE 1 | Parameters descriptions and values.

Symbol	Description	Dimension	Value
d	Dilution rate	Time^{-1}	0.8
q	Carbone-to-nitrogen ratio [a]	–	6
e_{PH}	Herbivore conversion efficiency [b]	–	0.45
e_{HC}	Carnivore conversion efficiency [b]	–	0.85
I	Nutrient input	mol.N.volume^{-1}.Time^{-1}	12
b_i	T° independent biomass loss rate	Time^{-1}	0.4
m_p	Primary producer body-mass	mg	1
m_h	Herbivore body-mass	mg	1.10^2
m_c	Carnivore body-mass	mg	1.10^4
c	Dry to wet mass conversion constant [c]	–	6.5
T	Temperature T°	Kelvin	285–315
T_{opt}	Optimal temperature	Kelvin	298
k	Boltzmann constant	eV.K^{-1}	$8.617.10^{-5}$
a_{ij}	Consumer-resource search rate	Volume.time^{-1}	(Equation 2)
z_i	T° dependent biomass loss rate	Time^{-1}	(Equation 2)
μ_i	Primary producer growth rate	Time^{-1}	(Equation 2)
β_a	Allometric scaling exponent for a [d]	–	0.25
$\beta_{z,\mu}$	Allometric scaling exponent for z & μ [e]	–	–0.25
$E_{a_{ph}}$	Activation energy for a_{ph} [f]	eV (electronvolt)	0.8
$E_{a_{hc}}$	Activation energy for a_{hc} [f]	eV (electronvolt)	0.74
E_{z_p}	Activation energy for z_p [f]	eV (electronvolt)	0.55
E_{z_h}	Activation energy for z_h [f]	eV (electronvolt)	0.43
E_{z_c}	Activation energy for z_c [f]	eV (electronvolt)	0.72
E_{μ}	Activation energy for μ [f]	eV (electronvolt)	0.53
E_D	De-activation energy [f]	eV (electronvolt)	1.15
a_{ph_0}	Scaling constant for a_{ph}	–	5.10^{13}
a_{hc_0}	Scaling constant for a_{hc}	–	3.10^{12}
z_{p_0}	Scaling constant for z_p	–	2.10^8
z_{h_0}	Scaling constant for z_h	–	4.10^6
z_{c_0}	Scaling constant for z_c	–	$1.5.10^{12}$
μ_0	Scaling constant for μ	–	3.10^8

References: [a]*Sterner and Elser (2002)*, [b]*Yodzis and Innes (1992)*, [c]*Peters and Peters (1986)*, [d]*Rall et al. (2012)*, [e]*Savage et al. (2004)*, [f]*Dell et al. (2011)*.

where J^* is the equilibrium density of consumer j. This index also corresponds to the coefficient of the Jacobian matrix, that describes the dynamics of species at equilibrium, in our model. It has been commonly used in ecology to quantify interaction strength (May, 1974) and is reviewed in Montoya et al. (2009). Finally, net IS, IS_{net}, is the net long term effect of the population of consumers j on the equilibrium density of the resource i and is equal to the (log) ratio of resource equilibrium densities, I^*, in absence I^*_- and in presence I^*_+ of the consumer, $log(I^*_-/I^*_+)$. This definition of IS is typically used in experimental removal studies (Paine, 1980; Laska and Wootton, 1998; Berlow et al., 2004).

We assess interactions between the three trophic levels. We thus consider the direct effect of herbivores on primary producers in absence of carnivores, IS^{H-P}; the direct effect of carnivores on herbivores, IS^{C-H}; and, for IS_{net}, the indirect effect of carnivores on primary producers, IS^{C-P}, as carnivores can indirectly impact primary producers by reducing herbivore density when feeding on them. In the following analyses, we focus on IS_{pp} and IS_{net} which are analytically derived as they are dependent upon equilibrium biomasses. We compare their thermal responses with the one of IS_{pc} which is given by Equation 2. Equilibrium densities, I^* for species i, are obtained by solving the system of differential equations (Equation 1) when $dI/dt = 0$. We first investigate how temperature directly affects IS. We then look at the effect of varying the temperature dependence of biological rates (by alternately fixing model parameters at their optimal value) and temperature independent mortality rates. Finally we explore how the indirect effect of temperature through decreasing body mass affects IS. Note that, for brevity, we mainly illustrate our results for the interaction between carnivores and herbivores.

3. RESULTS

3.1. Thermal Dependence of Biological Rates

When all parameters are temperature dependent, the relationship between temperature and consumer-resource IS follows the shape of Equation 2. Because of the definition of the search rate a_{ij}, IS_{pc} (which is equal to search rate in our model) follows

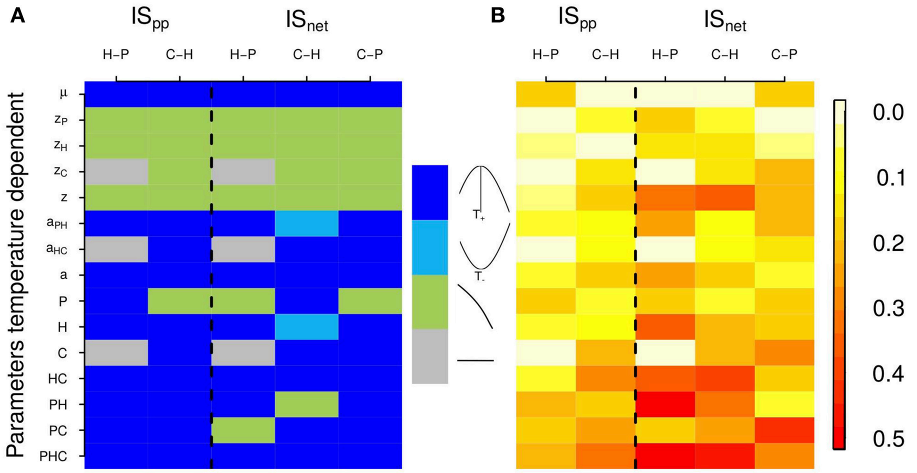

FIGURE 3 | Effects of temperature on two interaction strength measures: interaction strength per population, IS_{pp}, and net interaction strength, IS_{net}. Each column corresponds to different interactions between consumers and resources: H-P stands for the interaction between herbivores and primary producers in absence of carnivores, C-H for the interaction between carnivores and herbivores and C-P for the indirect interaction between carnivores and primary producers. (Note that to facilitate the comparison between those different interactions, we represented here the inverse of IS^{C-P}. Hence, for all interactions, a hump-shaped relationship means that IS first increases with temperature and a U-shaped relationship means that IS first decreases with temperature.) Each row corresponds to a different scenario of thermal dependence of parameters. Parameters that vary with temperature are specified on the left of the plot (e.g., second row: only z_P, the primary producer mortality rate, varies with temperature, other parameters being fixed). When the subscript is not indicated, biological rates of every trophic levels vary with temperature (e.g., 5th row: z, mortality rates of primary producers, herbivores and carnivores vary with temperature). When the trophic level is indicated (P, H and/or C), the parameters of the given trophic level(s) vary with temperature (e.g., 9th row: primary producer parameters, μ and z_p, vary with temperature). Hence for the last row (PHC), all parameters vary with temperature. Fixed parameters are set at their optimal value. **(A)** Qualitative representation of the shape of the thermal response of IS measures for different scenarios of parameters temperature dependence (as in **Figure 2**). The shapes of the thermal dependence of interaction strength are color coded; see color key, dark blue: hump-shaped, light blue: U-shaped, light green: decrease and gray: no temperature dependence. (In the last case, gray cells, there is no effect of temperature because all parameters are fixed for those interactions. Indeed, here the interactions between primary producers and herbivores are independent of carnivore's biological rates). **(B)** Thermal sensitivity of interaction strength for different scenarios of parameters temperature dependence, quantified as the standard deviation of interaction strength measures (color coded, see color key).

exactly the shape of the temperature-dependence of biological rates. This measure of IS propagates and thus affects IS_{pp} and IS_{net} similarly. All three measures of IS therefore increase with temperature, up to a point above which it starts decreasing (**Figure 3**). Importantly, the temperature-IS relationship holds for the interactions between all trophic levels: for the interactions between primary producers and herbivores (in the absence of carnivores), between herbivores and carnivores and between carnivores and primary producers (for IS_{net}). Note that for this indirect interaction, primary producers are more abundant in the presence than in the absence of carnivores. The log of IS_{net}^{C-P} is thus negative. A hump-shaped relationship demonstrates that trophic cascades also increase with warming under the PTR before decreasing at the warmest temperatures.

The sensitivity of IS to temperature varies significantly according to which parameter varies with temperature (**Figure 3**). The thermal response of IS can be hump-shaped, U-shaped or decrease with temperature. It is then determined by the temperature dependence of the biological rates that are expressed in the IS measures' formulas, which are based on equilibrium biomasses (see **Table S1** and **Figure S2**). In our model, mortality rate increases with temperature whilst growth and search rates follow a hump-shaped relation with temperature. These differences in the shape of the thermal responses of biological rates show in the thermal responses of IS measures. When only mortality rates z_i vary with temperature, intraspecific competition increases leading to a decrease in population biomass i at equilibrium, but also to an increase in equilibrium biomass of the resource of species i (if any). Equilibrium biomasses influence IS_{pp} and IS_{net}, which in turn decrease with increasing temperature. The intrinsic growth rate varies with temperature because of its effect on both mortality and consumption rates. The equilibrium biomass of a consumer species i decreases with mortality rate z_i, while the equilibrium biomass of its resource does increase because of lower regulation. The change of equilibrium with increasing temperature of both consumer and resource therefore influences both IS_{pp} and IS_{net}. When only search rates a_i vary with temperature, the thermal dependence of equilibrium biomasses can be hump-shaped or U-shaped. As equilibrium biomasses of the different trophic levels are interdependent, the relationships between biomasses at equilibrium and IS_{pp} and IS_{net} are not straightforward. IS_{pp} and IS_{net} are generally hump-shaped, although they can be U-shaped (for IS_{net}^{C-H}). This shows that generally, IS_{pp} and IS_{net} directly follow the scaling relationship of IS_{pc}. When consumption rates increase or decrease, IS increases/decreases too. We also vary the parameters by trophic level (i.e., mortality and growth or search rates are temperature dependent only for a given level). For these scenarios, the thermal response of IS measures is generally determined by search or growth rates (hump-shaped or

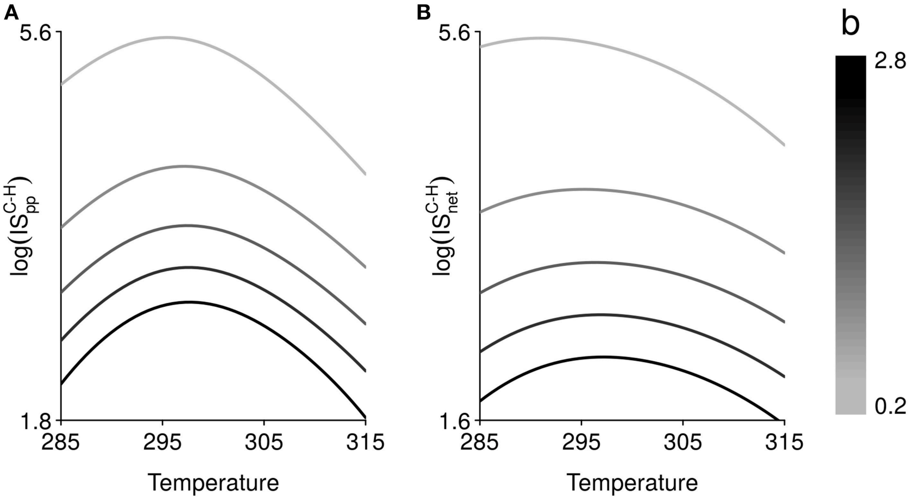

FIGURE 4 | Effect of temperature (in Kelvin) on, **(A)**, interaction strength per population, IS_{pp}^{C-H}, and, **(B)**, net interaction strength, IS_{net}^{C-H}, between carnivores C and herbivores H. The relationship between temperature and both interaction strength measures is hump-shaped and follows the thermal dependence function of search rate (or per capita interaction strength) and growth rate (**Figure 2**). Varying the mortality rate, from 0.2 to 2.8 time^{-1}, changes the magnitude of the temperature effect, the relative strength of interaction and shifts the temperature at which interaction strength is maximal.

U-shaped relationship) but can also be determined by mortality rates (decrease with temperature) according to IS measures. The variation in the shape of IS thermal responses is more important for IS_{net} than for IS_{pp}, which can be explained by the fact that IS_{net} is equal to the ratio of equilibrium biomasses of resources and consumers.

The shapes of the thermal responses of IS measures are qualitatively described in **Figure 3A**. However, the magnitude of the temperature effect, as well as the strength of the interaction, varies from one scenario of parameter temperature dependence to another. We find that the occurrence of temperature-independent rates can alter the thermal sensitivity of IS_{pp} and IS_{net} (**Figure 3B**), which is highly variable from one IS measure to another, and according to which rate is fixed. It tends to increase with the number of rates that are temperature dependent and is stronger for IS_{net}. The equilibrium biomass of a given trophic level is dependent upon equilibrium biomasses of other trophic levels (**Table S1**). These interactions between parameters and trophic levels in equilibrium biomasses can in turn lead to an increase in the temperature sensitivity of IS_{pp} and IS_{net}. We further investigate the response of IS between carnivores and herbivores, and its thermal dependence, to a change in temperature-independent biomass loss rate (**Figure 4**). The shape of the thermal response of both IS measures remains hump-shaped whatever the value of biomass loss rate. However, increasing biomass loss rate b_i decreases both IS measures and shifts the temperature at which IS is maximal toward higher temperatures, mainly for IS_{net}. Increasing mortality rate b_i diminishes carnivore equilibrium biomass, which in turn lead to a decrease in IS_{pp}. Increasing mortality rate b_i also decreases herbivore equilibrium biomass in absence of carnivores but increases its equilibrium biomass in presence of carnivores, resulting in a decrease in IS_{net} (see **Table S1** and **Figure S3**).

3.2. Temperature-Size Rule

Temperature, through its effect on body mass, can indirectly induce changes in IS (for the interaction between carnivores and herbivores in **Figure 5**). The TSR does not alter the shape of the thermal response of IS, which remains hump-shaped for all TS scenarios. According to Equation 4, the temperature of reference is 293.15 K. Organisms are larger for temperatures under 293.15 K and smaller for temperatures above 293.15 K. Hence IS values with and without TSR are equal at 293.15 K (lines are crossing at 293.15 K on **Figure 5**). However, below and above this temperature of reference, IS can either decrease or increase with the TSR. We also observe a shift in the temperature at which IS is maximal.

IS_{pc} (Equation 2, **Figure S1**) and IS_{pp} (**Figure 5A**) both increase for temperature below 293.15 K (increase in body mass) and decrease for temperature above 293.15 K (decrease in body mass). These IS measures then directly depend on species body mass. IS_{pp} gradually becomes lower as more trophic levels experience a decrease in body mass (**Figure 5A**). IS_{net} declines with decreasing carnivore body mass regardless of whether or not herbivore body mass also decreases (**Figure 5B**). However, when the three trophic levels follow the TSR, IS_{net} increases with reduced body mass compared to the case with no TSR effect. This is due to the fact that a reduction in body mass can affect equilibrium biomasses of the different trophic levels in distinct ways. The equilibrium biomass of herbivores increases in both the presence and absence of carnivores when the three trophic levels follow the TSR (**Figure S2**), which results in an increase of IS_{net}. Hence, the indirect effect of temperature through altering body mass does not qualitatively affect the relationship between temperature and IS except for a shift of the location of the maximal IS. However, it changes the relative strength of the interactions.

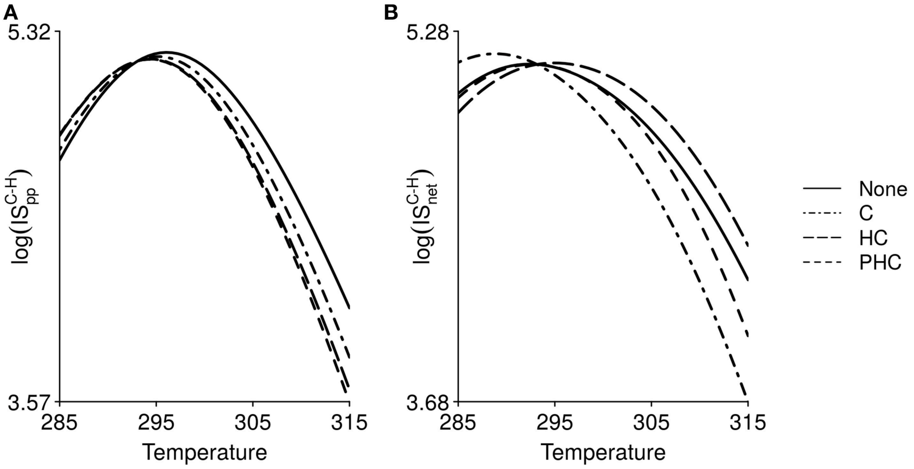

FIGURE 5 | Effect of temperature (in Kelvin) on, **(A)**, interaction strength per population, IS_{pp}^{C-H}, and, **(B)** net interaction strength, IS_{net}^{C-H}, between carnivores and herbivores, when organisms body mass decreases with temperature due to the temperature-size rule. Four scenarios are simulated: no TS response in either species (None), only carnivores follow a TS response **(C)**, herbivores and carnivores follow a TS response (HC) and the three trophic levels follow a TS response (PHC).

4. DISCUSSION

There is no consensus about the effect of temperature on trophic regulation, as studies are often based on different assumptions, models or measures of interaction strength (IS). It is known that temperature directly influences the physiology of organisms by changing their biological rates (Gillooly et al., 2001; Brown et al., 2004; Savage et al., 2004) and inducing a change in body mass (Forster and Hirst, 2012). These effects then propagate to the population- and community-level. The comparison of IS measures allows us to reveal three main mechanisms by which temperature affects trophic regulation : (i) temperature directly affects metabolic rates and body mass, which in turn induces changes in biological rates and in the rate at which individuals consume their resource (and in IS_{pc}). As a result, (ii) population sizes at equilibrium become temperature dependent, which in turn infuences IS_{pp}, the total effect of consumers on resource populations. Moreover, (iii) the effect of temperature propagates between trophic levels meaning that interactions between parameters (or trophic levels) that are temperature dependent may make more sensitive IS_{pp} and IS_{net} to temperature changes. We thus support the widely believed hypothesis that temperature has an effect on trophic interaction strength, but we also show that this effect can vary in direction, magnitude and location of its peak.

More precisely, in our analyses, the relationship between temperature and interaction strength follows the scaling relationship between search rates and temperature when all compartments respond to temperature. This result is obvious for a linear functional response but nonetheless underlines parameters that need to be better documented empirically. Sensitivity of the different IS measures to temperature increases when all parameters are temperature dependent. A precise definition of IS is therefore essential to link multiple experimental and theoretical studies. Yet many indices have been used, making it difficult to compare outcomes from different studies (Wootton and Emmerson, 2005). The coherence in the thermal response of the different IS measures considered here demonstrates that different indices can behave similarly to an increase in temperature.

When all parameters are temperature dependent, IS thus increases with temperature up to a certain threshold above which it decreases. Our result is consistent with previous studies that experimentally manipulated the presence of predators and measured either net IS (log ratio of prey biomass in absence/presence of predators) (Barton et al., 2009; Kratina et al., 2012; Shurin et al., 2012; Gray et al., 2015) or per capita IS (ratio of predation rate and resource density) (Sentis et al., 2014). Sentis et al. (2014) theoretically and experimentally measured omnivory strength, computed as the number of resources and consumers eaten. Their model predict that omnivory strength increases with temperature but rapidly decreases at extreme temperatures due to the hump-shaped thermal response of search rate. However, they did not experimentally measure this decrease at extreme temperatures because their warmest temperature was 30 °C. On a narrow range of temperature, Osmond et al. (2017) also found that net IS monotonically increases with temperature. Hence, most experimental studies found that temperature increases IS but few of them detailed the different rates that are temperature dependent. Our results also show that IS decreases at higher temperatures, in agreement with Sentis et al. (2014). These authors suggest that the effect of temperature on interaction strength is mediated by its effect on predator foraging activities. Temperature, through increasing search rate, promote predation of resources. However, at higher temperatures, search rate decreases and so does IS. It is therefore critical to characterize the thermal response of search rates and other biological rates over a large range of conditions to catch this peak. Yet few data or theories exist for the decline in individuals rate performance at higher temperatures (Dell et al., 2011) as the majority of studies concentrates on the rising part of biological rates responses to temperature. The decreasing phase has raised less attention, partly because organisms usually live within their physiological temperature range (PTR), and partly because a majority of experiments perform a marginal warming relative to current conditions (Sentis et al., 2014).

We also find that the relationship between temperature and IS can differ according to which biological rates are temperature dependent. Thermal sensitivity of IS when multiple rates are affected by temperature appears stronger than the sum of individual effects, suggesting interactions and synergies between trophic levels are taking place (**Figure 3B**). Indeed, effects of temperature propagate through the entire food chain, from primary producers at the bottom to carnivores at the top and conversely. For instance, when only the primary producer mortality rate z_{P} varies with temperature, the interactions between carnivores and herbivores, e.g IS_{pp}^{C-H}, still vary with temperature. This arises because z_{P} influences the equilibrium concentration of the nutrient, which in turn influences the equilibrium biomass of the primary producers, and so does the equilibrium biomass of the carnivores (**Table S1**), all together impacting IS_{pp}^{C-H}. Similarly, when only the carnivore mortality rate z_{C} varies with temperature, IS_{net}^{C-P}, which is the ratio of primary producers biomass in absence and in presence of carnivores, still varies with temperature (**Figure 3B**). z_{C} influences the equilibrium biomass of herbivores and subsequently the equilibrium biomass and concentration of primary producers and nutrients. The same reasoning applies for herbivore parameters. Hence, even though some parameters are not directly involved in IS measures, they can indirectly influence IS through the interdependence of equilibrium biomasses across trophic levels.

There is usually coherence in the thermal response of IS when multiple parameters from different trophic levels vary together. For instance, when mortality rates of all trophic levels vary with temperature (search rates and growth rates are fixed), the relationship between IS and temperature is no longer hump-shaped but instead exponential (**Figure 3A**). Similarly, when consumption rates of all trophic levels vary together, the thermal response of IS is unimodal. When multiple rates are temperature dependent, the thermal response of IS is also usually stronger than when a single parameter varies (**Figure 3B**). For instance, when the mortality rate z of the three trophic levels vary with temperature, the thermal sensitivity of IS_{pp} and IS_{net} is stronger than when the mortality rate of a single trophic level is temperature dependent. There may be however interactive effects that can lead in some cases to surprising IS thermal responses. We find this situation for instance when only the search rate of herbivore a_{PH} varies with temperature. In that case, the equilibrium biomass of herbivores in presence of carnivores is then temperature independent but the equilibrium biomass of herbivores in absence of carnivores is U-shaped (**Figure 3A**), resulting in a U-shaped thermal response for IS_{net}^{C-H}. All in all, this variation in the thermal response of IS indicates that there are multiple pathways by which temperature may affect IS.

Knowledge of which rates are influenced by temperature, and how, is therefore critical to document (Dell et al., 2011; Englund et al., 2011; Huey and Kingsolver, 2011; Vucic-Pestic et al., 2011; Burnside et al., 2014; Amarasekare, 2015). It will also be important to better measure activation energies for each rate since some parameters are more sensitive than others. It has been shown for instance that search rate can have a steeper temperature response than maximal intake rate or handling time (Englund et al., 2011; Sentis et al., 2014), and that it can be temperature independent for sit-and-wait predators (Sentis et al., 2017b). However, even when search rate (i.e., IS_{pc}) is fixed, IS_{net} can vary with temperature. This result is in agreement with previous experimental studies (Sentis et al., 2017b) and emphasize the importance of considering different IS measures. Temperature sensitivity can also vary across trophic levels. Climate sensitivity is assumed to increase with trophic levels (Voigt et al., 2003), possibly due to the fact that respiration increases faster than photosynthesis with warming (Pawar et al., 2015). On the other hand, upper trophic levels are often endotherms which can control their body temperature to a certain extent. According to our results, differences in the thermal sensitivity of species can in turn alter the shape of the thermal response of interaction strength but also its sensitivity. We also find that the thermal sensitivity of IS can be contingent on parameters that are not temperature dependent, such as mortality rates, that can magnify thermal responses. Mortality can increase via many other mechanisms than temperature. Natural disturbances or dilution, for instance, can affect mortality rates and in turn species biomasses leading to a change in the strength of their interactions. Hence, we show that, in addition to temperature, other factors can impact trophic regulation and, more importantly, magnify the temperature effect, without altering the shape of its thermal response.

Finally, we investigated the effect of a shift in body mass due to temperature on IS. Warming is assumed to have a negative effect on ectothermic organisms' body mass due to the temperature-size rule (Ashton et al., 2000). Despite body mass being a key determinant of trophic interactions (Brose et al., 2006; Sentis et al., 2017a), the ecological consequences of such phenotypic responses remain largely unexplored. Here we show that the unimodality of the relationship between temperature and interaction strength (for the case where all parameters vary with temperature) holds even when body mass decreases with temperature. However, per population interaction strength decreases with decreasing body mass whilst net interaction strength tends to either increase or decrease depending on which trophic levels follow the TSR. Osmond et al. (2017) found that the TSR had little effect on net IS but increases the stability of the interaction. While they considered symmetric TS responses between resources and consumers, we demonstrated, in agreement with (Sentis et al., 2017a) that heterogeneous TS reponses across trophic levels lead to different responses of IS. By altering resource and consumer body mass ratios, TS responses may alter IS. Increasing body mass ratio is expected to increase the relative rate of consumption per unit consumer biomass which decreases IS and stabilizes the food chain (Sentis et al., 2017a). We indeed find that when carnivores' body mass decreases, thus decreasing body mass ratio between carnivores and herbivores, the effect of carnivores on herbivores (IS^{C-H}) is lower. The indirect effect of temperature through body mass can then be opposite to its direct effect (which increases interaction strength under the PTR). Nevertheless, we also found that TS responses can further enhance the direct effect of warming on IS. We demonstrate that TS responses can impact IS in various directions depending on TS scenarios, consistent with Sentis et al. (2017a), but also show that these responses can vary from one measure of IS to another. This also raises the point that experiment duration is essential to accurately measure IS: experiments that are too short to observe a decrease in body mass could lead to under or overestimation of IS.

In summary, we find that temperature has numerous effects on IS. Presently, studies investigating how temperature influences ecosystem functioning mainly focus on only one effect of climate change at a time (Yvon-Durocher and Allen, 2012). Our results show that developing a framework that integrates the diverse effects of temperature on species' interactions is key to understand food web dynamics. Hence, through a simple model, we show that the impact of temperature on IS can be complex but that different measures of IS behave similarly with warming. Our approach however did not account for thermal adaptation of the species, which can reduce the physiological responses of organisms to warming. Furthermore, we considered a simple trophic chain, whereas a food-web approach would be relevant to investigate how various effects of temperature affect more complex communities. Hence, our analysis provides insights on various outcomes arising from communities under warming and demonstrates the importance of considering diverse effects of temperature.

DATA AVAILABILITY

Data have not been archived because this article does not contain data. Codes are available to download on https://github.com/Azenor/Temp_effect_trophic_interaction.

AUTHOR CONTRIBUTIONS

AB and DG conceived and developed the models. AB conducted the modeling work and wrote the first draft of the manuscript. All authors discussed the results and substantially revised the manuscript.

FUNDING

This work was supported by the University of Sherbrooke, the CRSNG and the Canada Research Chair program. ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

ACKNOWLEDGMENTS

We would like to thank A. Sentis, D. Watts, the Integrative Ecology (IE) lab and the Centre for Biodiversity Theory and Modelling (CBTM) members for enlightening discussions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00045/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 21 March 2019
doi: 10.3389/fevo.2019.00064

Scaling Contagious Disturbance: A Spatially-Implicit Dynamic Model

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Spatial processes often drive ecosystem processes, biogeochemical cycles, and land-atmosphere feedbacks at the landscape-scale. Climate-sensitive disturbances, such as fire, land-use change, pests, and pathogens, often spread contagiously across the landscape. While the climate-change implications of these factors are often discussed, none of these processes are incorporated into earth system models as contagious disturbances because they occur at a spatial scale well below model resolution. Here we present a novel second-order spatially-implicit scheme for representing the size distribution of spatially contagious disturbances. We demonstrate a means for dynamically evolving spatial adjacency through time in response to disturbance. Our scheme shows that contagious disturbance types can be characterized as a function of their size and edge-to-interior ratio. This emergent disturbance characterization allows for description of disturbance across scales. This scheme lays the ground for a more realistic global-scale exploration of how spatially-complex disturbances interact with climate-change drivers, and forwards theoretical understanding of spatial and temporal evolution of disturbance.

Keywords: landscape ecology, fire regime, heterogeneity, adjacency, fragmentation, LANDFIRE

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *01 November 2018*
Accepted: *20 February 2019*
Published: *21 March 2019*

Citation:
McCabe TD and Dietze MC (2019) Scaling Contagious Disturbance: A Spatially-Implicit Dynamic Model. Front. Ecol. Evol. 7:64. doi: 10.3389/fevo.2019.00064

INTRODUCTION

Disturbances pose a fundamental scaling problem as they both create and respond to spatial heterogeneity in the environment (Turner, 2010). Seminal theoretical and experimental work in scaling explore how disturbances introduce heterogeneity into ecosystem at varying scales: the patch-dynamics of Pickett and White, the "shifting-mosaic" of Bormann and Likens, and Turner's landscape equilibrium, all attempt to resolve the issue of how disturbances on a range of scales interact to create ecosystem-level patterns (Bormann and Likens, 1979; White and Pickett, 1985; Turner et al., 1993).

Among disturbance types, contagious disturbances, such as fire, are particularly important ecologically as they are not only large in total area, but can have large impacts on spatial pattern, process, and heterogeneity. Contagious disturbances mediate biogeochemical fluxes, are drivers of landscape ecology, and contribute uncertainty to understanding consequences of anthropogenic climate change. At the end of the twentieth century on average, 608 Mha of land burned per year globally, affecting nutrient cycles, community composition, and altering local energy budgets (Mouillot and Field, 2005; Marlon et al., 2012; Parks et al., 2016; Dannenmann et al., 2018). Anthropogenic land-use-change also often follows a contagious pattern, beyond its total area and carbon impact, it is a major driver of habitat fragmentation, with 75% of forests globally located <1 km from an edge (Haddad et al., 2015). Forest insects and pathogens also frequently spread as a spatially contagious process and impact a greater area in North America than fire and forestry combined (Hicke et al., 2012). Similarly, the spread of invasive species can alter nutrient cycling and change ecosystem composition by outcompeting local populations (Vitousek et al., 1996). Many of the disturbances listed here interact with one another, for example invasive plants and forest pests can alter the flammability of an ecosystem (D'Antonio and Vitousek, 1992), while land use creates breaks that alter fire regimes and other contagious disturbances (Carmo et al., 2011). In addition, most contagious disturbances are sensitive to climate—suggesting that anthropogenic climate change could cause novel behavior or interactions (Mitchell et al., 2014; Harris et al., 2016). Contagious disturbances are a central component of understanding an ecosystem, and to understand how ecosystems will behave in the future we need an understanding of how to predict contagious disturbances.

Contagious disturbances pose a particular challenge to scaling, as they not only create and respond to heterogeneity at a local scale, but they also respond to heterogeneity in neighboring locations, and in the process create a larger scale spatial pattern. To date, most efforts at modeling contagious disturbance have focused on spatially-explicit simulations (Seidl et al., 2011). In such models, rules are implemented that govern when and where a disturbance is initiated and whether it spreads contagiously to adjacent locations. Such rules are easy to formulate, typically invoking properties of the disturbance (e.g., fire intensity), adjacent locations (e.g., fuel load), and some degree of stochasticity, and are well-known for their ability to generate complex spatial pattern and temporal dynamics (Keane et al., 2004; Wolfram, 2017). While such simulation models have provided considerable insight into contagious disturbance, they have two critical limitations when it comes to scaling up disturbance. First, there are basic computational challenges to simulation at large scales. While contagious disturbance processes are common in landscape-scale models, they are absent from dynamic global vegetation models (DGVMs) because it is not currently possibly to run global models at the fine spatial resolution required to represent contagion, which has impacts on estimates of the carbon sink (Melton and Arora, 2014). Second, simulation models do not provide the same general theoretical insight found in analytical models.

The goal of this paper is to explore the development of a general, analytically-tractable, and spatially-implicit approach to modeling the scaling of contagious disturbance. This framework is general in the sense that it aims to capture a wide range of different disturbance types (including non-spreading disturbance as a special case) to provide a common framework for understanding their emergent scaling behaviors. It is spatially-implicit because we make the simplifying assumption that, when viewed from a large scale, the exact spatial locations of disturbances do not matter but rather their aggregate statistical properties. In moving up scales we are not focusing on the spread of individual disturbance events, but the broader distribution of disturbance size and shape that characterizes a disturbance regime spatially.

In developing this approach, we separate the problem of spatial scaling into two components, heterogeneity and spatial arrangement. Problems characterized by spatial heterogeneity are conceptually easier to scale. If an ecological process is only responding to its local environment, then even if those responses are non-linear, the emergent "whole" behavior at a larger scale is just the sum of all the local "parts." In this case spatial arrangement does not matter, just the frequency distribution of the different environmental conditions. This approach has been applied successfully to the upscaling of many key ecological processes, such as carbon and water fluxes, even when the heterogeneity of the process (e.g., distribution of vegetation stand ages) is evolving dynamically through time (Moorcroft et al., 2001; Fisher et al., 2018). In practice such approaches are typically modeled discretely, e.g., a finite number of age classes each with some fractional area on the landscape.

Ecological processes that depend on spatial arrangement are conceptually harder to scale, however we argue that not all spatial arrangement problems have to be spatially-explicit, as many only depend on *relative* spatial context. Herein we take the approach of focusing specifically on approximating the well-established landscape ecology concept of spatial adjacency, which is a key driver of many spatial processes. Similar to how we represent heterogeneity with a probability distribution, at a large scale we can likewise represent spatial adjacency with the probability that any two conditions will be adjacent to each other. And like with heterogeneity, this will typically be modeled discretely, in this case with a spatial adjacency matrix. If a vector of fractional abundances provides a first-order approximation of spatial variability, the combination of a vector of abundances and matrix of adjacencies thus provides a second-order model. Not all spatial processes can be approximated via adjacency, as sometimes higher-order shape and arrangement does matter, but we posit that this is a useful framework for considering contagious disturbance and spatial processes of adjacency or of dynamically evolving adjacency.

For processes where the heterogeneity in the landscape is fixed on ecological timescales (e.g., elevation, soils), fractional area and adjacency are likewise fixed and can be pre-computed (e.g., in GIS). Spatial processes, such as movement across a landscape, can then be approximated based on adjacency (e.g., what is the probability of moving from class A to class C directly vs. indirectly via B). The challenge with contagious disturbance arises because it not only responds to heterogeneity and adjacency, but it also alters both dynamically. Therefore, a successful approach to scaling contagious disturbance requires a means of updating both fractional areas and adjacencies in response to disturbances.

This paper examines three questions: First, how do we take advantage of adjacency to approximate spatial disturbance spread? Second, given that disturbance, how do we update the fractional areas and adjacencies (i.e., how do we make it dynamic)? Finally, given our ability to simulate disturbances in a spatially implicit manner, how does this theory compare to observations? Specifically, our spatially implicit disturbances model suggests that different disturbance regimes can be characterized by two metrics: (1) the size distribution of disturbances; and (2) the relationship between disturbance size and disturbance interior adjacency scaling. These two metrics were examined for different disturbance types and ecoregions for two contrasting locations, the states of Florida and Oregon, USA. We hypothesize: (1) that our metrics will distinguish between different disturbance types and different states; (2) our metrics will reflect the nested structure of the ecoregions, with ecoregions from the same state being more similar than comparisons across states. While many different configuration-based landscape metrics and indices exist and are used in management, evaluation of landscape change, and habitat analysis (Uuemaa et al., 2009), the strength of our metrics is that they are derived directly from a theoretical understanding of contagious disturbances, thus giving us an ability to predict how changes in either metric will translate into changes in future ecosystem processes, heterogeneity, and adjacency in both the short and long term.

METHODS

Simulating Disturbance Spread

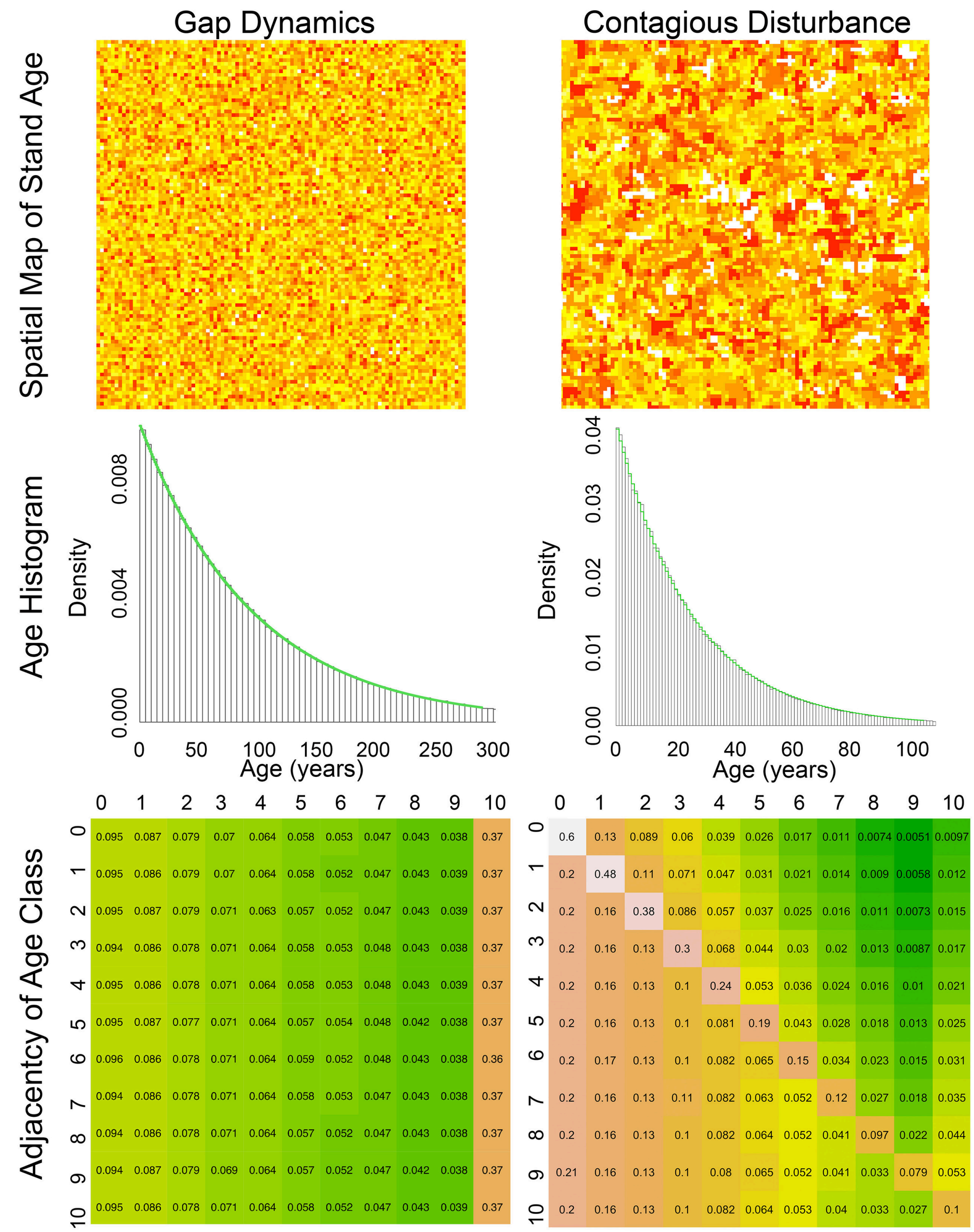
Before diving into how to approximate spatially-explicit models of contagious disturbance analytically, we first illustrate simple versions of these spatial models so as to clarify their key features. Arguably the simplest disturbance process is gap dynamics (e.g., mortality of individual canopy trees), which is often approximated as a stochastic process disturbing individual patches on a grid at random. If we simulate this process through time (**Figure 1** top left), keeping track of the age of each patch (time since disturbance), and running the simulation until the stand age distribution reaches steady state, we see that this age distribution converges to a geometric (discrete exponential) distribution (**Figure 1** mid left). Furthermore, since disturbance is random and does not depend on patch age or neighborhood, the spatial neighborhood of each patch is just a sample from this same geometric distribution. This can be shown by calculating an adjacency matrix, which tallies the probability that one age class is adjacent to another (**Figure 1** bottom left).

Compare this gap dynamics model with a simple model of a contagious disturbance (e.g., fire, insects, land use), which is described first by a probability of disturbance initiation and second, conditional on initiation, a probability of spread to adjacent patches. In more complex versions of such models both these probabilities can vary with age and environmental conditions (Mann et al., 2012). However, even in the simplest case, when both probabilities are fixed and disturbances are random, the model generates much more complex spatial patterns characterized by larger, contiguous disturbance patches (**Figure 1** right). As before, the overall stand age distribution remains geometric (**Figure 1** mid right), however the pattern of spatial adjacency is more complicated (**Figure 1** bottom right). First, most newly disturbed patches (age class 0) are adjacent to other newly disturbed patches (60% in the example simulation). As we move along the diagonal of the adjacency matrix, patches in a given age class continue to remain adjacent to other patches of the same age through time (i.e., larger even-aged patches remain), but this adjacency decays geometrically as new disturbances chip away at even aged patches, leaving them adjacent to younger disturbances. Above the diagonal we see a pattern similar to gap dynamics, where each age class has some probability of being adjacent to newly disturbed patches (which in this simple class is equal for all age classes) and then this adjacency decays equally for each age class. Matrix elements that are below the diagonal, which represent the probability that a patch is adjacent to a patch older than it, age classes likewise decay geometrically, but each age class is along a different curve because of the different cumulative probabilities. In other words, because the elements along the diagonal differ for each age class, and because the cumulative probabilities must sum to 1, the remaining cumulative probability is different for each age class.

Armed with a basic understanding of the patterns that spatially explicit simulations can produce, let us next consider how to develop a spatially implicit model to approximate the spread of contagious disturbance. As in the simulation, let us start by assuming an age or stage structured approach with n discrete age classes. Next, let us assume that the disturbance has some initiation probability, p_0, that is a vector with the same length as the number of age classes, n. In other words, the initiation probability could vary by age class. In this general derivation, our timestep or "t" represents any discrete timestep (annually, monthly, etc.). Because disturbance is simulated discretely in time, the probabilities map to that timestep and can be time varying (e.g., functions of environmental conditions) without loss of generality.

Given this initiation probability, the initial disturbance area (for disturbances with size = 1 patch) is given by $I_1 = p_0 \circ a$, where a is a vector of the fractional areas of each age class and $\circ$ denotes element-wise Hadamard multiplication. Next, let us assume that we know the current adjacency matrix, A_t, that describes the probability that a patch of a given age/stage class is adjacent to patches of the same or other age/stage classes at time t. Individual elements within A_t are probabilities, and thus must be between 0 and 1, and all patches must be adjacent to some other patch so each row represents a discrete probability distribution whose elements must sum to 1. However, A_t does not need to be symmetric (e.g., **Figure 1** bottom right). In practice the specification of these probabilities will depend on the spatial grain of the analysis (i.e., patch size) but this does not affect the mathematical derivation. Also, in practice the initial adjacency, A_0, would need to be derived from some sort of empirical GIS analysis or some steady-state assumption but this does not affect the derivation. Finally, except when deriving the dynamics of updating A_{t+1} given A_t we will drop the time subscript for simplicity, as we are not considering changes in A during a disturbance event.

To allow contagious disturbances to spread we also need to introduce a probability of spread, p_s, given initiation, which similar to I_1 is grain and timestep dependent and could be time varying. In the general case we will assume p_s is a $n \times n$ matrix describing the probability of spreading from one class into any other class, but in practice p_s could be a scalar or set to only vary by row (dependent on the class the disturbance is spreading from) or column (dependent on the class being spread into). It should also be noted that p_s does not need to be symmetric—the probability of spreading from one patch type into another (e.g., new regeneration into old-growth) need not be the same as the probability of spreading back. Given this framework we can next derive the probability of a disturbance spreading to a



	0	1	2	3	4	5	6	7	8	9	10
0	0.095	0.087	0.079	0.07	0.064	0.058	0.053	0.047	0.043	0.038	0.37
1	0.095	0.086	0.079	0.07	0.064	0.058	0.052	0.047	0.043	0.039	0.37
2	0.095	0.087	0.079	0.071	0.063	0.057	0.052	0.047	0.043	0.039	0.37
3	0.094	0.086	0.078	0.071	0.064	0.058	0.053	0.048	0.043	0.038	0.37
4	0.095	0.086	0.078	0.071	0.064	0.058	0.053	0.048	0.043	0.039	0.37
5	0.095	0.087	0.077	0.071	0.064	0.057	0.054	0.048	0.042	0.038	0.37
6	0.096	0.086	0.078	0.071	0.064	0.059	0.052	0.048	0.043	0.038	0.36
7	0.094	0.086	0.078	0.071	0.064	0.058	0.053	0.047	0.043	0.038	0.37
8	0.094	0.086	0.078	0.071	0.064	0.057	0.052	0.047	0.043	0.038	0.37
9	0.094	0.087	0.079	0.069	0.064	0.057	0.052	0.047	0.042	0.038	0.37
10	0.095	0.086	0.078	0.071	0.064	0.058	0.052	0.047	0.043	0.039	0.37

	0	1	2	3	4	5	6	7	8	9	10
0	0.6	0.13	0.089	0.06	0.039	0.026	0.017	0.011	0.0074	0.0051	0.0097
1	0.2	0.48	0.11	0.071	0.047	0.031	0.021	0.014	0.009	0.0058	0.012
2	0.2	0.16	0.38	0.086	0.057	0.037	0.025	0.016	0.011	0.0073	0.015
3	0.2	0.16	0.13	0.3	0.068	0.044	0.03	0.02	0.013	0.0087	0.017
4	0.2	0.16	0.13	0.1	0.24	0.053	0.036	0.024	0.016	0.01	0.021
5	0.2	0.16	0.13	0.1	0.081	0.19	0.043	0.028	0.018	0.013	0.025
6	0.2	0.17	0.13	0.1	0.082	0.065	0.15	0.034	0.023	0.015	0.031
7	0.2	0.16	0.13	0.11	0.082	0.063	0.052	0.12	0.027	0.018	0.035
8	0.2	0.16	0.13	0.1	0.082	0.064	0.052	0.041	0.097	0.022	0.044
9	0.21	0.16	0.13	0.1	0.08	0.065	0.052	0.041	0.033	0.079	0.053
10	0.2	0.16	0.13	0.1	0.082	0.064	0.053	0.04	0.033	0.027	0.1

FIGURE 1 | Comparison of Gap dynamics Contagious disturbance simulation. (Left column) Gap dynamic simulation. (Right column) Contagious disturbance simulation. (Top left) spatial map of stand age, with color on a log scale from youngest (red) to oldest (yellow), (Top right) spatial map of stand age for contagious disturbance, with color on a log scale from young (red) to old (yellow) and with new disturbances (age = 0) in white. (Middle left) simulated stand age distribution (black) when disturbance probability is 1% compared to geometric expectation (green), (Middle right) simulated stand age distribution (black) when disturbance probability is 1% and spread probability is 25% compared to geometric expectation (green), (Bottom) spatial adjacency matrix by age class aggregated into 10 year bins ([0 – 9] = 0, [10 – 19] = 1, etc.) with all patches 100 year or older in bin 10. Matrices are colored from white (highest adjacency) through orange to green (lowest adjacency).

second patch as depending on initiation, probability of spread, and adjacency:

$$I_2 = (p_s \circ A)I_1$$

Furthermore, we can see that $I_3 = (p_s \circ A)I_2$ and so on, leading to the more general recursion describing the probability of spreading to h + 1 patches, given that the disturbance has already spread to h patches.

$$I_{h+1} = (p_s \circ A)I_h = SI_h = S^h I_1$$

Where $S = p_s A$. Note that in this derivation the matrix A is fixed as it describes the adjacencies among the undisturbed age classes; the ongoing disturbance is not an explicit row/column in A and thus spread only occurs outward into undisturbed area, and there is no need to account for the spread of a disturbance backward into patches that were just disturbed. We also make the simplifying assumption that we are operating on a sufficiently larger scale that no single disturbance event changes the adjacency among undisturbed patches enough to invalidate this approximation (and require updating A during a disturbance event). That said, adjacency does need to be updated on our coarser model timestep as what we generally see is small year-to-year changes that gradually accumulate to appreciable landscape-scale adjacency shifts over longer time (e.g., decades).

Accumulating the spread over different disturbance sizes leads to an overall disturbance rate of

$$D = \sum_{h=1}^{\infty} I_h$$

where D is a vector by class. Overall, while there is slight underestimation of disturbance extent at high spread probabilities (**Figure 2**), the analytical approximation performs well and incurs a tiny computational cost relative to spatially explicit models. Also note that this general forward model has an important special case, $p_s = 0$, which corresponds to non-contagious disturbances, such as our initial gap dynamics simulation.

In practice an infinite sum is not actually computable, but the result will asymptotically approach the analytical result and thus can be approximated with a finite sum. Furthermore, the relative proportions of the different age/stage classes within the ith iteration in the sum (i.e., disturbance of size i), I_i, will rapidly approach a steady-state distribution. If $I_i / \sum I_i \approx \frac{I_{i+1}}{\sum I_{i+1}}$ then we approximate $I_{i+1} = I_i S$ with $I_{i+1} = I_i \lambda$ where λ is the dominant eigenvalue of A. The remainder of the summation $\sum_{h=i+1}^{\infty} I_h$ can thus be approximated as $I_i \sum_{h=i+1}^{\infty} \lambda^{h-i}$. This is just a geometric series, which has the analytical solution $I_i \lambda (1-\lambda)^{-1}$. Therefore, our strategy is to solve the first i terms explicitly and analytically approximate the tail of the distribution

$$D = \sum_{h=1}^{i} I_h + I_i \lambda (1-\lambda)^{-1}$$

As seen in **Figure 3**, this allows the full analytical model to be accurately approximated with only a small number of matrix multiplications (∼5 in this scenario)

Dynamic Updating

Fractional Areas

Once the overall disturbance rate, D, has been calculated we need to update both the fractional areas describing the landscape and the adjacency matrix between those fractional areas. First, let us assume that $a_t = \left[a_0\, a_1 \ldots a_{n-1}\, a_n\right]$ is a vector describing the fractional areas of each of our age classes. Let us also assume that all disturbances reset patches to age class 0, which is the conventional assumption in cohort-based vegetation demography models (Moorcroft et al., 2001; Fisher et al., 2018; VDMS). Note that we are not assuming that disturbance removes all of the vegetation and that age class 0 is bare ground, but rather we are using age 0 to semantically indicate 0 years since last disturbance. Following this assumption, the new fractional area in age class 0 at time t+1 is simply the sum of the disturbance rates in each age class times the current fractional area in each of those age classes, $a_{0,t+1} = \sum_{k=0}^{n} a_{k,t} D_{k,t}$. Next, for all other age classes, each age class ages by 1 year and is reduced by the amount of disturbance that occurred in that class

$$a_{k,t+1} = a_{k-1,t}(1 - D_{k-1,t})$$

Finally, the oldest age class is a special case, representing all stand equal or greater than the specified age, and thus is created by fusing the existing area in that class with the next youngest age class, minus the disturbance occurring in each

$$a_{n,t+1} = a_{n-1,t}(1 - D_{n-1,t}) + a_{n,t}(1 - D_{n,t})$$

Adjacency of Newly Disturbed Patches

In addition to updating the fractional areas in different age classes we also need to be able to update their adjacencies. This updating is done after the disturbance events of a given time-step, not as part of the disturbance simulation itself. This distinction means that the adjacency at a timestep (A_t) is not tied to a disturbance but rather represents the cumulative effects of disturbance on the landscape over a timestep.

Let us start by focusing on the adjacency of the newly disturbed age class, a_0, with itself, which we will denote as A_{00}. If we were assessing this adjacency in a spatially-explicit gridded dataset or simulation, we would estimate the probability of adjacency in terms of the frequency with which disturbed patches are adjacent to other disturbed patches vs. non-disturbed patches. For example, for a disturbance of size 1, all four edges are facing non-disturbed patches, so the adjacency is 0/4 = 0 (**Figure 4**). With a disturbance of size 2, the two patches have a total of eight edges, two of which are on the interior of the disturbance (disturbed patch adjacent to disturbed patch) and six external edges that are along the perimeter of the disturbance, giving an adjacency of 2/8 = 0.25. At size 3 there are two possible disturbance configurations (in a line or an L), but both cases have a total of four interior edges and eight external edges, giving an adjacency of 4/12. At size 4 there are five possible configurations, and the different configurations do not all have the same perimeter—the square configuration has an adjacency of 8/16 while all other configurations have an adjacency of 6/16. If disturbance shapes are completely random then we could work through the combinatorics of how often each shape is likely to occur (squares occur 20% of the time) and calculated a weighted average (0.4). More generally, if we look at the whole map across disturbances of different sizes the overall mean adjacency of disturbed patches will be

$$A_{00} = \frac{\sum Int}{\sum Int + \sum Ext}$$

where Int are interior edges and Ext are external edges.

Thus, far we have seen that the adjacency (interior/total edges) has tended to increase as the size of the disturbance increases.

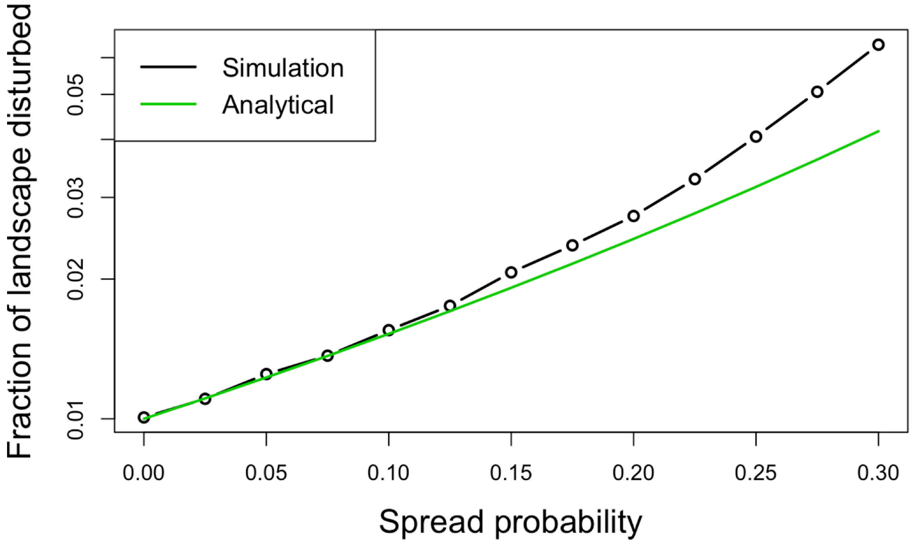


FIGURE 2 | Validation of the analytical model's ability to predict disturbance area as a function of spread probability (disturbance initiation probability of 1%). Simulations run on a 4-sided grid so, for example, a 0.25 spread probability corresponds to four independent chances, each 25%, to spread. The analytical approximation appears to underestimate disturbance at high spread probabilities.

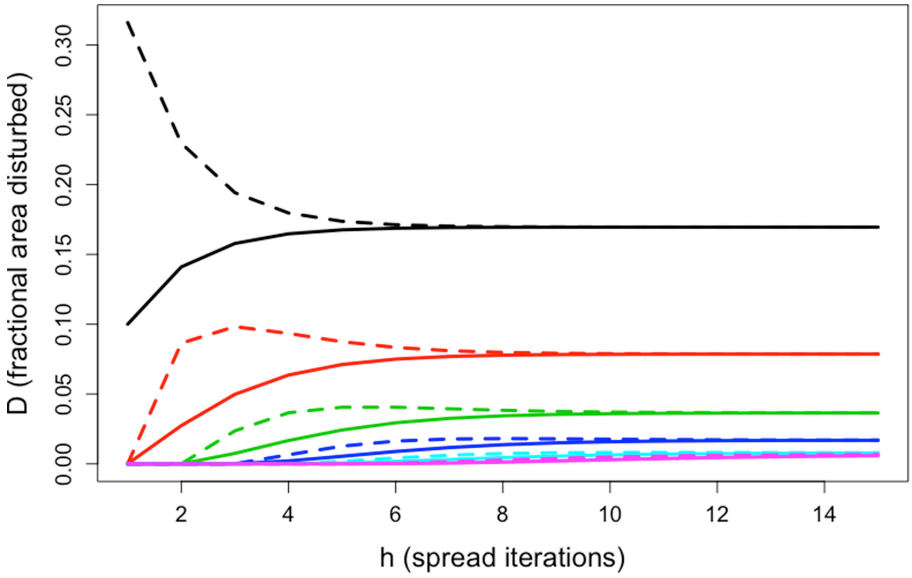


FIGURE 3 | In this scenario, disturbance was initiated in one class (black) at 10%, and then spread to other classes (spread probability of 25%) based on differing probabilities of adjacency between classes (50% self-adjacency, 50% adjacent to the next class). Solid and dashed lines are a comparison of how cumulative area disturbed increased with disturbance size for both the full model and the tail approximation (estimator).

We could continue calculating this pattern to larger disturbances with more complex shapes and harder combinatorics (e.g., for a size 5 disturbance there are 372 possible spread scenarios that produces thirteen possible shapes). However, at this point it is worth noting that different types of disturbances may be more likely to produce certain disturbance shapes than others. For example, some disturbances may tend to produce shapes that tend to be round (wildfire) while others might tend to be linear or dendritic (urban development, riverine systems). These different shapes tend to produce different characteristic interior/total ratios (i.e., different adjacencies). However, it is not the overall mean adjacency (interior/total) that characterizes a disturbance, nor any of the many other landscape metrics in use (e.g., Maximillian et al., 2019), but the functional relationship between disturbance size and adjacency, adj (size). For example, **Figure 5** shows the adjacency/size curves for

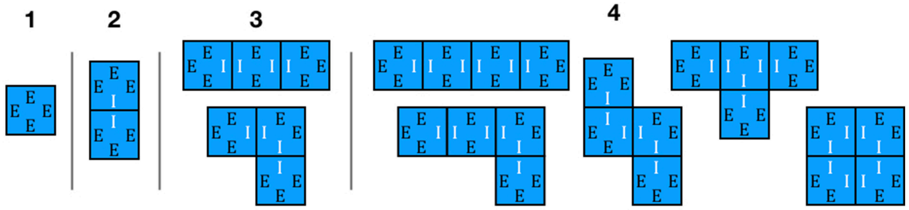


FIGURE 4 | Adjacency for small disturbances. Edges are labeled as (E)xterior and (I)interior. For size 1, there is 0 probability of self-adjacency (disturbed patches adjacent to other disturbed patches). For size 2 and 3 it is 1/4 and 1/3, respectively, while for size 4 the adjacency is either 1/2 (square configuration) or 3/8 (all other configurations).

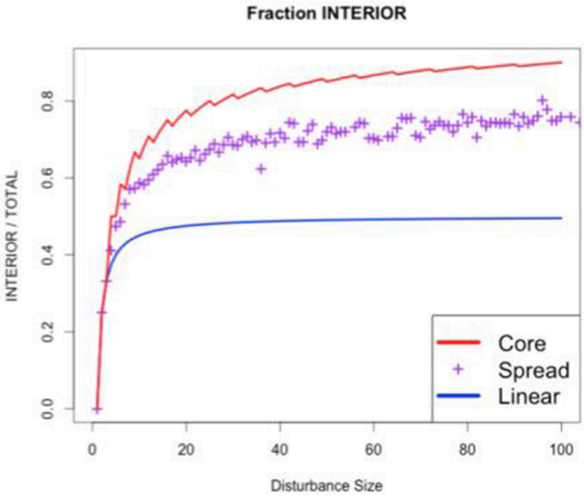


FIGURE 5 | Self-adjacency as a function of disturbance size for different disturbance shapes. Core and Linear are the bounding cases of disturbance shapes that maximize and minimize self-adjacency (respectively). Spread is a single realization of the stochastic contagious spread model (**Figure 2**).

three important cases: random spread (purple), the minimum adjacency (blue) achieved through linear disturbances, and the maximum adjacency (red) achieved by circular disturbances that minimize the interior:total ratio.

To get the overall A_{00} for the spatially implicit model, we next replace

$$A_{00} = \frac{\sum Int}{\sum Int + \sum Ext}$$

which sums over individual disturbances, with

$$A_{00} = \frac{\sum_{size} Int(size)p(size)}{\sum_{size} Int(size)p(size) + \sum_{size} Ext(size)p(size)}$$

which instead sums over each disturbance size. In this approximation, $Int\,(size)$ and $Ext(size)$ returns the expected number of interior and exterior edges while $p(size)$ is the probability of a disturbance of that size. In the denominator we can combine terms as $\sum_{size}(Int(size) + Ext(size))p(size) = \sum_{size} 4 \cdot size \cdot p(size)$ where the 4 arises from the assumption that patches are 4 sided. The size distribution itself can be calculated from the series of I_k, $p(h) = (I_h - I_{h+1}) \cdot h$, because $\mathrm{I_h}$ represents the probability of observing a disturbance of size greater or equal to size h+1. Differencing gives us the probability of a disturbance size h occurring, which is then multiplied by the disturbance size to give us the probability of encountering a disturbance of that size (e.g., the disturbances that stayed size 1 are the subset of disturbances that were initiated but did not spread to another grid cell). Finally, just as we truncated the calculation of D in section Simulating Disturbance Spread, the tails of this distribution can be approximated by noting that the geometric series implies a geometric PDF with rate λ. In the numerator we can use our previously discussed relationship between adjacency and size class, $adj(size)$ to calculate $Int(size) = 4 \cdot size \cdot adj(size)$. Putting these together we see that the assumption about the number of sides to a patch cancels out leaving us with just the mean adjacency weighted by disturbance size and the disturbance size probability distribution

$$A_{00} = \frac{\sum_{size} adj(size) \cdot size \cdot p(size)}{\sum_{size} size \cdot p(size)}$$

This derivation makes sense because large disturbances should contribute more to the adjacency, but usually occur at lower probabilities. Our derivation states that the second-order spatial scaling of any disturbance regime can thus be understood in terms of its size distribution and $adj(size)$. In the analysis of empirical disturbances section, we will evaluate these two components empirically for different disturbance types and ecoregions in Florida and Oregon. In evaluating this approach against simple simulation models, we discovered an important inconsistency in the model, as independent disturbances do sometimes end up adjacent to each other by chance. Consider again our earlier example of simulating gap disturbance ($p_s = 0$). In this case there is no spread, and thus our adjacency-based model makes the prediction that all disturbances are size $= 1$, and thus $A_{00} = 0$, but in practice we find adjacent disturbances. To correct our model, we thus added an additional term in the numerator that accounts for the adjacency between independent disturbances. The simplest such correction is to assume that other disturbances are encountered randomly at the overall disturbance rate, a_0.

$$A_{00} = \frac{\sum_{size} Int(size)p(size) + \sum_{size} a_0 Ext(size)p(size)}{\sum_{size} Int(size)p(size) + \sum_{size} Ext(size)p(size)}$$

$$A_{00} = \frac{\sum_{size} \left[adj(size) + a_0(1 - adj\,(size))\right] \cdot size \cdot p(size)}{\sum_{size} size \cdot p(size)}$$

The adjacency predictions corrected to account for this random self-adjacency performed well (**Figure 6**).

Adjacency of Non-disturbed Patches

In addition to needing to update the adjacency of disturbed patches to each other, there are three other cases that need to be considered: the adjacency of newly disturbed patches to non-disturbed, the adjacency of non-disturbed to newly disturbed, and the adjacency of non-disturbed to each other. For these cases we are going to make the simplifying assumption that the adjacency in each age class changes in proportion to the disturbance rate in that age class, D_k. This assumption is likely reasonable when spread rates are similar among age classes, but very large differences in spread rates, or large asymmetries in spread direction, could be tested through a detailed accounting of the adjacency, A, and spread, p_s, at every disturbance size, *I*, and age class, k. Doing so would come at the expense of considerably more complicated accounting and notational complexity, and thus this is left to future work.

For the first case of disturbances adjacent to non-disturbances, we want to normalize D by its sum to generate the probability that the disturbance was in that age class. As with the age-class distribution, we also want to shift the age classes by 1, to account for aging, and sum the final two elements in this vector to account for age-class fusion. Next, because rows sum to zero this vector of probabilities needs to be reduced by $1 - A_{00}$, giving

$$A_{0k,t+1} = \frac{D_{k-1}}{\sum D}(1 - A_{00,t+1})$$

Next, consider the case of non-disturbed patches adjacent to other non-disturbed patches. Here the adjacency should be reduced by the amount of disturbance in that age class, which is the disturbance rate normalized by the fractional area.

$$A_{j,k,t+1} = A_{j-1,k-1,t}(1 - D_{j-1}/a_{j-1})$$

As before, age classes are shifted by 1 and the final two classes are merged, however in this case the merge is an average (weighted by fractional area), rather than a sum.

Finally, because rows sum to 1, the adjacency of non-disturbed to newly disturbed patches are one minus the sum of the other elements in the row

$$A_{j,0,t+1} = 1 - \sum_{k=1} A_{j,k,t+1}$$

To test the performance of the analytical adjacency approximation, we compared the adjacency matrix predicted by this model to that generated by a fully spatial stochastic simulation, analogous to the one shown in the right column of **Figure 1** but with a disturbance initiation probability of 1% and a spread probability of 10%. In both the analytical model and stochastic simulation, we initiated the landscape from bare ground (age = 0) and ran the model for 1,000 years to reach a steady-state.

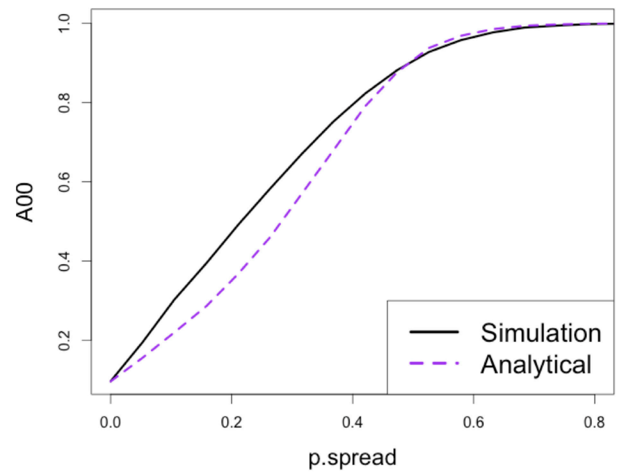


FIGURE 6 | Validation of the ability of the analytical approximation to predict self-adjacency of newly-disturbed patches as a function of disturbance spread probability (disturbance initiation probability set to 10%).

Analysis of Empirical Disturbances

Data Description

Our analysis looked at disturbances in Oregon and Florida from the LANDFIRE Disturbance product (Earth Resources Observation and Science Center, U.S. Geological Survey) for 2014, the most recent year available. Florida and Oregon were chosen as contrasting disturbance regimes because they are both areas with fire-based disturbance regimes and a large timber industry (Fox et al., 2007; Marlon et al., 2012; Mitchell et al., 2014). The LANDFIRE disturbance product is a 30 × 30 m resolution gridded raster covering the entire US, with each disturbed cell assigned one of twenty different disturbance types. Disturbances were determined by a combination of LANDSAT satellite imagery, MODIS satellite imagery, vegetation change detection techniques, and a database of disturbance events detected by other federal agencies (Rollins, 2009; Vogelmann et al., 2011). Specifically, the 2014 LANDFIRE Disturbance dataset was constructed with best-pixel composite imagery, other composite imagery, or majority focal filling to account for missing data after the decommissioning of LANDSAT 5. In our analysis we treated the LANDFIRE Disturbance product as given, and did not consider associated levels of uncertainty within different disturbance types and pixels.

We downloaded US state data from the LANDFIRE repository, available at https://landfire.cr.usgs.gov/disturbance_2.php. The authors then subset Disturbance dataset for each US state based on and Environmental Protection Agency level II Ecoregion boundaries (Ecoregions; McMahon et al., 2001).

Subsetting was done using with the R raster and rgdal packages (Hijmans, 2017; Bivand et al., 2018). We subset the US state-level rasters to focus on the two forested level II ecoregions within each state: Mississippi Alluvial and Southeast Coastal Plains (8.5) and the Southeastern USA Plains (8.3) in Florida; and the Western Cordilleras (6.2) and Marine West Coast Forest (7.1) in Oregon. In Oregon we excluded the Cold Deserts ecoregion (10.1) and in Florida we excluded the Everglades (15.4) (**Figure 7**). The resulting four rasters then had adjacency calculations done on all of the disturbance clumps within each raster (see below).

Calculation of Metrics

The analysis of empirical disturbances focused on the two metrics that emerged from our theoretical model: disturbance size distribution and the relationship between interior ratio and disturbance size. The analysis began by identifying individual disturbances that were surrounded on all sides by non-disturbance pixels. Adjacency was determined using the four cardinal "Rook's Case" pixels (for two pixels to be adjacent they had to share a side). For each disturbance we then identified the disturbance class and calculated the disturbance area and interior ratio (number of interior edges/total number of edges, **Figure 4**). After processing the four rasters, we ended up with a table of each disturbance event in Florida and Oregon, with a record of its type, size, interior/total ratio, eco region, and US state. This table is the basis of all further empirical calculations and is publicly available along with the scripts used to generate it on Github at https://github.com/mccabete/SpatialAdjacency. This analysis has no way of distinguishing distinct but adjacent disturbance events that occurred at different times within a year, therefore these distinct but adjacent disturbance events were considered the same clump. This analysis also did not account for relative area of different disturbance types mixed within a single clump. Clumps of mixed disturbance types accounted for a small number

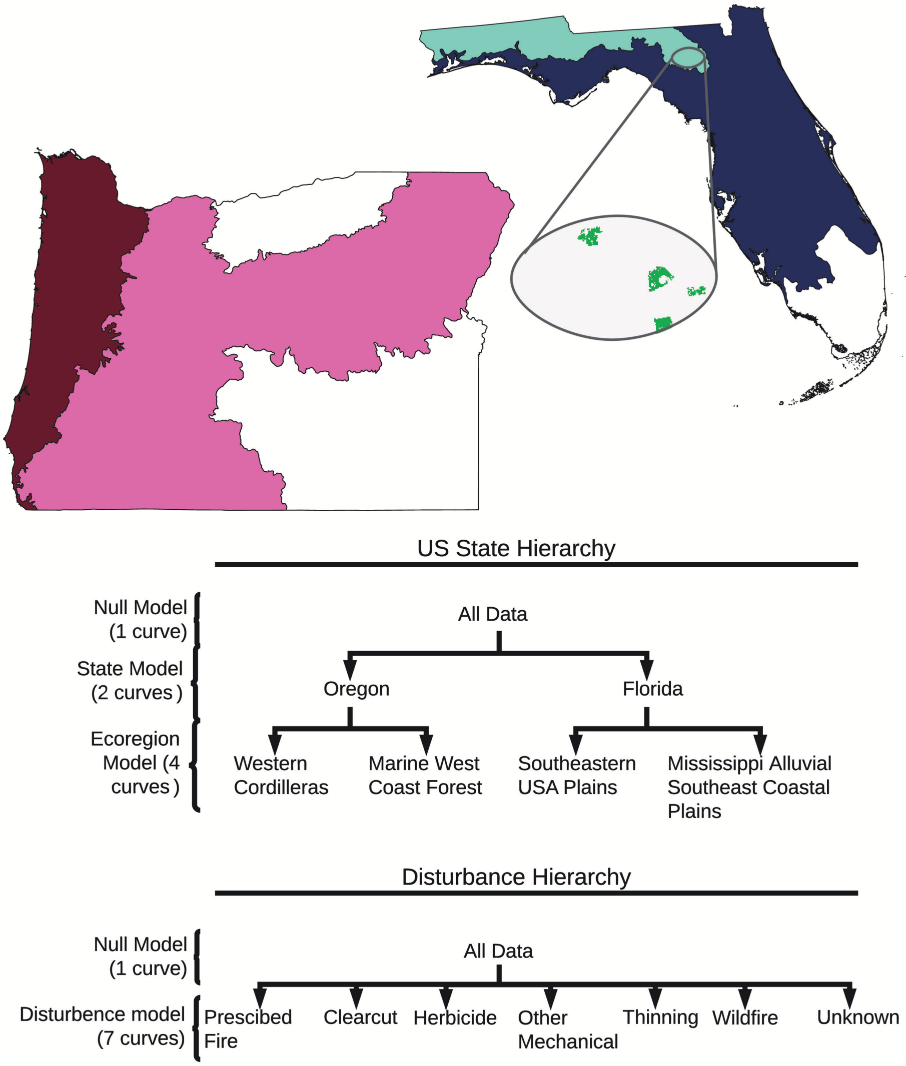


FIGURE 7 | Visualization of data subsetting and model hierarchies. Colored regions show what portions of Oregon and Florida were used in analyses. Cutouts show a sample of LANDFIRE raster file with disturbances in green. Model hierarchies show the different models compared, and the data used to make each curve.

of disturbance events (1%), but a large fraction of disturbance area (56%) (**Figure 9**; **Supplemental Table 1**). We treated Mixed disturbance as a separate class of disturbance in our comparison of size distributions. To calculate interior ratio curves these mixed disturbances were removed. Many of the disturbances most frequently co-occurring within mixed disturbances are represented in our curve fits (**Supplemental Figure 2**).

Assessing Statistical Significance

We used two different statistical tests for the two different disturbance metrics. For the size distributions, we compared the size distributions of disturbance type, US states, and ecoregions using a two-sided Kolmogorov–Smirnov test. We corrected the P-values using a Bonferroni correction (Massey, 1951; Bland and Altman, 1995). We compared size distributions of all disturbance types present within Florida and Oregon that had 20 or more disturbance events. This excluded biological and disease disturbance classes ($N = 4$, $N = 6$; **Supplemental Table 1**). We made 66 pairwise comparisons among 12 disturbance types, and three comparisons among state and two ecoregions. After correction, our alpha value was 0.000725 (**Supplemental Table 2**).

For the interior to total ratio, we fit and statistically compared curves corresponding to null models and different hierarchy levels. The curves were fitted using a modified Michaelis-Menten curves of the form $y = \frac{ax^c}{b+x^c}$ using a maximum-likelihood approach assuming Gaussian error (Michaelis and Menten, 1913). The form was chosen based on visual agreement with the data and maximum likelihood after comparison with six other functional forms (**Supplemental Figure 1**; **Supplemental Table 3**). Different curves were compared using a likelihood ratio test. Comparing the curves meant comparing different hierarchical levels (**Figure 7**). We fit two hierarchies, one starting at the US state level, and one at the disturbance-type level (**Figure 7**). In the US state hierarchy, an all-data null model was compared to a model where Oregon and Florida were fit separately. The US state-model was then compared to a model where each ecoregion was fit separately. In the second hierarchy, an all-data null model was compared to a model where each disturbance type was fit separately. The disturbance-model was then compared to a disturbance-by- US state model (**Figure 7**; **Supplemental Table 4**). We also separately compared a one-curve-Florida model to a two-curve-ecoregion model, and a one-curve-Oregon model to a two-ecoregion-curve model. We did this to see if the differences between ecoregions within Florida would be significant in isolation of the differences between Oregonian ecoregions (**Supplemental Table 4**). Because all single-pixel, double-pixel, and triple-pixel configurations produce the same interior ratio (**Figure 4**), curves were fit only to disturbances over 3 pixels (0.27 ha) large. To meet requirements of likelihood ratio tests, the data was subset to include only the disturbance types that were common amongst all ecoregions. Disturbance types included: clearcut, herbicide, other mechanical disturbances, prescribed fire, thinning, wildfire, and unknown. The distinction between wildfire, and prescribed fire is that a wildfire is an unplanned fire, prescribed fires are intentionally set and managed fires (LANDFIRE Disturbance, 2016). To contextualize modeled curves, we included hexagonal density plots, representing the spread and overall shape of all the data used to generate curves (ggplot2, 3.0.0; Wickham, 2016). To aid in interpretation, the upper and lower bounds for the interior ratio were also visualized based on calculations of the theoretical minimum (linear disturbance) and maximum (round disturbance) interior ratios for a given disturbance size. All analyses were performed in R (3.5.0; R Core Team, 2018) with adjacency calculations performed using the raster library (2.6-7; Hijmans, 2017).

RESULTS

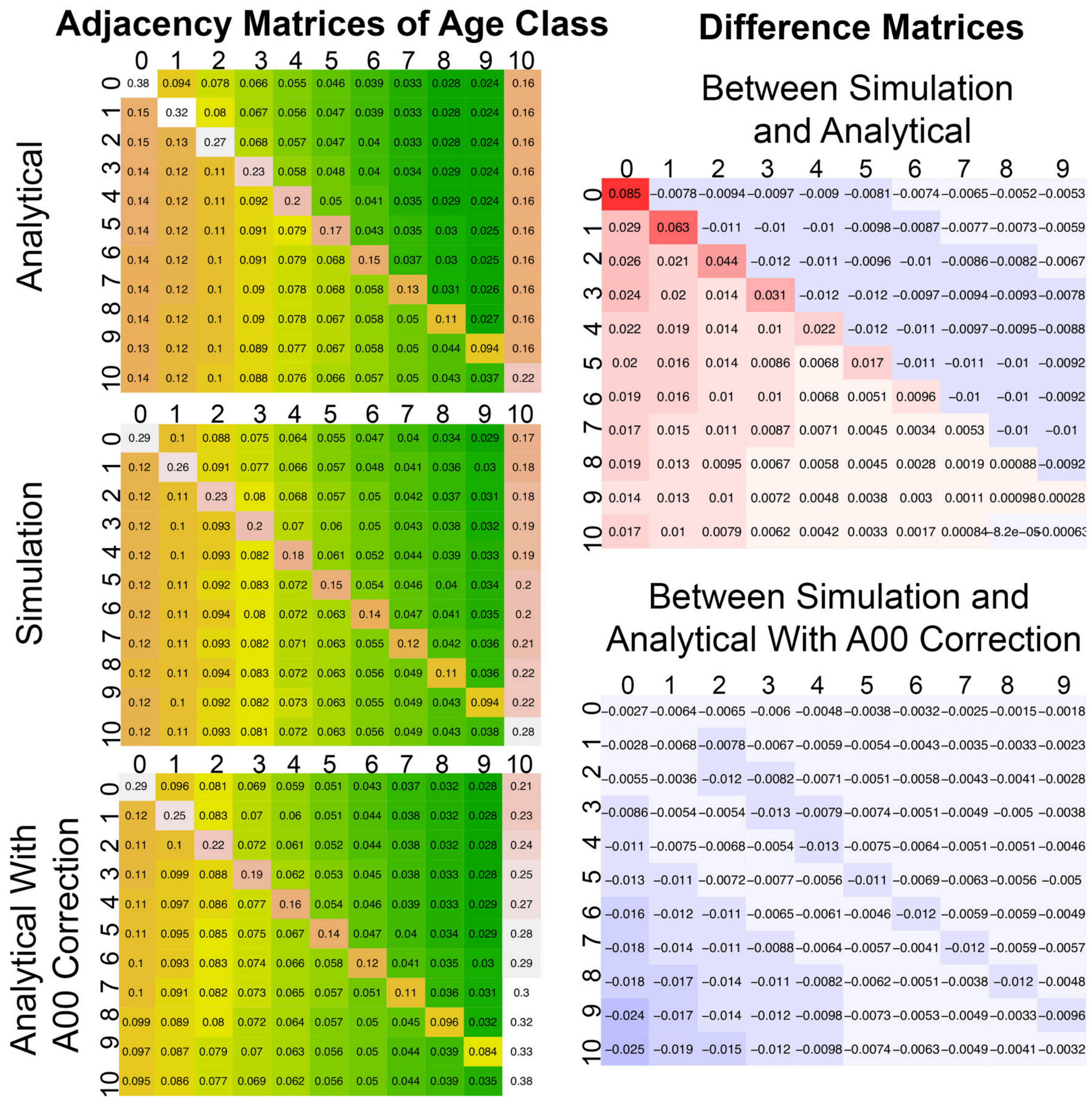
Dynamic Adjacency Updating

The analytical model for calculating disturbance spread and dynamically updating landscape adjacency was assessed by comparing the analytical model to a spatially-explicit stochastic simulation. In both cases the landscape was initiated from bare ground (age = 0) and run 1,000 years to reach a steady-state. **Figure 8** shows that the steady-state adjacency predicted by both models had the same structural features, as summarized in section Simulating Disturbance Spread: patches within an age class tended to be more self-adjacent, but that self-adjacency decays geometrically with age; there is also a geometric decay along rows, but with greater adjacency above the diagonal. Numerically, the predicted adjacencies were also very similar, though with the analytical model slightly overpredicting $A_{0,0}$. Because so many of the other rates in the adjacency matrix decay from $A_{0,0}$, there are slight biases elsewhere. However, the error propagation from $A_{0,0}$ is consistent with the underlying structure for updating the matrix being correct, because it means that structural elements are preserved as the landscape ages.

This impact of errors in $A_{0,0}$ on the overall adjacency calculation was tested with a third model (**Figure 8** bottom left), where the analytical model was run using the $A_{0,0}$ derived from the numerical simulation. Overall this model improved the overall pattern in the adjacency matrix, especially along the main diagonal. The remaining error (**Figure 8** bottom right) is largely concentrated in two places. First, there is greater adjacency with the oldest "absorbing" age class than observed in the simulation (left hand column). Second, because of this the bottom left corner (adjacency of old age classes to young classes) is a bit lower than observed. Matrix rows have a sum-to-one constraint, so some of these errors are inevitable compensating errors. It is also worth noting that in nudging $A_{0,0}$ directly we are not nudging the underlying terms used to calculate $A_{0,0}$ (I, D, a), which are also used in update the rest of A, meaning this test is not strictly internally consistent. An open question is how much of the remaining error in the adjacency matrix updating, is in the underlying analytical simulation of disturbance spread (I, D, a) vs. approximations in the updating of A? This is something we hope to investigate further in the future.

Disturbance Size Distribution

Our Kolmogorov–Smirnov pairwise comparison of disturbance type size distributions found that the majority of disturbance types had significantly distinct distributions ($p << 0.001$) (**Figure 9**; **Supplemental Table 2**). The three exceptions were



Adjacency Matrices of Age Class

Analytical

	0	1	2	3	4	5	6	7	8	9	10
0	0.38	0.094	0.078	0.066	0.055	0.046	0.039	0.033	0.028	0.024	0.16
1	0.15	0.32	0.08	0.067	0.056	0.047	0.039	0.033	0.028	0.024	0.16
2	0.15	0.13	0.27	0.068	0.057	0.047	0.04	0.033	0.028	0.024	0.16
3	0.14	0.12	0.11	0.23	0.058	0.048	0.04	0.034	0.029	0.024	0.16
4	0.14	0.12	0.11	0.092	0.2	0.05	0.041	0.035	0.029	0.024	0.16
5	0.14	0.12	0.11	0.091	0.079	0.17	0.043	0.035	0.03	0.025	0.16
6	0.14	0.12	0.1	0.091	0.079	0.068	0.15	0.037	0.03	0.025	0.16
7	0.14	0.12	0.1	0.09	0.078	0.068	0.058	0.13	0.031	0.026	0.16
8	0.14	0.12	0.1	0.09	0.078	0.067	0.058	0.05	0.11	0.027	0.16
9	0.13	0.12	0.1	0.089	0.077	0.067	0.058	0.05	0.044	0.094	0.16
10	0.14	0.12	0.1	0.088	0.076	0.066	0.057	0.05	0.043	0.037	0.22

Simulation

	0	1	2	3	4	5	6	7	8	9	10
0	0.29	0.1	0.088	0.075	0.064	0.055	0.047	0.04	0.034	0.029	0.17
1	0.12	0.26	0.091	0.077	0.066	0.057	0.048	0.041	0.036	0.03	0.18
2	0.12	0.11	0.23	0.08	0.068	0.057	0.05	0.042	0.037	0.031	0.18
3	0.12	0.1	0.093	0.2	0.07	0.06	0.05	0.043	0.038	0.032	0.19
4	0.12	0.1	0.093	0.082	0.18	0.061	0.052	0.044	0.039	0.033	0.19
5	0.12	0.11	0.092	0.083	0.072	0.15	0.054	0.046	0.04	0.034	0.2
6	0.12	0.11	0.094	0.08	0.072	0.063	0.14	0.047	0.041	0.035	0.2
7	0.12	0.11	0.093	0.082	0.071	0.063	0.055	0.12	0.042	0.036	0.21
8	0.12	0.11	0.094	0.083	0.072	0.063	0.056	0.049	0.11	0.036	0.22
9	0.12	0.1	0.092	0.082	0.073	0.063	0.055	0.049	0.043	0.094	0.22
10	0.12	0.11	0.093	0.081	0.072	0.063	0.056	0.049	0.043	0.038	0.28

Analytical With A00 Correction

	0	1	2	3	4	5	6	7	8	9	10
0	0.29	0.096	0.081	0.069	0.059	0.051	0.043	0.037	0.032	0.028	0.21
1	0.12	0.25	0.083	0.07	0.06	0.051	0.044	0.038	0.032	0.028	0.23
2	0.11	0.1	0.22	0.072	0.061	0.052	0.044	0.038	0.032	0.028	0.24
3	0.11	0.099	0.088	0.19	0.062	0.053	0.045	0.038	0.033	0.028	0.25
4	0.11	0.097	0.086	0.077	0.16	0.054	0.046	0.039	0.033	0.029	0.27
5	0.11	0.095	0.085	0.075	0.067	0.14	0.047	0.04	0.034	0.029	0.28
6	0.1	0.093	0.083	0.074	0.066	0.058	0.12	0.041	0.035	0.03	0.29
7	0.1	0.091	0.082	0.073	0.065	0.057	0.051	0.11	0.036	0.031	0.3
8	0.099	0.089	0.08	0.072	0.064	0.057	0.05	0.045	0.096	0.032	0.32
9	0.097	0.087	0.079	0.07	0.063	0.056	0.05	0.044	0.039	0.084	0.33
10	0.095	0.086	0.077	0.069	0.062	0.056	0.05	0.044	0.039	0.035	0.38

Difference Matrices

Between Simulation and Analytical

	0	1	2	3	4	5	6	7	8	9
0	0.085	−0.0078	−0.0094	−0.0097	−0.009	−0.0081	−0.0074	−0.0065	−0.0052	−0.0053
1	0.029	0.063	−0.011	−0.01	−0.01	−0.0098	−0.0087	−0.0077	−0.0073	−0.0059
2	0.026	0.021	0.044	−0.012	−0.011	−0.0096	−0.01	−0.0086	−0.0082	−0.0067
3	0.024	0.02	0.014	0.031	−0.012	−0.012	−0.0097	−0.0094	−0.0093	−0.0078
4	0.022	0.019	0.014	0.01	0.022	−0.012	−0.011	−0.0097	−0.0095	−0.0088
5	0.02	0.016	0.014	0.0086	0.0068	0.017	−0.011	−0.011	−0.01	−0.0092
6	0.019	0.016	0.01	0.01	0.0068	0.0051	0.0096	−0.01	−0.01	−0.0092
7	0.017	0.015	0.011	0.0087	0.0071	0.0045	0.0034	0.0053	−0.01	−0.01
8	0.019	0.013	0.0095	0.0067	0.0058	0.0045	0.0028	0.0019	0.00088	−0.0092
9	0.014	0.013	0.01	0.0072	0.0048	0.0038	0.003	0.0011	0.00098	0.00028
10	0.017	0.01	0.0079	0.0062	0.0042	0.0033	0.0017	0.00084	−8.2e−05	−0.00063

Between Simulation and Analytical With A00 Correction

	0	1	2	3	4	5	6	7	8	9
0	−0.0027	−0.0064	−0.0065	−0.006	−0.0048	−0.0038	−0.0032	−0.0025	−0.0015	−0.0018
1	−0.0028	−0.0068	−0.0078	−0.0067	−0.0059	−0.0054	−0.0043	−0.0035	−0.0033	−0.0023
2	−0.0055	−0.0036	−0.012	−0.0082	−0.0071	−0.0051	−0.0058	−0.0043	−0.0041	−0.0028
3	−0.0086	−0.0054	−0.0054	−0.013	−0.0079	−0.0074	−0.0051	−0.0049	−0.005	−0.0038
4	−0.011	−0.0075	−0.0068	−0.0054	−0.013	−0.0075	−0.0064	−0.0051	−0.0051	−0.0046
5	−0.013	−0.011	−0.0072	−0.0077	−0.0056	−0.011	−0.0069	−0.0063	−0.0056	−0.005
6	−0.016	−0.012	−0.011	−0.0065	−0.0061	−0.0046	−0.012	−0.0059	−0.0059	−0.0049
7	−0.018	−0.014	−0.011	−0.0088	−0.0064	−0.0057	−0.0041	−0.012	−0.0059	−0.0057
8	−0.018	−0.017	−0.014	−0.011	−0.0082	−0.0062	−0.0051	−0.0038	−0.012	−0.0048
9	−0.024	−0.017	−0.014	−0.012	−0.0098	−0.0073	−0.0053	−0.0049	−0.0033	−0.0096
10	−0.025	−0.019	−0.015	−0.012	−0.0098	−0.0074	−0.0063	−0.0049	−0.0041	−0.0032

FIGURE 8 | Comparison between adjacency matrices for a stochastic spatial simulation (simulation from **Figure 2**, middle) analytical approximation (top), and analytical approximation where a correction was applied to A00. All adjacency matrices are after 1,000 years (steady state). To the right are difference matrices between the simulation matrix and the two analytical matrices. Age class aggregated into 10 year bins ([0 − 9] = 0, [10 − 19] = 1, etc.) with all patches 100 year or older in bin 10. The 10th column of the error matrices was removed because of a summing to 1 constraint.

clearcut, wildland fire, and harvest, which had non-significant differences with roughly half of the disturbance classes. Finally, mastication had no significant difference between wildfire and chemical (**Supplemental Table 2**). The size distributions of Florida and Oregon were significantly different, as well as the two ecoregions nested within Oregon ($p < 0.001$; **Supplemental Table 4**). The two ecoregions size distributions nested within Florida were not found to be significantly different. However, in other size distributions significant differences were found despite visual similarity in part due to large sample sizes. The size distributions have a large range in sample sizes. US state-level size distributions were based on very large sample sizes (Oregon $N = 27{,}137$, Florida $N = 20{,}329$). Disturbance sample sizes range from harvest with $N = 22$ to unknown $N = 34{,}560$ (**Supplemental Table 1**). Unknown disturbances accounted for the majority of disturbance events in the overall dataset, and a large proportion of the area (20%). All four ecoregions had a similarly shaped size distribution, with peaks at single-pixel (0.09 ha) disturbances and at 7 ha disturbances. The 7-ha peak aligns with disturbance peaks in the disturbance categories unknown, thinning, wildland fire, mixed, harvest and wildfire. Within Oregon, the Western Cordillera ecoregion has more small and mid-level size disturbances than the Marine West Coast Forest, the Western Cordillera also had both considerably

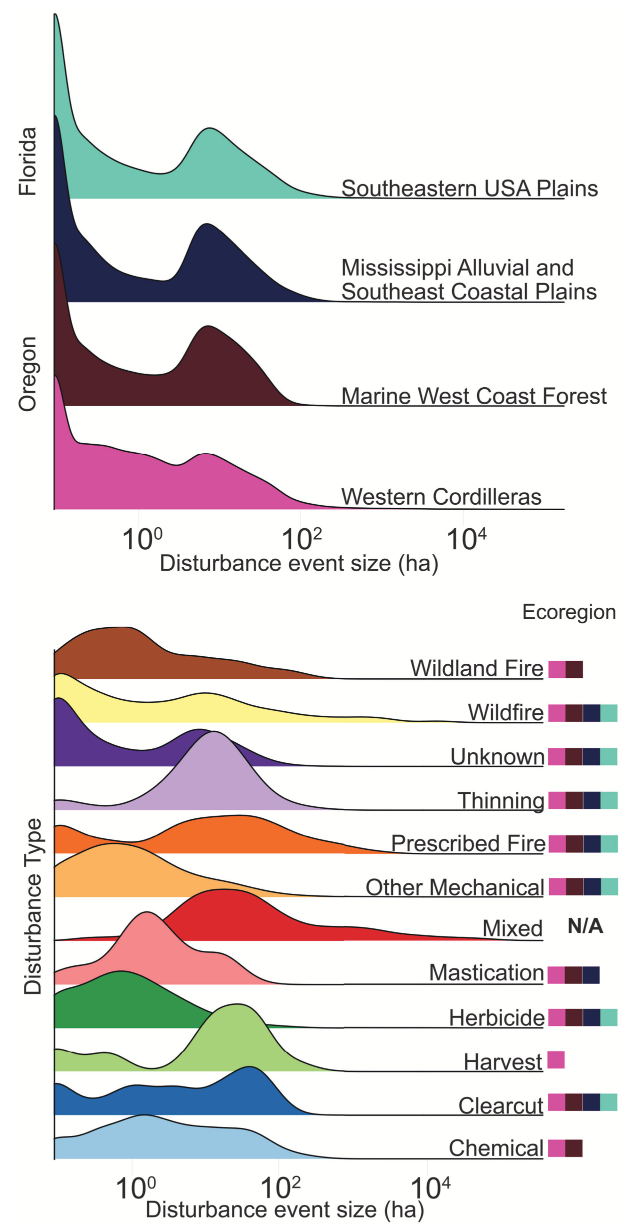


FIGURE 9 | Size density plots showing the contrasts between ecoregion/state and disturbance type. Colored boxes next to disturbance size density curves show what ecoregion contains the respective disturbance. Sample sizes associated with density plots can be found in **Supplemental Table 1**.

more disturbance events than the Marine West Coast Forest, and a larger area of disturbance (75%). Disturbance plots show more varied patterns, Wildfire and prescribed fire have a long tails, reflecting the influence of rare but large disturbances. In contrast, thinning and mastication have distinct peaks and sharper drop-offs, suggesting more standardized anthropogenic disturbances and smaller sizes. Mixed disturbance has the longest tail, and no peak at small disturbances. Herbicide and other mechanical disturbances have visually similar distributions but were found to be significantly different (Herbicide $N = 4{,}655$, Other Mechanical $N = 3{,}546$). Within mixed disturbances, herbicide and other mechanical disturbances co-occurred most frequently (**Supplemental Figure 2**).

Disturbance Interior Ratio Curves

We found a significant effect of US state ($p < 0.001$) and ecoregion nested within states ($p < 0.01$). Oregon had a wider range of interior ratios, with a higher occurrence of linear disturbances than Florida (**Figure 10**). Florida and Oregon have similar numbers of overall disturbance occurrence, but Oregon disturbances have a larger proportion of the total area of disturbances (%79). Within Oregon, small disturbances were more compact in Marine West Coast forests than in the Western Cordillera small disturbances, but this relationship crosses, such that Marine West Coast disturbances were less round at large disturbance sizes. The curves fit for the two ecoregions in Florida are nearly identical (**Figure 10**). Despite visual similarity, the two ecoregion curves were found to be significantly different even when compared to just a Florida curve model. Best fit parameters for all curves are provided in **Supplemental Table 5**.

In our second hierarchy, there was a significant effect of disturbance type ($p < 0.0001$), but not US state nested within disturbance ($p > 0.1$). Herbicide is the most distinctively linear, followed by other mechanical disturbances, and then unknown disturbances. Fire disturbance types (prescribed and wildfire) were closer to the maximum interior ratio curve, suggesting that fires tend to be compact and burned pixels were predominantly adjacent to other burned pixels (**Figure 11**). Disturbance-level curves show that prescribed fires are less compact at smaller sizes and larger sizes than natural fires, but at the most frequent size is similarly shaped. Thinning resembles other compact disturbances, but begins to become more linear at large sizes relative to wildfire. Clearcut follows a similarly compact pattern to wildfire. Individual disturbance curves and data plots can be found in the supplement (**Supplemental Figure 3**).

DISCUSSION

Theoretical Framework

Our framework for scaling spatially-implicit contagious disturbances is reasonably accurate, computationally efficient, and theoretically provocative. Our framework was able to estimate the fraction of the landscape that was disturbed as a function of disturbance initiation, adjacency, and spread probabilities (**Figure 2**). We were able to show that disturbance initiated in one age class would spread into stands of different ages based on their relative adjacencies (**Figure 3**). We demonstrated not only the ability to predict the self-adjacency of newly-disturbed areas (**Figure 6**), but also the adjacency of newly-disturbed areas to non-disturbed areas and the ability to update the adjacency of non-disturbed areas to each other in light of new disturbance. While the corrected self-adjacency predictions perform well (**Figure 8**), improving this correction is a useful area for future research, for example by accounting for the size of disturbed patches in calculating the probability that they will merge. In addition, it is important to note that when simulating disturbance using empirical *adj* functions that this correction term does not need to be included unless distinct,

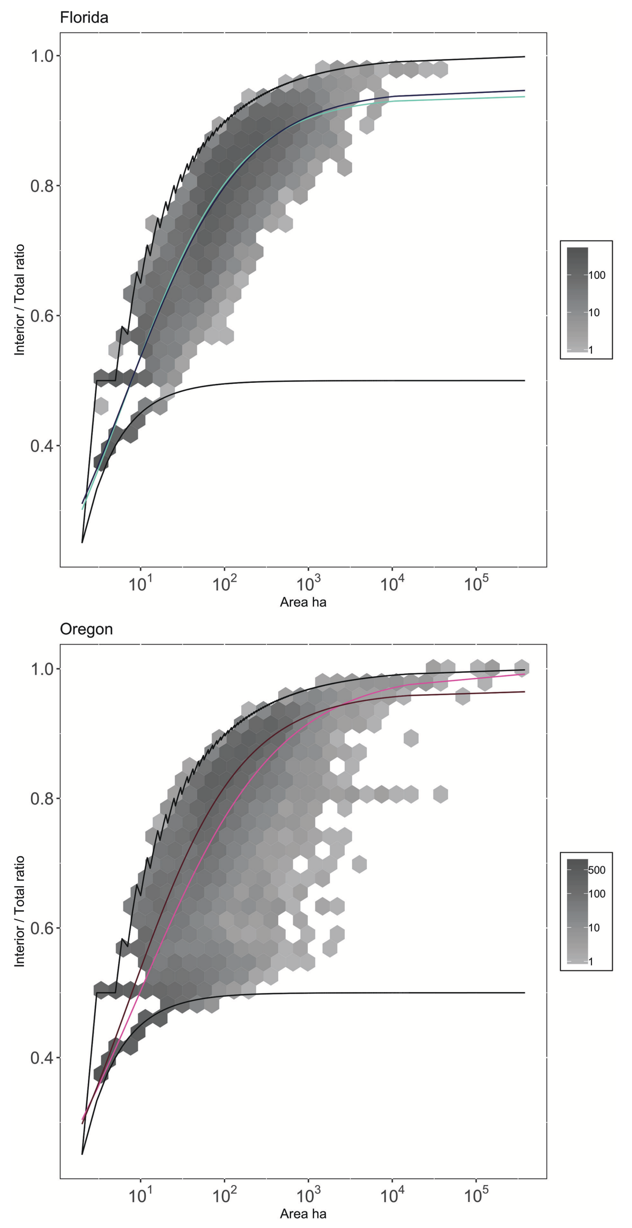


FIGURE 10 | Mean trends of Ecoregion within State. Curves match Ecoregion model curves referenced in **Figure 7**. Gray hexes correspond to binned-counts of number of disturbance events. Black lines correspond to core and linear bounding cases. Parameter values associated with curves can be found in **Supplementary Table 5**.

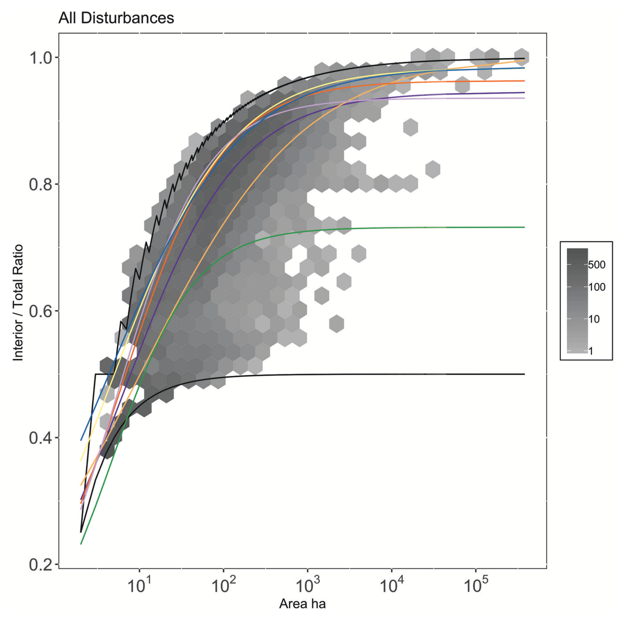


FIGURE 11 | Mean trends of disturbance type. Curves match Disturbance model curves referenced in **Figure 7**. Gray hexes correspond to binned-counts of number of disturbance events. Black lines correspond to linear bounding cases. Parameter values associated with curves can be found in **Supplementary Table 5**. Plots of individual curves against data can be found in **Supplementary Figure 3**.

but adjacent, disturbances occurring during the same time step, were separated in the original data (usually this is not possible). We were able to successfully update adjacency over 1,000 years within a reasonable level of accumulated error, and capture the major emergent features of contagious disturbance adjacency (**Figure 8**), such as the geometric decay of self-adjacency as even-aged stands mature and the geometric decay of adjacency within an age class (greater probability of being adjacent to newer disturbances) with greater adjacency above the diagonal (young) than old. That said, if older age classes are aggregated (bottom row) then considerable self-adjacency among old-growth stands can develop.

There are a number of important applications where this modeling framework can be immediately applied and expanded upon. At the top of this list is improving the incorporation of sub-grid scale disturbance processes within regional and global scale models, such as Dynamic Global Vegetation Models (DGVMs), Vegetation Demographic Models (VDMs, Fisher et al., 2018), and coupled Earth System Models. These models operate at a scale where spatially-explicit approaches are not computationally feasible– a typical landscape model operating at LANDSAT (30 × 30 m) resolution would require simulating hundreds of billions of grid cells to capture the Earth's land surface. As a result, disturbances that we know to be spatially contagious are either absent from these models altogether (Hicke et al., 2012; Dietze and Matthes, 2014; e.g., insects and pathogens) or represented using much simpler zeroth-order (spatially homogeneous) or first-order (fractional area) approximations (e.g., fire, land use). By using these simpler approximations, existing models miss important ecological phenomena, such as the spread of disturbance initiated in one age class or vegetation type into other vegetation within that grid cell. Depending on whether these models assume fractional areas are completely independent or randomly-distributed, these approaches will systematically either over- or underestimate (respectively) the degree of spatial adjacency occurring on the landscape. This will potentially bias estimates of dispersal limitation, lateral shading, microclimate, and lateral hydrologic and biogeochemical fluxes (Melton and Arora, 2014).

Even where spatially-explicit models are computable (e.g., landscape-scale models of vegetation communities and biogeochemistry), there is often considerable uncertainty in the initial conditions. Spatially explicit models require state variables to be estimated at a fine spatial resolution (Shifley et al., 2008), which is very data intensive and frequently underconstrained. Furthermore, the errors in spatial maps of initial conditions are not independent, so the uncertainties do not simply average out with the number of grid cells. In contrast, with spatially-implicit models we can often generate estimates of the probability distributions of age classes and their adjacency with much greater confidence (law of large numbers) than we can map explicitly. For example, one may be able to estimate the fraction of a landscape that is a certain age class (e.g., 10 to 20-years-old) much more precisely than one can estimate the age of a specific 30 × 30 m pixel. Because of this, the total predictive uncertainty in a spatially explicit model could be larger than a spatially-implicit approximation, for example if the initial condition uncertainties of the spatial model outweigh the approximation errors of the implicit model (Dietze, 2017). Without detailed inventory data, initializing a spatially explicit model presents a trade-off between feasibility and accuracy.

Beyond the global and vegetation modeling communities, our derivation can act as a null model for spatial processes like arrangement, location dependence, and absolute distance dependence. Arrangement can have an effect on certain contagious disturbances: for example, corridors can differentially affect seed dispersal dependent on angle relative to prevailing wind direction (Damschen et al., 2014). Habitat fragmentation can correlate with overall abundance of habitat, raising questions about the separability of configuration from size in occupancy modeling (Fahrig, 2002; Prugh et al., 2008; With and King, 2018). Absolute distance dependence is common in invasion ecology, where rare dispersal events over long distances can have a large effect on the subsequent colonization rates (Nathan et al., 2003). While some processes have spatial dependence that cannot be captured in our framework, the assumptions of our approach allow it to act as a non-trivial null-model to separate those effects (Rosindell et al., 2011). Explicitly accounting for size with adjacency is useful for disentangling the effects of size and arrangement, which often co-occur and can lead to misattribution (Prugh et al., 2008).

Empirical Analysis

In this analysis we characterized Oregon's and Florida's disturbance regimes based on their size distributions and the relationship between disturbance size and interior ratio. We hypothesized that these metrics would differentiate between contrasting US state-wide disturbance regimes and disturbance types, and would reflect the nested structure of ecoregions. Broadly, we found this to be true. Our interior ratio curves were able to significantly differentiate between US state, ecoregion, and disturbance types (**Supplemental Table 4**). In particular, different disturbances had characteristic interior ratio curves. Fire disturbances had compact configurations while several anthropogenically controlled classes (herbicide and other mechanical disturbances) spread dendritically. Relative to other mechanical disturbances and herbicide thinning spread in a compact way, but notably spread more dendritically at large disturbance sizes. This could indicate that thinning management strategies are fragmenting landscapes compared to natural disturbances. That said, the hierarchical structure of our analysis did not capture all possible permutations of lumping and splitting disturbance types, so similar curves (i.e., Clearcut and Wildfire; **Figure 11**) might have been lumped if evaluated independent of other disturbance classes. Overall, these results suggest that our metric captures the major features of the regions' disturbance regimes, and highlights the effects of anthropogenically mediated disturbances.

Size distributions of disturbances were generally distinct, but not sufficient to differentiate all disturbance types. That said, ecoregion-level size distributions had similar shapes (**Figure 9**). The consistent shape of the size distributions could be an artifact of the LANDFIRE disturbance attribution (Unknowns were the largest class of disturbance events) and could reflect the dominance of fire and thinning in both Florida and Oregon. Visually and statistically, the ecoregion size distributions support the nesting structure of the ecoregions: Florida ecoregions are more similar to each other than they are to the Oregon ecoregions (**Figure 9**; **Supplemental Table 2**). Disturbances reflect that high spreading probability creates larger disturbances: prescribed fire, wildland fire, and wildfire are the most long-tailed distributions (**Figure 9**).

Overall, a strength of this empirical analysis is that it describes disturbances in terms of size and of configuration separately, which contrasts with many spatial metrics which convolve the two (e.g., mean interior/total). That different sources of disturbance have different spatial patterns in disturbances alone is not an unexpected result. Intuitively, different disturbance mechanisms have different spatial signatures. A roadway-construction is smaller and narrower than a typical commercial thinning. These findings take that intuition a step farther and explore the patterns that emerge at larger scales. When an ecosystem's disturbance regime is changing, that change will manifest as changes to disturbance size, or disturbance configuration (the interior ratio curve), or both. In the future, if we characterize more disturbance regimes in terms of these metrics, and better understand what factors drive their variability in time and across large spatial scales, it should be possible to use these relationships to forecast the spatial scaling of changing disturbance.

As an example, consider a shift in disturbance regime that does not change the disturbance size, but shifts the shape from dendritic to compact. Dendritic disturbances create corridors through the landscape, which affects the demography of the ecosystem by changing migration, favoring certain dispersal mechanisms, and increasing the propagule pressure of certain areas. Size and shape of patch plays a role in the success of invaders (McConnaughay and Bazzaz, 1987; Fahrig, 2002). Dendritic disturbances alter the abiotic properties of a system through the creation of edges. Edge-effects have been found in forest systems to increase carbon uptake, increase available light, and increase nutrient deposition (Reinmann and Hutyra, 2017). At the other extreme, more compact disturbances could cause more evenly aged composition and introduce more within-patch homogeneity by having a larger fraction of the disturbed pixels "sheltered" from surrounding areas.

Many contagious disturbances are projected to change in magnitude, severity, and location with climate change (Flannigan et al., 2000; Bradley et al., 2010; Mitchell et al., 2014; Parks et al., 2016). Ultimately, these metrics will help us make concrete predictions of how to scale up these disturbances' regime changes. To be able to do this the variability within these metrics needs to be explored: How do they change year-to-year and place-to-place? How is this variability related to changes in weather, climate, and characteristics of the biotic and abiotic environment? This analysis demonstrates that interior ratio curves have the potential to communicate unique information about contagious processes and we encourage evaluating its utility in future work.

Opportunities and Challenges in Future Implementation

Implementing this spatially-implicit framework in real-world models requires that a number of inputs be derived through empirical analysis. First, the initial condition for adjacency, $A_{t=0}$, needs to be estimated for every large-scale grid cell. Given maps of current vegetation, this is computationally intensive but a relatively straightforward operation either within GIS or scripting languages with geospatial libraries (e.g., R). Next, users need to then decide whether to forward simulate disturbances and interior ratios based on initiation probability and spread probability (section Simulating Disturbance Spread), or to rely on empirically observed size distributions and interior ratios (sections Disturbance Size Distribution and Disturbance Interior Ratio Curves). For short-term simulations, relying on empirically-derived statistics, such as those derived here for Florida and Oregon, is probably the easiest way to implement a wide range of different disturbance types. The empirical analyses conducted here could be further broken down using empirical covariates, such as weather, to capture changes interannual variability in disturbance size and shape (Hu et al., 2010). For longer-term simulation, forward simulations have the advantage of being able to extrapolate to new conditions. In the simplest simulations explored so far, the initiation and spread probabilities were typically held constant through time, for different age classes, and as a function of disturbance size, but as discussed earlier, all of these can be made to vary based on either mechanistic models (e.g., fire ignition and spread; Kitzberger et al., 2012) or empirical observations. In these cases, there is a well-established body of literature deriving such relationships for spatially-explicit landscape models that should be directly translatable to inform spatially-implicit approaches (Seidl et al., 2011; Mann et al., 2012).

Once the concept of dynamic adjacency is in place within large-scale models, this opens the door for improving the representation of many other ecological processes within large-scale models. First and foremost is probably the addition of edge effects, such as lateral light penetration vs. shading, as 75% of forests globally located <1 km from an edge (Haddad et al., 2015). Depending on the default assumption, which varies from model to model, current approaches are either massively underestimating how bright large disturbances are, or treating small disturbances as receiving full sun. Edge effects are known to have large impacts on microclimate (temperature, humidity, wind, etc.), which will have impacts on all aspects of modeled ecosystem function (productivity, biogeochemistry, hydrology, carbon storage, etc.). In addition to edges, adjacency can also be used to improve representations of dispersal limitation within large scale models, which typically assume seed is equally available at all points within a large grid cell, using the same approach of iterative multiplication of an adjacency matrix that we used here to simulate contagious spread. This could also be particularly useful for representing invasive species in large-scale models. Finally, adjacency could also be used to improve the representation of other lateral fluxes, such as hydrologic or nutrient flows.

We have argued that our size distribution and interior/total ratio metrics describe disturbance regimes in a way that forwards our fundamental understanding of disturbances. However, for a metric to be useful it has to be practical to measure. How difficult are these metrics to estimate empirically? Potential challenges arise depending on the scale of interest. At scales where spatial data is common (remote-sensing products, GIS analyses) calibration is straightforward. More work needs to be done to see how these metrics vary with environmental variable and time to clarify exactly how much data is required to fully characterize a disturbance regime. However, our results suggest that these metrics capture nuanced information about a disturbance regime. Measuring these metrics across landscapes presents the dual opportunity to model disturbance and probe theoretical implications of these metrics.

CONCLUSION

In this paper we lay out a theoretical derivation for the spatially implicit scaling of disturbances and explore the descriptive capacity of metrics that emerge from our derivation. We found that we were able to capture how different spread probabilities alter a landscape, and could update adjacency dynamically with new disturbances and stand age. We note the implications of this technique apply widely to multiple problems in scaling, through the improvement of ecosystem models, development of null models and the characterization of disturbance regimes.

DATA AVAILABILITY

The publicly available LANDFIRE Disturbance dataset used in this study can be found at the LANDFIRE host website https://www.landfire.gov/disturbance_2.php. All code used to generate intermediate measures and analysis is publicly available at https://github.com/mccabete/SpatialAdjacency.

AUTHOR CONTRIBUTIONS

MD contributed to the conception of the study and mathematical derivation. TM implemented the simulation tools and MD ran the simulations. TM performed the empirical analysis. TM and MD both wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

FUNDING

This work was made possible by a grant from the Department of Defense's Strategic Environmental Research and Development Program (SERDP) # RC-2636.

ACKNOWLEDGMENTS

The authors would like to thank members of the Dietze lab for reviewing the manuscripts and Dennis Milechin for his help in optimizing the scripts used for analyses.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00064/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

PERSPECTIVE
published: 03 April 2019
doi: 10.3389/fevo.2019.00095

Integrating Multiple Data Types to Connect Ecological Theory and Data Among Levels

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Ecological theories often encompass multiple levels of biological organization, such as genes, individuals, populations, and communities. Despite substantial progress toward ecological theory spanning multiple levels, ecological data rarely are connected in this way. This is unfortunate because different types of ecological data often emerge from the same underlying processes and, therefore, are naturally connected among levels. Here, we describe an approach to integrate data collected at multiple levels (e.g., individuals, populations) in a single statistical analysis. The resulting integrated models make full use of existing data and might strengthen links between statistical ecology and ecological models and theories that span multiple levels of organization. Integrated models are increasingly feasible due to recent advances in computational statistics, which allow fast calculations of multiple likelihoods that depend on complex mechanistic models. We discuss recently developed integrated models and outline a simple application using data on freshwater fishes in south-eastern Australia. Available data on freshwater fishes include population survey data, mark-recapture data, and individual growth trajectories. We use these data to estimate age-specific survival and reproduction from size-structured data, accounting for imperfect detection of individuals. Given that such parameter estimates would be infeasible without an integrated model, we argue that integrated models will strengthen ecological theory by connecting theoretical and mathematical models directly to empirical data. Although integrated models remain conceptually and computationally challenging, integrating ecological data among levels is likely to be an important step toward unifying ecology among levels.

Keywords: Bayesian statistics, ecological modeling, population ecology, community ecology, ecological dynamics, integrated models, inverse models, individual based model

Edited by:
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University of Exeter, United Kingdom

Reviewed by:
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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *01 October 2018*
Accepted: *11 March 2019*
Published: *03 April 2019*

Citation:
Yen JDL, Tonkin Z, Lyon J, Koster W, Kitchingman A, Stamation K and Vesk PA (2019) Integrating Multiple Data Types to Connect Ecological Theory and Data Among Levels. Front. Ecol. Evol. 7:95. doi: 10.3389/fevo.2019.00095

INTRODUCTION

The search for unifying principles in ecology has spawned many ecological theories (Scheiner and Willig, 2011). These theories often span multiple levels of organization, connecting individuals to population, communities, and ecosystems (e.g., Brown et al., 2004; Falster et al., 2017). Although ecologists regularly translate theoretical models into mathematical frameworks (e.g., Hubbell, 2001; Brown et al., 2004; Kooijman, 2010), it has proven difficult to parameterize these complex, mathematical frameworks so that the resulting models are accurate, realistic, and applicable to real-world challenges (Marquet et al., 2014). We believe that attempts to parameterize complex, process-explicit models have been hampered by the isolation of data collected at different levels of organization. Although theoretical models regularly span multiple levels of organization, statistical models rarely connect data in this way.

Most models of ecological processes are fitted as "forward models," where model parameters are estimated from data measured at the level of the parameter (e.g., individual survival estimated from data on individuals through time) (Caswell, 2001; Tredennick et al., 2017). Although forward models usually support unique parameter estimates, it is challenging to collect the data required to parameterize forward models reliably while maintaining generality (Manning and Goldberg, 2010; Tredennick et al., 2017). Recently, several statistical advances have enabled "inverse models," where model parameters are estimated from data measured at higher levels of organization than the model parameters (e.g., Ghosh et al., 2012; González et al., 2016). For example, inverse modeling approaches have been used to estimate individual survival and fecundity from time series of population abundances rather than individual recapture histories (Ghosh et al., 2012). Inverse models make use of widely available data on higher levels of organization (e.g., population abundance surveys), which overcomes issues of data availability (Ghosh et al., 2012; Ovaskainen et al., 2016). However, inverse models often fail to identify unique parameter combinations because observed patterns at one level of organization are often consistent with multiple sets of parameters at lower levels of organization, leading to problems of non-identifiability (Peng et al., 2011; Ghosh et al., 2012).

In general, both forward and inverse models focus on a single type of data. For example, forward models of population dynamics typically are parameterized with data on survival and recruitment (e.g., life tables) (Fujiwara and Diaz-Lopez, 2017). By contrast, inverse models of population dynamics often are parameterized with data on populations (e.g., abundance time series) (Ghosh et al., 2012). Forward and inverse models face different challenges; a lack of data hampers forward models whereas a lack of specificity hampers inverse models. Importantly, these challenges are complementary, which suggests that a potential route is to combine forward and inverse modeling approaches to parameterize models from data collected at multiple levels of organization (Evans, 2012; Dietze, 2017). Connecting data collected at multiple levels—an "integrated" modeling approach—makes full use of available data and enables reliable parameter estimates without loss of generality (Besbeas et al., 2002; Schaub et al., 2007; Maunder and Punt, 2013).

Integrated models potentially overcome the practical challenge of estimating reliable, realistic parameters in complex mathematical models, such as dynamic energy budget models (Kooijman, 2010) or matrix population models (Caswell, 2001). This practical benefit has implications for fundamental ecology. For example, widespread estimates of demographic vital rates in natural conditions might give substantial new insights into spatial and temporal variation in life histories (e.g., McIntyre and Hutchings, 2003). Similarly, simultaneous analysis of data on individuals, populations, communities, and ecosystems might support realistic, data-driven models of biodiversity and ecosystem function (Isbell et al., 2018), and would bridge ecological analyses across distinct spatial scales, which is critical to the development of general ecological theory (Chave, 2013). In the following sections, we give a general introduction to integrated models, outline an illustrative application to real data, and discuss several open challenges.

CONNECTING MULTIPLE DATA TYPES WITH INTEGRATED MODELS

Integrated models connect multiple data types through a composite likelihood function (Maunder and Punt, 2013). Central to this approach is a core process model that connects multiple data types through appropriate likelihoods (Besbeas et al., 2002). With an appropriate process model, a component likelihood can be defined for each data type:

$$\mathcal{L}_i = f_i(process),$$

where the subscript i indexes different data types and the function $f_i(x)$ is specific to the i^{th} data type. Multiple component likelihoods can be combined into a composite (joint) likelihood function:

$$\mathcal{L}_{\text{composite}} = g(\mathcal{L}_1, \mathcal{L}_2, \ldots, \mathcal{L}_n),$$

where the function $g(\ldots)$ takes multiple component likelihoods and returns a single value for the composite likelihood. Commonly, component likelihoods are assumed to be independent, in which case the function $g(\ldots)$ is the product of all component likelihoods:

$$\mathcal{L}_{\text{composite}} = \mathcal{L}_1 \times \mathcal{L}_2 \times \ldots \times \mathcal{L}_n.$$

The composite likelihood $\mathcal{L}_{\text{composite}}$ can be used with any likelihood-based methods of inference (e.g., maximum likelihood, Markov chain Monte Carlo) (Maunder and Punt, 2013).

The choice of process model is critical to an integrated model. The process model must connect data collected at multiple levels of organization (e.g., individuals and communities) and must be computationally tractable. Existing applications of integrated models have focused predominantly on population processes (e.g., species' occurrences, demographic models; Bird et al., 2014; Koons et al., 2017; Lahoz-Monfort et al., 2017; Zipkin et al., 2017), which facilitates computation while remaining relevant to multiple levels. However, any process model that connects multiple data types could be used (e.g., models of individual or ecosystem dynamics). A potentially useful focus is individual-based models, which could be connected to many data types at the expense of increased computational demands (Grimm and Railsback, 2005).

The primary challenge in the development of an integrated model is computational. Integrated models include potentially complex and dynamic process models, as well as multiple likelihoods that differ in complexity. Although a composite likelihood function is suited to many inference methods, high computational demands mean that fully Bayesian implementations are rare (but see Brooks et al., 2004; Zipkin et al., 2017). In addition, many implementations are hard-coded for particular case studies (Maunder and Punt, 2013), and generalizing these models typically requires knowledge of software for Bayesian hierarchical models (e.g., BUGS or AD Model Builder; Maunder and Punt, 2013; Koons et al., 2017). Recent advances in computational statistics and software are enabling more flexible implementations of integrated models, and we give an example of one such model in the following section.

EXAMPLE: ESTIMATING FISH POPULATION DYNAMICS FROM MULTIPLE DATA TYPES

Background

Globally, freshwater river ecosystems are stressed by a combination of water extraction, changes to flow regimes, commercial and recreational fishing, the introduction of exotic species, and chemical and thermal pollution (Nilsson et al., 2005; Koehn et al., 2014). In many regions of the world, increased frequency of droughts and increases in consumptive water use have led to widespread water shortages, further exacerbating stresses on river ecosystems (Nilsson et al., 2005). In response to water shortages, many government agencies have invested heavily in programs to deliver environmental flows—releases of water to protect biological resources—often with an explicit focus on the viability of fish populations (Beesley et al., 2014; Koehn et al., 2014).

The Murray-Darling Basin in south-eastern Australia is highly valued environmentally, economically, and socially. Environmental values have been heavily affected by river regulation, particularly through the seasonal reversal of the timing of flows and reduced frequency and magnitude of flooding (Maheshwari et al., 1995). The Murray-Darling Basin supports over 40 native fish species, many of which have experienced substantial declines in abundance over the past century (Koehn, 2015). Here, we focus on Murray cod (*Maccullochella peelii* Mitchell, 1838), a large-bodied freshwater fish species listed as vulnerable under the Australian Commonwealth Environment Protection and Biodiversity Conservation Act, 1999. Murray cod are included in several state and federal conservation programs, which aim to identify management actions that will maintain viable populations, often with an explicit focus on environmental flows (Koehn, 2015). A key requirement of these programs is reliable models of population dynamics that can be used to predict population dynamics in different locations and under different management scenarios (Yen et al., 2013).

Data Types

We used data collected over 20 years in six rivers in the Murray-Darling Basin: the Murray (1999–present), Ovens (2007–present), Loddon (2007–present), Goulburn (2008–present), Campaspe (2007–present), and Broken (2008–present). Available data included sizes of all individuals captured in a given survey, size-at-age data from otoliths collected from 55 individuals from 1999–present, and mark-recapture data from 1999–2017 at several locations in the Murray River. All three data sets had similar ranges of individual sizes and ages.

Statistical Analysis

Our aim was to parameterize an age-structured model of population dynamics from data on size-abundance distributions,

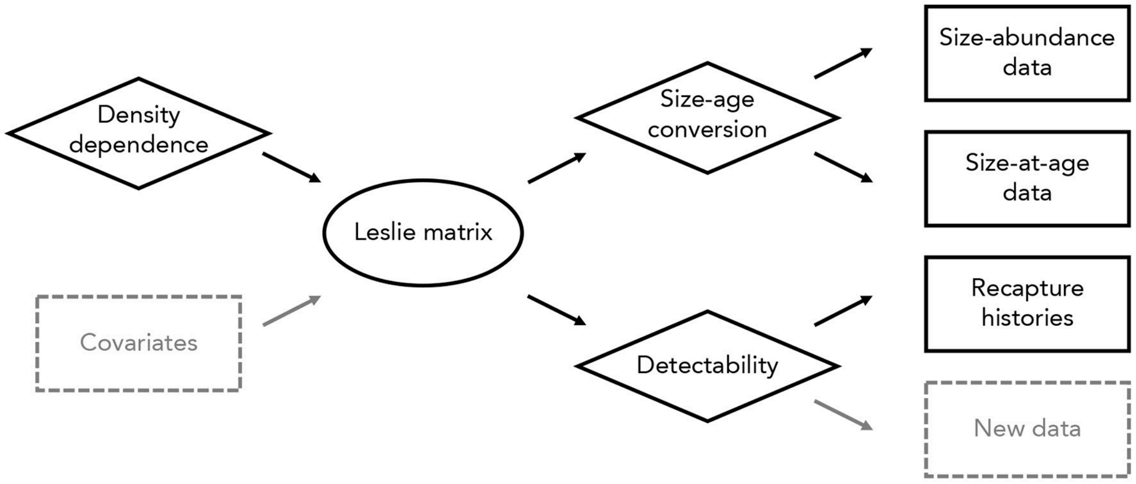

FIGURE 1 | Overview of the integrated modeling approach used here. Different data types (in rectangles) are connected to one another through a density-dependent Leslie matrix model (oval). Several sub-models (diamonds) incorporate density dependence, a conversion from sizes to ages, and detectability. New data types (dashed rectangles) could be included in this model without altering the overall modeling approach. Similarly, data and sub-models could be added or removed as needed, and the main Leslie matrix model could be replaced with an alternative process model (e.g., an integral projection model or individual-based model).

size-at-age data, and binary recapture histories (**Figure 1**). The underlying process model was a density-dependent Leslie matrix model with variation in vital rates among rivers (Caswell, 2001). We used five age classes and binned size-abundance data into eight size classes (round brackets exclude endpoints): [(0 , 200 g), (200 , 500 g), (500 , 1000 g), (1000 , 2000 g), (2000 , 5000 g), (5000 , 10,000 g), (10,000 , 20,000 g), and (20,000 , 60,000 g)]. These bins were chosen arbitrarily, with unequal bin widths to avoid the majority of individuals falling into one or a few size classes.

We connected size-abundance data, size-at-age data, and recapture histories to the underlying Leslie matrix with three component likelihoods (**Figure 1**). First, we assumed size-class abundances were independently Poisson-distributed, conditional on a detection probability, a conversion from size classes to age classes, and the matrix population model (i.e., dependencies among age classes are captured in the Leslie matrix). Second, we used binary recapture histories to estimate the probability of detection, assuming a Cormack-Jolly-Seber model with

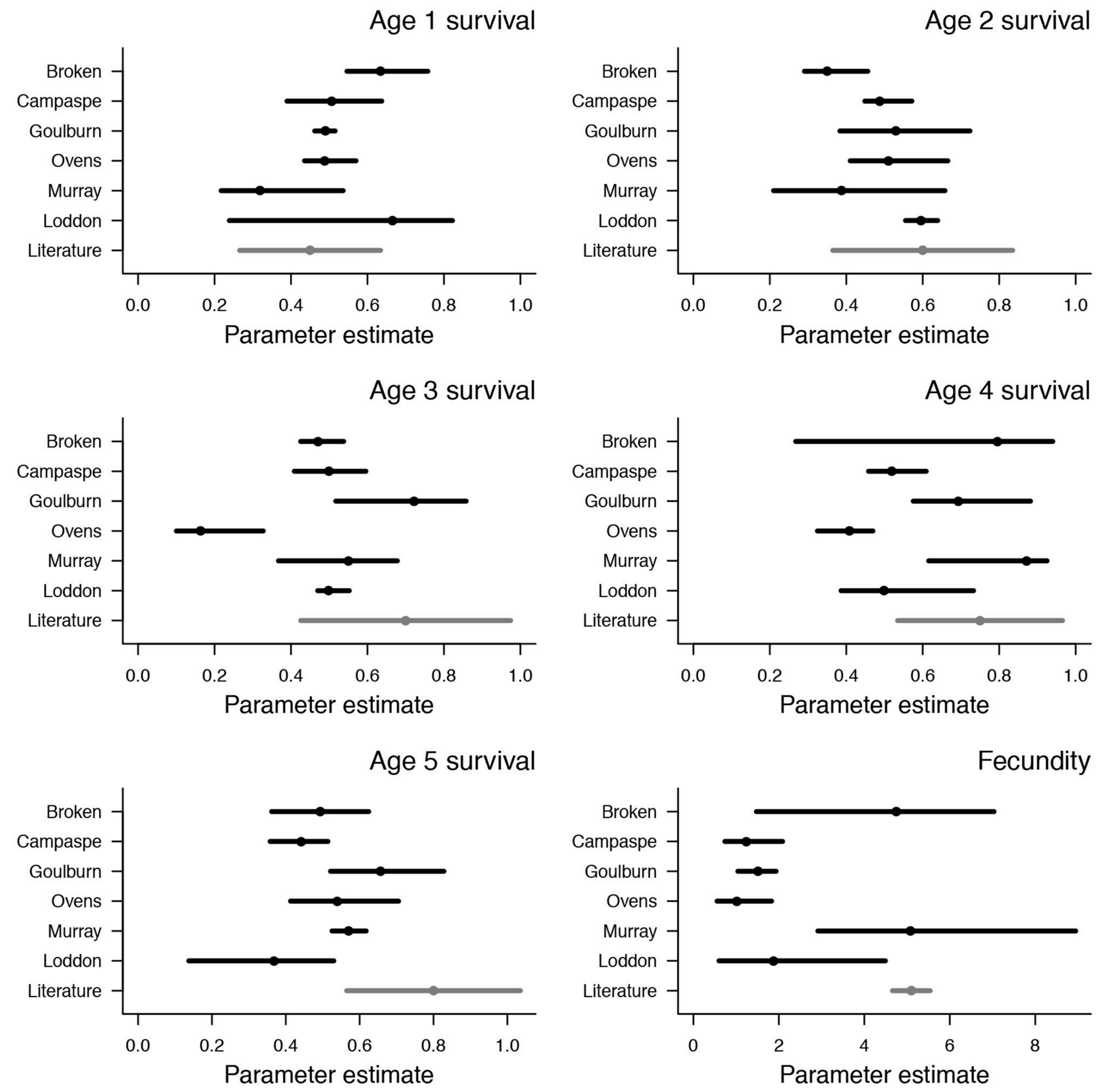

FIGURE 2 | Posterior distributions of survival and fecundity from age-structured population models of Murray cod. Values are shown for each of six rivers in south-eastern Australia (black points and lines), along with independent estimates from Yen et al. (2013) (gray points and lines). Points are median values and bars span 95% credible intervals.

time-varying survival probabilities (Lebreton et al., 1992). Third, we used size-at-age data to relate size-class abundances to age-class abundances, assuming that the distribution of individuals in a given size class among all age classes followed a multinomial distribution. We provide a detailed description of this model, including specification of prior distributions, in **Appendix S1**.

We assumed the three component likelihoods were independent, so that the composite likelihood was the product of all three component likelihoods:

$$\mathcal{L}_{\text{composite}} = \mathcal{L}_{\text{growth}} \times \mathcal{L}_{\text{abundance}} \times \mathcal{L}_{\text{capture}}.$$

Constructing models in this way is fully modular, and allows any or all elements of a given model to be changed (**Figure 1**). For example, the matrix population model could be replaced with an integral projection model or individual-based model, data sets of the same or different type could be added to the analysis, and data sets could be removed to estimate parameters using a forward or inverse modeling approach (**Figure 1**). The only requirement is that the component likelihoods can be defined; all other aspects of the modeling process are unchanged.

We used the *greta* R package to generate fully Bayesian parameter estimates (Golding, 2018). We based parameter estimates on 40000 random-walk Metropolis-Hastings Monte Carlo iterations (four chains of 100000 iterations, retaining every tenth sample), following a 100000 iteration warm-up and burn-in period. We assessed model convergence through visual inspection of chains and used Bayesian r^2 values to summarize model fit (Gabry and Goodrich, 2018). We did not use more-rigorous model validation (e.g., cross validation) because our goal was to illustrate the implementation of a simple integrated model rather than to present a full analysis of these data. Links to model code are in *Data availability*.

RESULTS AND DISCUSSION

The integrated model fitted observed abundances moderately well in five of six rivers, with median Bayesian r^2 values > 0.4 in all rivers except the Murray river (**Figure S1**, **Table S1**). Model fit was very poor in the Murray river (median Bayesian $r^2 = 0.00$) (**Figure S1**, **Table S1**). Poor model fit in the Murray river, which had the highest observed abundances, might be due to shared priors on vital rates drawing estimates toward those of other rivers. Fitted abundances did not always track observed abundances closely (**Figure S1**), due primarily to the constraints imposed by the matrix population model. Although a process-explicit approach might not match observed data as closely as alternative methods (e.g., a purely statistical regression model), the use of an explicit process model potentially guards against overfitting and, therefore, might be expected to yield more-accurate long-term predictions (Cuddington et al., 2013). We acknowledge that more-detailed model validation would be required to test this claim.

Median survival probabilities ranged from 0.32–0.67 in one and two year age classes, with the lowest values in the Murray river and highest in the Loddon river (**Figure 2**). Median survival probabilities of three and four year age classes was generally between 0.5 and 0.8, with lower values in the Ovens river (0.16 and 0.41 for three and four year age classes, respectively) (**Figure 2**). Median survival probabilities of the five year old age class were mostly between 0.4 and 0.6, with a slightly lower value in the Loddon river (0.37) and a slightly higher value in the Goulburn river (0.66) (**Figure 2**). Estimates of survival probabilities in one, two, and four year age classes were similar to values reported in the literature, but estimates in three and five year age classes were generally lower than values in the literature (**Figure 2**). Median fecundity estimates, which encompass egg and larval survival, ranged from 1 to 5, with low values (<2) in the Campaspe, Goulburn, Ovens, and Loddon rivers, and relatively high values (>4) in the Broken and Murray rivers (**Figure 2**). These higher estimates of fecundity in the Broken and Murray rivers match closely with existing estimates in the literature (**Figure 2**). Density dependence was weak in the Murray, Ovens, Goulburn, and Broken rivers ($k < 10^{-4}$) but strong in the Campaspe ($k = 0.01$) and Loddon rivers ($k = 0.02$), indicating relatively low carrying capacities in the Campaspe and Loddon systems (**Figure S2**, **Table S2**).

There are several possible extensions to this model. A relatively straightforward extension would consider temporal variation in vital rates, particularly in response to local or regional environmental conditions (**Figure 1**). Incorporating temporal variation in this way would enable projections of population abundances that are linked closely to contemporary and projected future environments (e.g., Yen et al., 2013). More challenging extensions might include size- or age-structured models of recapture histories or spatially explicit variation in vital rates. Although extensions such as these introduce computational challenges, it is conceptually straightforward to incorporate new data and models into the integrated modeling approach used here (**Figure 1**).

NEXT STEPS IN THE DEVELOPMENT OF INTEGRATED MODELS

The example presented here illustrates the use of an integrated model to estimate the parameters of a complex, process-explicit model. This approach enabled simultaneous estimates of demographic vital rates, detection probabilities, and size-age associations, which would not be possible without an integrated modeling approach. However, this example also illustrates several challenges. These include the computational demands of increasingly complex model structures (e.g., individual-based models), the development of generalizable likelihoods that allow novel data types to be included in arbitrarily complex model structures, and the development of more-sophisticated composite likelihoods that incorporate dependencies among data types. Rapid development of integrated modeling techniques suggest that these challenges will soon be overcome, enabling many new applications of integrated models. Two particularly exciting applications are the use of integrated models to connect data among many levels, and the use of integrated models to support advances in ecological theory.

Connecting Data Flexibly Among Many Levels

Most integrated models have focused on data collected at one or two levels. For example, integrated models of species distributions use data on populations (e.g., Lahoz-Monfort et al., 2017; Pacifici et al., 2017; Zipkin et al., 2017), while integrated models of demography use data on individuals and populations to estimate demographic vital rates (e.g., Brooks et al., 2004; Schaub et al., 2007; Bird et al., 2014; Koons et al., 2017). Few studies have moved beyond two levels to consider data spanning many levels (but see Péron and Koons, 2012). Given that individual behavior and movement, population dynamics, interspecific interactions, and ecosystem processes are all connected to the same underlying processes, it seems plausible that an integrated model could connect data among many levels.

Although integrated models are restricted by the computational demands of complex process models and likelihood functions, recent advances in computational software and hardware are rapidly overcoming these barriers. High-performance software libraries such as TensorFlow (Abadi et al., 2015) are enabling rapid computation of complex, dynamic models, supported by accessible libraries and packages in the R and Python computing environments (e.g., Golding, 2018). In addition, increasing availability and accessibility of high-performance computing environments is allowing non-specialists to undertake computationally demanding analyses. A major advance will be the development of flexible and modular software for integrated models that include different amounts and types of data.

Advancing Theory With Integrated Models

Integrated models have been used largely as a practical solution to data shortages and non-identifiable models (e.g., Maunder and Punt, 2013; Zipkin et al., 2017). However, a broader benefit of integrated models is their capacity to link ecological data directly with ecological processes. Ecological theory often is quantified through a mathematical process model. Therefore, connecting data with ecological processes supports close ties between theory and data, with theory informing the process models that underpin integrated data analyses. Similarly, an inability to parameterize process models from available data often limits the development of ecological theory. In this case, using all available data to parameterize complex process models has the potential to hasten the development of ecological theory. Examples include the refinement of life-history theory through more accurate demographic models and new insight into biodiversity-ecosystem function theory through models that connect population, community, and ecosystem dynamics. Although it is not entirely clear whether ecologists should emphasize theory developed from first principles or theory derived from data (Marquet et al., 2014), it is likely that close ties between theory and data will improve inferences, predictions, and understanding of ecological processes (Marquet et al., 2014; Rillig et al., 2015; Dietze, 2017).

DATA AVAILABILITY

All model code and data are archived at https://zenodo.org/record/2551819 (DOI: 10.5281/zenodo.2551819). Data are provided specifically for purposes of reproducibility. Raw data suitable for alternative analyses are publicly accessible through the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/).

AUTHOR CONTRIBUTIONS

JY and PV developed the statistical methods presented here. ZT, JL, WK, AK, and KS provided the case study and all data. JY conducted all analyses and wrote the first draft of the manuscript. All authors contributed to subsequent revisions of the manuscript.

FUNDING

JY and PV were supported by the Australian Research Council Centre of Excellence for Environmental Decisions (CE11001000104). Data collections used in this work were funded by the Murray Darling Basin Authority, the Commonwealth Environmental Water Office Long-Term Intervention Monitoring project, and the Victorian Environmental Flow Monitoring and Assessment Program, Department of Environment, Land, Water and Planning. JY received additional funds from The University of Melbourne and The Robert Johanson and Anne Swann Fund.

ACKNOWLEDGMENTS

We thank Diego Barneche, Julie Messier, Mary O'Conner, and Angelica Gonzalez for the invitation to write this perspective. Nick Golding provided advice on computational aspects of the work presented here. Many staff at the Arthur Rylah Institute contributed data used in this work, particularly Jason Lieschke, Joanne Kearns, John McKenzie, John Mahoney, Justin O'Mahony, Graeme Hackett, Andrew Pickworth, Scott Raymond, David Dawson, Matt Jones, Justin O'Connor, and Renae Ayres.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00095/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

PERSPECTIVE
published: 24 April 2019
doi: 10.3389/fevo.2019.00137

When Landscape Ecology Meets Physiology: Effects of Habitat Fragmentation on Resource Allocation Trade-Offs

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OPEN ACCESS

Edited by:
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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *29 August 2018*
Accepted: *05 April 2019*
Published: *24 April 2019*

Citation:
Ziv Y and Davidowitz G (2019) When Landscape Ecology Meets Physiology: Effects of Habitat Fragmentation on Resource Allocation Trade-Offs. Front. Ecol. Evol. 7:137. doi: 10.3389/fevo.2019.00137

Landscape heterogeneity is a general feature of natural environments, strongly affected by habitat fragmentation. It can affect a population's dynamics and probability of extinction. Fragmentation increases among-patch isolation and decreases patch size, resulting in a reduction in available resources in smaller patches. To persist, animals must be able to translate the variation imposed by fragmentation into adaptive energy allocation strategies that enable populations to avoid extinction. This means that physiological adaptations are expected to reflect changes in landscape configuration, especially in the size of the natural habitat patches and degree of isolation among them. We propose a novel, integrative conceptual framework in which spatial characteristics of the environment, imposed by fragmentation, lead to specific life-history traits that increase survival (at the individual level) and decrease the likelihood of extinction (as an emergent property at the population level). We predict that a resource allocation trade-off between the life-history traits of reproduction and dispersal along a fragmentation gradient will emerge. Populations occurring in patches of different sizes and isolations along gradients of fragmentation and productivity will exhibit differences in the strength of the dispersal-reproduction trade-off. Emerging from this framework are several explicit and testable hypotheses that predict that the dispersal-reproduction trade-off will be shaped by landscape heterogeneity imposed by fragmentation. Hence, this trade-off serves as the mechanistic link that translates environmental variation created by fragmentation into variation in species abundances and population dynamics by lowering local extinction probability and increasing overall population persistence.

Keywords: landscape ecology, habitat fragmentation, resource allocation tradeoff, dispersal-reproduction tradeoff, landscape physiology, productivity gradient, fragmentation gradient

INTRODUCTION

Here, we develop a framework that integrates two disparate fields of study, landscape ecology and evolutionary physiology; promoting an emerging new field, landscape physiology. Landscape ecology relies on correlations among landscape and population/community parameters but usually ignores individual-level mechanisms. Evolutionary and ecological physiology, in contrast, are mechanistic disciplines that focus on the microhabitat and often ignore landscape-level processes.

This framework generates explicit and testable hypotheses of how an organism translates habitat characteristics resulting from fragmentation *per se* (the condition of reduced patch size and greater isolation among patches), through the physiological mechanism of resource allocation strategies, into population dynamic parameters of reproduction, survival, and abundance. Integrating across physiology and the landscape in one unified framework will extend our ability to understand population extinction and persistence in light of current increases in habitat loss and climate change.

Landscape heterogeneity is one of the general features of natural environments. Habitats are distributed in space (hereafter, natural patches), are of different sizes and are at different distances. Natural patches of different size provide individuals with variable abiotic and biotic resources and niche opportunities and therefore may change the fitness of an individual. Different distances between natural patches require different dispersal efforts and may affect the energy and resources devoted to dispersal at the expense of energy and resources devoted to growth and fecundity in a particular natural patch. In the context of this paper, resources refer to nutritional and energy resources such as from carbohydrates, lipids, and proteins.

One form of landscape heterogeneity related to human impact is habitat fragmentation. Habitat fragmentation stresses the linkage between spatial elements and emphasizes the challenges organisms face in evolving strategies of resource allocation to life history traits. In this paper, we focus on the coupling of patch size and isolation in the context of habitat fragmentation, but also consider cases where size and isolation are decoupled to reflect large heterogeneous contexts.

Habitat fragmentation, a dominant feature of many landscapes, can result from habitat loss, due to, among others, road or city construction, and can affect a population's dynamics and probability of extinction (Fahrig, 2002, 2003; Reed, 2004; Hanski et al., 2013). This is especially true in regions where intensive use of agriculture has resulted in extensive fragmentation of natural habitats (Belanger and Grenier, 2002; Green et al., 2005; Millennium Ecosystem Assessment, 2005; Giladi et al., 2011). Climate change may possibly exacerbate the degree of fragmentation of natural habitats (Karieva et al., 1992; Klapwijk and Lewis, 2001; Opdam and Wascher, 2004). Fragmentation has multiple effects, leading to: (i) loss of total habitat area, (ii) reduced average habitat patch size, and (iii) increased distances among patches (the latter two reflect fragmentation *per se* effects; e.g., Gavish et al., 2012). Intensification of habitat fragmentation may result in a decline in species abundances and diversity, due to the differential within- and among-patch effects of fragmentation. At the within-patch level, small patch size leads to a reduction of suitable habitat, lower habitat quality and fewer resources, and thus to reduced population sizes and higher probability of extinction (MacArthur and Wilson, 1967). At the among-patch level, increased fragmentation may lead to greater distances among patches (low connectivity) and, possibly, to lower recolonization rates and a lower probability of replacement by individuals of that species from nearby habitats (Brown and Kodric-Brown, 1977; Hanski and Gilpin, 1997; Hanski and Gaggiotto, 2004).

For a population to persist, individuals within the population translate the abiotic and biotic variation they experience, including those imposed by fragmentation, into energy allocation strategies to life history traits. These life history traits in turn, affect demographic parameters that enable the population to avoid extinction. Life-history traits are strongly shaped by natural selection and result in adaptive states that should increase survival and enhance fitness (Roff, 1992; Stearns, 1992). In particular, natural selection acting on physiological priorities of energy allocation will result in tradeoffs in investment of limited energy and resources that maximizes fitness (Stearns, 1989; Zera and Harshman, 2001). A major physiological trade-off is one that involves dispersal and fecundity. We propose that a dispersal-reproduction trade-off serves as the physiological, mechanistic link by which organisms translate environmental variability experienced in fragmented habitats into life history traits that result in population persistence within those habitats (Hughes et al., 2003; Aguette and Schtickzelle, 2006; Guerra, 2011; King et al., 2011; Bonte et al., 2012). Here we focus on animals, but similar considerations are applicable to other organisms as well.

Life history evolution is largely concerned with phenotypic traits such as reproduction and survival that directly affect fitness (Roff, 1992; Stearns, 1992). Ecological and evolutionary physiology seeks to understand the mechanisms underlying these phenotypes (Garland and Carter, 1994; Feder et al., 2000; Karasov and Martinez del Rio, 2007). For example, the life history traits of body size and development time are regulated by eight signaling and hormonal pathways in insects (Nijhout et al., 2013; Gokhale and Shingleton, 2015), which result in 40,320 possible permutations of the control of growth (Davidowitz, 2016). This large number of possible combinations can be distilled into three physiological traits (Davidowitz, 2016) that explain 99% and 93% of the response of body size and development time, respectively, to simultaneous directional selection (Davidowitz et al., 2016). Thus, we can understand how two life history traits co-evolve, by understanding three underlying physiological mechanisms.

The allocation of resources is of major concern in understanding the physiology underlying life history traits: the strategies that have evolved to allocate resources and energy to one trait over another (Ricklefs and Wikelski, 2002). Such resource allocation strategies underlay constraints and tradeoffs among life history traits (Zera and Harshman, 2001; Boggs, 2009; Flatt and Heyland, 2011) and that of the landscape physiology framework presented here. Specifically, fecundity and dispersal are the life history traits of interest in this framework, whereas the strategies of resource allocation are the physiological mechanism that underlies these traits. Because this framework focuses on resource allocation strategies imposed by landscape fragmentation, it is considered a landscape physiology framework.

In this paper, we posit that spatial characteristics of the environment, imposed by fragmentation, force specific adaptive states of life-history traits to increase survival (at the individual level) and avoid extinction (as an emergent property at the population level). We argue that studies of life-history traits and population dynamics should incorporate spatial characteristics of fragmentation (e.g., landscape configuration and habitat patch characteristics) in order to better understand how physiology constrains an individual's allocation strategy. We propose the integration of two distinct fields—landscape ecology and evolutionary physiology—into Landscape Physiology. While the need to integrate these two fields has been previously suggested (Chown et al., 2004; Chown and Gaston, 2008; Bonte et al., 2012; Ellis et al., 2012), the integration of physiology and life-history into landscape-level processes is still extremely rare (Ellis et al., 2012). A deep understanding of populations in a fragmented landscape requires knowledge of population and life-history parameters that a physiological perspective can provide (Berwaerts et al., 1997; Templeton et al., 2001; Hanfling et al., 2004; Bakker et al., 2010; Willi and Hoffmann, 2012; Hanski et al., 2013). We are still lacking a clear understanding of the physiological mechanisms by which organisms are able to cope with the effects of fragmentation in ways that scale upwards and reduce the probability that populations will be lost.

Below, we first provide background on dispersal-reproduction resource allocation tradeoffs in general. We then present the landscape physiology framework that explains how animals translate habitat heterogeneity due to fragmentation into resource allocation strategies to dispersal and reproduction. Last, we describe three explicit hypotheses that emerge from this framework.

Similar to many other trade-offs, the dispersal-reproduction trade-off emerges because organisms have finite resources to invest in growth, maintenance, survival and reproduction. Allocation of resources to any one of these functions reduces the amount available to the others (de jong, 1993). Such resource allocation decisions directly affect fitness and therefore underlie the evolution of traits in general and life-history traits in particular (Stearns, 1989, 1992; Boggs, 2009). Resource allocation strategies are influenced by the amount of available resources: reduced nutrient availability can significantly magnify a trade-off (increase the slope of the tradeoff), whereas increased nutrient availability can reduce or eliminate a trade-off (decrease the slope of the tradeoff) (Kaitala, 1987; Chippindale et al., 1993; Nijhout and Emlen, 1998; Zera and Harshman, 2001; Harshman and Zera, 2007). Ever-changing physiological priorities throughout ontogeny govern the relative allocation of resources to organismal processes as a function of nutrient input (Zera and Harshman, 2001; Boggs, 2009). For example, under stressful conditions, allocation to storage or maintenance can take precedence over allocation to reproduction (Perrin et al., 1990; Rogowitz, 1996), or resources can be reallocated from existing structures, as in the case of flight muscle histolysis and the subsequent reallocation of these resources to reproduction (Marden, 2000; Stjernholm et al., 2005). Such dispersal-reproduction trade-offs are well-documented in the context of migration in birds (Proctor and Lynch, 1998; Gill, 2006) and insects (Johnson, 1963; Rankin and Burchsted, 1992; Dingle, 1996), where development of reproductive organs is postponed until after migration.

Dispersal-reproduction trade-offs are also evident at smaller geographic scales of daily dispersal and foraging patterns (Van Dyck and Baguette, 2005; Bonte et al., 2012). In Trinidadian guppies, *Poecilia reticulate*, fast-start locomotor performance decreases with increased wet mass as pregnancy advances (Ghalambor et al., 2004). Gravid females of the side-blotched lizard (*Uta stansburiana*) display diminished locomotory endurance relative to post-gravid females (Miles et al., 2000), reproductive effort and locomotor performance are inversely correlated in the garter snake, *Thamnophis sirtalis* (Seigel et al., 1987), and carrying single-egg clutches significantly affect stamina and sprint speed in brown anole lizards, *Anolis sagrei* (Cox and Calsbeek, 2009). Small-scale movement-reproduction trade-offs are well-documented in insects as well. By far the best-studied example is that of wing dimorphic morphs of insects (Harrison, 1980), in which wingless morphs typically invest more resources and invest them earlier into reproduction compared to winged morphs (Roff, 1986, 1990, 1994; Zera et al., 1999; Zera and Brink, 2000; Zera and Larsen, 2001). Flightless brachipterous male planthoppers, *Prokelisia dolus*, have a 3-fold mating advantage over long-winged, macropterous males (Langellotto et al., 2000). In wing monomorphic species, weight loads associated with reproduction in the cabbage white butterfly, *Pieris brassicae*, impair flight performance (Almbro and Kullberg, 2012). Range expansion in response to global warming in the speckled wood butterfly, *Pararge aegeria*, has led to increased dispersal ability associated with reduced reproductive investment (Hughes et al., 2003). A recent review, however, showed that flight-fecundity tradeoffs in wing monomorphic insects may not be universal (Tigreros and Davidowitz, 2019). The trade-off between dispersal and reproduction can be very sensitive, as seen in the grasshopper *Stenobothrus lineatus*, where mean egg laying was reduced by a rate of 0.36 eggs per day with each meter increase in mean daily dispersal radius (Samietz and Kohler, 2012). In the context of fragmentation—the focus of this paper—Gibbs and Van Dyck (2010) showed that females of the speckled wood butterfly from fragmented forest habitats that were forced to fly decreased investment into eggs, indicating the existence of a dispersal-reproduction trade-off. More importantly for the argument of this paper, they showed that butterflies from open, highly fragmented agricultural landscapes that were forced to fly did not suffer from reduced longevity as did butterflies from the unfragmented landscapes, suggesting that butterflies from fragmented landscapes were physiologically better able to cope with the increased dispersal demands relative to those from non-fragmented landscapes (Gibbs and Van Dyck, 2010).

THE LANDSCAPE PHYSIOLOGY FRAMEWORK

We present a novel framework that links physiological mechanism with landscape level processes to explain how fragmentation translates into population level persistence. Fragmentation increases the isolation among patches (among-patch effect) and decreases patch size (within-patch effect) (**Figure 1A**). Patch size may also affect among-patch processes. However, its major effects relate to local population dynamics (Andren, 1994; Fahrig, 2003; Burkey and Reeds, 2006; Ewers and Didham, 2006). Patch size decreases with fragmentation, which results in a reduction in available resources in smaller

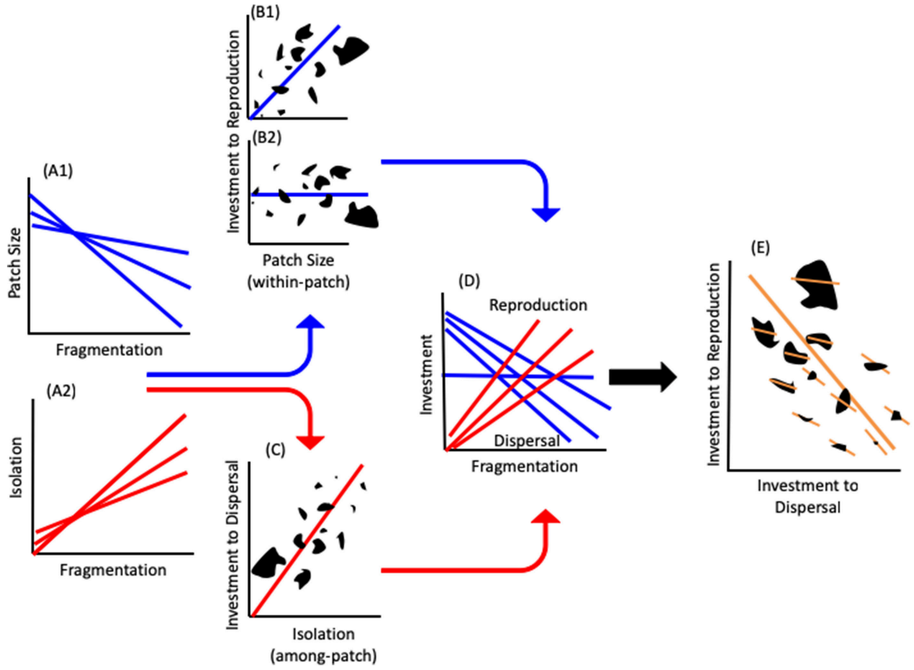

FIGURE 1 | The landscape physiology framework. The effects of fragmentation on patch size **(A1)** and isolation **(A2)**. The effects of patch size on investment to reproduction. Individuals in larger patches will invest more into reproduction **(B1)** or, if the landscape is exactly at carrying capacity equilibrium **(B2)** investment into reproduction will not change with patch size. **(C)** The effect of among-patch isolation on resource allocation to dispersal with higher investment to dispersal increasing with the degree of isolation. **(D)** Resource investment to reproduction and dispersal along a fragmentation gradient. **(E)** Resource allocation tradeoff at the physiological level (short, within patch, lines) create the landscape-level tradeoff (long line). Note that the within-patch slopes are shallower in larger patches. The multiple lines in **(A,D)** indicate that the specific slope and intercept of the relationships will vary with different combinations of patches **(B,C,E)**. The black shapes in **(B,C,E)** represent patches of different shapes and sizes.

patches (MacArthur and Wilson, 1967; Rosenzweig, 1995). This may consequently lead to two possibilities regarding the per-capita resource availability: (i) Constant per-capita resource availability, hence no change in density with area, due to the match between population size and resource quantity [e.g., Equilibrium theory (MacArthur and Wilson, 1967); and see empirical studies in Connor et al., 2000]. Consequently, investment to reproduction should stay constant with patch size (**Figure 1B2** and horizontal line in **Figure 1D**); (ii) Increased per-capita resource availability with area. Several reviews (Bowers and Matter, 1997; Bender et al., 1998; Debinski and Holt, 2000; Bowman et al., 2002) suggest that in almost half of studies, density has been shown to increase with a decrease in area, suggesting that individuals in larger areas may benefit from more per-capita resources. Therefore, reproductive investment should be higher in larger patches with more resources (**Figure 1B1** and decreasing blue lines in **Figure 1D**) (Wheeler, 1996; Papaj, 2000), whereas increased among-patch isolation should lead to increased allocation to dispersal ability and hence greater investment in dispersal structures (**Figure 1C**) (Gibbs and Van Dyck, 2010; Bonte et al., 2012; Stevens et al., 2012). Consequently, as fragmentation increases, organismal investment into dispersal should increase, whereas investment into reproduction should decrease or remains equal (**Figure 1D**). Thus, both scenarios lead to a resource allocation trade-off between reproduction and dispersal along a fragmentation gradient (**Figure 1E**).

It is important to note that there are two slopes that reflect the physiological and landscape levels of organization (**Figure 1E**). The first is the among-individual-within-patch slopes determined by the physiological processes governing the resource allocation strategies of the individuals within a patch (**Figure 1E**). The second is the slope generated among patches within the landscape which incorporates the physiology into landscape level processes (**Figure 1E**). The slope and intercept of the within-patch tradeoff (the allocation strategy) is context dependent and will change with any combination of individuals within a patch and the environmental conditions they experience (**Figures 1**, **2**). The among patch slope and position of each patch along it, is determined by the resource allocation strategies of the individuals within each patch. Thus, although we can make general predictions regarding the tradeoff within a landscape (**Figure 2**), the exact position of a given patch will be determined by the individuals and combination of patches measured (**Figure 1**).

We note that this framework is concerned with the tradeoff in the allocation of resources to dispersal vs. reproduction. We would expect the allocation of resources to these two traits to have cascading effects on the allocation of resources to other life

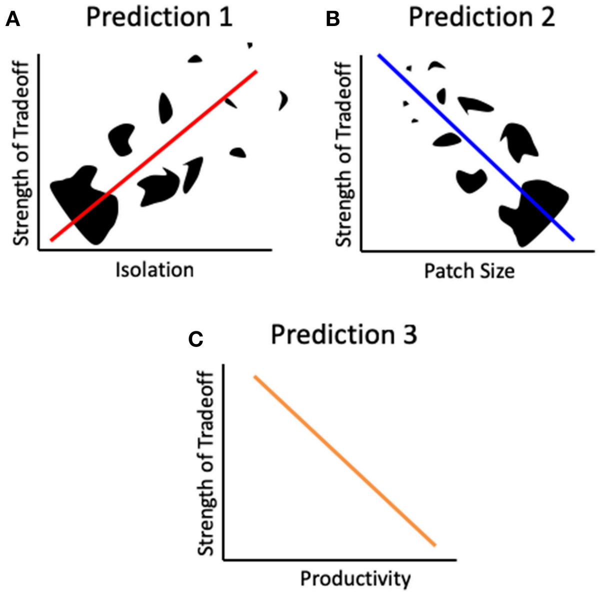

FIGURE 2 | Predictions derived from the landscape physiology framework. Patch isolation Black shapes represent patches of different shapes and sizes. The strength of the tradeoff between reproduction and dispersal will increase with patch isolation **(A)**, decrease with patch size **(B)** and patch productivity **(C)**.

history traits as well. Such additional affects are beyond the scope of this paper.

SPECIFIC HYPOTHESES

The landscape physiology framework offers a number of hypotheses regarding the effect of fragmentation on the dispersal-reproduction trade-off. We assume that the effect of the environment on the dispersal-reproduction dynamics is expressed by the strength of the trade-off. The strength of a trade-off can be expressed as the negative slope of the regression between reproduction and dispersal (however these are measured) so that a steeper negative slope indicates a stronger trade-off (**Figure 1E**), or by the strength of the (genetic) correlation among the traits where a stronger trade-off is indicated by a stronger negative correlation (Zera and Harshman, 2001; Roff and Fairbairn, 2007; Boggs, 2009; King et al., 2011). The strength of a tradeoff can also be influenced by the amount of variation about the slope, such that a higher variance (a lower R^2) indicates a weaker tradeoff. For simplicity, in this paper, we only use the slope as a measure of the strength of the tradeoff.

We propose three specific hypotheses, which we are testing in our ongoing research, regarding the relationship between the effects of habitat fragmentation and the strength of the dispersal-reproduction trade-off (**Figure 2**).

Hypothesis 1

Increased patch isolation leads to an increase in resource allocation to dispersal (**Figures 1C,D**). This hypothesis leads to the prediction of a positive relationship between the degree of isolation of a patch and the strength of the dispersal-reproduction trade-off, such that the trade-off will be stronger where isolation is higher (**Figure 2A**). This prediction will result in lower reproductive rates in the more isolated patches.

Hypothesis 2

Increased patch size leads to either a constant or an increase in resource allocation to reproduction (**Figures 1B1,D**). This hypothesis leads to the prediction of a negative relationship between patch size and the strength of the dispersal-reproduction trade-off, such that smaller patches will exhibit a stronger trade-off (**Figure 2B**). This prediction will result in lower reproductive rates in the smaller patches.

Hypothesis 3

An increase in patch productivity will provide enough resources for both dispersal and reproduction. This hypothesis leads to the prediction that the strength of the trade-off will decrease with increased productivity, i.e., in patches with higher resource availability (**Figure 2C**). This will result in lower reproductive rates in fragmented habitats of low productivity. This is supported by what is known of insect reproductive physiology: reproductive output is a function of the amount of resources acquired (Wheeler, 1996; Papaj, 2000). Resource abundance can affect the strength of a trade-off: it can be eliminated when resources are plentiful, or exacerbated when resources are limited, as described above.

Under landscape fragmentation, Hypotheses 1 and 2 are not independent, as more fragmented areas are more isolated and have smaller patches. Hypotheses 2 and 3 propose the same pattern, but in different spatial configurations: one along a fragmentation gradient (i.e., change in patch size) and the other along a productivity gradient. A landscape that includes both gradients, varying independently, will serve as an ideal model system to test the proposed hypotheses, as it can provide evidence that the shared mechanism works regardless of the spatial configuration and allows effects due to fragmentation to be separated from effects due to productivity.

STUDY SYSTEM

The appropriate study system in which to test how the dispersal-reproduction trade-off translates landscape fragmentation into population-level processes must fulfill the following criteria. First, fragments must be well-defined. Second, the fragmentation gradient must occur over a small enough area as to minimize abiotic variation from weather or other factors. Third, the gradient must have existed over sufficient evolutionary time to allow evolutionary responses in the dispersal-reproduction trade-off to emerge. Fourth, the study organism must be in high enough abundance to allow population-level effects to be measured. Finally, the fragmentation gradient must be at an appropriate grain for the organism's life-history (Baguette and van Dyck, 2007); the organism should be mobile enough so that dispersal is an important component of its life-history, but not so mobile that it can easily emigrate from the gradient.

Our current consideration and specific examples relate to terrestrial environments due to our own research interests. However, our framework should be relevant to any other environment where individuals face energy constraints and must allocate their resources to either fecundity or movement to another habitat patch. For example, in marine environments, isolated coral reefs are distributed at different distances and have different habitat quality (e.g., Belmaker et al., 2007, 2009). Dispersal among different coral reefs (Belmaker et al., 2011) is costly for individuals due the open-sea hostile environment, but may allow the new arrivals to have reduced predation pressure (Belmaker et al., 2005) and possibly an increase in fitness. Consequently, we expect that the dispersal strategies of individuals that are based on the heterogeneity of the coral reef system, will result in higher fitness and their fecundity-vs.-movement strategy will be favored by natural selection.

Although we present our framework and hypotheses in the context of fragmentation gradients, there is no reason this framework cannot be extended to other gradients of environmental variation. This means, that this framework is applicable to any natural situation where organisms have to prioritize between investment in dispersal and investment in fecundity to maximize their fitness. Given that in natural systems patch size and distance are not necessarily negatively correlated as they are along a fragmentation gradient, one can test the proposed framework in clusters of close habitat patches of different sizes or in clusters of similar sized patches of different distances. This allows for separate tests of hypotheses 1 and 2 independently. Such studies can be applied to different landscapes and taxa.

SUMMARY

The framework proposed here integrates two disparate fields, landscape ecology and evolutionary physiology, promoting the emerging new field of Landscape Physiology (Chown et al., 2004; Chown and Gaston, 2008; Bonte et al., 2012; Ellis et al., 2012). Landscape ecology relies on correlations between landscape and population/community parameters but usually ignores individual-level mechanisms. Evolutionary physiology, in contrast, is a mechanistic discipline that focuses on the microhabitat and often ignores landscape-level processes. This framework generates explicit and testable hypotheses of how an organism translates habitat characteristics resulting from fragmentation, through the physiological mechanism of resource allocation strategies, into population dynamic parameters of reproduction, survival, and abundance. This framework allows us to quantify and integrate both characteristics of habitat fragmentation and the dispersal-reproduction trade-off to produce response functions that can be used in inferring population persistence. All components of this framework are already well-supported in the literature of the respective fields: (a) habitat fragmentation reduces patch size and increases isolation, reducing species abundances and population persistence; (b) organisms in isolated, marginal, or fragmented habitats invest more in dispersal; and (c) dispersal-reproduction trade-offs are generally common. Previous studies have looked at qualitative differences among habitats (e.g., fragmented or not, (Gibbs and Van Dyck, 2010); or old or new populations, Hanski et al., 2006; Hanski, 2011). This framework extends beyond such studies in that it allows for the quantification of habitat characteristics and allocation strategies, such that we can determine the relationships between them to test explicit ecological and physiological predictions of resource allocation and life history strategies. Integrating across physiology and the landscape in one unified framework will extend our ability to understand population extinction and persistence in light of current increases in habitat loss and climate change.

AUTHOR CONTRIBUTIONS

YZ and GD contributed equally to the development of ideas and writing of the manuscript.

FUNDING

This study was supported by NSF grants IOS-1656279 and IOS-1053318 to GD and BSF grant 2016604 to YZ.

ACKNOWLEDGMENTS

We thank Judie Bronstein, Burt Kotler, Natasha Tigreros, Giorgi Kozhoridze, Julie Messier, and three reviewers for comments on previous versions of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 01 May 2019
doi: 10.3389/fevo.2019.00148

The Metabolic Basis of Fat Tail Distributions in Populations and Community Fluctuations

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Unveiling the mechanisms that molds populations fluctuations is central for understanding the dynamic of pest outbreaks, harmful algal blooms, or extinction risk. We hypothesize that metabolic restriction to maximum population abundance shapes single population and community fluctuations. Here, we derive a formal theoretical model linking metabolic limits to maximum population abundance with the distribution of fluctuations of single populations and communities. First, we show that the emergence of fat tails in the distribution of single population fluctuations is caused by the metabolic effect on maximum population abundance of periodic changes in resource supply or temperature. Second, we show an explicit link between single population fluctuations and the Laplace distribution of aggregated community fluctuations. Third, we derive a general relationship between population variance and body mass (called variance-mass allometry; VMA). This framework provides a theoretical mechanism to explain fat-tailed distributions of population fluctuations. It also predicts a double exponential or Laplace distribution of community fluctuations when the range of body size in the community is large. Finally, it provides a generalization of the VMA model which is able to generate theoretical predictions about patterns of variability among species lifestyles. This framework provides specific theoretical predictions that can be benchmarked against alternative competing models and empirical data, hence furthering our understanding about how metabolism determines abundance fluctuations.

Keywords: metabolic theory, variance mass allometry, population fluctuations, natural variability, power laws, size density distribution, energetic equivalence rule

OPEN ACCESS

Edited by:
Peter Convey,
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United Kingdom
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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *21 August 2018*
Accepted: *16 April 2019*
Published: *01 May 2019*

Citation:
Segura AM and Perera G (2019) The Metabolic Basis of Fat Tail Distributions in Populations and Community Fluctuations.
Front. Ecol. Evol. 7:148.
doi: 10.3389/fevo.2019.00148

INTRODUCTION

Deciphering the links between community structure and dynamics is a long-standing question in ecology. Scaling theories are an appealing approach to unify community size structure and population variability (Marquet et al., 2007; Cohen et al., 2012; Segura et al., 2017; Zaoli et al., 2017). Fundamental principles driving energy and mass conversion by organisms constrain processes at higher levels of biological organization and have therefore been useful to characterize community structure and dynamics (Brown et al., 2004).

Four scaling functions are ubiquitous in ecology: (i) the scaling of metabolic rates (B_i) with body mass (M_i); ($B_i \infty M_i^{\alpha}$; generally $0.5 < \alpha < 2$) (Damuth, 1981; Brown et al., 2004; DeLong et al., 2010), (ii) the scaling of population density (N_i) with body mass (size-density relationship, SDR; $N_i \propto M_i^{e_{SDR}}$; generally $e_{SDR} < 0$) (Damuth, 1981; Agustí et al., 1987; Blackburn and Gaston, 1997; White et al., 2007); (iii) the Taylor's scaling law, relating the average population abundance (*mean*(N)) with population variance (*var*(N_i)) (TL; $var(N_i) \propto mean(N_i)^{e_{TL}}$; $e_{TL} \sim 1$–2), and (iv) the scaling of population variance (*var*(N_i)) with body-mass (variance mass allometry, VMA; $Var(N_i) \propto M_i^{e_{VMA}}$; generally $e_{VMA} < 0$) (Marquet, 2005; Cohen et al., 2012). Multiple mechanisms have been proposed to explain these scaling relationships, and how they are interrelated (Zaoli et al., 2017), but the debate is far from being settled.

The form of the SDR varies with spatial scale and with the method of estimating population density (Blackburn and Gaston, 1997; White et al., 2007). At regional to global scales, the SDR often yields an exponent of approximately $-\alpha$, indicating that populations of different size can flux similar amounts of energy per unit area (Lawton, 1989), a phenomenon referred to as energy equivalence (Damuth, 1981). By contrast, density estimates obtained for all species present in local communities often produce weak triangular or polygonal (i.e., constraint envelope) relationships with exponents shallower than $-\alpha$, indicating that that larger-bodied species flux more energy (Marquet et al., 1995; White et al., 2007; Barneche et al., 2016). Under the hypothesis that only the abundance of dominant species are constrained by resource availability (Barneche et al., 2016; Ghedini et al., 2018), it is possible to derive some general predictions about population and community dynamics (**Figure 1**).

Fluctuations in abundance of single populations from time *t* to time *t+1* can be expressed as:

$$r_i = \log\left(\frac{N_i^{t+1}}{N_i^t}\right) \tag{1}$$

The distribution of fluctuations often show departures from the expected log-normal to fat-tailed distributions, implying reduced predictability for population outbreaks and extinctions (Halley and Inchausti, 2002; Lan and Chandran, 2011; Segura et al., 2013; Anderson et al., 2017a), but a mechanistic explanation for this phenomenon is currently lacking. At the community level, the aggregation of fluctuations of single populations across species (r_i) often follows a double exponential or Laplace distribution (**Figure 1**) which is a power law when the exponential of fluctuations ($exp(r_i) = N_i^{t+1}/N_i^t$) are evaluated (Keitt and Stanley, 1998; Allen et al., 2001; Marquet et al., 2007; Kalyuzhny et al., 2014; Segura et al., 2017). If the distribution of r_i values is centered on zero, it implies that an increase in one species is compensated by the decrease in another, consistent with zero-sum dynamics, which has important consequences for community dynamics (Marquet, 2005; Segura et al., 2017). Differently, VMA is a scaling law relating population variability with body size. Its scaling exponent has been theoretically predicted by combining the TL scaling exponent ($e_{TL} \sim 2$) and the SDR exponent ($e_{SDR} \sim -0.75$) giving an exponent $e_{VMA} \sim e_{TL} * e_{SDR} \sim -3/2$ (Marquet, 2005; Cohen et al., 2012). The VMA was succesfully evaluated using empirical data sets (Cohen et al., 2012; Xu, 2016) but the TL has been questioned as a statistical result of sampling from skewed distributions (Cohen and Xu, 2015). However, the ecological mechanisms generating skewed distributions remains unclear. Finding an expression for the VMA without invoking the Taylor's law would help to advance in the understanding of mechanisms behind populations and community variability (**Figure 1**).

Here, under the hypothesis that metabolic requirements constraint the maximum abundance of dominant species in a local community (Agustí et al., 1987; Belgrano et al., 2002; Brown et al., 2004; Barneche et al., 2016; Ghedini et al., 2018), we provide a formal link between body size, the distributions of population abundance, and population and community fluctuations in abundance. These links will help to advance our understanding of determinants of size structure, and population and community variability in natural communities. Based on the influence of body size, temperature, and resource flux on the metabolic limit to maximum population abundance, we derive a constraint envelope model that establishes: (i) a formal link with single-population variability that generates a fat-tailed distribution of fluctuations, (ii) an explicit relationship with the Laplace distribution of community fluctuations, and (iii) a general form of variance-mass allometry which, in a particular case, includes the VMA previously proposed by Marquet (2005) and Cohen et al. (2012).

THE METABOLIC RESTRICTION TO MAXIMUM POPULATION ABUNDANCE

The model is based on fundamental principles of resource network transport and enzyme kinetics and should therefore be applicable to many ecological systems (Brown et al., 2004). The basal metabolic rate (B_i) scale as a power law with body size (M_i) and have a near-exponential dependence with temperature (*T* in Kelvin)

$$B_i = b_0 \exp\left(\frac{-E}{kT}\right) M_i^{\alpha} \tag{2}$$

where b_0 is the size and temperature independent taxon specific constant, *exp()* is the exponential function, E is the activation energy (E ∼ 0.65 eV for heterotrophs and E ∼ 0.32 eV for autotrophs) and *k* is the Boltzmann constant (8.62×10^{-5} eV K^{-1}). Ideally, the scaling of field metabolic rate should be used, however, field metabolic data are not yet available for many groups (Nagy, 2005) and thus the scaling of basal metabolic rate is assumed. The allometric scaling of metabolism (α) showed variations among major evolutionary transitions (∼0.75–2; DeLong et al., 2010), but for the remaining of the article we will use the prototypical value found for metazoans (α ∼ 0.75). This choice does not modify the qualitative predictions of the theoretical model, as long as the scaling of metabolism is larger than that of the minimum population size (see below).

Total resource use (R_{tot}) in a local ecosystem (e.g., light or nutrients in case of autotrophs) is equal to the sum of the population-level rates of resource use per unit area or volume, R_i, across *S* cohabiting species ($R_{tot} = \sum_{i=1}^{s} R_i$). R_i, in turn,

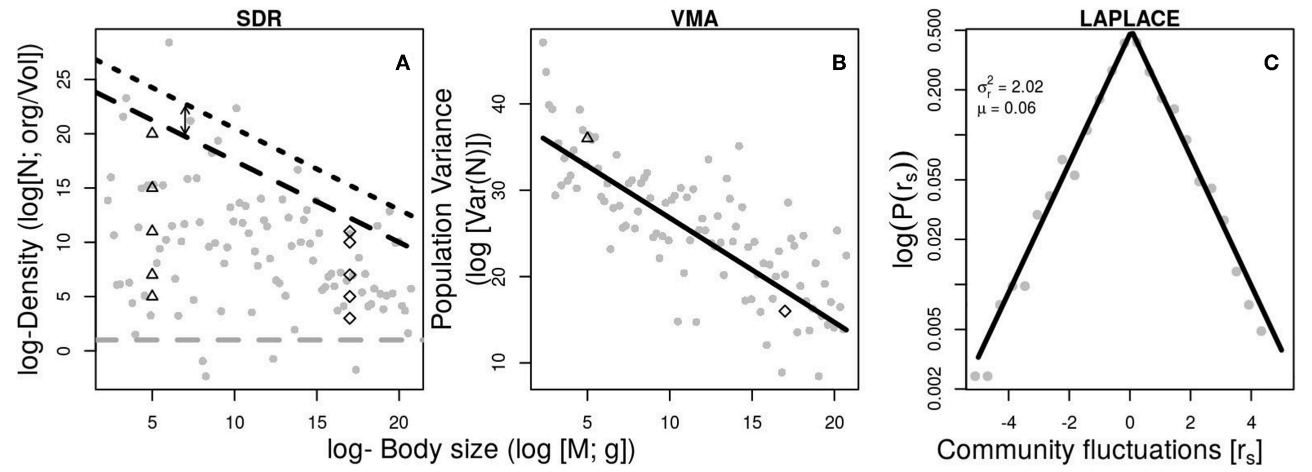

FIGURE 1 | Examples of relevant macroscopic community patterns simulated following Equations 5,6, 7, and 10. **(A)** The scaling of population density with body size (SDR) where maximum popupulation density (n_{max}; black dashed lines) scales as the inverse of the metabolic scaling ($-\alpha = -0.75$) and its intercepts increase with increasing resources supply from $R_{tot} = 0.1$ (dashed line) to $R_{tot} = 3$ (dotted line). Remaining parameters from Equation 5 are a = 1, T = 15°C. Minimum population abundance (gray dashed line) is assumed to have no relationship with body size ($\beta = 0$, b = 1 in Equation 6). Examples of possible temporal changes in the SDR space of a small sized (log(M)= 5; upper triangles) and large-sized (log(M)=17; open diamond) species. **(B)** The variance mass allometry (VMA) showing a decrease in population variance with body size (Equation 10; $\alpha = 0.75$, $\beta = 0$, b = 1, a = 1, $R_{tot} = 0.1$, T = 15°C, E = 0.65). The hypothetical positions of a small sized and a large-sized species from **(A)** are shown for comparison. **(C)** The Laplace distribution of aggregated population fluctuations. The Laplace distribution is the resulting distribution of aggregate temporal fluctuations of single populations (Equation 1). Simulated random normal variation (gray points) has been added to the equations.

is proportional to the product of metabolic rate (B_i) and the population density per unit area or volume (N_i),

$$R_i = N_i \quad B_i \tag{3}$$

Our interest is in understanding the upper limit to population density, $max(N_i)$. We assume that a dominant species can use no more than a fraction γ of R_{tot}. For simplicity, we further assume that this fraction is a constant independent of body size (i.e., $\gamma \propto M^0$). Given these assumptions, we can combine Equations 2 and 3, and then substituting γR_{tot} for R_i (Belgrano et al., 2002; Deng et al., 2012) for maximum population density:

$$max\,(N_i) = \gamma R_{tot} b_0^{-1} \exp\left(\frac{E}{kT}\right) M_i^{-\alpha} \tag{4}$$

and its logarithm:

$$n_{max} = \log\,(max\,(N_i)) = \left[a + \log\,(R_{tot}) + \frac{E}{kT}\right] - \alpha \log\,(M_i) \tag{5}$$

where $a = \log(\gamma\, b_0^{-1})$. As defined, n_{max} represents the upper limit for population density on the natural logarithmic scale. Similarly, we can define the equation for the lower population abundance bound on the logarithmic scale n_{min}:

$$n_{min} = b - \beta \log\,(M_i) \tag{6}$$

We will assume for simplicity that n_{min} is independent of body size ($\beta = 0$), and of temperature and resources (i.e., b is constant) (Pimm, 1991; Marquet and Taper, 1998). In the present context n_{min} is interpreted as the lower bound a local population can reach before getting locally extinct. For example, in the case of phytoplankton with asexual reproduction, the minimum abundance is one organism (thus $\exp(n_{min}) = 1$). We recall that this is not a metabolic scaling, and later we will discuss the qualitative effects of a different scaling exponent ($\beta > 0$) on specific predictions.

Equations 5 and 6 allow us to set the limits on local population abundance of a species in an ecosystem given its body size, resource supply rate and temperature (**Figure 1**; Lawton, 1989). In the following sections, we will derive a formal theoretical model relating the metabolic rate (Equations 2, 5, and 6) to the scope for single population fluctuations, the emergence of fat tails and the distribution of aggregated community fluctuations. The model predicts the potential limits of fluctuations (conditional to body size) within the boundaries imposed by metabolic restrictions, but it does not analyze the specific mechanisms that generates the variability (e.g., predation, environmental perturbations).

SINGLE POPULATION ABUNDANCE DISTRIBUTION

Because reproduction is a multiplicative process, a reasonable assumption for the distribution of abundances (N_i) through time for a single species in a local community is that it follows a Lognormal distribution (Halley and Inchausti, 2002). This implies that the logarithm of abundance follows a normal distribution with a mean μ and standard deviation σ (MacArthur, 1955; Halley and Inchausti, 2002). Defining n_{max}

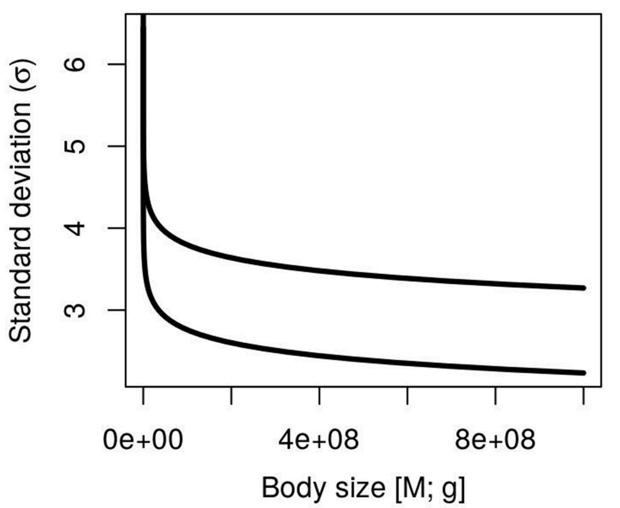

FIGURE 2 | Body size dependence of population standard deviation (Equation 7) at different resource levels ($R_{tot} = 3$ upper curve and $R_{tot} = 0.1$ lower curve). Remaining parameters used to draw the curve are $\alpha = 0.75$, $\beta = 0$, $a = 1$, $b = 0$, $T = 15°C$, $E = 0.65$.

and n_{min} (in Equations 5 and 6) as the expected 5th and 95th quantiles of the size-dependent (i.e., conditional) distribution of log abundances, the following formal relationship can be derived using Equations 2–6:

$$\begin{aligned} \mu &= \frac{n_{max}+n_{min}}{2} = \frac{a+\log(R_{tot})+\frac{E}{kT}+b}{2} - \frac{(\alpha+\beta)}{2}\log(M_i) \\ \sigma^2 &= \frac{n_{max}-n_{min}}{3.28} = \frac{a+\log(R_{tot})+\frac{E}{kT}-b}{3.28} - \frac{(\alpha-\beta)}{3.28}\log(M_i) \end{aligned} \tag{7}$$

These equations predict that μ will be negatively related to body size, consistent with empirical local size-abundance distributions (Damuth, 1981; Agustí et al., 1987; Blackburn and Gaston, 1997; Belgrano et al., 2002; White et al., 2007). If lower population limit is independent of body size ($\beta = 0$), as observed in most local size density relationships (Lawton, 1989; Blackburn and Gaston, 1997), the predicted average slope would be the half of the scaling exponent of metabolism (e.g., $-\alpha/2 \sim -0.375$) closer to the observed average in local communities of animals (-0.25; Blackburn and Gaston, 1997). In the particular case when there is a strong scaling of lower population limit with body size (e.g., $\beta \sim \alpha$) (e.g., Silva and Downing, 1994), the equations recover the energetic equivalence rule, as the predicted exponent of the SDR is the opposite to the metabolic scaling exponent ($e_{SDR} \sim -\alpha$) (Brown et al., 2004; White et al., 2007; Deng et al., 2012).

A novel explicit prediction is the link between metabolic constraints and the variance σ^2 of log-population abundance (**Figure 2**). Equation 7 predicts a decreasing function of σ^2 with body size (unless the extreme case $\beta = \alpha$), an inverse relationship with temperature and a positive relationship with the logarithm of resource supply. It provides the ecological conditions to observe a linear ($\alpha = \beta$) or a triangular ($\alpha > \beta$) relationship between log-size and log-abundance as has been observed (Lawton, 1989; Marquet et al., 1995; Blackburn and Gaston, 1997; White et al., 2007; Barneche et al., 2016). The decrease in population variance might be related to longer generation times in larger-sized organisms, which is closely related to body size. Those equation combine the physiological effect of the metabolic transport network (α, M_i) with the effect of local ecosystem properties (temperature and resource supply; T and R_{tot}) on population fluctuations. With the formal theoretical predictions on the mean and standard deviation of population abundance, it is possible to explore their role on populations and community fluctuations.

EMERGENCE OF FAT TAILS IN SINGLE POPULATION FLUCTUATIONS

The magnitudes of abundance fluctuations for a single population can be characterized as the log of the ratio of abundances, r_i, for two successive time periods, *t* and *t+1* (Equation 1) (Keitt and Stanley, 1998; Halley and Inchausti, 2002; Segura et al., 2013). The ratio of two lognormal distributions is itself a lognormal and in the long run, covariance of population abundance between successive times is zero, thus, the mean (μ_{ri}) and variance (σ^2_{ri}) of the fluctuations (r_i) are estimated as:

$$\begin{aligned} \mu_{ri} &= \mu_{t+1} - \mu_t \\ \sigma^2_{ri} &= \sigma^2_{t+1} + \sigma^2_t \end{aligned} \tag{8}$$

If mean abundance in successive times are similar, the expected mean of fluctuations μ_{ri} is on average zero, but the variance is the sum of the two variances (Equation 8), which amplifies the effect of size, temperature and resources on it (from Equation 7). The periodic changes in temperature or resources which naturally occur in natural ecosystems will shift the upper metabolic limit (n_{max}) and thus modify the scope for fluctuations of each population (σ^2_{ri} in Equation 8 and **Figure 1**). If the abundance of a single population is estimated over long periods (relative to its generation time), the fluctuations for a single species will follow a lognormal distribution with zero mean, but time-varying variances. This can be described as a mixture of lognormal distributions with different variances, which is a mechanism able to generate fat tail distribution of fluctuations (Halley and Inchausti, 2002; Segura et al., 2013; Anderson et al., 2017a). This provides a plausible metabolic-based explanations for the fat tails in the population fluctuations. This explanation is complementary to previous explanations based on environmentally-driven population crashes (Anderson et al., 2017a), migration (Anderson et al., 2017b) antropogenic disturbances (Quiroz-Martinez et al., 2012), or the long-range propagation of interaction among species in a food web (Keitt and Stanley, 1998; Allen et al., 2001). However, for a given community in a particular ecosystem in a defined period of time, present model allows to estimate quantitative predictions about the mixture of normal distributions and the resulting "fat-tailed" distribution for each species given their body size.

According to the present model, fat tails will be easily detectable in small-sized highly-abundant species because of their larger scope for fluctuations as opposed to large-sized species (**Figure 1**). If a short period of time is evaluated or if resources or temperature present a temporal trend as registered under antropogenic eutrophication or climate change, asymmetric distributions of population fluctuations could result as has been noted early (Halley and Inchausti, 2002; Segura et al., 2013; Anderson et al., 2017a). Short datasets might preclude detecting statistical differences between lognormal or their fat-tailed counterparts. Moreover, the ability to detect substantial differences would decrease with the size of the organism as the scope for fluctuations (σ^2_{ri}) is reduced. The patterns predicted by Equations 7 and 8 should be treated as the extreme limits into where population dynamics could act (Lawton, 1989). Finding deviations from the theoretically predicted scope for fluctuations could provide interesting clues about other ecological mechanisms reducing (e.g., predator-prey coupling) or amplifying (e.g., fishing) population variability.

LINK WITH THE LAPLACE DISTRIBUTION OF COMMUNITY FLUCTUATIONS

When the fluctuation (r_i) of multiple populations whitin a community spanning a large range in body sizes are aggregated, the Laplace distribution is the expected outcome as has been observed in empirical studies (Keitt and Stanley, 1998; Allen et al., 2001; Kalyuzhny et al., 2014; Segura et al., 2017). The link of single population fluctuations (Equation 8) to the community level is straightforward. There is a proposition that states that the aggregation of Lognormal distributions with mean zero and stochastic variance which has an exponential distribution generates a Laplace random variable (proposition 2.2.1 in Kotz et al., 2001). Single population fluctuations are approximately normal in the log space and its average is expected to be zero ($\mu_{rs} = 0$) and independent of body size (Equation 8) which fullfills the former criteria. The variance of the fluctuations (σ^2_{rs}) can be approximated as twice the variance of single population fluctuation (Equation 8; $\sigma^2_{rs} \sim 2\sigma^2$) which is related to metabolic rates and present a left skewed distribution with multiple shapes (**Figure 2**). When $\beta = 0$, the variances (σ^2) of populations distributed uniformly in the log body-size space are power laws with a scaling $\sim -\alpha/3.28$, and at the other end they are independent of size (when $\alpha = \beta$), and present an inverse relationship with absolute temperature and an exponenetial dependence on resource flux (R_{tot}). This distributions are close to an average of zero and an exponential distribution of the variances necessary to obtain a Laplace distribution of community fluctuations (Kotz et al., 2001).

Deviations from Laplace are expected because the distribution of variances (σ^2) are not strictly exponential, but this patterns have not been investigated yet (Kalyuzhny et al., 2014). Another source of discrepancies from the expected Laplace could arise if the fluctuations are estimated in a reduced period of time, where aperiodic fluctuations in abiotic conditions caused by nutrient pulses or systematic trends in temperature regimes modify the variance structure of fluctuations (Equation 7). Overall, Laplace distribution serves as a null model to test community fluctuations in real ecosystems or to analyze deviations from theoretical assumptions. This framework allows to generate theoretical predictions on the specific effect of increasing temperature or resource variability on population and community fluctuations.

A GENERAL MODEL FOR THE LINK BETWEEN POPULATION VARIANCE AND BODY SIZE

The variance-mass allometry has been defined theorethicaly by combining SDR and TL (Marquet, 2005; Cohen et al., 2012) and states that population variance (*Var*(N)) is a decreasing power function of body mass (M) which was supported by empirical tests (Cohen et al., 2012; Lagrue et al., 2015). However, the TL has been critiziced in statistical and biological grounds (Cohen and Xu, 2015). An alternative procedure to derive theoretical predictions on the variance-mass relationship without relying on fitting the Taylor's law can be performed based on the metabolic limits to density (Equations 5–8). The variance of population abundance ($Var(N_i)$) is defined in terms of μ and σ (Equation 7) as follows:

$$Var\,(N) = e^{2\mu+\sigma^2}\left(e^{\sigma^2} - 1\right) \tag{9}$$

Substituting Equations 7 into Equation 9 and then rearranging for M, we obtain an explicit relationship between organisms size and population variance as follows:

$$Var\,(N) = M^{-1.6\alpha-0.4\beta} + e^{1.6c+0.4b} - M^{-1.3\alpha-0.7\beta} + e^{1.3c+0.7b} \tag{10}$$

This equation includes the effect of resources and temperature into the term c=a+ log(R_{tot}) + E/kT. It is a combination of two power laws that generates a steeper slope toward large-sized organisms (**Figure 3**). In the special case in which the scaling of maximum and minimum population abundance are the same ($\alpha = \beta$) the Equation 10 is reduced to:

$$Var\,(N) \propto M^{-2\alpha} \tag{11}$$

Equivalent to the variance-mass allometry (VMA) proposed using a different derivation by Marquet (2005) and Cohen et al. (2012). The exponent equal to minus twice the scaling of metabolism (e.g., $-0.75{*}2 = -3/2$) match exactly their predicted theoretical value (Marquet, 2005; Cohen et al., 2012). Moreover, results showed that the metabolic limit to maximum population abundance generates a skewed distribution of species abundances, a necessary condition to generate TL (Cohen and Xu, 2015) but the model (Equation 11) does not depend on fitting Taylor's law to empirical data (Taylor, 1961). Therefore, our present method provides an advantage to conduct empirical tests, because contrary to TL, it does not require time series of population abundances to estimate temporal mean and variance.

The explicit link with metabolic scaling presented in Equation 10 could help to explain why free-living, free-living infested, and parasitic species exhibit different VMA relationships (Lagrue

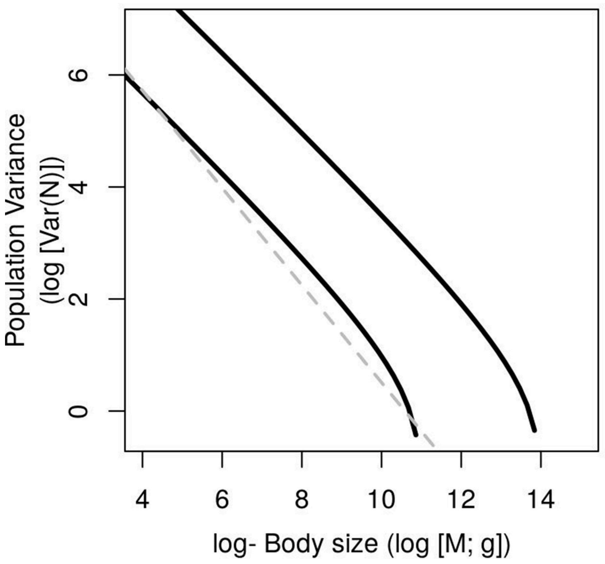

FIGURE 3 | General variance mass allometry (VMA) under different resource supply concentrations ($R_{tot} = 3$ upper line and $R_{tot} = 0.1$ lower line). The special case when $\alpha = \beta$ is a straight line (dashed line) whose slope is twice the opposite of the metabolic exponent $e_{VMA} = -2\alpha$.

et al., 2015). It is expected theoretically that both the intercept and slope of metabolic scaling (b_0 and α in Equation 2) differ between parasites and free-living species with direct implications in the VMA (Equation 10; Lagrue et al., 2015). Similarly, a fraction of the metabolic power of free-living species infested with parasites is not used to reproduce and increase population abundance, but to feed parasites, diminishing their effective scope for fluctuations with size as have been observed (Lagrue et al., 2015).

MODEL ASSUMPTIONS AND ALTERNATIVE MODELS FOR THE SIZE DEPENDENCE OF MAXIMUM POPULATION ABUNDANCE (n_{max})

There are three main assumptions required to derive specific predictions on variability of population and community fluctutations, namely: (i) there is a maximum to population abundance determined by body size, and ecosystem properties (T, R_{tot}), (ii) there is a lower bound to population abundance, and (iii) the distribution of population abundances is lognormal.

An important assumption in our proposed model is the existence of a metabolic determinant of maximum population density. While this assumption has received empirical support (Damuth, 1981; Belgrano et al., 2002; Deng et al., 2012) it has also been questioned and alternative models for the SDR have been suggested (e.g., Carbone and Gittleman, 2002; DeLong and Vasseur, 2012; Pawar et al., 2012). How do alternative SDR models fit into the framework propossed here? A group of consumer-resource models whose parameters are estimated based on scaling relationships provide quantitative predictions on the shape of the SDR by finding the body-size scaling of non-trivial steady-state consumer density (DeLong and Vasseur, 2012; Pawar et al., 2012). These models assume that the feeding processes (e.g., handling time, attack rate) and not the internal metabolic transport network determine the maximum population density of a consumer population. For example, under a simplified Lotka-Volterra predator-prey model, it was found that the SDR scaling exponent (e_{SDR}) was related to maximum population growth rate, attack rate efficiency and predator-prey size scaling, with specific body size-scalings exponents (ρ,δ,ω, respectively). A formal prediction of the body-size density scaling relationship was constructed ($e_{SDR} = \rho\omega - \delta$) (DeLong and Vasseur, 2012). Temperature will affect the normalization constant for each of these scaling rates, generating potentially more complex responses than the near-exponential response suggested in Equation 2. The quantitative predictions of consumer-resource models about n_{max} and its effects on the populations and communities fluctuations are able to be directly incorporated into the present framework (e.g., in Equation 4) and tested against empirical data. Any other quantitative model with formal predictions on the distribution of the SDR (e.g., Irwin et al., 2006; Pawar et al., 2012, among others) can be plugged into Equation 4 to generate specific testable hypothesis about the determinants of natural variability. However, the information on scaling relationships of feeding proceses required is sometimes not available and thus the metabolic approach here presented might serve as a first aproximation. We advocate for the empirical evaluation of alternative models on the determinants of SDR and its effect in the variability of populations and the community.

The limit of the lower population abundance (Equation 5) requires further exploration both in theoretical and empirical grounds (Traill et al., 2007). There is evidence for some groups suggesting that this pattern is flat (Marquet and Taper, 1998; Traill et al., 2007), after accounting for trophic group, temperature, species richness, and sampling area, the size scaling of population abundance is negligible for populations that are rare (Barneche et al., 2016). However, negative scaling exponents have been found for mammals (Silva and Downing, 1994) but the pattern is restricted to particular groups (Nagy, 2005) and we lack a robust theoretical framework to explain it (Lawton, 1989). As a first approximation and without further information, we suggest assuming β is independent of body size and temperature or resources. In the absence of information on the scaling of b, the parameter could be estimated by fitting a slope to the 5% quantile of the size-abundance distribution for the community under different resources or temperature regimes. More theoretical and empirical evaluations on the scaling of minimum population abundance is required to advance in the determinants of population and community variability.

The distribution of single species abundances following a Lognormal seems to be reasonable and have been proposed as a simple and ecologically meaningfull distribution to model population abundances (Halley and Inchausti, 2002). Present results are not sensitive to departures from the Lognormal, as long as the distribution of abundances be symetric in the log-scale. Under any other symetric distribution, the constant dividing standard deviation in Equation 7 will change, but will not qualitatively alter the results about the Laplace distribution. It will however change the derivation of a VMA which is based on the relationship between variance of the Lognormal and μ and σ. However, the lognormal is a reasonable first step and provides analytical results able to be tested with empirical data.

FINAL REMARKS

Our model is an asymptotic time model that defines the statistical boundaries for fluctuations in the long run and derive predictions on the shape of the distribution of fluctuations (conditional to body-size) at multiple ecological levels. Results present quantitative predictions of the fluctuation of population and community abundance with body size derived from the metabolic limits to maximum population abundance. Larger organisms are limited by metabolic constraints which defines maximum population density and limit population fluctuations. First, results showed how the metabolic constraints and the fluctuation of resources and temperature are able to generate fat tails in the fluctuation of single populations. Second, we derive a model for whole community fluctuations able to reproduce the observed double exponential or Laplace distribution. We also derived a variance-mass allometry independent from the fitting the Taylors' law and that recuperates the VMA previously proposed as a special case. Our approach provides a general framework to mechanistically link universal patterns observed in ecology, namely the metabolic scaling, species density distribution, and the Variance mass allometry.

Grounded on first principles our model provides a novel quantitative link between size structure and variability, two central tenets of ecological agenda. The universality of the patterns suggests that explanations should be rooted on first principles, and a great candidate is the scaling of the metabolic activity (Gillooly et al., 2001; Brown et al., 2004; Savage et al., 2004). An important aspect of our model framework is that parameters values can be fully assigned independently of size-variance data and have clear ecological interpretation. While α represents the scaling of metabolic rate with size, the relationship with temperature and resources is explicit. Empirical test of present model and alternative formulations for the maximum population abundance are required to advance in the comprehension of the mechanisms determining natural variability.

AUTHOR CONTRIBUTIONS

AS designed research and write the first draft. GP provided analytical tools and derived the equations. Both authors contributed to the writing of the final manuscript.

ACKNOWLEDGMENTS

We would like to specially thank the two reviewers of a previous version of this manuscript, whose comments and corrections greatly improved the quality of present manuscript. AS thanks Fondo Carlos Vaz Ferreira de Apoyo a Proyectos de Investigación en todas las Áreas del Conocimiento (D2C2) for economical support.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 15 May 2019
doi: 10.3389/fevo.2019.00146

Effects of Climate Warming on Consumer-Resource Interactions: A Latitudinal Perspective

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There is increasing evidence that climate warming is impacting biodiversity by disrupting species interactions. Trophic (consumer-resource) interactions, which comprise the fundamental units (modules) of food webs, are of particular importance because they have an intrinsic tendency to fluctuate in abundance, thus running to risk of stochastic extinction during periods of low abundances. Here I present a mathematical framework for predicting warming effects on consumer-resource interactions. This work differs from previous theory in two ways. First, it uses delay differential equations to realistically depict the developmental delays inherent in ectotherm life cycles, and incorporates mechanistic descriptions of phenotypic trait responses, derived from first principles of thermodynamics, into the dynamical delay model. Second, it tests the latest IPCC predictions on warmer-than-average winters and hotter-than-average summers. I investigate warming effects on three major axes: latitude (tropical vs. temperate), life stage attacked (juvenile vs. adult), and nature of consumer-resource dynamics in the absence of temperature variation (stable vs. complex). I report three findings. First, consumer-resource interactions in the tropics are more at risk of species losses due to warming while those in the temperate zone are more at risk of extreme fluctuations in species' abundances. Second, effects of warming are more detrimental when the consumer attacks the adult stage of the resource and when consumer-resource interactions exhibit complex dynamics. Third, hotter-than-average summers are more detrimental to consumer-resource interactions than warmer-than-average winters. I discuss implications of these results for biodiversity and biological pest control.

Keywords: ectotherm, intra-specific competition, life history, latitude, traits, temperature variation

Edited by:
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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *17 December 2018*
Accepted: *15 April 2019*
Published: *15 May 2019*

Citation:
Amarasekare P (2019) Effects of
Climate Warming on
Consumer-Resource Interactions: A
Latitudinal Perspective.
Front. Ecol. Evol. 7:146.
doi: 10.3389/fevo.2019.00146

INTRODUCTION

Trophic interactions between consumers and resources (e.g., predator-prey, plant-herbivore, host-parasite) play a fundamental role in all communities, be they natural or managed. A unique property that distinguishes trophic interactions from other species interactions is the conflict of interest between species: the consumer benefits from the interaction while the resource is harmed by it. This leads to unique dynamical outcomes such as intrinsic oscillations in abundance, and coevolutionary arms races (Murdoch et al., 2002, 2003).

The majority of consumer-resource interactions in nature occur amongst ectotherms (e.g., microbes, invertebrates, fish, amphibians, and reptiles) whose body temperature depends on the environmental temperature (Brown et al., 2004; Angilletta, 2009). It is well-known that temperature variation (e.g., diurnal, seasonal) has a strong effect on consumer-resource dynamics and persistence. For instance, differential adaptability of prey species to seasonal temperature regimes can generate temporal refuges, which can reduce overexploitation by predators and dampen predator-prey oscillations (Murdoch et al., 2003); differential adaptability of natural enemies can achieve more effective pest control through complementary action (Takagi and Hirose, 1994; Rochat and Gutierrez, 2001; Hunt-Joshi et al., 2005; Tuda et al., 2006).

There is increasing evidence that climate warming is disrupting consumer-resource interactions, causing phenological shifts and increasing the likelihood of species extinctions (Dunn and Winkler, 1999; Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Inouye, 2008; Miller-Rushing and Primack, 2008; Post et al., 2008). This has spurred a body of theory (Vasseur and McCann, 2005; van de Wolfshaar et al., 2008; OConnor et al., 2011; Ohlberger et al., 2011; Binzer et al., 2012; Dell et al., 2014; Gilbert et al., 2014; Amarasekare, 2015; Uszko et al., 2017), which has greatly enhanced our understanding of how temperature variation and climate warming influence the dynamics and persistence of consumer-resource interactions. There, however, remains two key gaps in our knowledge. The first is a biological one. No studies to date have incorporated the key feature that characterizes the complex life cycles of multicellular ectotherms: time delays induced by development from egg to adult. As we know from classical theory, developmental delays lead to types of complex dynamics (e.g., generation cycles, delayed feedback cycles) that are unobserved in models that do not account for the age/stage-structure (Gurney et al., 1983; Nisbet and Gurney, 1983; Murdoch et al., 2003). Importantly, such dynamics emerge even in the absence of temperature variation. A lack of knowledge on how temperature variation affects complex dynamics arising from developmental delays is one of the most crucial impediments to predicting how climate change will impact consumer-resource dynamics involving multicellular ectotherms. The second gap in our knowledge is a physical one. Existing studies do not incorporate recent IPCC predictions about warmer-than-average winters and hotter-than-average summers (IPCC, 2018).

Here I take a first step toward bridging these gaps. I develop a mathematical framework that realistically depicts the developmental delays that characterize ectotherm life cycles, and incorporates mechanistic descriptions of phenotypic trait responses to temperature into dynamical models of consumer-resource interactions. Its key feature is that it can predict population-level effects of warming at different latitudes based solely on trait response data, and completely independently of population-level information. This provides a powerful alternative to species distribution models that rely on population-level data to predict the effects of climate warming.

MATHEMATICAL FRAMEWORK

Consider a consumer-resource interaction in which the resource and consumer species each has two stages in the life cycle (juvenile and adult), and the consumer exploits the juvenile or adult stage of the resource species. We would expect the resource species to experience intra-specific competition for its own limiting factors (e.g., food, space). Such self-limitation can occur via density-dependent fecundity or mortality. Common examples of such interactions involve insect parasitoids attacking nymphal/larval or adult stages of other insects, lizards and spiders feeding on insects, and lady beetles feeding on aphids (Murdoch et al., 2003). The dynamics of the stage-structured interaction are given by:

$$
\begin{aligned}
\frac{dJ(t)}{dt} &= B\Big(T(t),A(t)\Big)A(t) - M_J(t) - D_J\Big(T(t),J(t)\Big)J(t)\\
&\quad - g(J(t))C(t)\\
\frac{dA(t)}{dt} &= M_J(t) - D_A\Big(T(t),A(t)\Big)A(t) - g(A(t))C(t)\\
\frac{dL(t)}{dt} &= fg(X(t))C(t) - M_L(t) - d_L(T(t))L(t)\ \ X = J,A\\
\frac{dC(t)}{dt} &= M_L(t) - d_C(T(t))C(t)\\
M_J(t) &= B\Big(T(t-\tau_J(t)),A(t-\tau_J(t))\Big)A(t-\tau_J(t))\\
&\quad \frac{m_J(T(t))}{m_J(T(t-\tau_J(t)))}S_J(t)\\
M_L(t) &= fg(X(t-\tau_X(t))\frac{m_L(T(t))}{m_L(T(t-\tau(t)))}S_L(t) \qquad (1)\\
\frac{dS_J(t)}{dt} &= S_J(t)\left[\frac{m_J(T(t))D_J(T(t-\tau_J(t),J(t-\tau_J(t))),J(t-\tau_J(t)))}{m_J(T(t-\tau_J(t)))} - D_J(T(t),J(t))\right]\\
\frac{dS_L(t)}{dt} &= S_L(t)\left[\frac{m_L(T(t))d_L(T(t-\tau_J(t)))}{m_J(T(t-\tau_J(t)))} - d_L(T(t))\right]\\
\frac{d\tau_J(t)}{dt} &= 1 - \frac{m_J(T(t))}{m_J(T(t-\tau_J(t)))}\\
\frac{d\tau_L(t)}{dt} &= 1 - \frac{m_L(T(t))}{m_L(T(t-\tau_L(t)))}
\end{aligned}
$$

where J and A depict juvenile and adult stages of the resource species, and L and C, those of the consumer species. The functions $B\Big(T(t),A(t)\Big)$ and $D_X\Big(T(t),X(t)\Big)$, $(X = J,A)$ describe the joint effects temperature and density on per capita birth and mortality rates, $g(X(t))$ is the consumer's functional response, and $d_Z(t)$, $Z = L,C$ depicts the density-independent mortality rates of the juvenile and adult consumer.

We consider g to be a saturating function of resource abundance given strong empirical evidence that saturating functional responses are the commonest observed in nature (Murdoch et al., 2003; Jeschke et al., 2004). Then, $g = \frac{a(T)J(t)P(t)}{1+a(T)h(T)X(t)}$ $(X = J,A)$ where $a(T(t))$ and $h(T(t))$ depict, respectively, the consumer's temperature-dependent attack rate and handling time. The stoichiometric properties underlying the consumer's conversion efficiency (f) makes it insensitive to temperature (Peters, 1983; Custer, 2005), and there is no empirical evidence suggesting systematic changes with temperature (Uszko et al., 2017). Density-dependent fecundity is typically depicted as $B\Big(T(t),A(t)\Big) = b(T(t))e^{-q(T(t))A(t)}$ (Murdoch et al., 2003; Amarasekare and Coutinho, 2014) where $b(T(t))$ is the temperature-dependent per capita birth rate, and $q(T(t))$, the temperature-dependent resource self-limitation strength. Density-dependent mortality is given by $D_X\Big(T(t), X(t)\Big) = d_X(T(t))(1 + q(T(t))X(t))$ (Amarasekare and Coutinho, 2014).

The function $M_Y(t)$ $(Y = J, L)$ is the temperature-dependent recruitment rate, which is the product of the recruitment rate into the juvenile stage $\tau_Y(t)$ time units ago and the fraction of juveniles (larvae) that survive to adulthood $(S_Y(t))$. The function $m_Y(T(t))$ $(Y = J, L)$ depicts variation in the per individual maturation rate with time due to the temperature dependence of juvenile developmental delay (τ_Y).

The population-level effects of climate warming we observe is the result of temperature effects on the underlying life history and consumption traits of consumers and resources. The first step therefore is to understand how temperature variation affects these traits.

TEMPERATURE RESPONSES OF LIFE HISTORY AND CONSUMPTION TRAITS

Life history and consumption traits of ectotherms exhibit plastic temperature responses (reaction norms, Roff, 1992) that represent the phenotypic-level manifestations of temperature effects on underlying biochemical processes (e.g., reaction kinetics, hormonal regulation; Johnson and Lewin, 1946; Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Nijhout, 1994; Van der Have and de Jong, 1996; Van der Have, 2002; Ratkowsky et al., 2005; Kingsolver, 2009; Kingsolver et al., 2011). Temperature effects on biochemical rate processes (e.g., reaction kinetics and enzyme inactivation) give rise to phenotypic-level responses that are left-skewed or monotonic increasing/decreasing (Van der Have and de Jong, 1996; Gillooly et al., 2001, 2002; Van der Have, 2002; Savage et al., 2004). Mortality and maturation rates exemplify such rate-controlled responses. This contrasts with temperature effects on on biochemical regulatory processes (e.g., neural and hormonal regulation; Nijhout, 1994; Hochachka and Somero, 2002; Long and Fee, 2008), which yield phenotypic-level responses that are symmetric unimodal (e.g., Gaussian). This is because regulatory processes are driven by negative feedbacks that push increasing and decreasing rate processes toward an intermediate optimum.

Temperature Response of Mortality

Density-independent per capita mortality rate of all ectotherms increases with temperature within the biologically relevant temperature range (Johnson and Lewin, 1946; Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Ratkowsky et al., 2005), i.e., the temperature range between the lower threshold below which body fluids freeze and the upper threshold above which proteins denature (Gillooly et al., 2001, 2002; Savage et al., 2004). Below this range, mortality starts to increase with decreasing temperature due to the freezing of body fluids and other related phenomena (Van der Have and de Jong, 1996; Gillooly et al., 2001, 2002; Savage et al., 2004; Dell et al., 2011). The complete mortality response can be described by a modified version of the Boltzmann-Arrhenius function (Van der Have and de Jong, 1996; Gillooly et al., 2001, 2002; Savage et al., 2004):

$$d(T) = d_{T_R} e^{A_d\left(\frac{1}{T_R}-\frac{1}{T}\right)}\left(1 + e^{A_L\left(\frac{1}{T_L}-\frac{1}{T}\right)}\right) \tag{2}$$

where $d(T)$ is the mortality rate at temperature T (in K), A_d is the Arrhenius constant, which quantifies how fast the mortality rate increases with increasing temperature, and T_R is a reference (baseline) temperature. The mortality at this temperature, d_{T_R}, represents the species-specific intrinsic mortality rate. The parameter T_L is the temperature threshold at which mortality starts to increase with decreasing temperature, and A_L quantifies how quickly the mortality rate decreases with decreasing temperature. Note that $A_d > 0$ and $A_L < 0$.

Temperature Response of Birth and Consumption Rates

A large number of studies spanning a range of ectothermic taxa show that per capita birth and consumption rates exhibit unimodal responses to temperature (Dreyer and Baumgartner, 1996; Carriere and Boivin, 1997; Morgan et al., 2001; Dannon et al., 2010; Hou and Weng, 2010; Jandricic et al., 2010; Dell et al., 2011; Englund et al., 2011; Amarasekare and Savage, 2012; Amarasekare, 2015). Both are well-described by a Gaussian function:

$$a(T) = a_{T_{\mathrm{opt}}} e^{-\frac{(T-T_{\mathrm{opt_a}})^2}{2{s_a}^2}} \tag{3}$$

where $T_{\mathrm{opt_a}}$ is the temperature at which the birth (consumption) rate is maximal $(a_{T_{\mathrm{opt}}})$, and s_a is a measure of the response breadth, the temperature range over which the species can reproduce and exploit resources.

Temperature Response of the Handling Time

Data from a number of ectotherm taxa spanning zooplankton to fish show that the handling time (inverse of the maximum uptake rate) exhibits a symmetric U-shaped response (Englund et al., 2011), which is well-described by an inverse Gaussian function:

$$h(T) = h_{T_{\mathrm{opt}}} e^{\frac{(T-T_{\mathrm{opt_h}})^2}{2{s_h}^2}} \tag{4}$$

where $T_{\mathrm{opt_h}}$ is the temperature at which the handling time is minimal $(h_{T_{\mathrm{opt}}})$, and s_h depicts the temperature range over which a consumer can handle its resource/prey species.

Temperature Response of the Maturation Rate

Maturation rate of ectotherms exhibits a left-skewed temperature response (Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Van der Have and de Jong, 1996; Van der Have, 2002; Kingsolver, 2009; Kingsolver et al., 2011) that results from the reduction in reaction rates at low and high temperature extremes due to enzyme inactivation. This response is well-described by a thermodynamic rate process model (Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Ratkowsky et al., 2005):

$$m(T) = \frac{\frac{m_{T_R} T}{T_R} e^{A_{m_J}\left(\frac{1}{T_R} - \frac{1}{T}\right)}}{1 + e^{A_L\left(\frac{1}{T_{L/2}} - \frac{1}{T}\right)} + e^{A_H\left(\frac{1}{T_H} - \frac{1}{T}\right)}} \tag{5}$$

where $m(T)$ is the maturation rate at temperature T (in K), m_{T_R} is the maturation rate at the reference temperature T_R at which the enzyme is 100% active, A_{m_J} (enthalpy of activation divided by the universal gas constant R) quantifies temperature sensitivity, $T_{L/2}$ and $T_{H/2}$ are, respectively, the low and high temperatures at which the enzyme is 50% active, and A_L and A_H are the enthalpy changes associated with low and high temperature enzyme inactivation divided by R (Johnson and Lewin, 1946; Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Van der Have and de Jong, 1996; Van der Have, 2002; Ratkowsky et al., 2005).

Temperature Response of Resource Self-Limitation

Self-limitation in the resource species arises from intra-specific competition. Experiments on temperature effects on competition in insects suggest that the temperature response of the per capita intra-specific coefficient ($q(T)$) can be monotonic or unimodal (Amarasekare and Coutinho, 2014; Amarasekare, 2015; Johnson et al., 2016). When the per individual demand for resources increases with temperature, due to higher activity levels at higher temperatures (Gillooly et al., 2001, 2002; Savage et al., 2004), self-limitation strength tends to increase monotonically with temperature. In this case, $q(T)$ is given by the Boltzmann-Arrhenius relationship:

$$q(T) = q_{T_R} e^{A_q\left(\frac{1}{T_R} - \frac{1}{T}\right)} \tag{6}$$

where $q(T)$ is the self-limitation strength at temperature T, A_q is the Arrhenius constant, which quantifies how fast the competition strength increases with increasing temperature, and T_R is a reference (baseline) temperature.

When the per-individual demand for resources is greatest during peak reproductive activity, which occurs at the optimal temperature for reproduction (Amarasekare and Coutinho, 2014; Amarasekare, 2015; Johnson et al., 2016), self-limitation strength exhibits a unimodal response with a maximum at the optimal temperature for reproduction. In this case $q(T)$ is unimodal and well-described by a Gaussian function (Equation 3). I use the Gaussian form in our analyses because empirical evidence (Amarasekare and Coutinho, 2014; Amarasekare, 2015; Johnson et al., 2016; Uszko et al., 2017) suggests this to be more common than the monotonic form.

PREDICTING WARMING EFFECTS ON CONSUMER-RESOURCE INTERACTIONS

Several large-scale data analyses show that the qualitative nature of phenotypic trait responses described above is conserved across ectotherm taxa (Dell et al., 2011; Englund et al., 2011; Kingsolver et al., 2011; Amarasekare and Savage, 2012). This allows us to make general predictions about trait responses to climate warming that applies across ectotherm taxa, habitat, and latitudes. By mapping various climate warming scenarios on to the phenotypic trait responses and comparing the result with the species' typical thermal regime, we can predict the effect of warming on trait responses. We can also predict the potential consequences of warming-induced changes in trait responses for population dynamics and species interactions.

There are two important aspects of trait responses that allow us to predict which traits are likely to be the most strongly affected by warming. The first is the distinction between rate-controlled and regulatory responses. The second is latitudinal variation in thermal adaptation. I will discuss each on in turn.

We see from the previous section that rate-controlled responses tend to be more skewed than regulatory responses. Because regulatory responses are more symmetrically unimodal, a negative deviation from the optimum (i.e., cooler temperatures) has the same detrimental effect as a positive deviation (i.e., warmer temperatures). This is not the case for skewed responses. For instance, the maturation rate exhibits a left-skewed response, with a faster decline at temperatures above the optimum than below it (Johnson and Lewin, 1946; Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Van der Have and de Jong, 1996; Van der Have, 2002; Ratkowsky et al., 2005). The mortality rate exhibits an inverted right-skewed response with mortality increasing rapidly with decreasing temperature at the low extreme (e.g., below freezing temperature) and increasing exponentially with increasing temperature above the low extreme (Johnson and Lewin, 1946; Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Van der Have and de Jong, 1996; Gillooly et al., 2001, 2002; Savage et al., 2004; Ratkowsky et al., 2005). This difference suggests that warming may have more detrimental effects on maturation and mortality than it does on the resource birth rate, and the consumer's attack rate and handling times.

Turning now to latitudinal differences, tropical thermal regimes are characterized by high mean temperatures and low-amplitude seasonal fluctuations, while temperate thermal regimes are characterized by low mean temperatures and high-amplitude seasonal fluctuations. As a result, tropical ectotherms exhibit trait responses with narrow breadths and thermal optima that coincide with the mean habitat temperature, while temperate ectotherms exhibit trait responses with wider breaths and optima that well-exceed the mean temperature (Deutsch et al., 2008; Tewksbury et al., 2008; Amarasekare and Johnson, 2017; Scranton and Amarasekare, 2017).

Climate Change Scenarios

Climate warming is expected to manifest as an increase in the mean annual temperature and/or a change in the seasonal thermal regime with warmer winters and hotter summers (IPCC, 2018). I consider the following three scenarios:

1. Warmer winters: the minimum temperature increases faster than the maximum temperature, resulting in an increase in the mean temperature and a decrease in the amplitude.

2. Hotter summers: the minimum temperature increases more slowly than the maximum temperature, resulting in an increase in the mean and amplitude both.
3. Warmer winters and hotter summers: the minimum and maximum temperatures change at the same rate, resulting in an increase in the mean while the amplitude stays the same.

By mapping these scenarios onto resource and consumer trait responses, I obtain the following general results.

Trait-Based Predictions

First, all warming scenarios lead to an increase in the mortality rate and a decrease in the maturation rate of both resource and consumer species. Because the maturation response is strongly left-skewed, the decrease in the maturation rate at high temperatures is much greater than those of birth and attack rates and self-limitation strength (**Figure 1**). This is significant because it means that species can develop faster and emerge earlier in the year because of warmer winter temperatures, but the decrease in the maturation rate during the hotter summers exceeds the increase in the maturation rate during warmer winters, resulting in a lower average maturation rate over the year.

Second, hotter-than-average summers are more detrimental to both tropical and temperate species compared to warmer-than-average winters. This is because maturation and mortality are most negatively affected by this warming scenario.

Third, all warming scenarios cause the mean habitat temperature to approach the physiologically optimal temperature in temperate ectotherms, and to exceed the optimal temperature in tropical ectotherms. Across all latitudes, this causes a decrease in the resource species' birth rate and self-limitation strength, and the consumer species' attack rate. The change in the mean temperature affects the consumer's handling time differentially depending on latitude, decreasing the handling time in temperate habitats and increasing it in tropical habitats. This is because the handling time exhibits a U-shaped response to temperature. The mean temperature becoming closer to the optimum in temperate habitats pushes the handling time toward its minimum, while the mean temperature exceeding the optimum pushes the handling time above the minimum (**Figure 1**).

Population-Level Predictions

The trait-based analysis suggests that maturation and mortality rates to be the most strongly affected by climate warming. If so, they should have a stronger detrimental effect on consumer-resource persistence in the face of climate warming. I explore this possibility by investigating consumer-resource coexistence in a constant thermal environment (i.e., the organism in question experiences the same temperature, on average, with few or no fluctuations around the mean), for which analytical expressions of resource and consumer persistence criteria can be derived.

Consider first the conditions for the resource and consumer species' viabilities when there is no developmental delay in either species (i.e., $\tau_J = 0, \tau_L = 0$). When resource self-limitation affects fecundity and the consumer attacks the adult stage of the resource, the resource can maintain a viable population (i.e., $R^\star > 0$) provided

$$\frac{d_C(T)}{a(T)\big(f - h(T)d_C(T)\big)} > 0, \tag{7}$$

and the consumer can persist on the resource (i.e., $C^\star > 0$) provided

$$\frac{q(T)d_C(T)}{a(T)\big(f - h(T)d_C(T)\big)} < \ln\Big(\frac{b(T)}{d_A(T)}\Big) \tag{8}$$

Note that when there are no developmental delays, the resource species' viability is determined by the consumer's temperature dependent attack and mortality rates [$a(T)$ and $d_C(T)$], its temperature-dependent handling time ($h(T)$), and conversion efficiency (f). Note that the product $h(T)d_C(T)$ is the fraction of the consumer's life span spent in handling food items at temperature T. The resource species' viability requires that the consumer species' efficiency in converting resources to consumer reproduction exceed the time it spends handling food items over its lifetime. Consumers with long handling times run the risk of driving their resources extinct.

When there are no developmental delays, the consumer species' viability is determined by the temperature responses of resource birth and death rates, resource self-limitation, the consumer's death rate and its consumption traits (conversion efficiency, attack rate, and handling time).

When both species exhibit developmental delays, the conditions for resource and consumer viabilities are, respectively:

$$\frac{d_C(T)}{a(T)\big(f\mathbf{e}^{-\mathbf{d_L(T)\tau_L(T)}}\big)} - h(T)d_C(T) > 0, \tag{9}$$

and

$$\frac{q(T)d_C(T)}{a(T)\big(f\mathbf{e}^{-\mathbf{d_L(T)\tau_L(T)}}\big)} - h(T)d_C(T)\big) + \mathbf{d_J(T)\tau_J(T)} < \ln\Big(\frac{b(T)}{d_A(T)}\Big) \tag{10}$$

where $\tau_X(T) = \frac{1}{m_X(T)}\;\; X = J, L$.

There are three key points to note. First, developmental delays cause a significant reduction in the upper temperature limit for viability in both resource and consumer species (**Figure 2**).

Second, the resource species' developmental delay has a stronger effect on consumer viability than the consumer's delay on resource viability. This is because the resource species' developmental delay enters the consumer's viability criterion as an additive term, while the consumer's delay enters the resource species' viability criterion only as an exponential term (compare Equation 9 and Equation 10). The resource species' developmental delay therefore causes a stronger reduction in the consumer's viability than does the consumer's delay on resource viability.

Third, the resource species' developmental delay has a stronger effect on consumer viability than the consumer's developmental delay. To see this, consider the consumer's viability criterion when the resource species' developmental delay is long relative to that of the consumer (i.e., $\tau_J > 0,\ \tau_L \rightarrow 0$):

$$\frac{q(T)d_C(T)}{a(T)\big(f - h(T)d_C(T)\big)} + \mathbf{d_J(T)\tau_J(T)} < \ln\Big(\frac{b(T)}{d_A(T)}\Big) \tag{11}$$

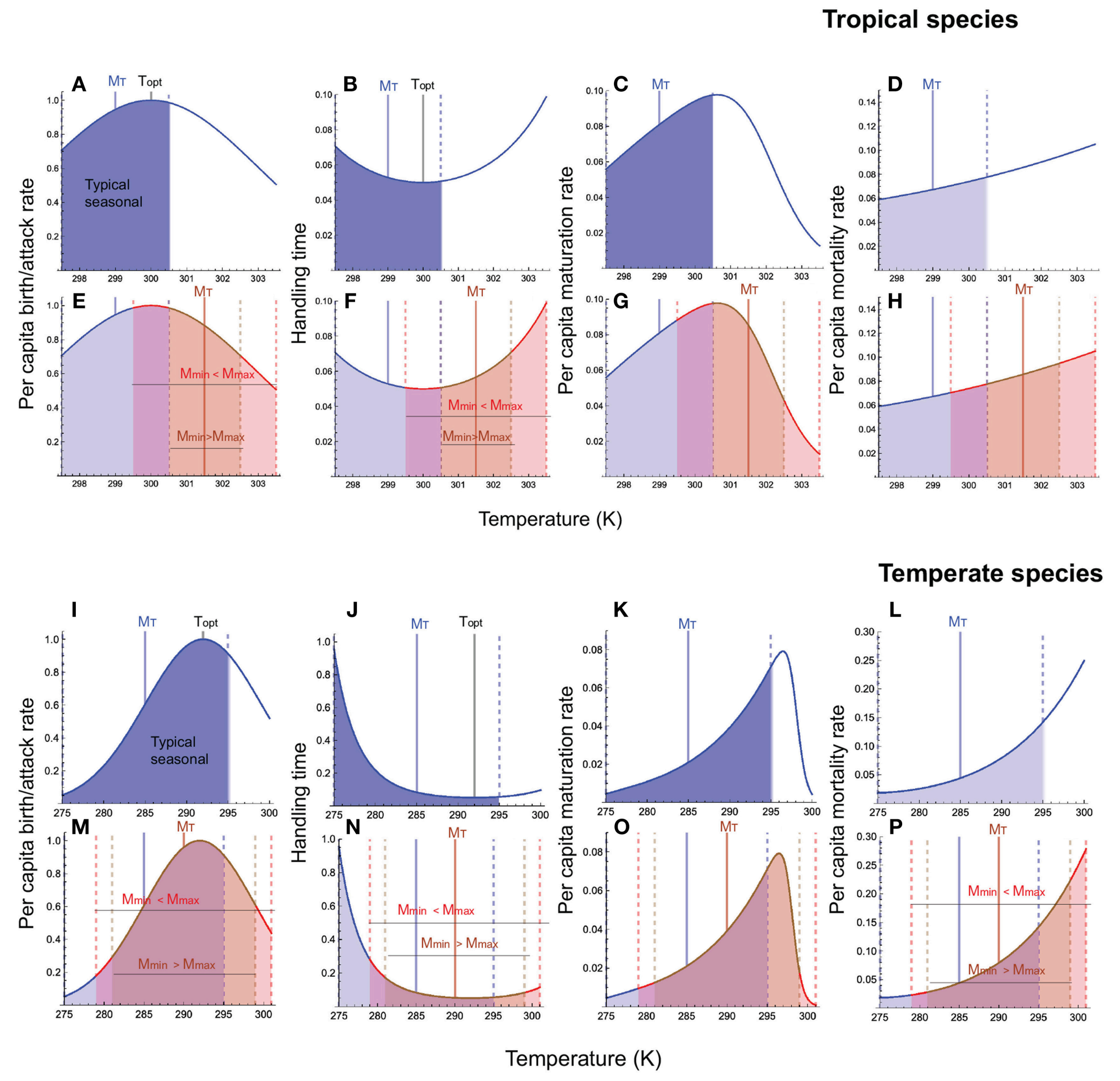

FIGURE 1 | Temperature responses of resource and consumer traits under typical seasonal variation and warming. **(A–H)** are for tropical ectotherms, and **(I–P)**, for temperate ectotherms. For each latitude, panels in the top row depict temperature responses under typical seasonal variation, and those in the bottom row, temperature responses under the two warming scenarios: minimum temperature increases faster than the maximum ($\text{Min}_T > \text{Max}_T$) and minimum temperature increases slower than the maximum ($\text{Min}_T < \text{Max}_T$). On panels in the bottom row for each species [**(A–D)** for tropical and **(I–L)** for temperate], the blue portion of the response curve depicts the response under seasonal variation, the brown portion of the curve when $\text{Min}_T > \text{Max}_T$, and the red portion of the curve, $\text{Min}_T < \text{Max}_T$. In each panel, the solid blue vertical line depicts the mean habitat temperature and the solid black line, the physiologically optimal temperature; the dashed vertical blue lines depict the temperature range experienced by species under typical seasonal variation, the dashed red lines depict the range when $\text{Min}_T < \text{Max}_T$, and the dashed brown lines, when $\text{Min}_T > \text{Max}_T$. For ease of comparison, increase in minimum and maximum temperature for the two scenarios are chosen such that the mean temperature (M_T) is the same. Note that the temperature range on the x-axis is smaller in the for tropical species (297.5–303.5 K) than for the temperate species (275–301 K). Parameter values for the tropical species are: $T_{\text{opt}_X} = 300, s_X = 3.0$(X=b, a, h, q), $T_{R_Y} = 297$(Y=R, C), $T_{L_Z} = 296, T_{H_Z} = 302$ (Z=J, L), $M_T = 299, A_T = 1.5°, m = 3, a = 2$ when the minimum temperature increases faster than the maximum and $m = 2, a = 3$ when the minimum increases more slowly than the maximum. Parameter values for the temperate species are: $T_{\text{opt}_X} = 292, s_X = 6.0$(X=b, a, h, q), $T_{R_Y} = 292$(Y=R, C), $T_{L/2_Z} = 275, T_{H/2_Z} = 298$(Z=J, L), $M_T = 285, A_T = 10°, m = 6, a = 4$ when the minimum temperature increases faster than the maximum and $m = 4, a = 6$ when the minimum increases more slowly than the maximum. Other parameters are: $b_{T_{\text{opt}}} = a_{T_{\text{opt}}} = 1.0, h_{T_{\text{opt}}} = 0.05, q_{T_{\text{opt}}} = 0.2, f = 1.0, d_{Y_{T_R}} = 0.1, d_{Z_{T_R}} = 0.1, m_{Z_{T_R}} = 0.05, A_{d_Y} = 10,000, A_{d_Z} = 10,000, A_{m_Z} = 10,000, A_{L_Y} = -25,000, A_{L/2_Z} = -50,000, A_{H/2_Z} = 100,000$.

as opposed to when the resource species' developmental delay is short relative to that of the consumer (i.e., $\tau_J \to 0, \tau_L > 0$):

$$\frac{q(T)d_C(T)}{a(T)\left(f\mathbf{e}^{-\mathbf{d_L(T)\tau_L(T)}} - h(T)d_C(T)\right)} < \ln\left(\frac{b(T)}{d_A(T)}\right) \tag{12}$$

Comparing Equations (11) and (12) shows that the resource species' developmental delay has a stronger effect on consumer viability for the same reason as above, i.e., it enters the consumer's viability criterion as an additive term, while the consumer's delay enters the its viability criterion only as an exponential term.

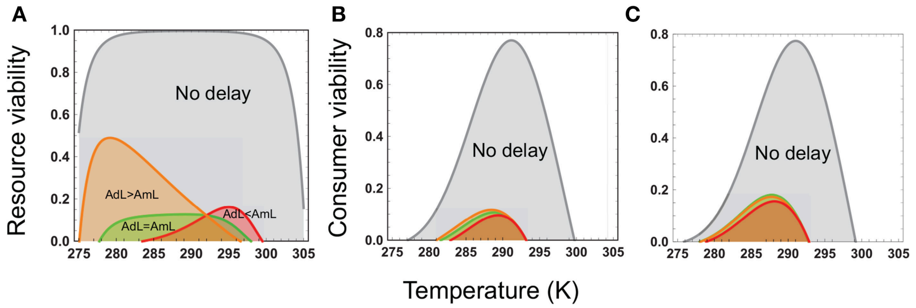

FIGURE 2 | Resource and consumer species' viabilities as a function of temperature. In each panel, the gray curve depicts the temperature range over which each species has a positive abundance in the absence of developmental delays (Equations 7, 8), and the orange, green, and red curves, the temperature range for viability in the presence of delays (Equations 9, 10). In **(A)**, the green, orange, and red curves represent, respectively, the resource species viability when the consumer's temperature sensitivities of maturation (A_{m_L}) and mortality (A_{d_L}) are the same ($k_1 = A_{d_L} - A_{m_L} = 0$), mortality has greater temperature sensitivity than maturation ($k_1 = 8,000$), and *vice versa* ($k_1 = -8,000$). In **(B)**, the green, orange, and red curves represent, respectively, the consumer species' viability when the resource and consumer species' temperature sensitivities of maturation are the same ($k_2 = A_{m_J} - A_{m_L} = 0$), resource's maturation has lower temperature sensitivity than consumer's ($k_2 = -4,000$) and vice versa ($k_2 = 4,000$). In **(C)**, the curves depict depicts consumer viability the consumer species' viability when the resource and consumer species' temperature sensitivities of mortality are the same ($k_3 = A_{d_J} - A_{d_L} = 0$), resource's mortality has greater temperature sensitivity than consumer's ($k_3 = 2,000$) and vice versa ($k_3 = -2,000$). Other parameters are as in **Figure 1**.

Importantly, the effect of developmental delays on viability is mediated by the multiplicative effect of the temperature responses of maturation and mortality rates. Differences between the resource and consumer in their temperature sensitivities of mortality and maturation therefore play a key role in determining the lower and upper thermal limits to viability. For instance, the resource species' viability is affected by the multiplicative effect of the consumer's maturation and juvenile mortality rates. As noted in the trait-based analysis above, the maturation rate decreases and the mortality rate increases with increasing temperature. This leads to a steep decline in viability as temperatures increase above the physiologically optimal range. Resource viability is lower when the consumer's maturation rate is more temperature-sensitive that its mortality rate (**Figure 2A**). This is because lower mortality and faster development means a larger adult consumer population and hence greater exploitation of the resource.

As with the resource species, differential temperature sensitivities of maturation and mortality rates have a strong effect on consumer viability. Thermal limits to consumer viability are narrower when the resource species' maturation rate is more temperature-sensitive, and mortality rate less temperature-sensitive, than those of the consumer (**Figures 2B,C**). This is because when the decrease in the resource maturation rate with increasing temperature exceeds the increase in the mortality rate, the resource developmental delay increases at both low and high temperatures. This causes a reduction in the adult resource population at temperatures below and above the optimal temperature range, narrowing the consumer's thermal limits to viability.

Summary of Predictions

Taken together, the trait-based and viability analyses make three testable predictions. First, warming has its strongest impact on viability through its effects on maturation and mortality rates. Second, the resource species' developmental delay has a greater negative effect on the consumer's viability than the consumer's delay. Third, because of the conflict of interest between species, we expect the consumer to be more susceptible to warming than the resource. This is because the resource is negatively affected by warming, but is positively affected by negative warming effects on consumer, while the consumer is negatively affected by warming and the negative effects of warming on the resource. The next step is to test these predictions with the dynamical model (Equation 2).

Consumer-Resource Persistence in a Variable Thermal Environment

Equation (1) is non-autonomous (i.e., long-term outcomes are not independent of time) and cannot yield analytical results on long-term outcomes. I conduct numerical analyses to investigate the consumer-resource dynamics and long-term outcomes under both typical seasonal variation and climate warming.

Let seasonal temperature variation be depicted by the sinusoidal function $T(t) = M_T + A_T S(t)$ where t is time in days, M_T is the mean habitat temperature in K, A_T is the amplitude of seasonal fluctuations ($A_T = \frac{T_{\max} - T_{\min}}{2}$), and $S(t) = \sin \frac{2\pi t}{yr}$ (or $-\cos \frac{2\pi t}{\tau}$) with $yr = 365$ days.

The change in the seasonal thermal regime under climate warming is given by $T(t) = (M_T + mt) + (A_T + at)S(t)$ with $m = (\text{mhigh} + \text{mhigh})/2$ and $a = (\text{mhigh} - \text{mhigh})/2$ depicting respectively, the daily rate of increase in mean and amplitude. The quantities $\text{mlow} = s_1/(n * yr)$ and $\text{mhigh} = s_2/(n * yr)$ where s_1 and s_2 are, respectively, the number of degrees by which the minimum and maximum temperatures increase in n years. When the minimum and maximum temperatures increase at the same rate ($s_1 = s_2$), the mean temperature increases over time with no net change in the amplitude. When the minimum temperature increases faster than the maximum (warmer-than-average winters; $s_1 > s_2$), the mean increases over time while the amplitude decreases. When the maximum

TABLE 1 | Temperature response parameters for tropical and temperate species.

	Tropical	**Temperate**
Seasonal temperature regime		
M_T	299 K	285 K
A_T	1.5°	10°
Resource species		
Birth rate		
$T_{\mathrm{opt_b}}$	300	292
s_b	3.0	7.0
Self-limitation strength		
$T_{\mathrm{opt_q}}$	300	292
s_q	3.0	5.0
q_{Topt}	0.2	0.2
Maturation rate		
T_R	298	292
A_{m_J}	12,000	12,000
$T_{L/2_J}$	296 K	275 K
$T_{H/2_J}$	302 K	298 K
A_{L_J}	−75,000	−50,000
A_{H_J}	75,000	175,000
Juvenile mortality rate		
A_{d_J}	7,000	8,000
$d_{J_{T_L}}$	290	275
A_{d_L}	−50,000	−25,000
Adult mortality rate		
A_{d_A}	8,000	9,000
$d_{A_{T_L}}$	290	275
A_{d_L}	−50,000	−25,000
Consumer species		
Attack rate		
$T_{\mathrm{opt_a}}$	300 K	292 K
s_a	3.0	6.0
Conversion efficiency		
f	1.0	1.0
Handling time		
$h_{T_{\mathrm{opt}}}$	0.05	0.05
$T_{\mathrm{opt_h}}$	300 K	292 K
s_h	3.0	6.0
Maturation rate		
T_R	298	292
A_{m_L}	10,000	10,000
$T_{L/2_L}$	296 K	275 K
$T_{H/2_L}$	302 K	298 K
A_{L_L}	−75,000	−50,000
A_{H_L}	75,000	175,000
Juvenile mortality rate		
A_{d_L}	9,000	8,000
$d_{L_{T_L}}$	290	275
A_{d_L}	−50,000	−25,000
Adult mortality rate		
A_{d_C}	9,000	8,000
$d_{C_{T_L}}$	290	275
A_{d_L}	−50,000	−25,000

temperature increases faster than the minimum (hotter-than-average summers; $s_1 < s_2$), the mean and the amplitude both increase over time. I incorporate warming as a liner increase in the mean, minimum and maximum temperatures. The formulation, however, is general and can accommodate any form of empirically observed warming regime.

The nature of consumer-resource dynamics is an important axis of investigation because developmental delays can lead to complex dynamics even in the absence of temperature variation (Gurney et al., 1983; Nisbet and Gurney, 1983). In this case, the steady state outcomes of Equation (1) depend on the developmental delay relative to adult longevity (Murdoch et al., 2003). When the resource species' developmental delay is short relative to adult longevity but longer than the consumer's developmental delay, the outcome is a stable equilibrium (Murdoch et al., 2003). When the reverse is true, the ensuing delay in the operation of density-dependence can lead to delayed feedback cycles. When density-dependence operates through fecundity and the consumer attacks the juvenile stage, such delayed feedback is manifested as single generation cycles with a period approximately equal to the resource species' generation time; when the consumer attacks the adult stage, the feedback cycles have a delay equal to the resource species' developmental delay (Murdoch et al., 2003).

I ran the model (Equation 1) for a period of 100 years and recorded long-term abundances in the 101th year. I analyzed six cases along three axes of biological relevance: resource life stage attacked (juvenile vs. adult resource), latitudinal variation in temperature regime (tropical vs. temperate), and nature of consumer-resource dynamics in the absence of temperature variation (stable vs. complex). For each case analyzed, I checked for deterministic extinction of consumer and resource, and calculated the variability in abundances as the coefficient of variation (standard deviation of the time series of abundance in the 101th year scaled by the mean abundance). I used parameter values (**Table 1**) that are realistic for insect species in tropical and temperate habitats (Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Kooijman, 1993; Van der Have and de Jong, 1996; Amarasekare and Savage, 2012; Amarasekare and Johnson, 2017; Scranton and Amarasekare, 2017). In accordance with empirical findings (Gao et al., 2013; Johnson et al., 2016), I considered the unimodal temperature response of competition to have the same parameter values as the temperature response of reproduction, i.e., competition is strongest at the temperature optimal for reproduction ($T_{\mathrm{opt_q}} = T_{\mathrm{opt_b}}$), and operates on the same temperature range within which the species can reproduce ($s_q \leq s_b$).

RESULTS

Analysis of the dynamical model both confirms predictions of the trait-based analysis and yields new insights. Three generalities emerge. First, consumer-resource interactions in the tropics are more at risk of species losses due to warming, while those in the temperate zone are more at risk of extreme fluctuations in species' abundances. Second, effects of warming are more detrimental when the consumer attacks the adult stage of the resource and when consumer-resource interactions exhibit complex dynamics. Third, hotter-than-average summers are more detrimental to consumer-resource interactions than warmer-than-average winters. Below I explain these results in detail.

First, as predicted by the trait-based analysis, warming poses a greater risk of deterministic extinction for tropical consumer-resource interactions. The consumer goes extinct once the minimum temperature exceeds 2° when the adult stage is attacked (**Figures 3B,F,J,N,R,V**), and 3° when the juvenile stage is attacked (**Figures 4B,F,J,N,R,V**); the resource goes extinct once the minimum temperature exceeds 3 and 4°, respectively, in these two cases (**Figures 3**, **4A,E,I,M,Q,U**). In contrast, deterministic extinction of temperate resources and consumers does not occur until the maximum temperature increases by 6° (**Figures 3**, **4C,D,K,O,S,W** for resource, **Figures 3**, **4D,H,L,P,T,X** for consumer). However, both resource and consumer species exhibit large fluctuations in abundance (**Figure 5**). Fluctuations are more extreme when the consumer attacks the adult resource stage and consumer-resource dynamics are complex rather than stable (compare **Figure 3** and **Figure 4**).

The second result involves two new insights that were not anticipated by the trait-based and analytical viability analyses. The first is that warming is more detrimental when the consumer attacks the adult stage of the resource. Not only does warming cause more extinctions when the adult stage is attacked compared to when the juvenile stage is attacked, but it also leads to greater variability in abundance in both resource and consumer species (compare **Figure 3** and **Figure 4**). These outcomes ensue regardless of latitude or nature of consumer-resource dynamics (**Figure 5**).

The second insight is that warming has a greater detrimental effect when consumer-resource interactions exhibit complex dynamics. As noted in the previous section, when the juvenile developmental delay is long relative to adult longevity, delay in the operation of density-dependence can lead to delayed feedback cycles in the absence of temperature variation. When consumer-resource interactions exhibiting such cycles are subject to warming, the interplay between intrinsic non-linear dynamics and non-linear trait temperature responses to warming can predispose species to extinction. Indeed, when consumer-resource dynamics are complex, we see the deterministic extinction of resources and consumers at lower levels of warming than when dynamics are stable (compare **Figure 3** and **Figure 4**). We also see greater variability in abundances (**Figure 5**).

The third result concerns the effect of warming scenario. As predicted by the trait-based analysis, hotter-than-average summers are more detrimental to consumer-resource interactions than warmer-than-average winters. It causes a greater number of resource and consumer extinctions across latitudes, and leads to greater variability in abundances. Greater variability in abundances is more clearly seen in the resource rather than in the consumer, in tropical rather than in temperate habitats, and when the consumer attacks the adult rather than the juvenile stage of the resource. Of note, as the strength of warming increases the difference between the two warming scenarios diminishes, as can be seen by the increasing similarity in the CVs of abundances between scenarios as warming proceeds from 1 to 6°. Interestingly, the effects of warming scenarios are more apparent when one examines the temporal trajectories of population trajectories rather than the summary measures of variability in abundances (CV). We see that, across the board, the dynamical effects of hotter summers alone are more similar to the scenario with warmer winters and hotter summers, indicating that hotter summers tend to override the effect of warmer winters. The reason for this can be seen by looking more closely at how phenology and population trajectories change over the year as a result of warming. Warming causes earlier emergence because winters are warmer. However, warming causes summers to also be hotter, causing a reduction in birth, attack and maturation rates and increasing mortality rates. This in turn leads to a lowering of summer abundance. As warming proceeds summer abundance declines further, causing population growth to be restricted to early spring and fall. When extinction occurs, it is because summer abundances fall too low for species to recover from.

DISCUSSION

Evidence for the detrimental effects of climate warming on biodiversity is rapidly accumulating (Dunn and Winkler, 1999; Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Inouye, 2008; Miller-Rushing and Primack, 2008; Post et al., 2008). An accurate gauge of these detrimental effects requires that we understand the effects warming has on key components of biodiversity. Consumer-resource interactions (e.g., predator-prey, plant-herbivore, host-parasite) constitute the fundamental building blocks of all communities. They therefore serve as a key indicator for gauging the effects of warming on biodiversity. Understanding how warming affects consumer-resource dynamics and persistence is therefore a key research priority.

Here I develop a mathematical framework for predicting the effects of warming on consumer-resource interactions. This framework, based on delay differential equations, realistically captures the developmental delays that characterize the life cycles of multicellular ectotherms. It also incorporates mechanistic descriptions of consumer and resource trait responses to temperature, and the latest IPCC predictions about warmer-than-average winters and hotter-than-average summers. I use a trait-based analysis to generate predictions about population-level consequences of warming, which I then test with the dynamical model. I report three key findings.

First, tropical consumer-resource interactions are more at risk of species losses due to warming, while temperate interactions are more at risk of extreme fluctuations. Second, warming is more detrimental when the consumer attacks the adult stage of the resource and when consumer-resource dynamics exhibit complex dynamics. Third, hotter-than-average summers are more detrimental than warmer-than-average winters.

The first finding, that tropical consumer-resource interactions are more prone to species losses while temperate interactions

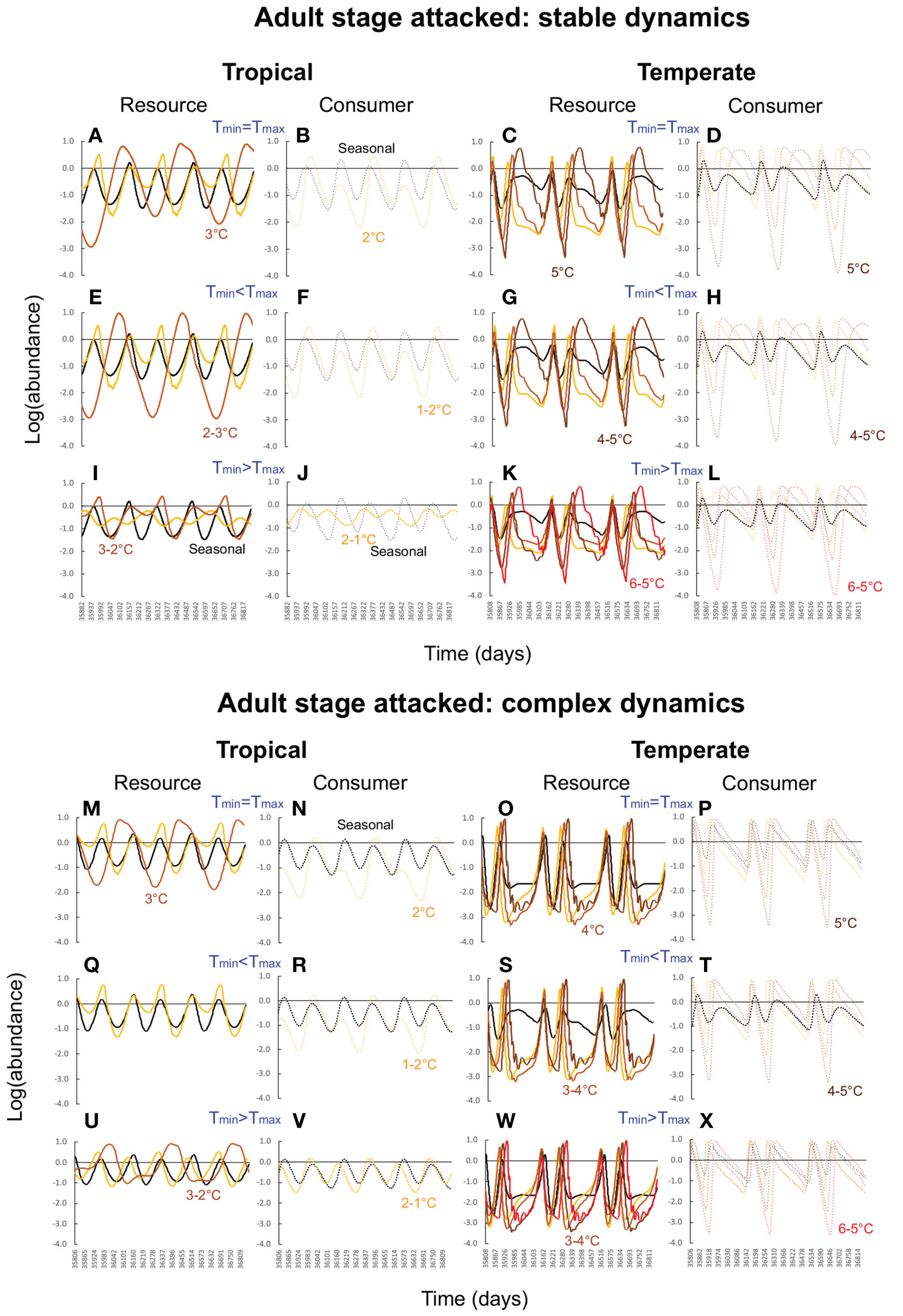

FIGURE 3 | Consumer-resource dynamics in tropical and temperate habitats when the consumer attacks the adult stage and consumer-resource dynamics are stable **(A–L)** vs. complex **(M–X)**. In all panels, the black curves (solid for resource, dashed for consumer) depict abundances under typical seasonal variation. Yellow, light brown, dark brown, and red curves depict progressively higher levels of warming (1–4°C for tropical habitats, 2–6°C for temperate habitats). For each latitude, the top row of panels depict effects of warming when the minimum and maximum temperatures increase at the same rate (mean increases, amplitude unchanged). The second row depicts warming effects when the maximum temperature increases faster than the minimum (mean and amplitude both increase), and the third row, when the minimum temperature increases faster than the maximum (mean increases, amplitude decreases). Parameter values for the tropical community are: $b_{T_{\mathrm{opt}}} = 5.0, m_{J_{T_R}} = 0.05$ ($\tau_{J_{T_R}} = 20$), $d_{J_{T_R}} = 0.1, d_{A_{T_R}} = 0.05, a_{T_{\mathrm{opt}}} = 1.0$ for stable dynamics, and $b_{T_{\mathrm{opt}}} = 2.0, m_{J_{T_R}} = 0.07$ ($\tau_{J_{T_R}} = 15$), $d_{J_{T_R}} = 0.05, d_{A_{T_R}} = 0.01, m_{L_{T_R}} = 0.1$ ($\tau_{L_{T_R}} = 10$), $d_{L_{T_R}} = 0.1, d_{C_{T_R}} = 0.01, a_{T_{\mathrm{opt}}} = 0.5$ for complex dynamics. Parameter values for the temperate community are: $b_{T_{\mathrm{opt}}} = 1.0, m_{J_{T_R}} = 0.04$ ($\tau_{J_{T_R}} = 25$), $d_{J_{T_R}} = 0.1, d_{C_{T_R}} = 0.1, a_{T_{\mathrm{opt}}} = 0.5, m_{L_{T_R}} = 0.1$ ($\tau_{J_{T_R}} = 10$), $d_{L_{T_R}} = 0.1, d_{C_{T_R}} = 0.05$ for stable dynamics, and $b_{T_{\mathrm{opt}}} = 1.0, m_{J_{T_R}} = 0.05$ ($\tau_{J_{T_R}} = 20$), $d_{J_{T_R}} = 0.05, d_{R_{T_R}} = 0.01, d_{L_{T_R}} = 0.1, d_{C_{T_R}} = 0.05, m_{L_{T_R}} = 0.1$ ($\tau_{J_{T_R}} = 10$) for complex dynamics. All other parameters values are as in **Table 1**.

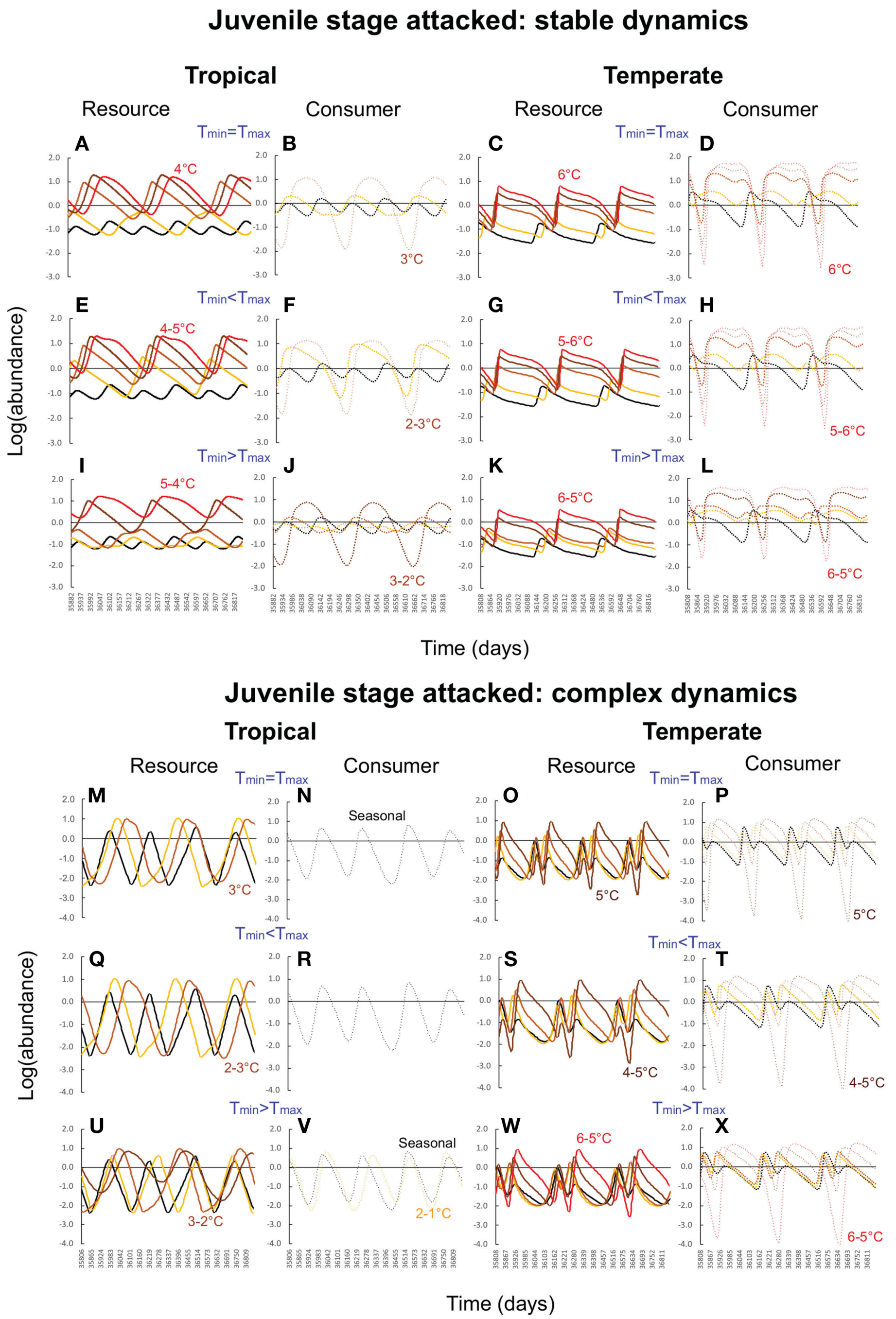

FIGURE 4 | Consumer-resource dynamics in tropical and temperate habitats when when the consumer attacks the juvenile stage and consumer-resource dynamics are stable **(A–L)** vs. complex **(M–X)**. In all panels, the black curves (solid for resource, dashed for consumer) depict abundances under typical seasonal variation. Yellow, light brown, dark brown, and red curves depict progressively higher levels of warming (1–4°*C* for tropical habitats, 2-6°*C* for temperate habitats). For each latitude, the top row of panels depict effects of warming when the minimum and maximum temperatures increase at the same rate (mean increases, amplitude unchanged). The second row depicts warming effects when the maximum temperature increases faster than the minimum (mean and amplitude both increase), and the third row, when the minimum temperature increases faster than the maximum (mean increases, amplitude decreases). Parameter values for the tropical community are: $b_{T_{\mathrm{opt}}} = 2.0, m_{J_{T_R}} = 0.07$ $(\tau_{J_{T_R}} = 15), d_{J_{T_R}} = 0.05, d_{A_{T_R}} = 0.01, a_{T_{\mathrm{opt}}} = 0.5, d_{L_{T_R}} = 0.1, dP1TR = 0.05, m_{L_{T_R}} = 0.1$ $(\tau_{L_{T_R}} = 10)$ for stable dynamics, and $b_{T_{\mathrm{opt}}} = 2.0, m_{J_{T_R}} = 0.05$ $(\tau_{J_{T_R}} = 20), d_{J_{T_R}} = 0.05, d_{A_{T_R}} = 0.05, a_{T_{\mathrm{opt}}} = 0.5, d_{L_{T_R}} = 0.1, dP1TR = 0.05, m_{L_{T_R}} = 0.1$ $(\tau_{L_{T_R}} = 10)$. Parameter values for the temperate community are: $b_{T_{\mathrm{opt}}} = 2.0, m_{J_{T_R}} = 0.04$ $(\tau_{J_{T_R}} = 25), d_{J_{T_R}} = 0.1, d_{C_{T_R}} = 0.01, d_{L_{T_R}} = 0.1, d_{C_{T_R}} = 0.05, m_{L_{T_R}} = 0.1$ $(\tau_{J_{T_R}} = 10)$ for stable dynamics and $b_{T_{\mathrm{opt}}} = 1.0, m_{J_{T_R}} = 0.05$ $(\tau_{J_{T_R}} = 20), d_{J_{T_R}} = 0.05, d_{R_{T_R}} = 0.05, d_{L_{T_R}} = 0.1, d_{C_{T_R}} = 0.05, m_{L_{T_R}} = 0.07$ $(\tau_{J_{T_R}} = 15)$ for complex dynamics. Other parameter values are as in **Table 1**.

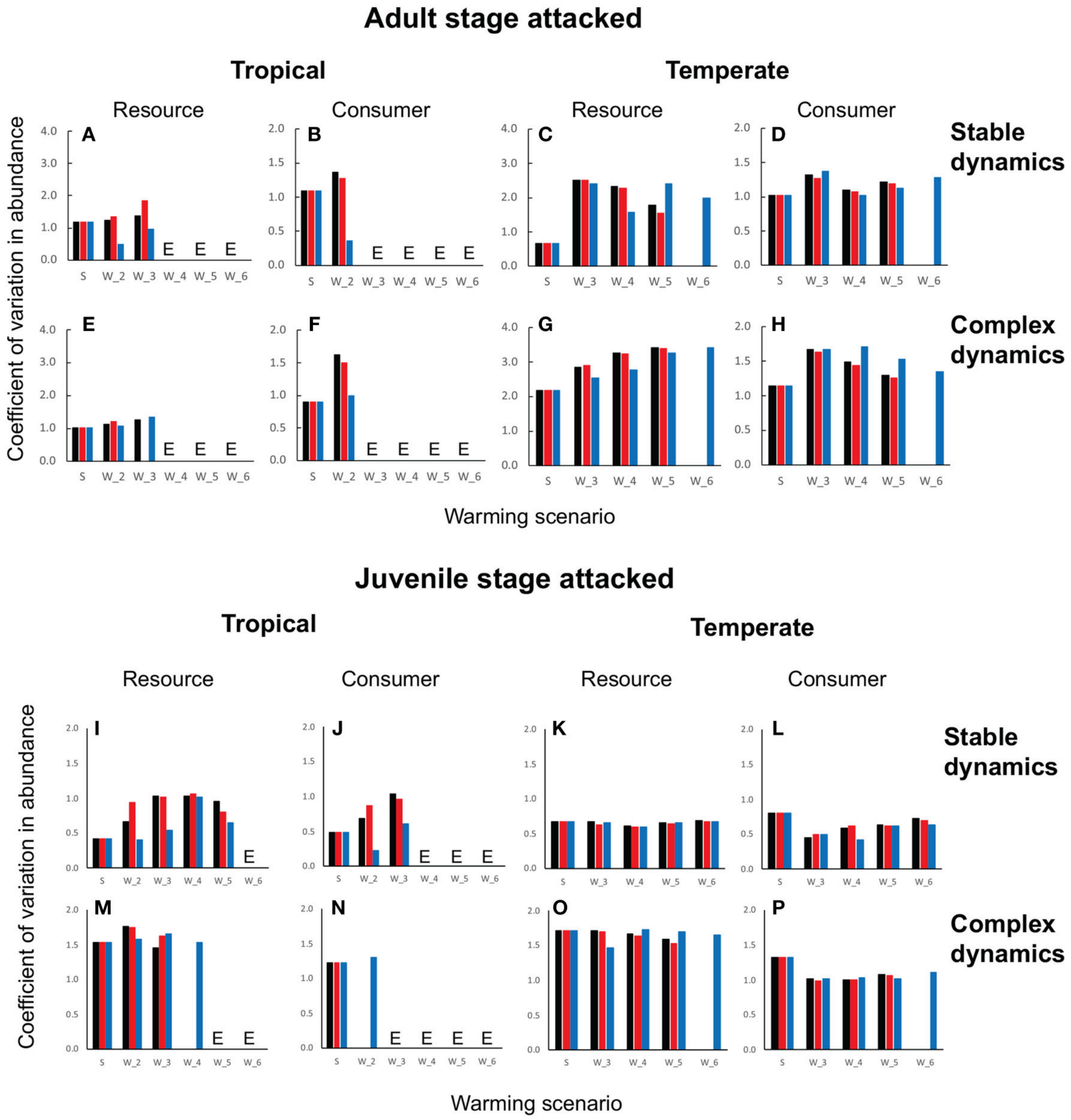

FIGURE 5 | Coefficient of variation in resource and consumer abundances in tropical and temperate habitats when the consumer attacks the adult stage **(A–H)** vs. the juvenile stage **(I–P)**. In all panels, the x-axis gives the CV in abundance under typical seasonal variation (S) and successively increasing levels of warming ($W_2 \cdots, W_6$) where W_i ($i = 1, 6$) depicts a warming scenario in which the maximum temperature increases by $i^{\star}$ [e.g., W_2 denotes W_{22} (black column), W_{12} (red column), and W_{21} (blue column). In each panel, the black column depicts warming effects when the minimum and maximum temperatures increase at the same rate, the red column depicts effects when the maximum increases faster than the minimum, and the blue column, when the maximum increases slower than the minimum. In each case (juvenile vs. adult), the top row of panels depicts stable dynamics **(A–D)** when the adult is attacked and **(I–L)** when the juvenile is attacked] and the bottom row, complex dynamics **(E–H)** for adult and [m-(p) for juvenile]. Cases marked with E depict warming-driven extinctions of resource and/or consumer. Parameter values are as in **Figures 3**, **4** and **Table 1**.

are more prone to extreme fluctuations, highlights the different challenges that climate warming poses to ectotherm communities inhabiting different latitudes. Since tropical ectotherms exhibit thermal optima that coincide with the mean habitat temperature (Deutsch et al., 2008; Tewksbury et al., 2008; Amarasekare and Savage, 2012; Amarasekare and Johnson, 2017), an increase in the mean temperature, regardless of whether it is through an increase in the minimum or maximum temperature, pushes the species into a thermal realm in which birth, attack and maturation rates decrease and mortality rates increase. The resulting negative per capita growth rate causes deterministic extinction. In contrast to the tropics, which see warming-induced extinctions, temperate habitats see an increase in the fluctuations of resource and consumer abundances. In all cases, the decrease in fluctuations are greater in magnitude than the increase, which means that species are less prone to outbreak densities in the face of warming than they are to stochastic extinction during periods of low abundances.

The expectation based on the trait-based analysis that warming is more detrimental to the consumer than to the resource is borne out by the dynamical model analysis. The tropics see more cases of consumer rather than resource extinction, while the temperate realm sees greater declines in consumer rather than resource abundance, and hence a greater risk of stochastic extinction. These outcomes ensue because of the conflict of interest between species inherent in consumer-resource interactions. The resource species is negatively affected by warming, but positively affected by warming effects on the consumer, while the consumer is negatively affected both by warming and the negative effects of warming on the resource species.

The second finding is that warming has a greater detrimental effect when the consumer attacks the adult stage of the resource and when consumer-resource interactions exhibit complex dynamics. The reason that warming has differential effects based on the life stage attacked can be explained as follows. Temperature affects juvenile development through the multiplicative effect of juvenile maturation and mortality. Warming both decreases the maturation rate and increases the mortality of the juvenile resource stage, resulting in a smaller adult resource population that the consumer then overexploits. Such overexploitation can lead to increasing consumer-resource fluctuations and eventual extinction, effects compounded by warming-induced reduction in consumer attack rate and increase in handling time. When the consumer attacks the juvenile stage of the resource, the invulnerable adult resource stage acts as a buffer (particularly when fecundity and adult longevity are high), making the consumer less resource-limited and reducing the tendency for extreme fluctuations and warming-induced extinction.

The reason why warming has a greater detrimental effect on consumer-resource interactions exhibiting complex dynamics is because the interplay between population cycles resulting from delayed density-dependent feedback and temperature variation can cause resource abundances to fall to levels at which the consumer cannot maintain itself. Even when deterministic extinction does not occur, this interplay can lead to large fluctuations in abundance that can predispose species to stochastic extinction.

The third result is that hotter-than-average summers is more detrimental to consumer-resource interactions than warmer-than-average winters. This is an interesting finding in light of the fact that it is the warmer-than-average winters that lead to advanced emergence and phenological asynchrony (Dunn and Winkler, 1999; Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Inouye, 2008; Miller-Rushing and Primack, 2008; Post et al., 2008). The crucial insight to emerge from the comparative analysis of warming scenarios is that asynchrony in emergence is not the issue. It is what follows that matters. While warmer-than-average winters cause advanced emergence and higher spring abundance due to faster maturation rates and the concomitant reduction in juvenile mortality, hotter-than-average summers cause a steep decline in birth and maturation rates and a steep increase in the mortality rate. This is because maturation reaches its lowest and mortality its highest under this warming scenario. The population-level outcome is a large decline in abundance during summer. The hotter the summers become, the more difficult it is for species to recover from the large decline in summer abundance. Since the consumer is dependent on the resource, a large decrease in resource abundance makes recovery from low abundances an extra challenge for the consumer.

These findings have implications for both biodiversity and biological control. Regarding biodiversity, two general results emerge. The first concerns life history and consumption trait attributes that increase susceptibility to warming. Interactions in which resource species' maturation rate is more temperature-sensitive (i.e., large Arrhenius constants and narrower response breadths), and mortality rate less temperature-sensitive (smaller Arrhenius constants), than those of the consumer are more susceptible to the detrimental effects of warming, as are those in which consumer's maturation rate is more temperature-sensitive that its mortality rate. In the former, greater susceptibility to warming ensues because when the decrease in the resource maturation rate with increasing temperature exceeds the increase in the mortality rate, the resource developmental delay increases at both low and high temperatures. This causes a reduction in the adult resource population at temperatures below and above the optimal temperature range, narrowing the consumer's thermal limits to viability. In the latter, greater susceptibility to warming occurs because lower mortality and faster development of the juvenile resource stage means a larger adult consumer population and hence greater exploitation of the resource. Similarly, interactions in which the resource species has high fecundity and long developmental delays relative to adult longevity and the consumer has a long developmental delay relative to that of the resource are more at risk of extinction due to warming as are those in which the adult resource stage is attacked.

The second general result regarding biodiversity is that consumer-resource interactions in the tropics are more at risk of extinction due to warming while temperate interactions are more vulnerable to extreme fluctuations. This generates a latitudinal difference in the nature and timing of extinctions. Warming causes deterministic extinction of tropical resources and consumers, leading to immediate disruption of species interactions. In contrast, warming predisposes temperate resource and consumers to stochastic extinction during low abundances, which means that interaction disruptions are likely to occur with a time delay. Such extinction debts may lead to unexpected outcomes since it is difficult to predict *a priori* the order and timing of species losses. If the consumer goes extinct first, diversity may be recovered through natural recolonizations or reintroduction of the consumer; if the resource goes extinct first, the entire interaction will be lost and recovery would be much more challenging.

Regarding biological control, warming-induced loss of natural enemies that serve as biological control agents can cause pest outbreaks that can compromise the supply of essential food items, thus creating a significant threat to food security. Pests whose adult stages are attacked are more likely to lose their natural enemies, particularly in tropical climates where many important crops are grown, leading to greater pest damage. At the same time, pests with invulnerable adult stages are likely to benefit from warming and resist the effects of biological control. Warming-induced failure of biological control can lead to greater pesticide use and greater pollution, thus compounding existing environmental problems. One key finding of this study is that one can make predictions about population-level outcomes of warming based solely on how temperature affects ectotherms' phenotypic traits. When choosing natural enemy agents to attack a particular pest, it is crucial to compare their maturation and mortality responses to determine whether the enemy has greater tolerance of the high-temperature extremes projected for the region such that its maturation-mortality response allows for a sustainable adult population in the face of warming.

In this study I have focused on pairwise consumer-resource interactions, a necessary first step in developing a framework that incorporates developmental delays and mechanistic temperature response functions. Extending the framework to incorporate additional tropic levels and competition between species is an important future direction. While the results of the trait-based and analytical viability analyses are general and can apply across ectotherm taxa from any latitude or habitat type, the dynamical model was analyzed using parameter values realistic for insects and other terrestrial ectotherms. Determining whether the latitudinal, life stage, and warming-scenario effects found for terrestrial consumer-resource interactions generalize to aquatic ones is a fruitful future exercise.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

FUNDING

This research was supported by a Complex Systems Scholar Grant from the James S. McDonnell Foundation and National Science Foundation grant DEB-1457815 to PA.

ACKNOWLEDGMENTS

I thank two referees for constructive comments that greatly improved the manuscript.

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ORIGINAL RESEARCH
published: 12 June 2019
doi: 10.3389/fevo.2019.00202

Interaction Dimensionality Scales Up to Generate Bimodal Consumer-Resource Size-Ratio Distributions in Ecological Communities

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Understanding constraints on consumer-resource body size-ratios is fundamentally important from both ecological and evolutionary perspectives. By analyzing data on 4,685 consumer-resource interactions from nine ecological communities, we show that in spatially complex environments—where consumers can forage in both two (*2D*, e.g., benthic zones) and three (*3D*, e.g., pelagic zones) spatial dimensions—the resource-to-consumer body size-ratio distribution tends toward bimodality, with different median *2D* and *3D* peaks. Specifically, we find that median size-ratio in *3D* is consistently smaller than in *2D* both within and across communities. Furthermore, *2D* and *3D* size (not size-ratio) distributions within any community are generally indistinguishable statistically, indicating that the bimodality in size-ratios is not driven simply by *a priori* size-segregation of species (and therefore, interactions) by dimensionality, but due to other factors. We develop theory that correctly predicts the direction and magnitude of these differences between *2D* and *3D* size-ratio distributions. Our theory suggests that community-level size-ratio bimodality emerges from the stronger scaling of consumption rate with size in *3D* interactions than in *2D* which both, maximizes consumer fitness, and allows coexistence, across a larger range of size-ratios in *3D*. We also find that consumer gape-limitation can amplify differences between *2D* and *3D* size-ratios, and that for either dimensionality, higher carrying capacity allows coexistence of a wider range of size-ratios. Our results reveal new and general insights into the size structure of ecological communities, and show that spatial complexity of the environment can have far reaching effects on community structure and dynamics across scales of organization.

Keywords: body size, consumer-resource dynamics, interaction dimensionality, metabolic scaling, consumption rate, coexistence

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *31 August 2018*
Accepted: *16 May 2019*
Published: *12 June 2019*

Citation:
Pawar S, Dell AI, Lin T, Wieczynski DJ and Savage VM (2019) Interaction Dimensionality Scales Up to Generate Bimodal Consumer-Resource Size-Ratio Distributions in Ecological Communities. Front. Ecol. Evol. 7:202. doi: 10.3389/fevo.2019.00202

INTRODUCTION

For at least a century, biologists have wondered why "*Spiders do not catch elephants in their webs, nor do water scorpions prey on geese*" (Elton, 1927; Riede et al., 2011). That is, why does only a subset of all possible resource-consumer body size ratios exist in nature? Answering this question is important because it could reveal general principles underlying the ecological and evolutionary dynamics of communities (Yodzis and Innes, 1992; Cohen et al., 1993; Brose et al., 2006a,b; Tang et al., 2014; Pawar et al., 2015). Indeed, a prominent hypothesis for why size-ratio distributions show strong central tendencies within and across communities is that only certain size combinations permit species coexistence (Emmerson et al., 2005; Brose et al., 2006a; Otto et al., 2007; Tang et al., 2014). Also, size-ratio distributions exhibit multiple peaks within and across communities; for example, predators tend to be much larger than their prey in water than on land, invertebrate predators tend to be closer in relative size to their prey than vertebrate predators, filter feeders may be a million times larger than their resources, and parasitoids and ectoparasites can be 10 or down to 1 million times smaller than their hosts (Peters, 1986; Cohen et al., 1993; Brose et al., 2005, 2006a). These different peaks likely reflect different regions of feasible coexistence, population stability, or fitness, influenced by both abiotic (e.g., spatial habitat complexity) and biotic (e.g., foraging strategy) factors (Brose et al., 2006a; Cohen, 2008).

Several studies have developed mathematical models to understand how body size determines the feasibility of consumer-resource size-ratios in specific taxa and trophic interaction types (e.g., McArdle and Lawton, 1979; Persson et al., 1998; Aljetlawi et al., 2004). Others have generalized such models by incorporating metabolic scaling (Schmidt-Nielsen, 1984; Peters, 1986; Brown et al., 2004; Savage et al., 2004) into consumer-resource interaction and life history models (Brose et al., 2005; Weitz and Levin, 2006; Williams et al., 2007; Riede et al., 2011; Kalinkat et al., 2013; Carbone et al., 2014). However, studies thus far have failed to yield systematic predictions about central tendencies or the shapes of community-level size-ratio distributions (Brose et al., 2006a).

Arguably, the key to a more nuanced understanding of variation in community size-ratios is to incorporate community- and environment-specific biomechanical constraints into models of consumer-resource interactions (Vucic-Pestic et al., 2010; Dell et al., 2011; Pawar et al., 2012, 2015; Portalier et al., 2019). In this paper, we investigate this possibility by including biomechanical and physiological constraints on the components of consumption rate—search, detection, and handling (attack, pursuit, subjugation, and ingestion) (**Figure 1**). In particular, we focus on whether interaction dimensionality combined with other biomechanical (velocity, handling) and physiological (metabolic rate) constraints affect consumer-resource size-ratios in local ecological communities. Recent work suggests that the dimensionality of trophic interactions—Euclidean dimension of the space in which the consumer searches for resources (*2D* vs. *3D*)—is a ubiquitous and important factor that strongly affects consumer-resource interactions via encounter rates (McGill and Mittelbach, 2006; Pawar et al., 2012; Carbone et al., 2014). Specifically, if the chance of finding a resource is roughly the same in all directions, then increasing either the dimensionality of resource dispersion (Ritchie, 2009) or the consumer's detection region will increase encounter rates (McGill and Mittelbach, 2006; Pawar et al., 2012, 2015). This leads us to hypothesize that the size-ratio distributions of interacting species in communities should vary systematically with spatial complexity of the habitat. This would be driven by variation in conditions for energetically-feasible stable coexistence of consumer-resource species pairs within different sub-habitats (e.g., pelagic vs. benthic zones in aquatic ecosystems). We first derive theoretical predictions for differences in limits to feasible size-ratios in *2D* vs. *3D* interactions. We then use an extensive dataset of 4,685 consumer-resource interactions from nine aquatic and terrestrial communities to test our predictions.

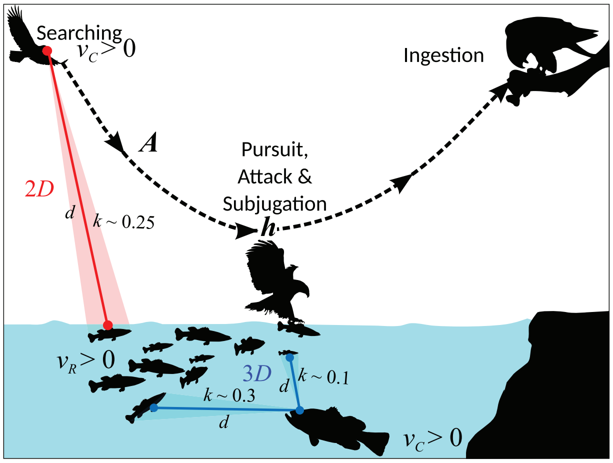

FIGURE 1 | An illustration of components of consumption rate and environmental constraints on them. The parameters shown belong to our model for size-mediated consumer-resource dynamics. Feasible body size-ratios depend on consumer and resource body velocities (v_R and v_C), reaction distance (d), attack success probability (A) following attack and pursuit, handling time h (sum of pursuit, attack, subjugation, and ingestion times), and interaction dimensionality (D). Our theory predicts that *3D* interactions, by allowing an additional dimension for detection (depicted here by the largemouth bass' search space), can allow *3D* consumers to subsist on a wider range of resource sizes (k denotes consumer-resource size ratio; see text after Equation 3). Thus, feasible size-ratios for the fishing eagle searching in *2D* (water surface) are expected to be more strongly constrained than the largemouth bass searching in *3D* (water column), although they are both feeding on the same resource.

METHODS

Theory

We develop a mathematical model to predict the feasibility of community-wide resource to consumer size-ratios. To this end, we first incorporate body size constraints on components of consumer-resource interactions—relative velocity, detection distance, attack success, and handling time (**Figure 1**)—which altogether determine per-capita biomass consumption rate. Consumption is a fundamental rate controlling the energy budget of an individual (net energy gain or loss) and population dynamics (coupled changes in consumer and resource population biomasses or numbers) (DeLong and Vasseur, 2012; Pawar et al., 2012, 2015; Carbone et al., 2014). We then derive feasible size-ratios from both energetic and population dynamical perspectives.

We begin with a general equation for consumption rate c (mass × time^{-1}) (Pawar et al., 2012, 2015; Carbone et al., 2014):

$$c = a\, A\, x_R\, m_R\, f \tag{1}$$

Here, x_R is resource number density (individuals × m^{-2} or m^{-3}), m_R is resource body mass, a is per-capita area or volume search rate (m^2 or m^3 × s^{-1}), A is probability of attack success (conditional on an attack occurring), and f is a dimensionless prey risk function that determines the shape of the consumer's functional response (Pawar et al., 2012; Dell et al., 2014). In principle, f can be of any form, but we focus on the commonly observed Type II form

$$f = \frac{1}{1 + a\, A\, h\, x_R} \tag{2}$$

where h is consumer's handling time (s). If h is instantaneous (→ 0), Equation (2) reduces to the linear Type I functional response ($f = 1$). Our subsequent results about feasible size-ratios from both energetic and population dynamical perspectives remain qualitatively unchanged if we use a Type III functional response (**Appendix 3**; **Figure S2**).

We now define size-dependence of the components of c. In **Appendix 3** we show that our results are robust to considerable variation in parameterizations of the following scaling equations. The parameterizations are listed in **Table S3**. First, for search rate we use an empirically well-supported scaling model (Pawar et al., 2012; Dell et al., 2014; Rizzuto et al., 2018):

$$a = a_0 m_C^{p_v + 2p_d(D-1)} k^{p_d(D-1)}\,. \tag{3}$$

Here, a_0 is a constant that includes effects of temperature and dimensionality, p_v is the scaling exponent for consumer body velocity, p_d is the scaling exponent for reaction distance between consumer and resource, D is interaction dimensionality defined by the space in which the consumer can search for and detect a resource ($2D$ or $3D$; **Figure 1**), and $k = m_R/m_C$ is body size-ratio. We emphasize that this simple definition of interaction dimensionality arises because resource detection typically occurs in Euclidean space, regardless of which sensory modality is used. Later, we discuss how our model can be extended to more complex definitions of dimensionality by considering non-sensory components (such as relative velocity) of consumer-resource interactions. As such, Equation (3) is a scaling model for grazing (i.e., consumer searching for sessile resources) but also well-approximates the scaling of search rate in active-capture interactions (i.e., both consumer and resource moving actively across the landscape) when $m_C > m_R$ (**Appendix 3**) (Pawar et al., 2012; Dell et al., 2014). We use just the grazing model because our dataset is dominated by grazing and active-capture interactions with $m_C > m_R$ (**Appendix 1**, **Table S2**; see also **Table S5**). Furthermore, in **Appendix 3** we show that relative to dimensionality, foraging strategy is expected to have minor effects on feasible size-ratios.

Next, for attack success probability A, we use an empirically supported function (**Appendix 1**; **Figure S1**),

$$A = \left(1 + k^{\gamma}\right)^{-1}, \tag{4}$$

where γ is a constant that governs the decrease in attack success as resources get very large relative to consumer size ($m_R \gg m_C$). The exponent γ in Equation (4) captures biomechanical constraints that appear at upper size-ratios (McArdle and Lawton, 1979; Persson et al., 1998; Aljetlawi et al., 2004; Weitz and Levin, 2006). In particular, increasing γ can emulate increasing consumer gape-limitation, which was previously suggested to be a bigger constraint on size-ratios in aquatic interactions relative to terrestrial ones (Hairston and Hairston, 1993). Hairston and Hairston (1993) argue that gape limitation is stronger in aquatic interactions because the bodies and appendages of aquatic organisms are modified for efficient locomotion in water, and thus are of limited use for handling resources. As a result, aquatic consumers cannot be too close to or smaller in size than resources (relative to terrestrial consumers). By increasing γ, we can explore the importance of gape-limitation relative to detection dimensionality in constraining feasible size-ratios. Similarly, by relaxing γ we can consider interactions where attack success and therefore consumption rate is relatively insensitive to size-ratio, such as in the case of ecto-parasites, which are largely limited by encounter (therefore, search) rate, and can successfully feed on wide range of resource sizes once they are encountered.

Substituting Equations (3, 4) into (1) and rearranging to gives the scaling of per-capita (biomass) consumption rate:

$$c = a_0\, m_C^{p_v + 2p_d(D-1)+1}\, k^{p_d(D-1)+1}\, \left(1 + k^{\gamma}\right)^{-1}\, x_R\, f. \tag{5}$$

Note that here the resource mass term m_R from Equation (1) has been absorbed into the size-ratio term. This equation captures four essential features of consumption rate:

(i) For a given resource size and therefore size-ratio k, consumption rate c increases with consumer mass m_C because larger consumers have greater body velocity,

(ii) Consumption rate c increases with size-ratio k because when $m_R < m_C$ (i.e., $k < 1$) search rate increases with resource mass m_R due to increasing reaction distance (and for active-capture, also increasing relative velocity; **Appendix 3**, Equation S14),

(iii) When resource mass far exceeds consumer mass ($k \gg 1$), c declines because resources become difficult for the consumer to attack and handle due to the $(1 + k^{\gamma})^{-1}$ term. That is, the product of per-capita search rate (a monotonically increasing function with respect to size and size-ratio; Equation 3) and attack success probability A (monotonically decreasing function), aA, yields an empirically realistic unimodal (hump-shaped) function (McArdle and Lawton, 1979; Persson et al., 1998; Aljetlawi et al., 2004; Brose et al., 2008) (**Appendix 1**; **Figure S5**).

(iv) Consumption rate c increases faster with consumer mass m_C and size-ratio k when consumers forage in $3D$ ($D = 3$;

e.g., pelagic zones in lakes and oceans) than $2D$ ($D = 2$; e.g., benthic zones) because above a threshold consumer size, $3D$ search space (m^{-3}) allows higher detection probability than $2D$ search space (m^{-2}) (Pawar et al., 2012, 2015).

Finally, for handling time we use another empirically well-supported model (Pawar et al., 2012):

$$h = h_0 m_C^{-\beta_h} m_R \tag{6}$$

where h_0 is a constant and β_h is the scaling of the metabolic rate of a consumer during pursuit, subjugation, and ingestion of resources.

Energetically Feasible Size-Ratios

We first derive feasible ranges of size-ratios that meet consumer energy requirements for somatic maintenance, by setting a lower bound on energy gain from resource consumption (Carbone et al., 2014; Rizzuto et al., 2018):

$$ec > B_C \tag{7}$$

Here, B_C is the rate of the consumer's energy use converted to mass units (kg/s) while resting (resting metabolic rate, RMR), e the efficiency of conversion of resource biomass into consumer biomass (a proportion). All other parameters are as defined in Equations (1)–(6). Conversion efficiency e is approximately independent of body size (Peters, 1986; DeLong et al., 2010; Lang et al., 2017), and between 0.5 and 0.85, with carnivores having higher values than herbivores (Yodzis and Innes, 1992; Lang et al., 2017). Our results remain qualitatively robust to a even wider variation in e than this (**Appendix 3**). Convert B_c to mass units (like the quantity ec on the left hand size) we assume $1\,\mathrm{kg} = 7{\times}10^6$ J (the combustion energy content per unit of wet biomass) (Peters, 1986). Note that the Inequality (7) sets a lower bound on consumption rate because B_C is RMR, which is an underestimate of maintenance energy needs because it typically does not include the energy required for somatic growth, producing offspring, storage, and bursts of activity (such as during foraging). These may cause significant additions to the energy needs of adult animals in certain periods of their lifetime (Rizzuto et al., 2018). Therefore, we expect the coexistence bounds to be somewhat narrower than those we predict below; but this does not change our conclusions about the differences in coexistence due to dimensionality. Also, assuming there are no systematic differences in conversion efficiency in $2D$ vs. $3D$ interactions, variation in e will have negligible effect on our subsequent results.

We already have the size scaling of a and A, but require the scaling of B_C and biomass abundance $x_R\, m_R$. For B_C, we use the scaling of basal or resting metabolic rate (Peters, 1986; Nagy, 1987; Brown et al., 2004; DeLong et al., 2010):

$$B_C = B_0 m_C^{\beta} \tag{8}$$

where B_0 is a constant that includes the effect of temperature and converts metabolic rate units (J/s) to mass use rate units, and β is the scaling exponent of metabolic rate. For biomass abundance we use (Peters, 1986; Brown et al., 2004):

$$x_R m_R = x_0 m_R^{1-\beta_x} \tag{9}$$

Where x_0 is a normalization constant that includes the effect of temperature, and β_x is the scaling exponent of numerical abundance. Substituting the scaling (Equations 5, 6, 8, 9) into (7) and solving for m_R gives the bounds on resource mass m_R and therefore size-ratios that guarantee a balanced energy budget. To obtain an exact solution for this we set $h = 0$ [Type I $f(R)$] and solve for m_R, which gives:

$$m_R > c\left(m_C^{\beta-p_d(D-1)-p_v}\left(1+k^{\gamma}\right)^{-1}\right)^{\frac{1}{1+p_d(D-1)-\beta_x}} \tag{10}$$

Where $c = (B_0/ea_0x_0)^{\frac{1}{1-p_d(D+1)-\beta_x}}$. In **Appendix 3** we show that our subsequent results are qualitatively unchanged if $h > 0$. Substituting the values of scaling exponents (**Table S3**) into Inequality (10) gives

$$\begin{aligned} m_R &> m_0 m_C^{0.64}\left(1+k^{\gamma}\right)^{-2.22} \ \mathit{in}\ 2D \\ m_R &> m_0 m_C^{0.14}\left(1+k^{\gamma}\right)^{-1.54} \ \mathit{in}\ 3D \end{aligned} \tag{11}$$

where $m_0 = (B_0/ea_0x_0)^{2.22}$ in $2D$ and $(B_0/ea_0x_0)^{1.54}$ in $3D$. Inequalities (10) and (11) yield three important theoretical insights and predictions (illustrated in **Figure 2**):

(i) The smaller m_C and k exponents for $3D$ compared with $2D$ in Equation (11) imply that size constraints weaken as dimensionality increases. Therefore, relative to $2D$, a wider range of resource sizes become feasible for larger $3D$ consumers. Conversely, $3D$ foraging allows an increased range of consumer sizes on a given sized resource because for a given size-ratio, larger consumers enjoy a greater mass-specific search rate in $3D$ than in $2D$ [$a/m_C \propto m_C^{0.04}$ in $3D$ but $m_C^{-0.34}$ in $2D$, from parameterized Equation (3)].

(ii) Within either $2D$ or $3D$, feasible size-ratios for coexistence are predicted to be constrained by baseline resource density (x_0) through the term m_0. In particular, following empirical data (Peters, 1986; Pawar et al., 2012), if we assume baseline abundance (x_0) is about two orders of magnitude higher in $3D$ than $2D$, the widening of energetically feasible size ratios is magnified because then the advantage of $3D$ detection dimensionality is enhanced. In this context, note that although biomass density is expressed in per-volume units in $3D$ and per-area units in $2D$ (**Table S3**), what matters is that a greater amount of resource biomass can be packed into a $3D$ space, which boosts consumption rate due to increased detection dimensionality.

(iii) The upper bound on size ratios (where $m_R > m_C$ so $k > 1$) is set by the scaling of A through the exponent γ. Therefore, all these results are qualitatively robust as long as decline in attack success at high size-ratios is strong enough to render consumption rate (Equation 5) unimodal with respect to k. Values of the exponents in Equation (5) dictate that consumption rate will be unimodal with respect to size-ratio as long as $\gamma > 0.2$ in $2D$ and >0.4 in $3D$ (also see **Figure S4**). Our meta-analysis (**Appendix 1**) shows this condition generally holds for real interactions and is in agreement with previous studies (Aljetlawi et al., 2004; Brose et al., 2008).

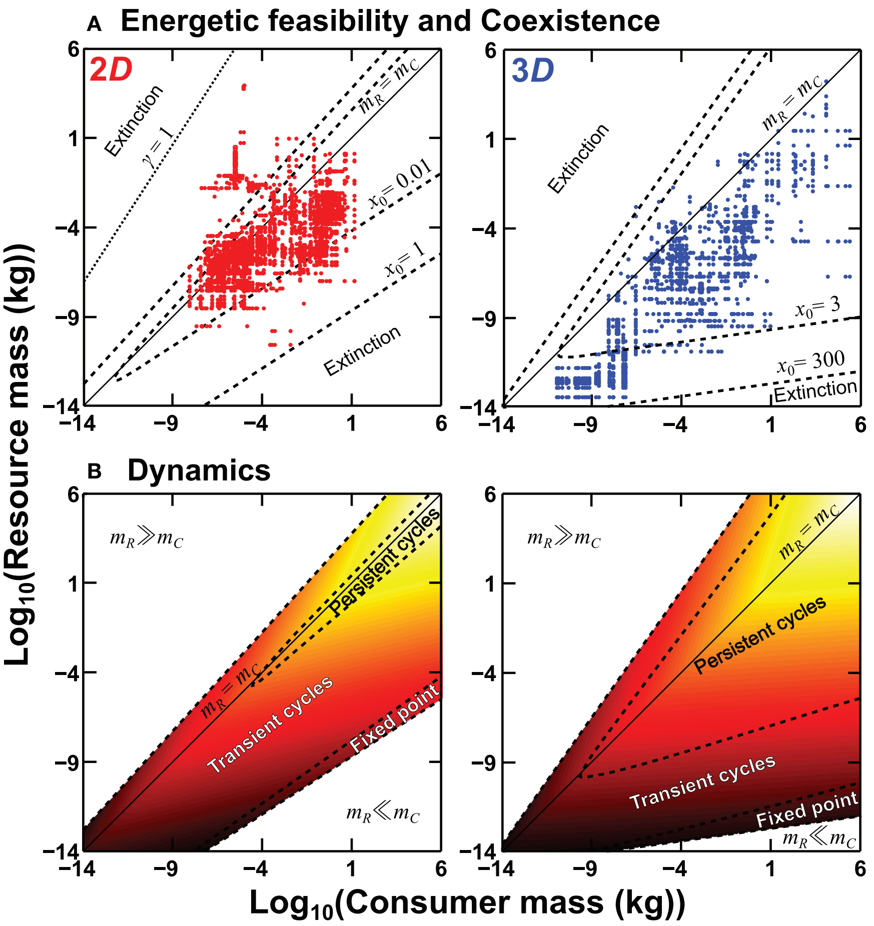

FIGURE 2 | Predicted effects of interaction dimensionality on consumer energetic feasibility and consumer-resource coexistence **(A)** and population dynamics **(B)**. In **(A)** real consumer-resource pairs (dots) from nine communities have been overlaid ($n = 3{,}055$ in *2D* and 1,630 in *3D*; **Table 1**), with dashed lines delineating predicted coexistence regions for different baseline carrying capacities x_0 (because baseline abundances tend to be higher by orders of magnitude in *3D* than *2D*; see main text). In **(B)** dashed lines delineate population stability regimes and equilibrium abundance is represented by a heat-map of $\log_{10}$ number density (darker means more abundant). These results are for $h_0 = 10^4$ s (Equation 6) and $\gamma = 2$ (Equation 4; cf. **Table S3**). When attack success declines more weakly (γ decreases) at size-ratios $m_R \gg m_C$, possibly due to decrease in gape-limitation, coexistence becomes possible at those extreme ratios, illustrated by the dotted $\gamma = 1$ line (at $x_0 = 1$, with other parameter values remaining the same) in the *2D* plot in **(A)**.

Population-Dynamically Feasible Size-Ratios

The above theory based upon the consumer's energetic considerations does not account for consumer-resource population dynamics. Therefore, we consider whether accounting for population dynamics changes our predictions about the effect of dimensionality on feasible size-ratios. Using a general consumer-resource model, in **Appendix 2** we show that both consumer-resource coexistence and mutual population stability yield similar predictions as above. Specifically, coexistence is possible only if

$$m_R > m_0\left(m_C^{\beta-p_d(D-1)-p_v}\left(1+k^{\gamma}\right)^{-1}\right)^{\frac{1}{1+p_d(D-1)-\beta}} \qquad (12)$$

where $m_0 = \left(\frac{B_0}{e a_0 x_0}\right)^{\frac{1}{1+p_d(D-1)-\beta}}$. This is same as inequality (10), except that β (consumer's RMR scaling exponent) replaces resource carrying capacity scaling exponent β_x. That is, the above predictions (i)–(iv) from the energetic model also hold for the population dynamics model. We also show that local asymptotic stability to small perturbations around equilibrium abundances of consumer and resource (Equations S8–S9) differs between *2D* and *3D*. **Figure 2** shows that regions of cycles over the size-combination plane coincide with regions of low abundance (along the $k = 1$ line). Consistent with consumer-resource theory, as $h \to 0$ and the functional response becomes Type I, regions of persistent cycles are replaced by transient cycles (**Appendix 3**). Furthermore, in **Appendix 3**, we show that the scaling of coexistence in Equation (11) is qualitatively similar for Type II and III functional responses. These results and those from the energetic model above are robust even if decline in attack success (Equation 4) is not strictly a power-law (**Figure S6**).

Theoretical Predictions

Next, we calculated community-specific predictions about the magnitude of difference in central tendency of 2*D* and 3*D* size-ratio distributions to compare with the empirical data (next section) on size ratios. For this, for each community, and for a given K and γ (which set the lower and upper bound of the coexistence region, respectively; **Figure 2**), we generated 10,000 random interactions by first generating model consumer and resource size distributions within that community's observed size limits. The size distributions were generated using the beta distribution, using the method used by Pawar (2015). This approach allows realistic, right-skewed size distributions of different shapes to be generated. As long as the size distribution is right-skewed, the following results remain qualitatively robust. We then determined what subset of size-ratios in these random interactions allowed stable population coexistence (criteria i–ii in **Appendix 2**). This is equivalent to "carving out" the general predicted coexistence region (**Figure 2**) into its stable community-specific sub-regions. Differences in the median of these feasible and stable $\log_{10}$-transformed 2*D* and 3*D* size-ratios were then the predicted difference for that community. This difference was compared with the empirically observed difference (see data analysis below). We use the median ($\log_{10}$-transformed) size ratio of each local community as a measure of central tendency because most communities exhibit skewed and multimodal size-ratio distributions (**Figure 3**). Also, we focus on predicted differences in medians and not the absolute values of medians themselves, because feasible size-ratios are expected to depend on carrying capacity [**Figure 2**; also see text following Inequality (11)], which is an unknown parameter in all our community datasets.

Empirical Data

To study size-ratio distributions and test our theoretical predictions we compiled published data on interacting consumer-resource pairs for nine communities (four terrestrial, five aquatic; **Table S5**). If average body mass for a particular taxon was not reported in the original study, it was estimated using methods previously described (Dell et al., 2011, 2013, 2014). Each consumer-resource interaction was assigned a 2*D* or 3*D* search-space dimensionality by combining information on the consumer's movement space and foraging strategy—sit-and-wait, active foraging, or grazing—and the resource's movement space (**Table S1**). Classification of interactions by dimensionality in this way requires knowing the taxonomy, feeding behavior, body size, and foraging strategy of individual taxa (see **Table S1**). Although there are many communities with data on trophic links, few have the adequate body size and taxonomic information required for this level of classification. These nine communities are the available datasets for which all these pieces of information are available or could be obtained from the literature. The final dataset comprised 4,685 interactions between 964 taxa, comprising 3,055 2D and 1,630 3D consumer-resource interactions (**Table S5**).

Data Analysis

We tested whether, as predicted by our theory, 2*D* and 3*D* size-ratio distributions had significantly different central tendencies, both within each of the nine communities as well as the overall dataset. A parametric approach to testing this statistically is not appropriate because size-ratios within communities are often not independent (multiple resources may be fed upon by the same consumer and multiple consumers often feed on the same resource). Furthermore, the ($\log_{10}$) size-ratio distributions are often right-skewed with long tails and/or multi-modal (**Figure 2**). Therefore, we developed the following bootstrap-like test for significance of differences in size-ratios. For each community we separately generated 10^5 lists of random 2*D* and 3*D* consumer-resource interaction pairs by independently sampling (with replacement) the observed pairs of consumers and resources. Each randomly generated 2*D* and 3*D* "sub-community" was constrained to have the same number of interaction pairs as observed in the original 2*D* or 3*D* sub-community. We then calculated differences in median $\log_{10}$-transformed size-ratios (3*D* or 2*D*) across the 10^5 random lists. The distribution of these 10^5 differences is an approximation of the sampling distribution of differences assuming random partitioning of the community into 2*D* and 3*D* sub-communities. Thus, the proportion of times the observed difference between median values of log-transformed 2*D* and 3*D* size-ratios matches or exceeds a value in the sampling distribution can be used as an estimate of the one-tailed *p*-value of the observed difference. We also compared each community's predicted difference in median 2*D* vs. 3*D* size ratios (see "*Theoretical predictions*" above) with its sampling distribution of random differences in medians to test whether these also significantly matched the observed differences in median size-ratios.

As an even more stringent test in the face of non-independent size-ratios, we also re-analyzed the data for differences between 2*D* and 3*D* size-ratios as described above after collapsing all the links of a single consumer to a single size ratio by taking the geometric average of the sizes of all its resources. After doing so, our results about significant differences in central tendencies of 2*D* vs. 3*D* size-ratio distributions remain qualitatively the same (**Appendix 3**; **Table S4**).

Finally, to determine whether size ranges $[m_{C,\min}, m_{C,\max}]$ and $[m_{R,\min}, m_{R,\max}]$ are influenced by factors independent of dimensionality, such as oxygen limitation, physical medium for locomotion, and phylogenetic history (Allen et al., 2006), we also tested for differences in median sizes of all 2*D* an 3*D* species using the Wilcox test after removing consumers and resources that were in both the sets, and also tested for differences in variances around the median values using the Brown–Forsythe test.

RESULTS

We find strong and statistically significant empirical evidence that median 3*D* size-ratios are consistently lower than 2*D* size-ratios across all nine communities (**Figure 3**), with observed differences in median size-ratios closely matching our theoretical predictions (**Table 1**). The magnitude of difference between 2D and 3D size-ratios varies with community, ranging from the median 3*D* size-ratio being about four times smaller than 2*D* for the Scotch Broom community to 2.29 orders of magnitude smaller for the Eastern Weddell Sea community.

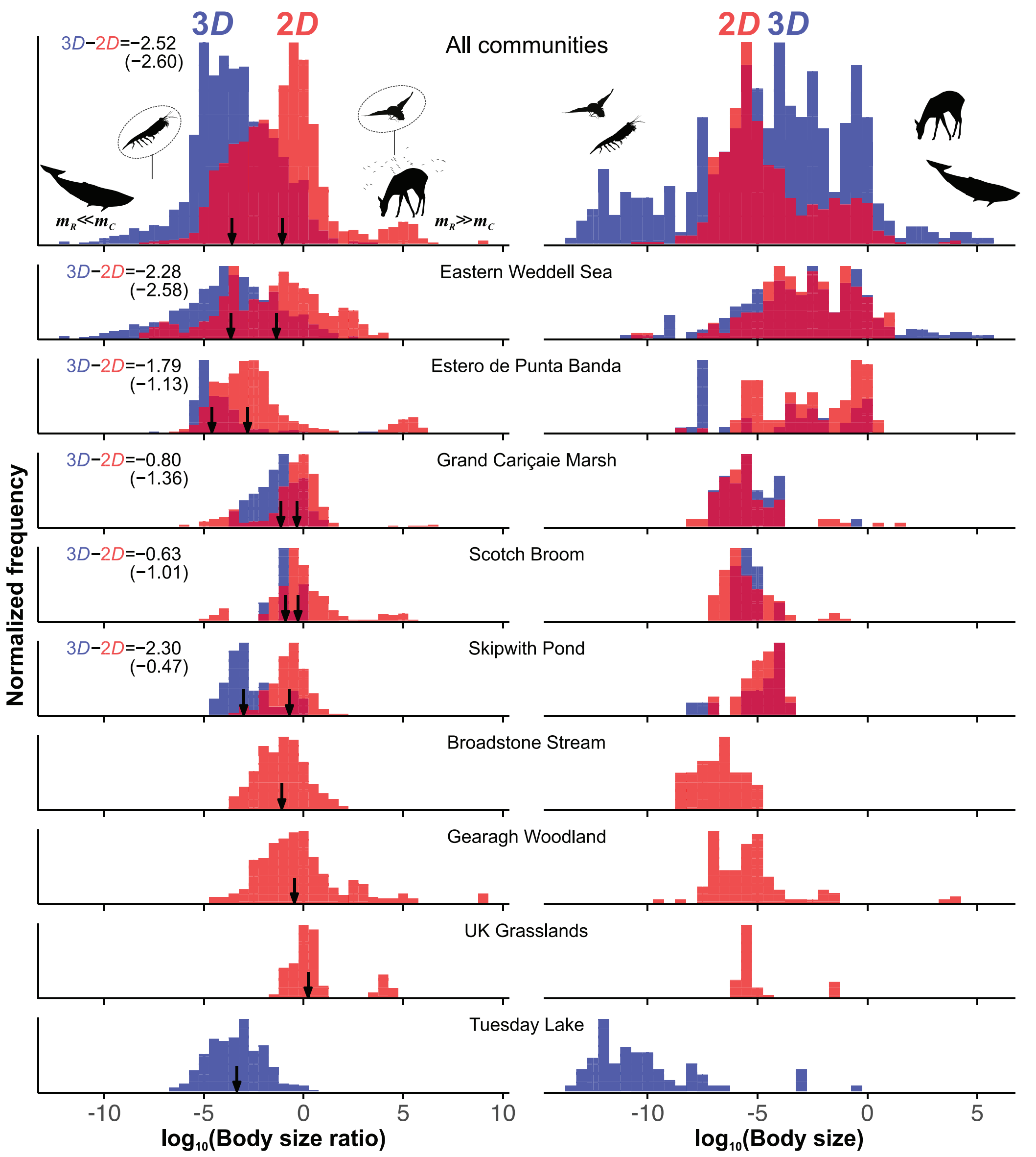

FIGURE 3 | Effect of interaction dimensionality on species' $\log_{10}$ size-ratio and size (mass, kg) distributions across communities. All pairs of *2D* (red) and *3D* (blue) distributions have been normalized by respective peak frequency to allow comparison within and between communities. In all sub-plots a darker shade of red represents the overlap between the *2D* and *3D* distributions. Black vertical arrows mark locations of observed median *2D* and *3D* interaction size-ratios, along with their observed and predicted (in parentheses) differences. In all communities, the range and median of $\log_{10}$ size in *2D* and *3D* are similar while median *3D* size-ratios are significantly lower than *2D* as predicted by our theory (**Table 1**). Note that there are three pure *2D* and one pure *3D* community. Two real interactions are shown to illustrate extreme size-ratios: Blue Whale eating Krill ($m_{R \ll} m_C$; $k \sim 10^{-10}$) in the Eastern Weddell Sea, and Deer Flies on Roe Deer ($m_{R \gg} m_C$; $k \sim 10^{6.5}$) in Grand Cariçaie Marsh.

Even in the case of pure *2D* communities, size-ratios tend to be higher than *3D* ratios observed in other communities. Similarly, in the single pure *3D* community (Tuesday lake), size-ratios are generally lower than the *2D* ratios from the other communities (**Figure 3**; **Table 1**).

We also found multimodalities in *2D* size-ratio distributions (**Figure 3**), one at extremely small size-ratios ($m_R \ll m_C$) and another at extremely large ratios ($m_C \ll m_R$). The lower *2D* peak (where $m_R \ll m_C$) found in several communities corresponds to grazing. Scotch Broom, UK Grasslands, and Estero de Punta Banda also each have a peak at very high *2D* size-ratios ($m_R \gg m_C$), corresponding to macroparasites, parasitoids, herbivores, and micropredators. Indeed, these types of interactions are why only 87.8% of *2D* interactions lie within the predicted *2D* coexistence region (the $\gamma = 2$ and high x_0 case in **Figure 2**), while 99.9% of *3D* interactions

TABLE 1 | Differences between *2D* and *3D* size-ratio distributions.

Community	Median $\log_{10}$ (Size-ratio)			Median $\log_{10}$ (Size)		Taxa			Interactions			*2D*/*3D* overlap	
	2D	*3D*	*3D*−*2D*	*2D*	*3D*	All	*2D*	*3D*	All	*2D*	*3D*	Con	Res
All communities	−1.07	−3.59	−2.52* (−2.60)	−4.79	−4.05	964	704	463	4685	3055	1630	0.09	0.20
Eastern Weddell Sea	−1.37	−3.65	−2.28* (−2.58)	−2.78	−2.51	314	137	270	979	258	721	0.11	0.30
Estero de Punta Banda	−2.81	−4.60	−1.79* (−1.13)	−2.48	−2.73	105	102	47	1388	1086	302	0.34	0.19
Grand Cariçaie Marsh	−0.34	−1.14	−0.80* (−1.36)	−5.55	−5.44	88	86	45	623	460	163	0.00	0.46
Scotch Broom	−0.28	−0.91	−0.63* (−1.01)	−5.44	−5.28	150	147	11	362	347	15	0.00	0.22
Skipwith Pond	−0.71	−3.01	−2.3* (−0.47)	−4.69	−4.55	33	31	17	321	284	37	0.78	0.23
Broadstone Stream	−1.09	–	–	−6.71	–	28	28	0	138	138	0	–	–
Gearagh Woodland	−0.46	–	–	−5.56	–	113	113	0	370	370	0	–	–
UK Grasslands	0.22	–	–	−5.40	–	61	61	0	112	112	0	–	–

The Median $\log_{10}$(Size-ratio) column shows observed medians of $\log_{10}$ transformed size-ratios, and their observed and predicted (in parentheses) difference in medians (3D−2D). All observed and predicted differences are significantly different from 0 ($p < 0.05$; flagged with an asterisk) based upon a randomization test (see main text). Note that although median 2D and 3D size-ratios are significantly different in each community, median 2D, and 3D consumer and resource sizes are not ($p > 0.05$; Wilcoxon–Mann–Whitney test with shared taxa removed). The 2D/3D overlap column shows proportion of consumers in each community feeding on both 2D and 3D resources (Jaccard index) (Con), and proportion of resources exploited by both 2D and 3D consumers (Res). If such an overlap exists, the total number of taxa (Taxa-All) within a community will be smaller than the sum of 2D and 3D taxa.

fall within the predicted *3D* coexistence region. This is not surprising because macroparasitism, parasitoidism, herbivory, and micropredation are likely to be more limited by search and detection than attack success. We can account for this by decreasing the value of γ in Equation (4) and recalculating coexistence bounds. Doing so relaxes constraints on coexistence at high size-ratios ($k \gg 1$ or $m_R \gg m_C$) (**Figure 2**, **Figure S4**), and helps explain deviation of these interactions from predicted coexistence bounds. Note that, as $\gamma \to 0$, the upper coexistence bound (**Figure 2**) will vanish because attack success probability A becomes independent of size-ratio. We chose $\gamma = 1$ to illustrate that a weaker decline in attack success with size-ratio can explain feasibility and coexistence of interactions at those size-ratios. The value of $\gamma = 1$—where A declines weakly with decreasing size-ratio (resources get very large relative to consumers)—is necessarily arbitrary because we have practically no information about A at those extreme size-ratios, which future work needs to address.

Eastern Weddell Sea, Grand Cariçaie Marsh, and Scotch Broom also show a secondary *2D* peak at very small size-ratios ($m_R \ll m_C$) (**Figure 3**), mostly corresponding to large endothermic vertebrates feeding on arthropods—effectively grazing interactions because of the large size difference between consumer and resource, and therefore in their body velocities **Appendix 3**; (Pawar et al., 2012; Dell et al., 2014). This is also qualitatively consistent with our theory, which predicts a relaxation of coexistence constraints in grazing interactions where $m_R \ll m_C$ (**Figure S3**).

In communities that have both interaction dimensionalities, median body size distributions of species in *2D* and *3D* interactions are statistically indistinguishable (**Figure 3**; **Table 1**). Body size ranges of species involved in *2D* and *3D* interactions also tend to be similar, with only Eastern Weddell Sea and Estero de Punta Banda showing significant differences in variance of sizes ($p < 0.001$, Brown-Forsythe test of unequal variances). Thus, bimodality in size-ratios is not driven simply by different *2D* and *3D* size distributions. Indeed, the high overlap between *2D* and *3D* size distributions supports an assumption implicit in our theory: that size ranges of consumers or resources are set by factors extrinsic to dimensionality. The similarity in size distributions partly stems from the fact that although consumers forage on completely different resources (and therefore potentially different habitat zones) in *2D* and *3D* in certain communities (i.e., Eastern Weddell Sea, Skipwith pond, and Estero de Punta Banda), a relatively constant proportion of resources are fed upon by both *2D* and *3D* consumers in all communities (compare consumer and resource *2D*/*3D* overlap in **Table 1**). An example of how the same resource can be exploited in both *2D* and *3D* is shown in **Figure 1**. Thus, *2D* and *3D* components of each community are consistently coupled through shared resources.

DISCUSSION

By combining theory with extensive empirical data, we have shown that interaction dimensionality strongly constrains resource-to-consumer size ratios in ecological communities. Specifically, *3D* interactions allow a lower median size-ratio as well as a wider range of size-ratios than *2D*, with the magnitude of observed difference in most communities similar to the difference predicted by our theory (**Table 1**). This emergent difference between *3D* and *2D* size-ratios arises because in *3D*, the additional dimension for resource detection usually elevates baseline encounter rates and steepens the scaling of consumption rate with body size (Pawar et al., 2012). As a result, communities from spatially complex environments that can support both *2D* and *3D* interactions show distinct size-ratio distributions (**Figure 3**). For example, bimodal size-ratio distributions exist in the Eastern Weddell Sea, which has pelagic (mostly *3D*) and benthic (mostly *2D*) zones, and in the Grand Cariçaie Marsh, which has shallow-water (mostly *2D*), grassland (mostly *2D*), and tree-dominated zones (mixture of *2D* and *3D*). We emphasize that the difference in median $2D$ and $3D$ size-ratios is repeatedly observed across communities, despite considerable variation in habitat (e.g., aquatic vs. terrestrial), consumer foraging behaviors (e.g., $2D$ benthic vs. $2D$ water surface foraging), and organismal types (e.g., vertebrates vs. invertebrates).

Our results provide an explanation for three important empirical patterns in the body size structure of communities. First, our theory predicts that wider ranges of size-ratios become feasible as consumer size increases in both $2D$ and $3D$ (**Figure 2**). This explains why smaller consumers tend to be restricted to a narrower range of resource sizes (Cohen et al., 1993), and therefore why invertebrate predators tend to be closer in size to their prey than vertebrate predators (Peters, 1986; Brose et al., 2006a). Second, our theory predicts that the widening of coexistence bounds with consumer size is much more pronounced in $3D$ than $2D$, and that this widening occurs in the direction of lower size-ratios. That is, consumers are able to coexist with resources much smaller than themselves in $3D$ in comparison to $2D$. This helps explain why pelagic predators ($3D$) tend to be so much larger than their prey in comparison to terrestrial ($2D$) predators (Cohen and Fenchel, 1994; Brose et al., 2006a). Similarly, we would also expect size-ratios in other $3D$ interactions, such as those for aerial predators, to be more extreme than in terrestrial 2D interactions. Indeed, the mean size-ratio of terrestrial $3D$ interactions from real communities—all from Grand Cariçaie Marsh, Gearagh Woodland, Scotch Broom, or UK Grasslands—is about an order of magnitude lower than $2D$ interactions (0.07 in $3D$ vs. 0.51 in $2D$). Third, if coexistence bounds widen with body size, it follows that if consumer size increases systematically with trophic level then so will size-ratios. This can explain why the traditional Eltonian paradigm (Elton, 1927) of invariance of size-ratios with trophic level does not always, or even typically, hold (Cohen and Fenchel, 1994; Brose, 2010; Riede et al., 2011).

Our theory also predicts that irrespective of dimensionality, size-ratios will be smaller in magnitude (closer to $k = 1$) and show less variance (i.e., be more constrained) in resource-poor environments (with low carrying capacity; **Figure 2**). Although we could not test this directly, carrying capacity may account for additional variation in size-ratio distributions across communities. Furthermore, abundance of resources is particularly important to consumer-resource coexistence in $3D$ because the potential advantage of stronger scaling of search rate from the additional dimension is not realized if resources are not sufficiently abundant. For example, the higher encounter of resources in $3D$ would not be realized if resources have the same numbers (but not densities) in $2D$ and $3D$ habitats (e.g., 1 kg/m^2 and 1 kg/m^3), irrespective of whether abundance was high or low.

Hairston and Hairston (1993) suggest that size-ratios in aquatic interactions are more constrained than in terrestrial environments because of gape-limitation. That is, they argue that gape-limitation is stronger in aquatic interactions because bodies and appendages of aquatic organisms are modified for efficient locomotion in water, and thus are of limited use for handling resources. As a result, aquatic consumers may be larger, but not too close to or smaller in size compared to resources. However, we find that size-ratios exhibit $2D$-$3D$ bimodality even within aquatic environments, suggesting that gape-limitation may not be the primary constraint on size-ratios.

Our theory can partly explain multimodalities found in $2D$ size-ratio distributions (**Figure 3**) in terms of foraging strategies. The $2D$ peak in several communities where $m_R \ll m_C$ corresponds to grazing. Our theory predicts that grazing allows a wider range of size-ratios (**Figure S3**), although observed size-ratios peak at even more extreme values than predicted. Similarly, by decreasing γ, which determines the strength in decline of attack success (A) as resources become much larger than consumers ($m_R \gg m_C$), we are able to explain the $2D$ peak in size-ratios at $m_R \gg m_C$ (corresponding to macroparasitism, parasitoidism, herbivory and micropredation) seen in several communities. This is also consistent with the fact that the empirical data on consumption rates we used to obtain estimates of γ are only from predator-prey interactions, not macroparasitism, parasitoidism, herbivory or micropredation. At the same time, we did not find multimodalities in $3D$ size-ratio distributions. This could occur because strategies, such as macroparasitism and micropredation are less feasible in $3D$ environments than in $2D$ (which is possible if γ itself increases with dimensionality), or because such interactions are simply under-sampled in $3D$. In either case, further research is needed. This is particularly important given the important role of parasitism in food webs (Hechinger et al., 2011). For example, the addition of parameters that account for the biomechanics of attack and escape (which must differ with foraging strategy) will likely help explain some of this additional variation and multi-modalities.

Empirical biases also need to be considered while interpreting our results. For example, the fact that no observed species pairs lie in the predicted feasible regions at smallest and largest consumer sizes in $2D$ likely reflects a lack of sampling of interactions for the smallest (e.g., microorganisms and microinvertebrates) and largest (e.g., large carnivores) consumers (Brose et al., 2006a). More importantly, sampling biases are also likely to skew the estimate of the proportion of $2D$ and $3D$ interactions in each community—the "pure" $2D$ and $3D$ communities likely contain interactions with both dimensionalities and only more accurate trophic and foraging data will resolve this issue.

Our theoretical analysis assumes that the criteria for energy balance and stable coexistence of two-species systems approximately hold even when these pairwise interactions are embedded in food webs. We are encouraged by the fact that we are able to correctly predict the differences between median $2D$ and $3D$ size ratios, even without incorporating higher-order or indirect effects. This is consistent with the result that community stability is most strongly determined by the strengths of the direct coupling between consumer-resource interactions (Pawar, 2009; Tang et al., 2014). Thus, we have shown for the first time, that a combination of environmental, behavioral, and biomechanical constraints on species interactions scale up to an emergent property (the community-wide size-ratio distribution) through a combination of natural selection (the energetics constraint; inequality 10) and species sorting (the coexistence constraint; inequality 12). This scaling up and emergence effectively results in the reorganization of communities from more spatially complex environments into distinct compartments (in terms of food web topology), as evidenced by the typically low overlap in 2*D* and 3*D* consumer and resource species and interaction identities (last two columns of **Table 1**). This stems from localization or specialization of consumers as well as resources to a specific, preferred sub-environment (2*D* or 3*D*). Nevertheless, future extensions of our work to multispecies interactions should account for the stability consequences of indirect interactions and polyphagy, and these modifications may lead to more accurate predictions about the effect of dimensionality on size-ratio distributions in real communities. Given the apparently ubiquitous difference in 2*D* and 3*D* size-ratios within communities, food web models with coupled 2*D* and 3*D* sub-communities should be especially enlightening for these questions and might explain some of the differences between predicted and observed features of size-ratio distributions reported here. In this respect, we were intrigued to find that 2*D* and 3*D* sub-communities are coupled, as must be the population dynamics, through shared resources in all the communities we analyzed.

Our classification of interactions according to dimensionality of the search and interaction space is appealingly simple, and necessarily so because detection typically occurs in Euclidean space (McGill and Mittelbach, 2006; Pawar et al., 2012). An extension of our model would be to include more complex habitats with non-integer dimensionality by relaxing the assumption of random movement of the consumer and/or resource. For example, non-random searching by consumers for resources that are dispersed or moving in fractal dimensions (Ritchie, 2009)—a more continuous measure of dimensionality—could alter how spatial complexity influences size-ratios. Testing these additional factors would require more detailed knowledge of foraging behavior for specific taxa and of habitat complexity in local communities.

In conclusion, our study helps explain a number of empirical observations in which community size structure varies with habitat, type of consumer-resource interaction, and foraging strategy (Elton, 1927; Cohen et al., 1993; Brose et al., 2006a,b; Riede et al., 2011). Our theory generalizes previous models that incorporate body size into components of consumer-resource interactions (McArdle and Lawton, 1979; Persson et al., 1998; Aljetlawi et al., 2004; Weitz and Levin, 2006) to multiple foraging strategies—active-capture, sit-and-wait, or grazing—and interaction dimensionalities. Thus, our framework can be used to develop models for specific organisms and habitats by relying on estimates of body sizes, foraging strategies, and interaction dimensionalities. Ultimately, models that explicitly incorporate biomechanical and environmental constraints on the components of consumer-resource interactions should form the foundation of a general theory that can explain variation in the structure and function of ecological communities across environments.

AUTHOR CONTRIBUTIONS

SP and VS developed the theory. SP and TL conducted the theoretical and numerical analyses. SP and AD collected empirical data for the main analysis and meta-analysis. SP, AD, and DW analyzed the empirical data. SP, AD, TL, DW, and VS wrote the manuscript.

FUNDING

SP, AD, and VS were supported by UCLA Biomathematics start-up funds and by NSF DEB Award 1021010. SP was supported by UK NERC Grant NE/M003205/1. TL, DW, and VS were supported by a McDonnell Complex Systems Scholar Award.

ACKNOWLEDGMENTS

We thank P. Amarasekare, C. Johnson, and the reviewers for helpful discussions and comments.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00202/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

HYPOTHESIS AND THEORY
published: 18 June 2019
doi: 10.3389/fevo.2019.00219

Principles of Ecology Revisited: Integrating Information and Ecological Theories for a More Unified Science

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: 31 December 2018
Accepted: 24 May 2019
Published: 18 June 2019

Citation:
O'Connor MI, Pennell MW, Altermatt F, Matthews B, Melián CJ and Gonzalez A (2019) Principles of Ecology Revisited: Integrating Information and Ecological Theories for a More Unified Science. Front. Ecol. Evol. 7:219. doi: 10.3389/fevo.2019.00219

The persistence of ecological systems in changing environments requires energy, materials, and information. Although the importance of information to ecological function has been widely recognized, the fundamental principles of ecological science as commonly expressed do not reflect this central role of information processing. We articulate five fundamental principles of ecology that integrate information with energy and material constraints across scales of organization in living systems. We show how these principles outline new theoretical and empirical research challenges, and offer one novel attempt to incorporate them in a theoretical model. To provide adequate background for the principles, we review major concepts and identify common themes and key differences in information theories spanning physics, biology and semiotics. We structured our review around a series of questions about the role information may play in ecological systems: (i) what is information? (ii) how is information related to uncertainty? (iii) what is information processing? (iv) does information processing link ecological systems across scales? We highlight two aspects of information that capture its dual roles: *syntactic information* defining the processes that encode, filter and process information stored in biological structure and *semiotic information* associated with structures and their context. We argue that the principles of information in living systems promote a unified approach to understanding living systems in terms of first principles of biology and physics, and promote much needed theoretical and empirical advances in ecological research to unify understanding across disciplines and scales.

Keywords: information theory, semiotic, entropy, organization, first principles, ecology, evolution

PRINCIPLES OF ECOLOGY, REVISITED

Information is fundamental to life and living systems, from subcellular processes to the biosphere (Gatlin, 1972; Davies and Walker, 2016; Tkačik and Bialek, 2016). Information is contained in the improbable organization and configuration of flows of matter and energy arising from activities and interactions of assemblages of atoms, molecules, cells or organisms (MacArthur, 1955; Ulanowicz et al., 2009; Frank, 2012; Kempes et al., 2017). All these structures—their composition and configuration—can be described using information measures, but some structures also carry, or encode, information that is interpreted and processed (Patten, 1959; Odum, 1988; Ulanowicz et al., 2006; Harte, 2011; Kempes et al., 2017). Information processing affects population dynamics (Donaldson-Matasci et al., 2010; Battesti et al., 2015; Fronhofer et al., 2017; Gil et al., 2018) and evolutionary processes (Ulanowicz, 1997; Giraldeau and Caraco, 2000; Dall et al., 2005; Frank, 2008; Ulanowicz et al., 2009; Schmidt et al., 2010; Wagner, 2017), and is part of every aspect of ecological change and human interactions with rest of the biosphere (Munday et al., 2009; van der Sluijs et al., 2010; Rossi-Santos, 2015; Altermatt and Ebert, 2016; Goldstein and Kopin, 2017; Gordon et al., 2018). Therefore, ecological science has much to gain by incorporating the fundamentals of information theories and information processing to understand and describe our changing world (Wicken, 1987; Schneider and Kay, 1994; Holt, 2007; Farnsworth, 2013).

Despite evidence that information plays fundamental roles in ecological systems, information does not yet feature prominently in the ecological principles at the center of our textbooks and theories (**Appendix 1**). This omission is problematic and isolating for ecology from other scientific disciplines (Schneider and Kay, 1994). Advances in other realms of science including physics, molecular biology and astrobiology increasingly recognize information, energy and material as the joint pillars of living systems (Frank, 2012; Woods and Wilson, 2013; Davies and Walker, 2016; Walker et al., 2016; Kempes et al., 2017; Wagner, 2017). Ecology, however, tends to emphasize organisms as fundamental units, and traits, environmental conditions and contingencies as fundamental concepts (**Appendix 1**). In expressions of ecological principles, energy and materials play important roles in explaining resource supply or environmental conditions, and information is rarely mentioned. Information processing is included by acknowledging evolution as an ecological principle (**Appendix 1**), but evolution is only one of many examples of information processing in ecological systems.

The costs of omitting something as fundamental as information from our general, mainstream scientific models are great. For example, ecologists have failed to anticipate the effects of environmental change on population dynamics mediated by disruptions in information processing. Studies showing that environmental change (e.g., ocean acidification) alters organisms' abilities to sense their environment and to act appropriately on environmental information such as cues for the seasonal events they use to find food or mates (Munday et al., 2009; Martín and López, 2013; Gordon et al., 2018) are often presented as surprising. A greater acceptance of the role information flow plays in population dynamics might lead to ecological theory to accommodate these effects, and deepen our understanding of the ecological consequences of disruptions of information (Schneider and Kay, 1994; Gil et al., 2018).

Another blind spot in ecological understanding concerns the roles of information flow in networks and organization. Social information (Gil et al., 2018), social learning systems (Aplin et al., 2015) and other forms of information can be central to the organization and stability of symbioses (Davy et al., 2012), social groups (Flack et al., 2006), and other living systems. The stabilizing and organizing consequences of information networks (MacArthur, 1955; Jorgensen et al., 2000; Ulanowicz et al., 2009; Babikova et al., 2013; Sentis et al., 2015; Lee et al., 2016) would be missed from a perspective of ecology that exclusively focuses on energy and material relations among individual organisms, or the interaction between an organism and its environment. Human activities may destroy the integrity of information networks and their adaptive capacities before they are ever known to science. Finally, biodiversity is a form of information; it is information stored in genes, morphologies, traits and behaviors that reflect the ecological and evolutionary history of life on earth. Ecological science is still ill-equipped to fully understand the consequences of this information (biodiversity) loss for future information processing, and flows of energy and materials. While concepts relating biodiversity and ecosystem functions have been developed (Loreau), they have not yet been grounded in the more general relationships between information and energy flows, though similar efforts have been made in information theories (Schneider and Kay, 1994; Ulanowicz et al., 2009; Coscieme et al., 2013; Norton and Ulanowicz, 2017). Thus, though it is well accepted that biodiversity is being lost at an alarming rate on the planetary scale, we do not have first principles to guide our understanding of the consequences of this information crisis.

We aim to fill the gap between information theories and modern ecological thinking by articulating principles for ecological systems that are consistent with our understanding of the role played by information in the structure and function of living systems (**Box 1**). We seek principles that are consistent with broader scientific knowledge and might, with additional theoretical development, allow unification of ecological theories and concepts that share a conceptual foundation (Margalef, 1963; Schneider and Kay, 1994; Jorgensen et al., 2000; Scheiner and Willig, 2008; Patten et al., 2011; Marquet et al., 2014; Patten, 2014).

Here, we review major concepts in the information theories that lead to these ecological principles. We structured our review around a series of questions about the role information may play in ecological systems: (i) what is information? (ii) how is information related to uncertainty? (iii) what is information processing? (iv) how does information processing link ecological systems across scales? Answers to these questions draw upon literatures as diverse as thermodynamics to cybernetics, statistics to evolution, behavioral ecology to semiotics (**Boxes 2–4**). As a consequence of seeking common ground and intellectual themes across such diverse literatures, we take care to define terms and introduce concepts that might be elemental in one literature

Box 1 | Five principles that integrate information in ecological understanding.

Drawing upon multiple research themes with domains spanning physics, information theory, ecology, evolution and semiotics, we identified a set of principles that integrate information and information processing into our understanding of ecological systems. These principles rest on the success of many decades of scientific knowledge development, but also represent the first step from this point forward to a more unified understanding of ecological systems. This is not an exhaustive set of principles for ecology, we have not considered principles of energy and matter other than how they interact with information. The principles presented here address two main concepts: the fundamental nature of information and its dual relationship with thermodynamic entropy and uncertainty (Information is Fundamental to Living Systems), and the multiscale causes and consequences of information processing (How is Information a Dynamic Part of Living Systems?). We use the term **living system** to include any energy-matter-fluxing life form, or aggregate of life forms, so it includes the smallest living organism up to the entire biosphere. It does not assume *a priori* an organism-centered, perspective on ecological systems that is typical of modern Darwinian approaches, but our concept of living systems is also not incompatible with assuming organisms are the fundamental unit of living system. These principles are not themselves a framework or research guide, but rather the minimum set of statements about nature that are the basis for theory and knowledge gain. We illustrate how a canonical model of eco-evolutionary dynamics can be modified to be consistent with these 5 principles (**Box 5**). Development of theories founded on these principles should lead to the development of hypotheses for how ecological systems across scales of organization grow, change and persist.

Principle 1: Information is a fundamental feature of living systems, and therefore also of all ecological systems. Syntactic and semiotic information (**Table 1**) constitute the two fundamental forms of information, and each is essential to the structure and function of living systems, from molecular systems to the biosphere. Consequently, some information within ecological systems is directly related to energetics in terms of thermodynamic entropy (Uncertainty and Entropy), while other aspects of information define sign systems that interact with energetics to produce life processes (**Figure 1A**).

Principle 2: Syntactic and semiotic information interact in feedbacks, with energetic processes and material cycles, to influence structure, function and organization in ecological systems. Ecological systems use semiotic information to structure how they expend energy for work (e.g., growth, reproduction, and consumption). (**Figure 1**) ecological processes are partly responsible for syntactic information (nonrandom distribution of matter on the Earth's surface). For example, reproduction represents the replication and transmission of information as encoded genetically within and across generations. Reproduction requires energy and resources, which are allocated to somatic growth or reproductive effort by information processes within the organism or between the organism and its environment.

Principle 3: Information processing requires energy and materials, therefore supply of energy and materials and thermodynamic constraints can limit information processing. The infrastructure for storing, transmitting, receiving and using information requires energy and materials (**Figure 2**), consequently the supply and physical constraints on the efficiency of energy and material systems may affect how much and how quickly information may be processed. These constraints are expected to lead to evolution of information systems that balance energetic and material efficiency, stability and durability with information processing capacity and reliability.

Principle 4: Information processing allows components of living systems to measure the environment and their own state and to measure the relationship between their state and past and expected environments. Subsets of information processing systems (cells, organs, individuals, etc.) receive and use cues and signals in the context of their environment (**Figure 2**). Organisms use evolved information processing systems to relate measurements of their current environment to expectations of their future environment [anticipation *sensu* (Rosen, 1985)]. This measurement combined with processing permits goal directed agency in living systems.

Principle 5: Information processing systems are linked within and across scales of biological organization. Strong positive feedbacks in information processing can define or reinforce levels of organization—from a cell to an individual to symbioses all the way to an ecosystem and the biosphere (**Figures 1**, **2**). Information stored at higher order levels of organization, such as social groups, communities or ecosystems, can be used by lower level systems, such as individual organisms and cells. In this way, information processing occurs across scales of space and time, and can create and maintain physical or energetic structures.

but foreign to another (**Table 1**). We then consider briefly how ecological science might proceed to test, refine and build upon these principles This review and synthesis is intended to explain and justify our proposed set of fundamental principles for ecology (**Box 1**), and provide common conceptual ground for further scientific exploration of the role information plays in ecological systems.

INFORMATION IS FUNDAMENTAL TO LIVING SYSTEMS

What Is Information?

A basic definition of **information** is the difference between a set of realized events relative to the possible sets of those events (**Table 1**; **Figure 1** and **Box 3**). Defining "what is possible" is not always easy, and entails a judgment by an observer. Sometimes "possible" is considered a random state, other times, it is considered a perfectly ordered state, or a known state (see Reference States for more explanation of reference states). The set of differences that constitutes information contains consequences of historical events that shaped the arrangement of elements in a living system. For example, the distribution, arrangement and structure of nucleic acids in a DNA molecule differs from a randomly assembled set (or any other arrangement) of the same nucleic acids. The difference between the arrangement of nucleic acids in the DNA strand and a random assemblage of the same set of nucleic acids reflects the recent history of those molecules and their translation within the ribosome, as well as the longer-term history of evolutionary processes that resulted in that particular allele's structure. We can also consider the information in the difference between two DNA molecules, identical except for a single nucleic acid. Again, the difference between the two DNA molecules reflects their shared (or different) histories of evolution and recent synthesis. But the consequence of the small differences for subsequent protein synthesis and biological function may be great. These DNA molecules, and their differences, contain ***syntactic information*** (**Table 1**). Syntactic information exists in any spatial or temporal arrangement of events or objects, including the species or functional diversity of a set of interacting species (Pielou, 1967; Jost, 2006), the notes and rhythms in a bird's song (Farina and Belgrano, 2006; Sánchez-García et al., 2017), or temporal pattern of sunrise and sunset (Edgar et al., 2012; Kinmonth-Schultz et al., 2013).

Information contained in structure, reflecting the structure's history, can (but does not need to) represent signs or symbols that convey meaning as interpreted by an observer (***semantic information***, **Table 1**). **Semiotic information** is the content and

Box 2 | Timeline of selected milestones of information science.

Concepts of thermodynamic entropy and surprise emerged in the Twentieth century, setting the stage for later developments in concepts of entropy and information. But it was with Schroedinger's argument that information is central to life, followed closely by Shannon's insight that information can be considered as a quantifiable capacity for communication, that initiated a scientific revolution around information. Information has emerged in ecological thinking across scales since Shannon's work and we highlight some of these contributions to illustrate the breadth and progression of these concepts.

Year	Milestone
1925	Introduction of information in statistical inference (Fisher, 1925)
1929	Information could be included in the second law of thermodynamics (partially resolving the problem posed by Maxwell's demon) (Szilard, 1929; Parrondo et al., 2015)
1945	Information (negative entropy) is fundamental to life (Schrodinger, 1944)
1948	Introduction of the concept of cybernetics and communication control systems in biology and in machines (Wiener, 1948)
1948	Shannon information, a non-thermodynamic entropy measure, is introduced as an expected value that expresses the information content of a message (Shannon, 1948)
1953	First edited volume on information in biology, including attempts to quantify information in living structures (Quastler, 1953)
1955	Shannon index introduced to ecology to estimate energy flow among species (MacArthur, 1955)
1956	The distinction is made between information content in structure, and the subset of information transferred in observations; the term "negentropy" is coined (Brillouin, 1956)
1957	Maximum entropy principle (MEP) is published (Jaynes, 1957); Information theory is connected to ecological diversity indices and community structure (Margalef, 1957)
1959	Calls for a cybernetic approach to ecosystems; first empirical estimate of the information flow (consumption) of Silver Springs FL ecosystem from Odum's 1957 work (Patten, 1959). Brillouin derived a relationship between the energy required by Maxwell's Demon to acquire 1 bit of information, thereby relating information and energy in the context of thermodynamics.
1970	Progress in biological information theory in biology is reviewed, and qualitative information concept is proposed, along with the idea of closed biological systems for conservation laws (Johnson, 1970)
1972	Information theory is used to argue that "living is computing", and new theory for biology is introduced (Gatlin, 1972)
1972	Information is described as "a difference that makes a difference", and argued to be fundamental to human culture as well as ecology (Bateson, 1972)
1981	Debate in ecology about whether ecosystems are cybernetic systems abates, limited by methods (Patten and Odum, 1981)
1986 1987	Publication of *Evolution as entropy: toward a unified theory of biology* (Brooks and Wiley, 1988) Wicken synthesizes, reviews and critiques information and entropy concepts, bring some semantic clarity to these terms in the literature
1997	A new perspective on ecosystem as ascendant information systems is introduced (Ulanowicz, 1997)
2000	Calls to consider the importance of information in biology and evolution are renewed (Maynard Smith, 2000; Szathmáry and Smith, 2002)
2015	Renewed interest in information as fundamental to the origin of life (Davies and Walker, 2016; Davies et al., 2017)
2017	Information theory is mainstream in molecular biology (Sherwin et al., 2017; Wagner, 2017).

Box 3 | Information theory and statistical inference.

For many ecologists and evolutionary biologists, the most common application of information theory is probably as a tool for statistical inference. The Akaike Information Criterion (AIC; Akaike, 1974), Bayesian Information Criteria (BIC; Schwarz, 1978), and related measures have become so familiar to ecologists as model selection procedures (Burnham and Anderson, 2002) that the philosophical and conceptual underpinnings are rarely given a second thought. For example, we use AIC to compare the relative performance of a candidate set of models, where we measure performance as the balance between fit (likelihood, L, of the data given the model) and the number of parameters k ($\text{AIC} = -2\ln(L) + 2k$). Rather remarkably, the AIC computed for a model is proportional to the amount of information lost—measured as the Kullbeck-Leibler divergence, D_{KL}—in using a given statistical model $\boldsymbol{p}$ to approximate the true model that actually generated the data $\boldsymbol{p^*}$. For discrete distributions the divergence is equal to

$$D_{KL} = -\sum_{i=1} p^*(x_i)\ \log\left(\frac{p^*(x_i)}{p(x_i)}\right)$$

Even though we do not know the true model, the AIC values from several candidate models can be compared. Similarly maximum entropy methods (Jaynes, 1957), which make use of information theoretic principles have been widely used to fit Species Distribution Models to location data (Phillips et al., 2006; Phillips and Dudik, 2008) and in the Maximum Entropy Theory of Ecology to estimate the parameters of macroecological distributions (Harte et al., 2008; Harte, 2011).

In one sense, the use of information theoretic principles in model selection and estimation is deeply related to the quantities we discuss throughout the manuscript: it is the structure inherent in ecological systems (i.e., their information content) that allows us to make inferences about the processes that might have generated the data we observe and predictions about that which we have not. On the other hand, such inference requires both an observer (i.e., us) and a theory about how the world works (i.e., a mathematical model) and in this article, we are concerned primarily with how information structures ecological systems, even when no one is looking.

the quality of semantic information as it is carried by signs (Sebeok and Umiker-Sebeok, 1992; Kull, 1999; Dall et al., 2005; Barbieri, 2008; Schmidt et al., 2010). Semiotic information is central to interactions among molecules (proteins, enzymes, etc.), cells, physiological systems and organisms, and has long been recognized as important to ecological and evolutionary dynamics (von Uexkull, 1992). General sign theory was developed by Pierce (Atkin, 2006), and emphasized the triad of signs, objects and interpretants, highlighting how meaning in information requires not only an object and a sign that may represent it, but also an interpretation of that sign that associates the sign with the object (Atkin, 2006). Biosemiotic theories of ecology (Farina, 2008, 2011; Hoffmeyer, 2009) build on Peirce's triadic theory of signs (Atkin, 2006). The interpretant is often associated with an organism in which case this topic is the purview of the fields of behavioral ecology (e.g., evolution of signals and communication), chemical ecology and cognitive ecology. Biosemiotics, therefore, brings to ecology an understanding of information as signification and representation in ecological interactions, and its consequences are often considered in terms of fitness. For example, predators associate coloration with toxicity and avoid eating prey that exhibit these signs (Stevens and Ruxton, 2011). Another example is

Box 4 | Relationships between common information terms and concepts through a single information definition.

This formula is a measure of the **thermodynamic entropy** of a system when *k* is equal to the Boltzmann's constant ($1.38064852 \times 10^{-23}$ J/K)

In order for Boltzmann's thermodynamic entropy definition to apply, the natural logarithm must be used (i.e., $b=e$). In the context of Shannon entropy, the scale of the logarithm can be chosen for convenience. For state spaces defined by binary decision trees, $\log_2$ is typically used so that one unit of information (one **bit**) reduces uncertainty by a half.If one uses $\log_{10}$, one unit of information reduces uncertainty 10 fold (a quantity termed a **Hartley** of information).

Shannon generalized information theory to non-thermodynamic systems by demonstrating that this formula can be used to quantify the carrying capacity of any channel of communication. In this general case, *H* is referred to as **Shannon entropy**. Here the value of *k* is arbitrary and unitless and often set to 1 for convenience.

Given a probability distribution **p** $p(x_i)$ defines the probability that the system is in a specific state

If all *m* states of a system are equally probable, the uncertainty is maximized. This is often a useful reference point for comparison (see Box 3). In this case, the formula reduces to $H = -k \log_b(m)$ (or, $S=k \ln(W)$ using Boltzmann's famous notation).

$$H = -k \sum_{i=1}^{m} p(x_i) \log_b p(x_i)$$

As discussed in Box 2, the **Kullbeck-Leibler divergence** D_{KL} measures the "distance" between two probability distributions (**p** and **p***). It is called a divergence and not a distance because it asymmetrical and depends on what is chosen as the reference (or prior, in Bayesian contexts) distribution. If **p** is the reference, then:

$$D_{KL}(\mathbf{p}^*, \mathbf{p}) = -\sum_{i=1}^{m} p^*(x_i) \log\left(\frac{p^*(x_i)}{p(x_i)}\right)$$

If, and only if, **p** is a uniform distribution (such that all states are equally likely), then

$$D_{KL}(\mathbf{p}^*, \mathbf{p}) = H(\mathbf{p}) - H(\mathbf{p}^*)$$

If **p*** and **p** are marginal posterior and marginal prior distributions respectively, the quantity $H(\mathbf{p}) - H(\mathbf{p}^*)$ is referred to as **Lindley information**. More generally, the sum of $D_{KL}(\mathbf{p}^*,\mathbf{p}) + D_{KL}(\mathbf{p},\mathbf{p}^*)$ is called **Jeffrey's divergence**, which is proportional to **Fisher's information**, a widely used statistical measure of uncertainty. Frank (2009, 2012) has demonstrated that natural selection maximizes Fisher's Information.

Knowledge of the state of one variable can also provide information (reduce uncertainty) about the state of another variable. This is called **Mutual information**. Mutual information (which we denote $I(X,Y)$ is simply the difference between the **marginal** $H(X)$ and the **conditional** $H(X|Y)$ **entropies** (or because unlike the Kullbeck-Leibler divergence [right], it is symmetrical, $H(Y) - H(Y|X)$). We can compute this as

$$I(X, Y) = \sum_{i=1}^{m} \sum_{j=1}^{n} p(x_i, y_j) \log\left(\frac{p(x_i, y_j)}{p(x_i)p(y_j)}\right)$$

If the variables are independent, then knowledge of the state of one provides no information on the state of the other and the $I(X,Y) = 0$.

For derivations and details, see the excellent treatments by Lindley (1956), Cover and Thomas (2001), Amari and Nagaoka (2000), Burnham and Anderson (2001), and Frank (2009, 2012),

phenological cues associated with day length that many taxa use as signs of future favorable environmental conditions; these environmental cues have meaning because of regular variation in the environment (Helm et al., 2013).

Semiotic information plays an important role in ecological systems. In birdsong, the temporal structure of sounds carries information (and energy) imparted to it by the singing individual. The information may or may not be a reliable cue of its state; the bird's song also signifies semantic information to other birds that interpret the song. The information in a bird's song may even signify its fitness and an expectation of its own future—its likelihood of finding a mate or defending its territory, perhaps. The pattern of sounds in birdsong has meaning to other organisms, and that meaning depends on the receiver—e.g., the species or individual—and the context (Farina and Belgrano, 2006; Pijanowski et al., 2011). Even the aggregate biophony—the collective sound that vocalizing animals create in an environment—of a landscape's acoustic diversity presents a community-level semiotic context for the actions and ecology of any individual bird (Farina, 2008; Pijanowski et al., 2011) (**Figure 1B**). Semiotic information is important, even when signs are interpreted by biological systems that are not organisms. In the DNA example, the interpretant may be associated with a ribosome or protein, as the "observer" of the sign. The syntactic information of a gene is received by ribosomes' structure, and ribosomes encode and transcribe the information in a gene if the information matches what the ribosomes can interpret.

These two concepts—syntactic and semiotic—capture the dual nature of information (**Figure 1**). On the one hand, information is defined as signals sent and received by the individuals participating in the system. Their use of semiotic information drives ecological and evolutionary dynamics within the system (Patten, 1959; Gatlin, 1972; Giraldeau and Caraco, 2000; Ulanowicz et al., 2009; Gil et al., 2018) (**Figure 1**). On the other hand, information influences dynamics in ways not driven by individual organisms or mediated by communication; some forms of information stored in biological structures have energetic value (Parrondo et al., 2015), decay (Tkačik and Bialek, 2016), and constrain future possible states of a system (Shannon, 1948; Ulanowicz et al., 2009; Davies and Walker, 2016). The difference between a set of realized events relative to the possible sets of those events can be framed and measured in both senses we describe here. An ecological science

TABLE 1 | Glossary for general terms and concepts.

Term	Definition and context
Information theory	The study of flow, utilization and storage; also described as the study of coding and transmission of information. Often abbreviated IT.
Information	The reduction in uncertainty associated with the difference between two states of a system. Example units: bits. Does not consider any meaning or interpretation of the information. Also called: *potential information* (Farina and Pieretti, 2013), *intrinsic information* (Wiener, 1948), *physical information* (Farnsworth, 2013) and *syntactic information* (Schmidt et al., 2010). See **Figure 1** for specific examples.
Functional information	Many have argued that syntactic information concepts alone are insufficient to describe information in biology. Functional information is defined by a structure's ultimate function and probability of a set of units to achieve that function (Szostak, 2003). Others have defined functional information as the part of a structure (e.g., a genome) that is the minimum required to reconstruct the organism (Johnson, 1970; Jiang and Xu, 2010; Farnsworth et al., 2012). Johnson (1970) referred to it as the information that once lost cannot be regained.
Entropy	The smallest possible average size of lossless encoding of messages sent from a source to a destination (Shannon, 1948). Also called: *uncertainty*, *equiprobability, indeterminacy, complexity*.
Epistemological uncertainty	Uncertainty in the knowledge of a process, due to data or model limitations.
State of a system	A particular spatial or temporal arrangement of elements, for example, atoms in a molecule, individuals in a habitat, relative abundances of species, or pathways of energy flow in a network
Cybernetics	The study of biological systems with feedback.
Observer	The object or system measuring the difference between the two states in the information measurement.
Reference state	A benchmark state with which to compare another state, such as an observed state. Examples include: maximum entropy, full information, thermodynamic zero; or, other observed states.
Thermodynamics	The science dealing with energy and relations among different kinds of energy, and relations among energy and properties of matter.
Entropy	A measure of the irreversibility of a process in the context of the number of possible processes for using energy. Example units: J/Kelvin
Information	Negative entropy or organization, taking a value explicitly convertible or comparable to energy. Example unit: bits.
Observer	The observer of the two states in question (see Wicken, 1987 for a critical review of observers and information in thermodynamics).
Biosemiotic theory	Study of the communication of information in living organisms.
Semantic information	Signs or symbols that convey meaning as interpreted by an observer.
Semiotic information	The content and quality of semantic information as it is carried by signs.
Interpretant	The understanding an observer has of the relationship between a sign and an object (Pierce/Atkin, 2006). Pierce and others developed this idea further so that the interpretant is considered a translation of the original sign. Thus, the interpretant is not the observer, *per se* (Atkin, 2006).
Sign	Along with *object* and *interpretant*, one of the three inter-related elements of a sign in Pierce's sign theory (a leading semiotic theory). In ecology, we often use the word "cue" as synonymous with "sign."

*For specific models and technical definitions, see **Boxes 3**, **4** and **Figure 2**.*

that fully includes information will need to integrate syntactic and semiotic information (Bridging Syntactic and Semiotic Information; **Box 1**).

For many ecologists, the vast and varied literature on information, the related concepts of entropy, and their role in living systems is uncharted territory. This literature dates back at least a century in ecology and complex systems science (**Box 2**). It is a rich literature in which terms such as information and entropy are used with a plurality of definitions, meanings, and contexts (Wicken, 1987; Schneider and Kay, 1994; Gatenby and Frieden, 2006). To facilitate progress toward an ecological science that more effectively integrates information, we highlight some of the major concepts of information and their relationships to each other (**Table 1**). We present a brief review of thermodynamic entropy and information, and then proceed with greater emphasis on information theoretic concepts, though we highlight the continued need to bridge these gaps.

How Is Information Measured?

In ecology, as in any science, measurements are central to how we learn about our subjects, and how we visualize and operationalize theories. Measuring information and information flow in living systems is done in several ways (**Figure 1**). To understand which information measures or concepts are appropriate for a given context, and how metrics may or may not be comparable, we consider how information concepts are related to entropy, energy, cues and communication (**Table 1**).

Information can be measured in the context of information theory as the reduction in **uncertainty** of a system when comparing two (realized vs. possible) states of that system (**Box 3**, **Figure 1**, **Table 1**). We can measure information by comparing the **entropy** or **uncertainty** of an observed state relative to another state or states—a previous observation, a theoretical possible state (or set of states) such as a random state or thermodynamically dead or maximally entropic state (**Box 4**). In a thermodynamic context, information can be measured as negative entropy (**Table 1**), taking a value explicitly convertible or comparable to energy (Gatenby and Frieden, 2006; Schneider, 2010; Kempes et al., 2017). The unit of the measured information (bit, Hartley, etc.) depends on the configuration of the equation in **Box 4**, the reference states used or implied (Reference States), the base of the logarithm and the value of k. In the context of biosemiotics, information is measured

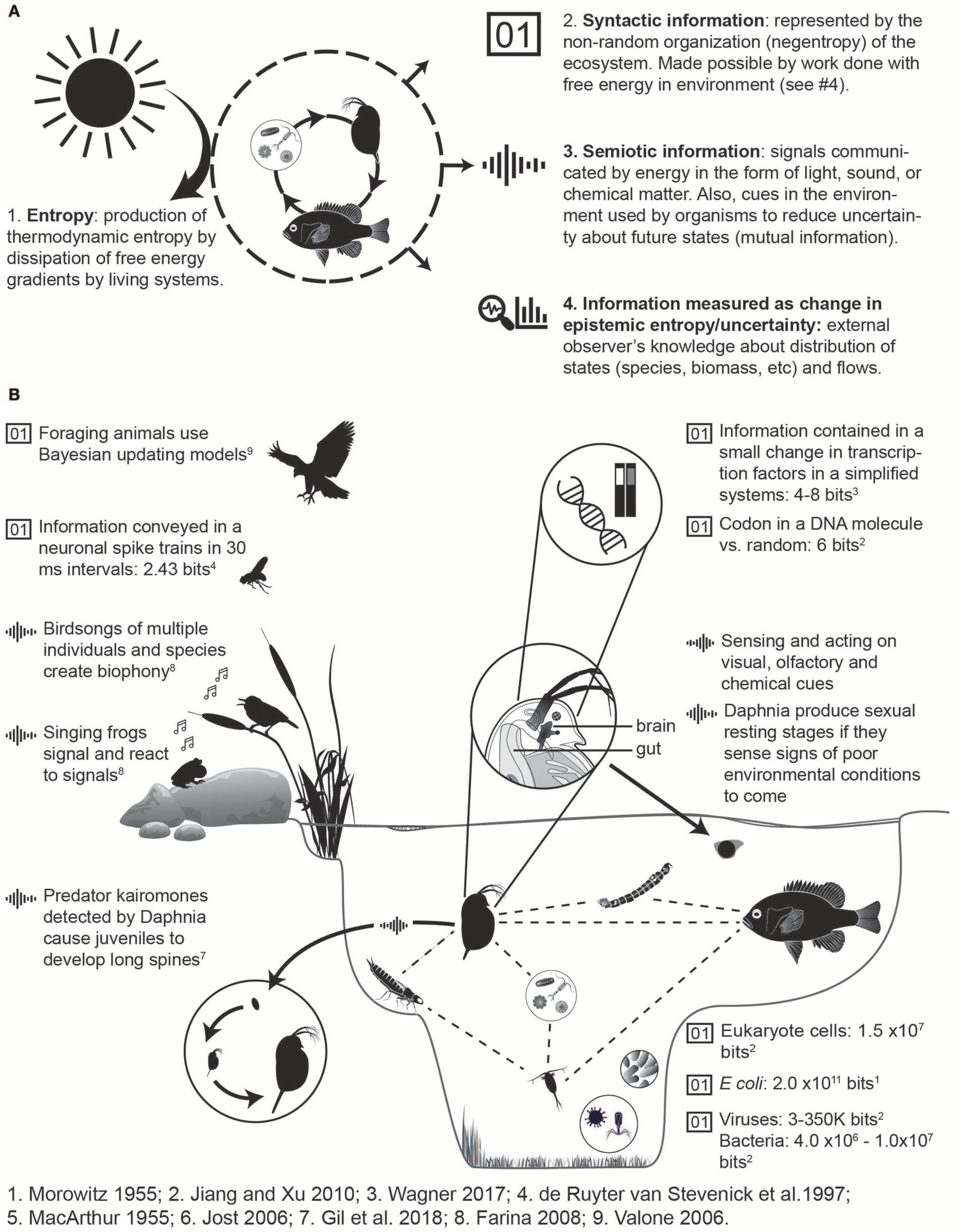

FIGURE 1 | Information takes a variety of forms in ecological systems. **(A)** In an ecological system such as a simple aquatic food chain (center circle), information is present as latent information, semiotic information, and information change as states change. This living system dissipates energy, and therefore has entropy. **(B)** In an

(Continued)

FIGURE 1 | example aquatic system, information has been measured and reported at many levels of ecological scale, from transcription binding factors to food webs. Examples of syntactic information (01) contained in structures such as genes, cells, viruses, networks, and communities. Information is also contained in differences or changes in structure. Semiotic information (〰), such as frog calls, kairomones from dragonfly larvae to daphnia, or use of cues and signals among organisms mediates ecological and evolutionary processes. Information can be measured using theory and equations in **Box 4**.

in a different way, typically by comparing the results of the information for fitness. For example, syntactic information in the DNA and birdsong examples can be quantified using a Shannon index for allele diversity, or spectral analysis on bird song, and the semiotic information in these structures can be quantified in terms of the fitness of individuals who carry the allele or can act on the message in the song to find a fit mate (**Figure 1**). Measurements of information—by a scientist, or an organism or other participant in the ecological system—therefore involve assumptions or specifications about signs, observers and reference states that require consideration of fundamental aspects of the system, such as entropy (Erill, 2012).

Uncertainty and Entropy

Information is most generally considered to be a reduction in uncertainty. Uncertainty is sometimes used as a measure or synonym of entropy. There are two distinct uses of the term "entropy" in the context of information—one associated with information theory (likened to uncertainty), and another associated with thermodynamics (**Table 1**). Both entropy concepts can be expressed with the same equation (**Box 3**), though the terms and their relationships are interpreted differently depending on whether the context is thermodynamics or information theory (**Table 1**). Though the same word "entropy" is used for these two entropy concepts, they are actually distinct ideas and are not fully and directly interchangeable or convertible (Wicken, 1987).

Thermodynamic entropy

Living systems take energy and process it to produce more organized systems with lower entropy (Schrodinger, 1944; Schneider and Kay, 1994; Jorgensen et al., 2000) (**Table 1**). Understanding ecological systems in terms of thermodynamic entropy has played an important role in theories of ecosystem services, human-nature interactions, and systems ecology (Odum, 1988; Jorgensen et al., 2000; Coscieme et al., 2013). The reduction in entropy associated with processing energy has been related to information (Patten, 1959; Margalef, 1985). This form of information is explicitly related to the energy required to obtain or produce the information, in a famous solution to the physics problem of Maxwell's daemon (Wicken, 1987; Parrondo et al., 2015). The thermodynamic concept of entropy and information predates, and has been distinct from, the information theoretic concepts (Wicken, 1987) (**Table 1**). Work focused on understanding ecological systems in terms of thermodynamics of non-equilibrium (living) systems has moved away from using information in this context and instead emphasizes self-organization and entropy reduction (Wicken, 1987; Schneider and Kay, 1994) (**Table 1**).

Information theoretic entropy

Information has also been defined relative to a concept of entropy in information theory (**Table 1**, **Box 4**). This entropy is the information theoretic entropy introduced by Shannon when the parameter $k = 1$ (**Box 4**) (Shannon, 1948). The Shannon equation can be used to estimate information by calculating the entropy (H) of two states of a system (an observed state *1* and a reference state *R*), and taking the difference in entropies:

$$\mathrm{I} = \mathrm{H_R} - \mathrm{H_1} \tag{1}$$

Uncertainty is maximized, and information is minimized, when the probability of the observed state of a system may be drawn from a uniform distribution of possibilities (one in which any state of the system is equally probable).

Though Shannon introduced his concept of syntactic information using the term entropy, and the use of the term entropy in this context does still persist (Jost, 2006; Sherwin et al., 2017; Gaggiotti et al., 2018), information theoretic entropy is not explicitly related to thermodynamic entropy (see Wicken, 1987 for an explanation of some of the core differences). Instead, information theoretic entropy is often related to the concept of equiprobability or disorder (without any explicit thermodynamic value to disorder). However, somewhat conversely to the trajectory of terminology in thermodynamics, the term entropy in information theory has in many cases been replaced by synonyms *uncertainty* (Dall et al., 2005; Gatenby and Frieden, 2006), *indeterminacy* (Ulanowicz et al., 2009), or *complexity* (Wicken, 1987).

Reference States

Information is a reduction in uncertainty between two states of the same system (**Box 4**). Central to this concept is the question, which two states are being compared? These two states may be defined in several ways. How they are defined influences how the observer interprets the information measured—how it may be related to energy, entropy and how it may be compared to other estimates of information.

There are absolute reference states. For a change in thermodynamic entropy, one reference state is thermodynamic zero (no entropy) (Jorgensen et al., 2000; Kempes et al., 2017). In early efforts, several researchers estimated the information content in cells based on the number of binary steps required to construct a biological structure from an unstructured arrangement of elements. They then verified these estimates using energetic methods, assuming that the information content of the structure was convertible to energy content via its inverse relationship to thermodynamic entropy. For example, Morowitz's estimate of 2×10^{11} bits in an *Escherichia coli* cell generally matched estimates based on calorimetric analyses (Morowitz, 1955). For non-thermodynamic entropy, maximum entropy is another absolute reference state. Full information may also be an absolute reference state. Full information is a known set of all possible states of a system and their probability of occurrence (Parrondo et al., 2015), but this one requires knowing the system. Pioneering attempts to integrate information theory into ecology drew on this idea of quantifying information by estimating all binary differences in a realized biological or ecosystem structure relative to all possible differences (Margalef, 1957, 1985; Patten, 1959). However, it was recognized relatively early on that knowing all possible states of an ecosystem was prohibitively difficult (Patten and Odum, 1981), and that thermodynamic zero is not always the most relevant reference state for comparing information between different life forms far from equilibrium. Approaches to estimate information in energetic terms had to make assumptions about these probabilities (Patten, 1959).

When observers (scientists, or participants in systems) define reference states other than absolute reference states, the accuracy of an absolute estimate of information depends on how well observers know (have a model) of the set of possible events and their relative probabilities—the set of possible nucleic acids, species, or letters in an alphabet. For entropy defined in terms of any value of k other than the Boltzmann constant in Equation 1 (**Box 4**), there is no explicit reference state to ground comparisons of states of a system. Any reference state can be specified by the recipient or user of the information (**Boxes 3**, **4**). The reference state could be another known state of the system. For example, Jiang and Xu (2010) used the Shannon entropy index and data on genome size to estimate the information content of viruses and a variety of prokaryote and eukaryotic cells by estimating all the binary differences between their DNA structure ($b = 2$, **Box 4**), minus "junk DNA," and the reference state of a completely disordered arrangement of base pairs but respecting the known probabilities of occurrence. They calculated information values ranging between 3 K and 340 K bits in viruses, 3.2×10^6 to 1.2×10^7 bits in bacteria taxa, and 1.5×10^7 to 8.4×10^8 bits in eukaryotes (**Figure 1**). Foraging animals use internally defined reference states based on their recent experiences of their environment and foraging activities when they use Bayesian updating processes to forage or choose mates in a dynamic environment (Dall et al., 2005; Valone, 2006). Erill (2012) argued that evolution acts as the informed observer for genetic information processes underlying evolution.

Examples of Information Measures in Ecological Studies

The earliest major effort to take an information theoretic perspective on ecological systems was Robert MacArthur's 1955 paper on diversity and stability (MacArthur, 1955). He introduced the Shannon entropy index to ecology to quantify uncertainty in how energy might flow through a community based on the number of possible energy flow pathways. In this example, MacArthur was exploring the idea that uncertainty is an attribute of the ecological system, in this case, a food web. Within a food web, he considered a probabilistic "indeterminacy" regarding the pathway in the network that energy might travel between two nodes. He used the Shannon index to model $p(x_i)$ (the central term, **Box 4**) as the proportion of energy flow through a particular node in the food web (not the proportion of individuals comprising that node, as we do today when we apply the Shannon index to describe diversity in ecological communities). His reference state was a uniform distribution (maximum uncertainty). The advantage of using the concept of entropy is that he did not need to know the exact energy flow pathways at any given time, or even which is most probable. He simply needed to know that the energy flow pathways are indeterminate; that there is an entropy of the network. Stability in a food web energy-flow network arises from indeterminacy in energy flow (Ulanowicz, 2001), or in other words, from uncertainty within the system about which pathway energy will flow through. This approach considers indeterminacy is an attribute of the network, not an attribute of an observer's (the scientist's) knowledge of the network.

Since this initial pioneering use of information theory to gain new insight in ecology, the Shannon index has been used extensively to estimate diversity in ecological systems (Pielou, 1967; Jost, 2006). The conventional definition of Shannon diversity (H') based on individuals of different species in a species assemblage is attributed to (Margalef, 1957, 1961; Ulanowicz, 2002). Estimates of diversity using Shannon or Simpson indices are examples of the use of an information theoretic measure of diversity, and these are applied to genetic systems or species assemblages (Jost, 2006; Sherwin et al., 2017; Gaggiotti et al., 2018). In fact, the development of metrics to measure diversity as information using entropy-based measures (Hill numbers) has played a key role in unifying understanding of diversity across ecological and evolutionary paradigms (Gaggiotti et al., 2018). Recent developments in the theory of using information metrics for diversity estimates of biological systems allow comparison of diversity across levels of an ecological system (e.g., genetic diversity and species diversity for a single species assemblage) (Gaggiotti et al., 2018).

Structural information has been an influential concept in community, ecosystem, and systems ecology (Patten, 1959; Margalef, 1985; Ulanowicz, 1997), in molecular biology (Gatenby and Frieden, 2006; Erill, 2012; Sherwin et al., 2017), and biodiversity science (MacArthur, 1955; Jost, 2006; Sherwin et al., 2017). For example, research on non-equilibrium thermodynamics has developed an understanding of ecosystem services, and even information in human societies (Odum, 1988) that is explicitly related to thermodynamic entropy and its related information (Jorgensen et al., 2000). Extensive work has employed structural information concepts and theory to understand macrostates in biological and ecological systems (Sole et al., 1996; Harte, 2011; Seoane and Solé, 2018).

Semiotic information is typically quantified in terms of the outcomes of situations in which living systems are exposed to sources of information that vary in their semantic content and context. These procedures are common in chemical ecology, where semiochemicals, such as pheromones and kairomones, can elicit many direct and indirect effects on development and survival within and among species. These effects can cascade up to higher levels of ecological organization. For example, predator kairomones can trigger cascading effects on the structure and functioning of aquatic food webs (Marino et al., 2015), or pheromones in insect pest outbreaks affecting primary production across large geographic areas. This information science has advanced to application with the development of databases of semiochemicals (http://www.pherobase.com/) for arthropod pest management, among other uses. Other approaches are used to assess the presence and importance of semiotic information as it mediates behavior, demography, and evolution (Dall et al., 2005; Schmidt et al., 2010). For example, the empirical studies of the role semiotic information plays in evolutionary or ecological processes have measured the consequences of information processing for the state of a receiving organism (Schmidt et al., 2010) such as its fitness at individual (Mery and Kawecki, 2005; Donaldson-Matasci et al., 2010) and population levels (Clobert et al., 2009; Fronhofer et al., 2017; Jacob et al., 2017).

Bridging Syntactic and Semiotic Information

Despite proliferation of information theory in several areas in ecology, an empirical synthesis of information stocks and flows is still elusive because different uses of information definitions and reference states makes it impossible to compare many estimates of entropy across systems. One issue is that the term $p(x_i)$ can take a variety of values that impart distinct meanings or interpretations on the resulting estimates of information. For example, when applying Shannon information to estimate the information contained in a genome or gene, the possible elements (nucleic acids) are finite and known (now), and their relative probabilities can be estimated (Jiang and Xu, 2010; Sherwin et al., 2017). This allows for the definition of a standard reference state for estimation of information in genetic systems for which these probabilities are already known. For a given species pool or sample, information theoretic methods now allow comparison and quantification of diversity across levels of biological organization (Gaggiotti et al., 2018). However, even with these advances, the values of these estimates do not constitute comparable estimates of information contained in biodiversity, in the sense of syntactic information that we are using here; a meta-analysis or synthetic assessment of information contained in would be un-interpretable diverse systems by comparing Shannon or Simpson measures. The reason for this incomparability is that entropy measured using the Shannon index depends on the estimate set of possible species, and this depends on the completeness of sampling or knowledge of the possibilities (e.g., species) in a system. Usually, this information is lacking; the choice of possible species and their relative probabilities is arbitrary because species pools are difficult to establish and are scale dependent (Jost, 2006; Gaggiotti et al., 2018). Approaches to estimating the full species pool are rarely reported or standardized. Thus, it is rarely possible to meaningfully compare reported values of Shannon diversity among different communities (Jost, 2006).

Bridging the gap between modes of studying and measuring syntactic and semiotic information also remains a major challenge (Adams, 2003). We still lack the ecological theory to relate the different measures and concepts of information to each other; we cannot track or account for information stocks and fluxes across studies or systems. For example, estimates of Shannon diversity using Hill numbers are not clearly comparable, in terms of information theories, to absolute references states that might allow a test of their relationship to energetics (Ulanowicz et al., 2009; Harte, 2011; Wagner, 2017; Hansen et al., 2018). The two entropy concepts that underlie thermodynamic and information theoretic definitions of information are not fully and directly interchangeable (Wicken, 1987). We should not view this gap to be a dead end; a similar situation occurs for energy, which also takes a variety of forms (e.g., radiant, thermal, chemical) that are difficult to quantify exactly and interconvert in living systems. Yet, we use energy and energetic models throughout ecological disciplines. As we have done with energetic models, we must explore relationships between different forms of information in nature. By attempting to understand the multiple information processes in ecological systems, we may overcome come of the challenges associated with diverse concepts and connect information use and its consequences in living systems.

Ecological systems integrate structural and syntactic information (**Figure 1**), just as they comprise multiple forms of energy and material. In fact, the way we understand ecological and evolutionary processes begins to bridge the gap between semiotic and syntactic information concepts. Two of the principles we propose for ecological knowledge explicitly recognize information of both kinds as fundamental to ecological systems (**Box 1**). We can continue to use thermodynamic, information theoretic and biosemiotic theories to gain insight about nature, and consistent with these principles (**Box 4**), do so in research that allows us to explore relationships between these information concepts. We believe such an approach may lead to deeper understanding of the extent and nature of relationships among the ways we observe and measure information in different contexts for different reasons. To help integrate information concepts with how we understand ecological systems, we can consider how information flows and accumulates in ecological systems. We refer to the flowing and accummulation of information as "information processing."

HOW IS INFORMATION A DYNAMIC PART OF LIVING SYSTEMS?

What Is Information Processing?

Information is a dynamic feature of living systems because it is stored, transmitted, received, and used (Gatenby and Frieden, 2006; Erill, 2012) (**Figure 2**). In other words, living systems process information by combining semiotic and syntactic facets of information that we have reviewed so far (Gatlin, 1972; Maynard Smith, 2000; Farnsworth, 2013; Davies and Walker, 2016). Storage occurs in material or energy structures that reflect the events that created those structures. Structure stores information, thereby providing memory, about past events. Neural networks, social structures, morphologies, and learned behaviors are all examples of information storage, and therefore subject to general properties and constraints

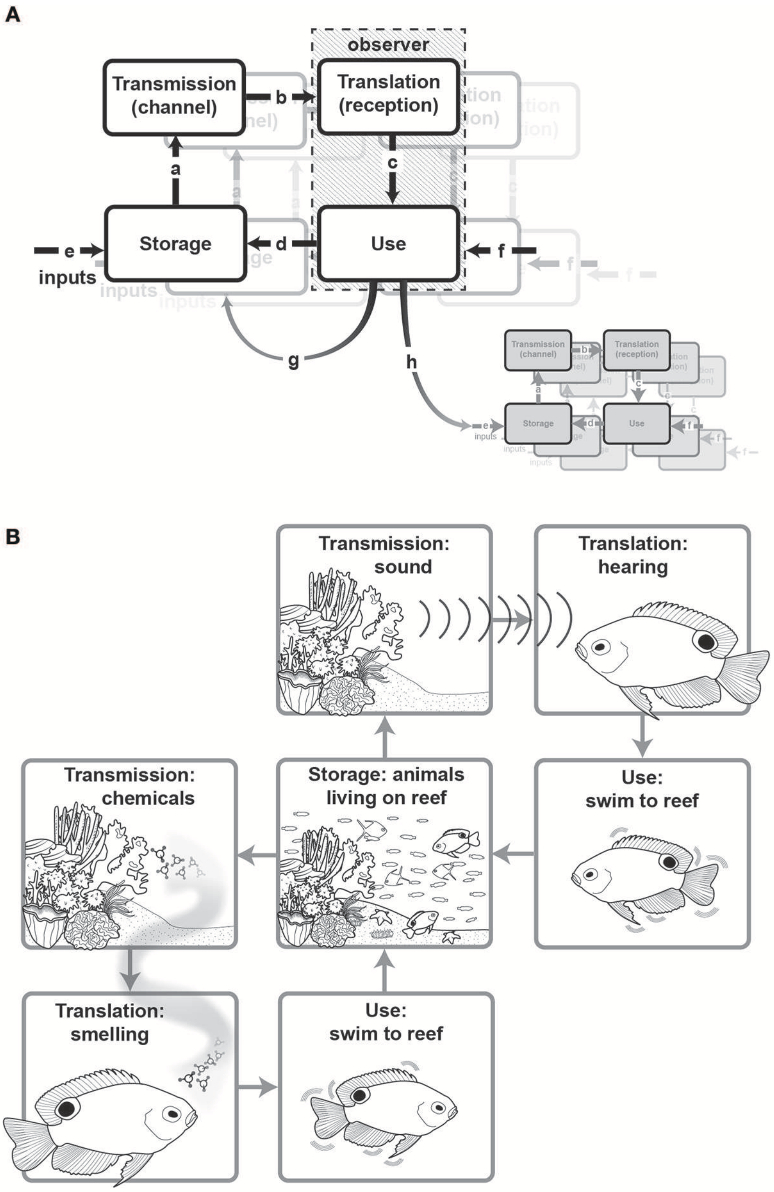

FIGURE 2 | Four steps of information processing. **(A)** Information processing can occur within a closed feedback loop (a -> b -> c-> d), or by accepting information from outside the loop (e -> a-> b -> c…) and can lead to information that is used by the processing systems outside the focal system (e.g., c -> h or c->g). Information processing requires an observer, which often constitutes the reception and use of information. Inputs to any processing system may be information instantiated in chemical, electrical, energetic, or material structures. **(B)** Coral reef fish use olfactory (*Osterhinchus doederleini*) (Gerlach et al., 2007) and auditory (Gordon et al., 2018) information to relocate their home reef. The information stored in the sound or chemical patterns in the water are received by fish sensory systems—themselves information systems—and used to guide behavioral responses such as swimming to the reef and remaining there, and the recruitment of fish to these reefs contributes to structure at population and community levels.

of information systems. Transmission occurs when stored information influences some informational, energetic or material process. Reception is the decoding and integration of the transmitted information in the receiving system or observer; reception of semiotic information involves a decoding process in which the state and previous information of the decoder is relevant. Reception is the physical receipt of information interacting with the state of the recipient. Use is the consequence in terms of what is done with the information received. Examples of information use include conversion of received information to stored information (e.g., observation to memory), and conversion of received information to work or function (observation to use) (Gatenby and Frieden, 2006) (refs in **Figure 2**). Transmission and reception are subjects of much of information theory and the literature on their role in communication and biology is vast (Dall et al., 2005; Chaine et al., 2013; Tkačik and Bialek, 2016). In this view, information transmission occurs through "channels," and the information transmitted depends on the ability of the channel to transmit, and the receiver to receive, a signal relative to noise. Information transmission and reception can be modeled quantitatively using equations relating the probability of information received relative to what was possible based on a reference state (e.g., the properties of the transmitting channel, the expectation of the receiver, the context, etc.) (**Figure 1**).

When we consider information processing in living systems, we can quantify syntactic information stored, transmitted and received in objectively quantifiable units (**Box 4**). For example, the potential information stored in the action potentials that constitute neuronal communication (Tkačik and Bialek, 2016) (**Figure 1**) and the amount transmitted by neurons in flies (de Ruyter van Steveninck et al., 1997) has been estimated in bits, and even compared to the amount of information encoded by someone typing on a keyboard (Bergstrom and Rosvall, 2009). The amount of information associated with a particular ATP-binding phenotype is quantifiable (36.6 bits), and comparable to the amount of information needed for any single amino acid sequence [estimated at 345.8 bits; (Wagner, 2017)]. However, these quantitative measures of information processing fail to capture the content of information or the consequences of information processing, which are more often measured in terms of changes in the state or behavior of the user of the information (**Figure 2**).

Information processing systems confer general attributes and properties upon biological systems. These attributes include plasticity, memory, self-regulation, amplification, anticipation, cross-scale connections, and dependence upon energy and materials. The same information content can be stored in different structures and processed in different ways at different stages of an information processing system (**Figure 2A**). This property allows transfer of information among entirely different material or energetic systems, allowing the structure and materials of information processing systems to be plastic without necessarily compromising information flow. Information processing systems are typically characterized by indeterminacy in channels, and plasticity in the particular flows of information confer stability on the processing network (Patten and Odum, 1981; Flack et al., 2006; Moses et al., 2016), much as MacArthur showed in his idealized food web (MacArthur, 1955). Information processing systems can adapt to changing conditions, often reversing structural patterns in ecological networks (MacArthur, 1955; Ulanowicz, 2001; Flack et al., 2006; Ulanowicz et al., 2009; Valdovinos et al., 2016). For example, organismal processing systems such as visual or olfactory systems allow organisms to sense their environment, and based on a comparison of detected information with a reference state, act on that information (**Figure 2**).

Information processing systems relate past experiences and current conditions to anticipate likely future conditions so that the processing system (e.g., an organism or physiological system) can act accordingly (Rosen, 1985; Helm et al., 2013; Kinmonth-Schultz et al., 2013). Plasticity allows information processing systems to update, taking in new information from the environment or about the state of the processing system itself (Valone, 2006). For example, Fronhofer et al. (2017) and Jacob et al. (2017) have recently demonstrated experimentally that microbial organisms' abilities to sense their environment and select habitats where they are likely to perform well affects movement of individuals in ways that facilitates species' range expansion dynamics and local adaptation, thereby enhancing persistence in a changing environment. Many diverse information processing systems have evolved to allow organisms to perceive their environment and act upon that information. These evolved systems allow organisms or groups of organisms to use predictable environmental temporal patterns in day length or temperature to anticipate changing environmental conditions and to trigger developmental processes or other life history events. The genetic underpinnings—though diverse—of phenology and circadian rhythms constitute a *memory* of past successes associated with regularly occurring environmental conditions (Edgar et al., 2012; Kinmonth-Schultz et al., 2013). Another example of anticipation is the case when trees release and exchange infochemicals, often via mycorrhizal networks in the soil, and used by other individuals to infer, for example, the occurrence elsewhere of plant-insect interactions (especially pest insects) to change physiologically to minimize a likely future pest or disease attack (Barto et al., 2012).

The study of control and communication is the focus of the field of cybernetics. Self-regulation of a system's state through feedbacks is another attribute characteristic of the many information processing systems in ecology (Wiener, 1948; Patten and Odum, 1981; Farnsworth, 2013; Krakauer et al., 2014). For example, a self-regulating system is the physiological maintenance of thermal homeostasis in mammals (Woods and Wilson, 2013). Relevant to this review is the distinction between first- and second-order cybernetics as, respectively, the cybernetics of observed systems and the cybernetics of observing systems (von Foerster, 1974; Scott, 2004). Self-regulation in observing systems (e.g., organisms and their aggregates) requires information processing and an internal model of the world and of self to relate outputs to inputs and maintain feedbacks among sets of distinct steps; cybernetic systems also allow amplification of information as it is processed. Low or trace elements of chemicals (e.g., kairomones produced by predators) can elicit large behavioral, evolutionary and demographic responses in prey as that information is processed through physiological, neurological and genetic systems. Then, indirectly, population dynamics and even trophic cascades may be affected.

Information and the dynamics it elicits in ecological systems result in its inter-dependence on energy and material systems. The relationships between information and energy take a variety of forms. Information is carried by variations in the spectra of electromagnetic fields (e.g., light and magnetism) that are directly controlled by energy demanding organs of communicating organisms. Information processing requires energy and materials and is thereby subjected to physical and chemical constraints (Odum, 1988; Laughlin et al., 1998; Parrondo et al., 2015; Tkačik and Bialek, 2016; Kempes et al., 2017). Energy is required to create, maintain, and operate infrastructure to process information. This need for energy and materials has been considered as a "cost" of information. Information storage infrastructure, such as a brain or a gene, can be metabolically and materially expensive to build and maintain. The energetic and material requirements to maintain an information processing system may lead to changes in the network structure and its information processing over time, particularly as the external environment changes. Cybernetic models of information highlight relationships between information processing and system stability and energy fluxes in ways that are grounded in first principles of physics (O'Neill et al., 1986; Parrondo et al., 2015; Davies and Walker, 2016). In another approach, emphasizing semiotic information, behavioral ecologists have developed theoretical frameworks that relate use of private and social information (Danchin et al., 2004; Gil et al., 2018) to increased success in resource foraging and acquisition, suggesting that energetic and material costs of information processing systems may be balanced by resource gains. These examples illustrate how information-energy relationships have emerged as important in ecological studies; yet, as with other questions concerning information and energy, fully understanding how these different relationships fit together remains an important challenge for research, both in ecology and in physics.

Information processing systems occur within traditional levels of the ecological hierarchy (cells, organisms, populations), but also across levels, thereby linking ecological and evolutionary dynamics in what Koestler (1967) called a holarchy (**Box 5**). Holarchic systems are hierarchies where there is not a strict top-down flow of cause and effect; information flows up and down across levels mediating the dynamics of a system (Kay, 1999). The holarchic nature of information processing networks allows information to be stored and accessed at different levels of organization than the level at which it used. For example, genetic information in interaction with the environment may mediate phenotypic variation in physiology, communication, and species' interactions, with the emergent outcome that in turn affects patterns of selection and evolution. Eco-evolutionary processes are the direction expression of different modes of information flow in holarchic structured ecosystems.

Information processing networks also have the capacity to perform computations at the local level that have far-reaching consequences at the macroscopic level. For example, insect societies are able to perform complex behaviors, including possibly computations, even though individual behaviors are simple, and these society-level behaviors produce and store information with emergence properties of long-range order (Solé et al., 2016). Though many apparent examples of information processing center on organisms and how they receive external signals and act on them, information processing also occurs within genetic, physiological, and neurological systems process information using analogous processing systems (Laughlin et al., 1998; Maynard Smith, 2000; Woods and Wilson, 2013; Tkačik and Bialek, 2016; Wagner, 2017) (**Figure 2**). Information is also processed at levels of organization above individuals (Frank, 2008) such as within social networks (Flack et al., 2006; Aplin et al., 2015), and even in non-Darwinian units such as communities (Gerlach et al., 2007; Farina, 2008; Gordon et al., 2018) and ecosystems (Patten, 1959; Odum, 1988) (**Figure 1B**). A cybernetic perspective, in particular a second-order perspective, challenges the heavily reductionist, mechanistic view of ecology because it demonstrates that flows of information among levels of organization mediate a living system's dynamics (Ulanowicz, 1997; Jablonka and Szathmary, 2004; Ulanowicz et al., 2006; Davies and Walker, 2016).

Are Organisms Causes or Consequences of Information Processing?

Taking a synthetic perspective on information in ecological systems reveals an additional duality: individual organisms are drivers of information processing, but organisms and other biological structures can be seen as emergent to the process of information processing (Davies and Walker, 2016). Much of mainstream ecological theory (e.g., **Appendix 1**) is predicated on the view that organisms are the fundamental agent of information processing and the consequences of information processing are behavioral, fitness, and population outcomes (Dall et al., 2005; Schmidt et al., 2010; Burns et al., 2011; Gil et al., 2018). However, another theme in how information theory has been used in biology, specifically to better understand the origin of life, suggests that organisms, like other levels of organization, may be emergent properties of information processing systems (Schrodinger, 1944; Schneider and Kay, 1994; Kay, 1999; Krakauer et al., 2014; Marshall et al., 2017). The information processing systems that allow organisms (or agents) to emerge and persist are not restricted to any particular biological scale. Therefore, there may be no reason to think that information processing and the stability and evolvability that comes with it are restricted to what we traditionally perceive as an "organism," based on physical attributes of organisms. Indeed, recent discoveries on the holobiont (host-symbiont, host-parasite relationships) nature of the organism blurs our notions of individuality. There is substantial evidence for information processing to have cross-scale consequences and connections, and we will review these in the next section.

Together, the perspective that organisms are fundamental units in ecological systems, combined with the view that organisms are emergent properties of ecological information processing systems, suggests that there are feedbacks between information use and processing across scales of ecological organization (Ulanowicz, 1997). This dual relationship between information processing and the individual has been argued to underlie major evolutionary transitions from unicellular organisms to multicellular organisms as evolutionary units (Szathmáry and Smith, 2002; Jablonka and Szathmary, 2004; Jablonka and Lamb, 2005). In this way, information dynamics and the informational, material and energetic efficiency and stability they confer appear to have shifted the way evolutionary biology recognizes elements of living systems as "organisms" in recent decades. Some have extended the concepts of fundamental units of selection even further, based on information processing dynamics, to include kin, social groups, symbioses and even some species associations (Ehrlich and Raven, 1964; Szathmáry and Smith, 2002; Guimarães et al., 2011).

Box 5 | Eco-evolutionary model of information use processing.

Here we outline a model taking into account the fitness consequences of the information acquisition, storage, communication, and use. We first introduce the maximal information in an ecosystem accounting for the fitness of information traits of all phenotypes. In the second part of the box, we connect our maximal information criteria into a quantitative trait dynamics model. From first principles of thermodynamics an important reference point of interest is the maximum entropy, and around this point is a distribution of possible thermodynamic states (**Table 1**). For a living system defined by phenotypes with fitness, an analogously important reference point is that all phenotypes have equal frequency and equal fitness, and we assume this holds maximal information in the ecosystem. Around this point, there is a distribution of possible configurations of the ecosystem, with units of fitness. These distributions are intimately connected (Principle 2), but the former is abstracted in the following model derivation of information processing.

Information processing ecosystems are comprised of traits that influence a component of fitness variation, particularly those involved in information acquisition, storage, communication, and use (i.e., decision making) (**Figure 2A**). These we refer to as information processing traits, and as with other evolving traits, they are involved in tradeoffs among one another and with traits associated with energy (e.g., metabolic traits) and materials (e.g., resource acquisition traits) (Principle 3). The relationships among information traits, including the covariance matrix and the trait hierarchy taking into account processes across biological levels (Melián et al., 2018), define the occurrence and nature of these tradeoffs (Jablonka and Lamb, 2005). Information processing traits have cost functions. For example, acquiring and storing information about past environmental conditions and trait distributions could be adaptive during decision making (e.g., information usage), but there are likely significant energy costs associated with gathering social, habitat or species interactions information (e.g. movement across a landscape) and storing it for later use (e.g., metabolic costs of memory) (Giraldeau and Caraco, 2000).

Consider a population characterized by individuals each containing four information traits (acquisition, z_a, storage, z_s, communication, z_c, and use, z_u), where the mean trait value of the information traits contained in each individual z_i at time t in site x is given by:

$$Z_{ix}^{t} = \frac{1}{4}[z_a \leftarrow exp(c_a T) \oplus z_s \leftarrow exp(c_s \Psi) \oplus z_c \leftarrow exp(c_c \Omega) \oplus z_u \leftarrow exp(c_u \Upsilon)], \tag{1}$$

where c_a, c_s, c_c, and c_u represent the information cost of acquisition, storage, communication and use, respectively, and T , Ψ, Ω, and Υ represent information from past environmental conditions, storage energy cost, the cost of gathering social and habitat information, and information usage cost, respectively.

In this example, perhaps the metabolic cost of memory increases exponentially with the total amount of information stored over the lifetime of an organism, including information acquired via movement through space and stored over time. These cost functions vary among traits, organisms types, individuals and development. Most individuals will use information from the most recent and spatially restricted state, with the variance depending on the cost of each information trait. In the canonical model of evolution, individuals use no information from previous states (i.e., strong costs), thus excluding adaptive strategies that involve information processing from prior states.

We consider the fitness function of each individual as the sum of information processing traits and other traits that underlie fitness variation. We can build a fitness functions based on these two components. For the non-information traits, fitness is often calculated from how well it matches a fitness optimum determined by the environment, specifically an environment that is determined by trade-offs associated with energy and material traits. For the information traits there is also an information environment, and we propose that its relationship between information processing traits, can also be a significant component of fitness variation (Principle 4). For example, individuals acquire information from their surroundings, and the canonical model does not incorporate how that information might be shared among individuals in a way that could influence both individual and population mean fitness. The adaptive use of information might build over time in a population and become a significant component of the fitness function (Principle 4). The fitness of individual i accounting for these two components can be expressed as:

$$W_{ix}^{t} = \frac{1}{2}[exp(-\alpha(Z_{ix}^{t} - \theta_{lx}^{t})^{2}) + exp(-\gamma(Y_{ix}^{t} - \theta_{Ex})^{2})] \tag{2}$$

where Z_{ix}^{t} is the information trait value of individual i in time t and site x (Equation 1), θ_{lx}^{t} is a measure of the optimal information content obtained from the population at time t, Y_{ix}^{t}, is the non-information trait value of individual i in site x and θEx is the optimum determined by the environment. α and γ determine the interaction sensitivity to deviations from the information content optimum and from the environmental optimum, respectively. The effects of information and non-information trait correlations on fitness of each phenotype can be included by adding the covariance matrix with a multivariate fitness optimum (Melo and Marroig, 2015).

Modeling these two fitness components is a useful distinction and expansion of the canonical model. First, it adds more realism because information traits are now explicit in the evolutionary process alongside other evolving traits (Principle 1). Second, it allows us to contrast models of evolution with and without evolving information traits. This could also include models where the feedback between trait and the environment vary among traits. Information traits might have a more explicit feedback or feedforward relationship with the environment than other traits. Third, it is possible that information traits are evolving differently from other traits and experience different tradeoffs, such that modeling them separate from other traits might be a useful starting point. For example, information processing traits likely arise from different hierarchical levels of biological organization (Principle 5). In a plant- pollinator system, for example, the interactions in a typical evolutionary model do not incorporate the abilities of pollinator to acquire, access, and use prior foraging experience to make local decisions about which flowers to interact with. As such, there is no variation in the population with respect to decision making based on individual memory and learning potential (Watson et al., 2016). We posit that including such semiotic information into models of evolution will reveal new insights about natural populations, species interactions and the stability of ecological communities. The model outlined above can be run for many generations and for each time step, the phenotypes after selection and changes driven by structural modifications or plasticity in the information and the non-information traits can be used to update the fitness values (Melo and Marroig, 2015; DeLong and Gibert, 2016; de Andreazzi et al., 2018). Fitness will then determine the ecological dynamics and the total information content in the ecosystem. This total information content for each scenario can be compared with our reference point with all types having both equal frequency and equal fitness (i.e., maximal information in the system).

An information theory perspective suggests that Darwinian evolution is one fundamental form of information processing that produces structure and persistence in living systems (Gatlin, 1972; Maynard Smith, 2000; Frank, 2012; Wagner, 2017). But, evolution is not the only form of information processing prevalent or necessary for ecological systems—evolution at levels of organization other than the genetic population would be consistent with information processing, by cellular structure and contents, by mixed species communities and social systems, social learning, and thermodynamic information conversion to energy (Margalef, 1957; Wicken, 1987; Odum, 1988; Ulanowicz, 1997; Farnsworth, 2013; Kempes et al., 2017). From the perspective of life as non-equilibrium thermodynamic systems, ecosystems are considered holarchic systems that grow and accumulate information and organization over time (Schneider and Kay, 1994; Kay, 1999; Jorgensen et al., 2000); evolution is one mode of information accumulation, but not the only mode. This fact has profound implications for how we approach understanding ecology at this time because mainstream ecological theory is predominantly based on Darwinian models, assumptions and concepts, resulting in a strong emphasis in ecological theories on evolvable "Darwinian" units—individuals, symbioses, etc. (Szathmáry and Smith, 2002; Jablonka and Szathmary, 2004; Jablonka and Lamb, 2005). Taking the perspective that information and information processing is fundamental, and evolution is one manifestation of it, opens up additional perspectives on how living systems grow, change, and persist (Wicken, 1987; Ulanowicz, 1997; Frank, 2008; Farnsworth, 2013).

ADVANCING THE ROLE OF INFORMATION IN ECOLOGICAL UNDERSTANDING: CHALLENGES AND OPPORTUNITIES

We have outlined five fundamental principles for ecological science that integrate information and its role in living systems (**Box 1**). The five principles provide a foundation upon which new theories may be developed (or existing concepts and theories rooted). To build a theory for how ecological systems process information, conceptual and theoretical models need to be articulated (we offer one such approach in **Box 5**), and experiments will be needed to test their assumptions and derived hypotheses and predictions. Building this theory is a major challenge for ecological and evolutionary science. It will require synthesis of existing frameworks in molecular ecology and evolution, (semio)chemical ecology, behavioral ecology, physiology, systems ecology, and thermodynamics (to name a few). To inform this new direction, we can begin by drawing upon the rich theoretical and empirical literature on the role of information in evolution, behavioral ecology, and molecular biology (Dall et al., 2005; Ulanowicz et al., 2009; Schmidt et al., 2010; Farnsworth, 2013; Gil et al., 2018). We highlight two immediate challenges here.

Develop and Employ Empirical Approaches for Quantifying Information and Its Flow in Ecological Systems at Multiple Scales

The five principles capture the importance of information and its relationships with energy and materials. Yet, studying information empirically has been extremely difficult historically. Estimates of information content in cells, organisms, communities, and ecosystems were in the past severely constrained by infrastructure for measuring or observing structural information or behaviors associated with communication (Patten and Odum, 1981). Now, existing approaches allow information to be estimated in quantifiable and comparable terms (e.g., Jiang and Xu, 2010; Kempes et al., 2017) (**Figure 1**). Using physics concepts and models (Kempes et al., 2017), have recently estimated the thermodynamic information content of the biosphere based on estimates of the information content in cells. These approaches could be further developed and adapted to quantify information in communities and ecosystems, allowing tests of hypotheses related to principle 2. Other approaches we now have that were not available until recently were the computational and technological infrastructure to sample sounds, colors, and chemicals in the environment, and to analyze their possibilities and probabilities to then estimate information. Expanding the use of these approaches to generate estimates of information processing in living systems is an essential next step to understanding how information processing is driven by and changes energy and material processes as outlined by principles 3 and 4. These can be used to quantify information in ecological systems under different conditions and to further develop empirical knowledge of where and when information is processed.

An empirical, data-rich body of knowledge is essential to produce a more general and testable theory of ecology. Theory (Develop and Apply New Ecological Theory of Information) is also essential, because even though it is possible to assemble more and new kinds of data, we still face basic challenges comparing these measurements. In some ways the capacity to measure information (e.g., eDNA or remotely sensed observations) has outpaced our ecological theory for how to use these observations of information to understand ecological and evolutionary dynamics. For example, for a freshwater planktonic food web, it is possible estimate information content of the genomes of *Daphnia* and its phytoplankton prey, of the kairomone chemical indicator of a predator, of the interaction network and diversity of the community (**Figure 1**). However, it is not yet clear how to compare these to track information in the system over time or in response to environmental change. Yet another challenge arises when we consider the question, if information is defined by the sender and receiver, how is a third party to find meaning in it? This was precisely the problem faced by code breakers in World War II. It was from this challenge that a solution was found to objectively quantify information—this is was Claude Shannon's contribution, published in 1948. To build a more complete set of observations of information and information processing in ecological systems, we require new methods and theories to guide and interpret those methods.

Develop and Apply New Ecological Theory of Information

Calls for the integration of information theories with ecological theories have drawn on information concepts with distinct historical roots: semiotic information (Barbieri, 2008; Schmidt et al., 2010; Farina, 2011), structural information (Gatenby and Frieden, 2006; Tkačik and Bialek, 2016) and genetic information (Maynard Smith, 2000; Frank, 2008), and information criteria to support inference (Harte, 2011). This duality of syntactic vs. semiotic is a basic dichotomy in the literature that needs resolving if we are to develop an integrated theory of information for ecological systems. More explicit consideration of the interpretant—the scientist as the user of information, the relational roles of living systems as they use information—may bridge these information concepts (Atkin, 2006). Theories that admit semiotic information, syntactic information and the role of interpretants will integrate information approaches based on entropy measures of the structure and flows in communities and ecosystems (MacArthur, 1955; Margalef, 1957, 1985; Patten and Odum, 1981; Ulanowicz, 1997), with approaches in behavioral ecology and evolution (Maynard Smith, 2000; Dall et al., 2005; Farina, 2008; Frank, 2008; Schmidt et al., 2010; Pijanowski et al., 2011) that emphasize how organisms gather and use information to mediate their development, and their interactions with the environment that mediate their fitness (Holt, 2007). This joint description of ecological information dynamics will capture the principles outlined above and allow exploration of their consequences for the ecological patterns and processes we study. Resolving these gaps in information theory would then allow other theoretical advances to model dynamics of information in ecological systems (Gatenby and Frieden, 2006). Ultimately, this theory will allow us to interpret information flows across scales and how they map to fluxes of energy and materials and in so doing connect behavioral and cognitive ecology with community ecology and biogeography.

CONCLUSION

Ecological systems integrate information in multiple forms—syntactic and semiotic—with diverse relationships to energy and materials. We reviewed fundamental concepts in information theories, distinguishing between syntactic information and semiotic information. Information processing links these two forms in living systems, connecting processes across scales in holarchies. Taking this perspective on ecological systems may advance efforts to unify understanding across scales of life by drawing on knowledge systems related to different scientific disciplines. This unification brings challenges—understanding the relationships between different forms of information and energy, and developing methods for observing, quantifying and tracking information remain the focus of research efforts across disciplines.

Understanding ecology in terms of information and its links with energetic and material processes may help to bridge complex ideas and literatures in ecology and information sciences. To encourage such synthesis, we have articulated five principles for ecological systems that integrate diverse concepts of information in living systems (**Box 1**). Relating ecological ideas and questions to these principles to build a more coherent understanding of life is possible, and these principles lead to operational statements and empirical testable hypotheses.

Scientific and philosophical thinking and work has now placed information firmly "as one of three elemental components of existence (along with space/time and energy/matter)" (Atmar, 2001) in living and non-living systems, though this perspective is only just re-emerging in ecological thinking. A synthesis of information concepts in ecology is not that farfetched. It is well underway and operational in molecular biology, physiology and physics. Ecology has the opportunity to draw from these recent advances, and see our world from a new perspective.

A more robust and complete understanding of nature that is not restricted to a single research paradigm or scale of nature is not only an essential goal of science, but also critical to understanding how our world is changing. Harries-Jones (2009), drawing on the work of Douglas Bateson (Bateson, 1972), argued that the collapse of ecosystems *follows* the more subtle collapse of communicative order. This is a plausible hypothesis. Yet, modern ecological science is simply not equipped—theoretically or methodologically—to even test this hypothesis, nevermind to dismiss it. But we can remedy that, with rapid growth in an integrated science of the dynamics of information, energy, and materials in ecological systems. A synthesis in ecology could begin with explorations and tests of existing hypotheses about the role of information in living systems. A more unified and multi-scale ecological science that integrates information dynamics is not only possible but essential to pursue.

AUTHOR CONTRIBUTIONS

MO, AG, and MP conceived of the study, reviewed literature and wrote manuscript. CM and BM developed model (**Box 5**). MO, MP, FA, BM, CM, and AG contributed to the development of the 5 principles and editing.

FUNDING

Funding is from the Swiss National Science Foundation Grants No PP00P3_179089 and 31003A_173074 and the University of Zurich Research Priority Programme URPP Global Change and Biodiversity (to FA). Funding from the EAWAG Socio-Economic-Technological Synthesis Center (SETS) to MO.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

APPENDIX 1. EXISTING ECOLOGICAL PRINCIPLES

Fundamental principles are broad statements about empirical patterns and the processes that operate to create patterns (Scheiner and Willig, 2008) that are central to any scientific understanding expressed by theory. Fundamental principles are not novel statements but instead are true and foundational for modern accepted theories of ecology, often invoked to understand new problems or to organize or synthesize diverse ideas (Margalef, 1963; Allen and Gillooly, 2009; Gurevitch et al., 2011). Here we present a few examples of recently published principles of ecological science. These sets of principles are taken to be uncontroversial and consistent with any basic ecological text or training. Scheiner and Willig offer these 7 principles as central to a general and broad theory of ecology. The other two sets illustrate how ecological principles are typically referenced as starting points to understand a more specific, novel or applied subject. We find these are not foundational for an ecological science for the future, changing world, because they do not adequately reflect information processes that define living systems and the relationships they mediate between information, and energy and material flows.

7 Principles of the Theory of Ecology (Scheiner and Willig, 2008), articulated after an extensive review of recent progress in ecological understanding:

1. Organisms are distributed in space and time in a heterogeneous matter
2. Organisms interact with their abiotic and biotic environment environments
3. The distributions of organisms and their interactions depend on contingencies
4. Environmental conditions are heterogeneous in space and time
5. Resources are finite and heterogeneous in space and time
6. All organisms are mortal
7. The ecological properties of species are the result of evolution

Principles of Conservation Biology cites these as the shared principles with ecology (Groom et al., 2005).

1. Evolution is the basic axiom that unites all biology
2. The ecological world is dynamic and largely non-equilibrial
3. Human presence must be included in conservation planning

Three basic principles of ecology invoked to understand ecogeoscience research (Allen et al., 2014)

1. Biological traits exist in a distribution due to species diversity
2. Biological traits are adaptable and dynamic through time
3. Dynamically coupled relationships between species and their environments create biotic-abiotic feedback cycles.

frontiers
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ORIGINAL RESEARCH
published: 07 August 2019
doi: 10.3389/fevo.2019.00242

The Scales That Limit: The Physical Boundaries of Evolution

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Organisms are subject to the laws of physics, so the process of evolution by genetic variation and natural selection is constrained by these fundamental laws. Classic and recent studies of the biophysical limits facing organisms have shown how fundamental physical constraints can be used to predict broad-scale relationships between body size and organismal biomechanics and physiology. These relationships often take the form of power laws across a wide range of body sizes for organisms sharing a common body plan. However, such biophysical perspectives have not been fully connected with the detailed dynamics of evolution by natural selection, nor with the variation between species around the central scaling relationships. Here we first discuss what a general biophysical theory of evolution would require and provide a mathematical framework for constructing such a theory. We discuss how the theory can predict not only scaling relationships, but also of identifying the types of tradeoffs made by different species living in particular niches. In addition, we discuss how a key higher-order requirement of a biophysical theory of evolution is its ability to predict asymptotic behavior and the limits of a particular body plan. We use several examples to illustrate how dominant physical constraints can be used to predict the minimum and maximum body sizes for a particular body plan, and we argue that prediction of these limits is essential for identifying the dominant physical constraints for a given category of organisms. Our general framework proposes that a major portion of fitness should be the overlay of how all traits of a particular body plan interact with fundamental physical constraints. To illustrate this concept, we investigate multiple physical limits on particular traits, such as insect legs, and show how the interaction of a number of traits determines the size limits on entire body plans, such as those of vascular plants. We use bacteria as an example of the shifts in which physiological traits and physical constraints are most limiting at various organism sizes. Finally, we address the effects of environmental conditions and ecological interactions in determining which of the physical constraints faced by organisms are most likely to affect their growth, survival, and reproduction, and hence their fitness. We consider such ecological effects on our examples of bacteria, insects, mammals and trees, and we nest the constraints-perspective in the broader picture of evolutionary processes.

Keywords: biophysical constraints, allometry, metabolic scaling, safety factors, evolutionary transitions

OPEN ACCESS

Edited by:
Diego Barneche,
University of Exeter, United Kingdom

Reviewed by:
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University of Exeter, United Kingdom
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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *24 December 2018*
Accepted: *11 June 2019*
Published: *07 August 2019*

Citation:
Kempes CP, Koehl MAR and West GB (2019) The Scales That Limit: The Physical Boundaries of Evolution. Front. Ecol. Evol. 7:242. doi: 10.3389/fevo.2019.00242

1. INTRODUCTION

The classic view of evolution is that individual species become adapted to specific niches through the process of genetic variation and natural selection, where the temporal trajectories of particular populations are noisy and often unpredictable in detail. From this perspective, the myriad physiological functions performed by one species can only be fully understood through the lens of a specific evolutionary history and the numerous selective pressures in a particular ecological setting that lead to selection for one physiological/morphological local optimum (of potentially many). A contrasting perspective to focusing on these detailed processes that lead to speciation is that evolution occurs in the physical world, and that the consistency of basic physical laws produces broad-ranging regularities across biological diversity (Thompson, 1917; Rashevsky, 1944, 1960; Brown et al., 1993; Alexander, 1996; Niklas and Hammond, 2013). A prime example of such regularities is the observation of scaling relationships such as the metabolic power law relationship between body size and metabolic rate noted by Kleiber (1932). This type of systematic behavior has been shown to be the consequence of the global optimum configuration of a trait within a range of possibilities with respect to a particular physical law or constraint (e.g., Brown et al., 2004). How much of detailed evolution can we predict from such a constraints-first perspective, and how do we reconcile such a perspective with the detailed processes of the evolution of a particular species?

Here we review constraint-based perspectives on evolution, and show how they are nested within the broader framework of evolutionary biology. We discuss contexts under which certain physical constraints are dominant and/or independent of other constraints, thus producing scaling relationships across diverse species. In particular, we focus on the ultimate limits of particular categories of organisms as prime examples of where physical constraints dominate. We define a limit as the point where the optimal performance of a physiological function or morphological trait is not effective enough to allow an organism to survive. These limits set a minimum or maximum allowable body size. Such limits are known for microbes, arthropods, vascular plants, and mammals, each of which we will later discuss as detailed examples. These limits illustrate how the constraints perspective on evolution is useful, not only for predicting regular trends within a category of organisms (such as allometric scaling), but also for predicting higher-order features such as the size limits of a body plan or a transition to an alternate body plan that allows for expansion into bigger or smaller body sizes.

Understanding or predicting such limits gives us insight into macroevolutionary processes, including major evolutionary transitions (e.g., DeLong et al., 2010; Kempes et al., 2016), and is the first step in building a more detailed perspective on how physical constraints shape microevolution. In addition, another reason to focus on these constraints is as a test of theories for scaling relationships. If a particular theory proposes that a dominant constraint predicts a particular scaling relationship, then it should also predict at what scales that constraint becomes asymptotically limiting to organism physiology and architecture. That is, the scaling theory should also predict the minimal and maximal sizes for organisms that share a body plan.

2. EVOLUTION, PHYSICAL CONSTRAINTS, AND THE BODY PLAN

One could think of evolution from the perspective of overlaying multiple physical constraints (e.g., constraints arising from immutable physical laws such as gravitational force). This could be done from the perspective of evolutionary history in which life sequentially encounters new constraints with increasing complexity or body size, or from the perspective of distinct physical constraints that each lead to scaling relationships, all of which apply to an organism simultaneously. In this latter case the overall physiology of an organism can be seen as the overlay and interaction of multiple constraints and associated scaling relationships (**Figure 1**). This combination can lead to more complex evolutionary optimizations if many constraints are equally consequential, as will be discussed formally below.

Studying evolution using the constraints perspective is further complicated by the fact that, although a specific feature of an organism is constrained by a number of physical laws that may scale differently with size, the selection pressure on that feature is ultimately based on how the interaction of many such interrelated features affects the fitness of the entire organism. The way that traits affect the fitness of an organism depends on the physical environment in which the organism must function and its ecological interactions with other organisms, both of which can change over a life span. Thus, the organism is the product of a history of adaptation to particular physical constraints and ecological conditions, as well as of the evolutionary constraints of its structural components and physiological machinery. Indeed, it should be noted that the constraints that affect organism performance represent a subset of the overall evolutionary process. The full picture of evolution is one in which genes are mapped into a phenotype, that phenotype defines the performance of an organism, and performance ultimately becomes fitness via many interactions with a particular ecological context where factors such as predation, likelihood of reaching reproductive maturity, resource availability, parental nurturing, and niche construction all play important and complicated roles (**Figure 2**). Classic and well-developed models of trait evolution typically consider the heritability, covariation, and rate of change in traits to assess how traits affect fitness and are genetically connected (e.g., see Lynch et al., 1998 for a broad review and Lande (1979) for an allometric application). This traditional perspective has been successful in predicting a wide variety of evolutionary regularities and in uncovering genetic correlations. The overall dynamics of trait evolution in traditional evolutionary models (such as the Price equation) can, in principle, be partitioned into the contributions from each of the processes described in **Figure 1** (Queller, 2017).

Our focus in this paper is mainly on one such component, the mechanistic determination of performance from the set of physical constraints and organism traits (phenotype), without consideration of how those traits are genetically determined

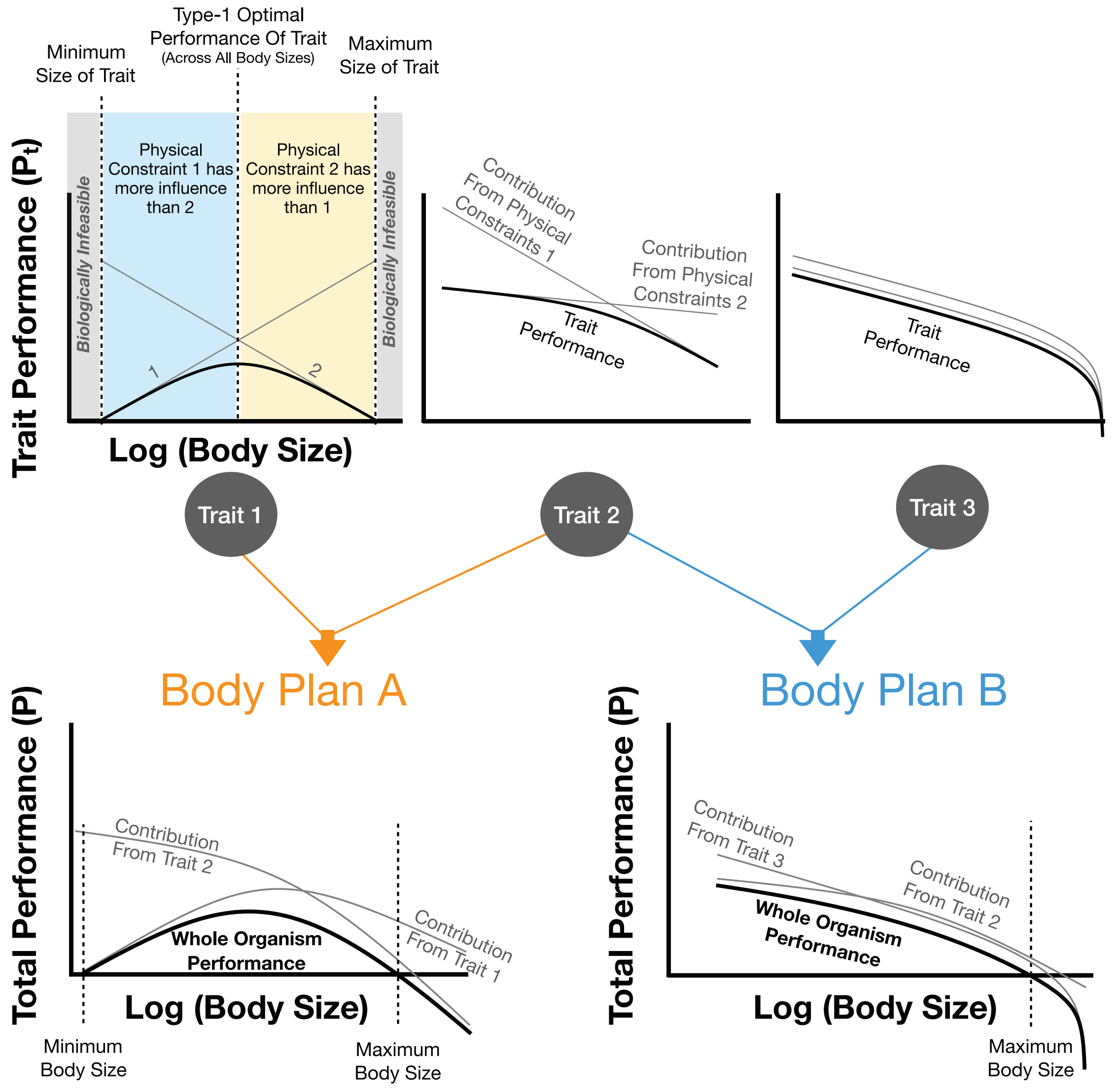

FIGURE 1 | The impact of physical constraints on trait performance and body plan performance. Each trait is the sum of the performance costs, P_t, from individual physical effects. It is assumed that each physical effect curve and the overall summed trait performance are all optimized. For trait 1 it can be seen that the optimal trait performance has a maximum value at intermediate body sizes representing the best performance across all individuals of this body plan (an example of a type-2 optimum in **Figure 3**). Trait 1 also illustrates a minimum and maximum body size for this trait, both of which are the point at which the cost of the trait would equal total metabolism. This figure also shows how combinations of traits combine to form overall body plans which in turn may illustrate a type-2 optimum (see Body Plan A) along with minimum and maximum body sizes where the cost of the overall body plan exceeds total metabolism. It should be noted that this figure is representative, and real organisms would combine an arbitrary number of traits with a wide variety of performance-curve shapes. In many cases one or two traits could dictate the total value of P.

(including correlations between gene effects), which processes influence inheritance, or how the performance fully interacts with the complicated set of ecological constraints described above. We show that physical constraints can be used to determine the intrinsic growth rate of an individual, which is a major component of fitness. Furthermore, we consider cases in which particular constraints become asymptotically challenging so that performance of an organism goes to zero, thereby dominating fitness and predicting the ultimate limits of a body plan, independent of other ecological considerations.

In considering these examples throughout the paper we suggest that the constraints perspective could eventually be integrated into a broader framework incorporating the underlying genetics, ecological considerations, and population structure in order to determine overall fitness and evolutionary dynamics (**Figure 2**). For example, the connection between traits, physical constraints, and fitness could be nested within adaptive dynamics models (e.g., Abrams, 2001; McGill and Brown, 2007), which are aimed at determining evolutionary stable strategies of complex trait combinations within a population (e.g., see Falster and Westoby,

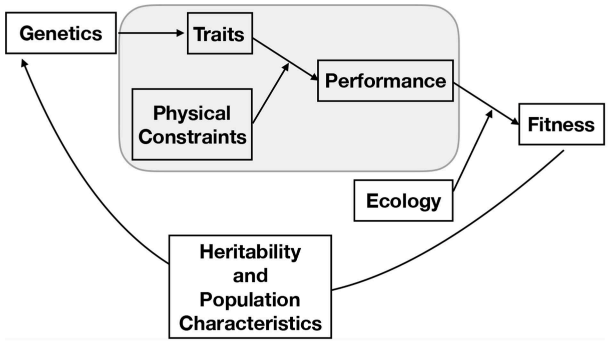

FIGURE 2 | A conceptual representation of the full process of evolution, where the gray box represents the main focus of this paper. From this perspective, genes produce a phenotype, that phenotype defines the performance of an organism given a set of physical constraints, performance becomes fitness through the many features of an ecological context, and the population of genetics evolves given this fitness and the nature of the population, mechanisms of heredity, and mutation. It should be noted that the connection between traits and physical constraints may become the dominant component of fitness in particular contexts. For example, we illustrate here that in many cases the ultimate limit of a particular body plan occurs when one physical constraint becomes asymptotically challenging taking fitness to zero.

2003; Falster et al., 2016 for considerations of plant traits). We also discuss the contexts in which the physical optimizations can be performed without an explicit treatment of the evolutionary dynamics, and why such optimizations can be, and have been, successful in predicting allometric scaling relationships and ultimate limits.

2.1. Abstract Formalism of Constraints and Fitness

With the complications and caveats listed above in mind, we provide a simple formalism for evolution in the context of physical constraints. Below we connect this formalism to the aspects of fitness that can be directly calculated, specifically, the growth rate of an individual. There are a wide variety of models for evolutionary dynamics which typically connect the rate of change in the abundance of a gene or specific genome to its fitness given specific assumptions about inheritance and mutation (e.g., Lynch et al., 1998; Nowak, 2006; Frank, 2011a,b, 2012a,b,c; Queller, 2017). All of these frameworks rest on the ability to quantify the fitness, f_j of each genotype and/or phenotype j in the population, and in each case we can connect a particular model to constraints so long as we can specify the physical determinants of fitness. A classic example of an earlier attempt to connect physical constraints and fitness comes from McNeil Alexander, where he formalized the evolution of safety factors using the equation $\phi(s) = l(s)F + U(s)$, where $\phi(s)$ is the overall cost of a trait given a safety factor s, F is the cost of failure, $l(s)$ is the probability of failure, and $U(s)$ is the cost of growing, using, and maintaining a trait as a function of the safety factor (Alexander, 1996). From this perspective, trait evolution is the minimization of this total cost where an increasing safety factor typically decreases the likelihood of failure but increases the cost of production, use, and maintenance. Our approach is to further generalize this concept and connect it to fitness, rather than just safety factors, by defining the interconnection between all organism traits and physical constraints. Take t_t to be the contribution of a particular trait to overall fitness, then

$$\begin{bmatrix} t_1 \\ t_2 \\ \vdots \\ t_T \end{bmatrix} = \begin{bmatrix} g_{1,1} & g_{1,2} & \cdots & g_{1,P} \\ g_{2,1} & g_{2,2} & \cdots & g_{2,P} \\ \vdots & \vdots & \ddots & \vdots \\ g_{T,1} & g_{T,2} & \cdots & g_{T,P} \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \\ \vdots \\ p_P \end{bmatrix} + \begin{bmatrix} e_{1,1} & e_{1,2} & \cdots & e_{1,P} \\ e_{2,1} & e_{2,2} & \cdots & e_{2,P} \\ \vdots & \vdots & \ddots & \vdots \\ e_{T,1} & e_{T,2} & \cdots & e_{T,P} \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \\ \vdots \\ p_P \end{bmatrix} \tag{1}$$

or

$$\vec{t} = \mathbf{g}\vec{p} + \mathbf{e}\vec{p} \tag{2}$$

where p_p is a particular physical constraint, $g_{t,p}$ is the net benefit attributed to a particular trait due to physiology interacting with a physical constraint, and $\mathbf{e}\vec{p}$ is the portion of the net benefit that strongly depends on ecological interactions in combination with physical constraints (e.g., predator avoidance given the density of predators; see **Appendix A.1** for a more detailed treatment). The first subscript, t, refers to the trait of interest, and the second, p, to a particular physical constraint. Here lowercase subscripts refer to an arbitrary element of a matrix or vector, such that t_t is an arbitrary element of $\vec{t}$, and uppercase subscripts refer to the last element where P is the length of $\vec{p}$, T is the length of $\vec{t}$, and $\mathbf{g}$ is a $T \times P$ matrix.

It is important to note that this formalism could be setup to address traits at various levels of organization—ranging from detailed considerations of the functional proteins to entire morphological features—depending on the questions of interest. For example, the first column of the matrix $\mathbf{g}$ might be the relationship that describes whether a hollow cylinder will develop a local kink over its length. The second column might be the relationship for how far a cylinder bends, and the third column might be the relationship for the weight of the cylinder. In this same matrix the rows would then describe different traits, so that the first row could be the trait of a leg and the second the trait of a wing. Thus, in this example, $g_{1,1}$ relates to the performance of a leg resisting kinking, and $g_{2,1}$ to the performance of a wing resisting kinking, both in combination with p_1. Similarly, $g_{1,2}$ and $g_{2,2}$ relate to the performance of a leg and wing, respectively, in resisting bending, and $g_{1,3}$ and $g_{2,3}$ relate, respectively, to the performance of the weight of a leg and wing.

In this formalism, performance, as described by $g_{t,p}$, refers to a net consideration of both the cost and return to fitness for a particular trait, where $g_{t,p}$ could be either positive or negative depending on a trait's current form (e.g., the current genotype and phenotype of an organism). Fitness is then defined as

$$f = \sum_{t=1}^{T} t_t. \tag{3}$$

It is important to note a few features of this formalism. First, t_t is meant to represent the lifetime contribution to fitness such that $\mathbf{g}$, $\vec{p}$, and $\mathbf{e}$ should be constructed as lifetime quantities. Second, the main challenge of this formalism is in constructing the matrix **g** and also deciding on the level of granularity with which to describe the traits t. For example, should one consider all properties of a bone together or should one partition a bone into its various sub-traits such as its of cross-sectional shape, material composition, and dimensional ratios? Constructing the lifetime values of **e** is equally challenging given a particular ecological setting. As already emphasized, the focus of this paper is on investigating the consequences of the physical contribution, $\mathbf{g}\vec{p}$, to fitness, ignoring ecological effects, $\mathbf{e}\vec{p}$. However, it should be noted that future efforts that attempt to systematize the variation around scaling relationships will often need to quantify $\mathbf{e}\vec{p}$.

2.2. Dominant Constraints and Scaling Relationships

In light of the complicated dynamics of overlapping physical and evolutionary constraints for organism evolution discussed earlier, it is perhaps surprising that *any* scaling relationships exist relating diverse organisms. For example, one can imagine contexts in which many physiological traits are equally consequential, and organisms with different combinations of traits have equivalent fitness. In other contexts, ecological processes might be more important than physiological effects and might shift unpredictably across body size. In some cases the interrelation of traits (e.g., due to the underlying genetics) might produce very complicated relationships across body sizes that cannot be easily interpreted and would include signals of phylogenetic relatedness. In contrast, scaling relationships for a particular trait highlight that a single constraint (or possibly a small set of constraints) dominates over a wide range of sizes and is consistently optimized, and/or that the optimization of one trait to a particular physical constraint is independent from other traits. In this paper, the term "optimization" here has two interrelated meanings: (1) A type-1 optimum, which is determined for one body size and is the best functionality that can be achieved by a single trait, or set of traits, in organisms with a particular body plan (**Figure 3**). We hold body size constant and optimize across different values of the parameters that determine the performance of that trait, or set of traits. An allometric scaling law is the set of type-1 optima, each performed at a particular body size. (2) A type-2 optimum, which is the best functionality that can be achieved for a particular body plan considering all body sizes. The procedure for finding a type-2 optimum is to first find the type-1 optimum at each body size for a trait or set of traits, and then to find the body size that has the best type-1 optimum. A type-2 optimum represents the body size that outperforms all others. The type-2 optimum would be the best point along the relationship between body size and the type-1 optima. In the case of a power-law for the set of type-1 optima, the type-2 optimum would occur at the smallest or largest size. In other cases, performance may not change with body size (i.e., the type-1 optima are all equivalent across different body sizes for a given measure of performance).

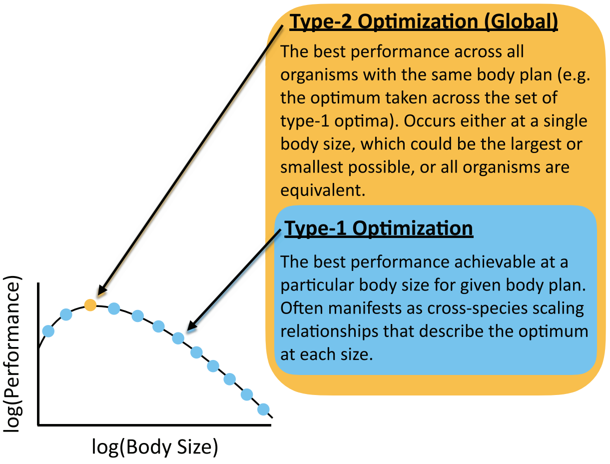

FIGURE 3 | Definition of Type-1 and Type-2 optimizations with reference to a body-size performance curve.

In the context of the formalism that we have introduced above, the layered hierarchy of constraints that define a single species is represented by the relative size of the entries of **g** (e.g., $g_{t,p}$). The existence of scaling laws indicate that a small subset of elements in **g** are significantly larger than all other elements across a range of body sizes for a class of organisms. Formally, this situation can be expressed as

$$\sum_{p,t\in\mathbf{s}} g_{p,t}p_p \approx \sum_{p,t}^{P,T} g_{p,t}p_p \tag{4}$$

where **s** represents a subset of **g**. Ultimate limits would indicate that a subset of entries of **g** become increasingly or asymptotically large and negative at a particular scale and $t_{t\in\mathbf{s}} \rightarrow 0$. In this context the type-1 optimization has vanishingly small fitness at a particular body size and this body size then represents either an upper or lower bound on the possibilities for a particular body plan.

3. APPLYING THE CONSTRAINTS FRAMEWORK

3.1. Explicit Connections to Growth

The preceding formalism is meant to be an abstract representation of the evolution of organism traits with body size under a set of physical constraints considering both physiological and ecological effects. As such we have assumed a linear form for the determination of fitness. More generally, we should expect that the contribution of an individual trait to fitness should follow $t_t = g_t(\vec{t}, \vec{p}, \vec{o})$, where g_t is a function of fitness contribution for a particular trait given the entire set of traits, $\vec{t}$, physical constraints, $\vec{p}$, and other species in the same environment, $\vec{o}$, and may not be representable as a linear combination of the form of Equation (1). This general relationship makes it clear that there may be many traits with fitness contributions that are contingent on the value of other traits. Although the physiological optimization problem may not be of the form of Equation (1), that does not mean that it cannot be fully quantified and solved.

To make such optimizations more explicit we should first concretely connect traits with aspects of fitness. A variety of recent efforts have shown that the growth curves of a variety of organisms can be predicted from a model that considers the budgeting of total metabolic rate, B, into growth and maintenance purposes as $B = E_m \frac{dm}{d\tau} + B_m m$ (where E_m and B_m are the unit costs of synthesizing and maintaining biomass, respectively, and τ is time) (West et al., 2001; Kempes et al., 2012). Typically this model is solved by rearranging for $dm/d\tau$ and recognizing that B scales as a power law with mass. However, the power law of B is the result of an optimization and we can relax this assumption and instead specify this budget in terms of the effect of each individual organism trait

$$\frac{dm}{d\tau}(\tau) = \frac{1}{E_m}\left[\sum_i B_i(\tau) - \sum_i C_i(\tau)\right] \tag{5}$$

where $B_i(\tau)$ (W) is the contribution of trait i to total metabolic power, $C_i(\tau)$ (W) is the metabolic cost of each trait, and E_m (J/g) is the energy to synthesize biomass given all of the current traits. Each of these terms is taken as a function of time as an organism progresses through a life cycle. In connection with our general framework we have that

$$\vec{t}(\tau) = \frac{1}{E_m}(\mathbf{b} - \mathbf{c})\vec{p} \tag{6}$$

and

$$\frac{dm}{d\tau}(\tau) = \sum_i t_i(\tau) \tag{7}$$

where $B_i(\tau) = \sum_j b_{i,j}(\tau) p_j(\tau)$, $C_i(\tau) = \sum_j c_{i,j}(\tau) p_j(\tau)$, and $\mathbf{g} = \mathbf{b} - \mathbf{c}$ in connection with the notation in Equations (1) and (2).

As written, these equations describe the growth rate of an organism along ontogeny. These equations are often converted into population growth rates by first solving Equation (5) for the growth trajectory $m(\tau)$ and then using this to find the time to reach reproductive maturity G (e.g., West et al., 2001; Kempes et al., 2012). From this generation time the specific growth rate of the population is given by $\mu = \ln(k)/G$, where k represents the expected number of offspring produced by an adult and could in principle be a complicated function of the traits themselves and thus parameterize the variety of ecological features discussed earlier (e.g., for bacteria without any mortality $k = 2$). In general, one could combine our framework for the growth rate of an individual with a complicated model for the expected offspring to reach maturity, $\langle k\rangle(\vec{t})$, to form a μ that represents total fitness in an evolutionary model. Here $\langle k\rangle$ is a function of the set of current traits, $\vec{t}$, and all effects from the environment and other species, $\mathbf{e}\vec{p}$. Given a body plan, our goal is to find the set of trait values that maximize the population growth rate for each organism size, or

$$\mu_{opt}(m) = \max\left(\mu(\mathbf{b}, \mathbf{c})|m\right). \tag{8}$$

The optimization procedure should hold adult size fixed (type-1 optimization) and solve for the $\mathbf{b}$ and $\mathbf{c}$ that maximize population growth rate which integrates over the full life-history. As a result, the optimum population growth rate $\mu_{opt}(m)$ is a function of size, and the $\mathbf{b}$ and $\mathbf{c}$ that produce this optimum will also change with body size. In many cases it may be more practical to consider lifetime averages for all of the traits and optimize the average individual growth rate, $\overline{\frac{dm}{d\tau}}$, which is what we consider in our examples. Note that for a fixed k optimizing $\overline{\frac{dm}{d\tau}}$ is equivalent to optimizing μ. Again each of these optimization problems may not have analytically tractable forms, but it should be possible to perform the numerical optimization using a wide variety of known techniques.

3.2. A Single-Cell Example

There are many cases where it is possible to concretely and simply calculate the tradeoffs associate with investment in various traits for an organism along with the optimization of those traits. To illustrate how this procedure is done, along with some of the challenges of operationalizing the conceptual framework outlined in Equation (1), we begin with the simple example of optimizing a single trait. Consider the case of a non-motile spherical bacterium that is acquiring resources via diffusion through the cellular surface followed by active transport via membrane-bound protein structures. The total metabolic energy available to the organism is proportional to the number of molecules, say O_2 during respiration, acquired by the cell. It has been shown that the diffusive uptake rate is given by $4\pi S_\infty Da \frac{ns}{ns+\pi a(1-ns^2/(4a^2))}$ where n is the number of uptake sites, a is the radius of the cell, s is the radius of an uptake site, and S_∞ is the background concentration of the resource in the fluid (e.g., Fiksen et al., 2013). This implies that

$$B_n = Y4\pi S_\infty Da \frac{ns}{ns + \pi a\left(1 - \frac{ns^2}{4a^2}\right)} \tag{9}$$

where Y is the yield coefficient (Joules per mole) for the limiting resource. We also know that each of these transporters requires some amount of energy, β_n to produce, and thus the total cost of n transporters is

$$C_n = \beta_n n. \tag{10}$$

Taken together, these two relationships imply that the average growth rate over a lifetime is given by $\overline{\frac{dm}{d\tau}} = 1/E_m(B_n - C_n)$ and can be rewritten in the form of our framework as

$$\begin{aligned}\overline{\frac{dm}{d\tau}} &= \frac{1}{E_m}\left(\begin{bmatrix} a\frac{ns}{ns+\pi a\left(1-\frac{ns^2}{4a^2}\right)} & 0\end{bmatrix} - \begin{bmatrix}0 & n\end{bmatrix}\right)\begin{bmatrix} Y4\pi S_\infty D \\ \beta_n\end{bmatrix} & (11)\\ &= \frac{1}{E_m}\begin{bmatrix} a\frac{ns}{ns+\pi a\left(1-\frac{ns^2}{4a^2}\right)} & -n\end{bmatrix}\begin{bmatrix} Y4\pi S_\infty D \\ \beta_n\end{bmatrix}. & (12)\end{aligned}$$

where we are considering the trait to be uptake sites and $\vec{p}$ to be composed of terms related to the limits of diffusive uptake and the costs of protein construction. Since we are only considering a single trait, $\overline{\frac{dm}{d\tau}}$ is a simple scalar and already represents the entire sum for fitness. **Figure 4** gives the energetic values of each term along with the resulting growth rate for a single cell of size

$a = 10^{-6}$ (m), and shows that as a cell adds transporters there is an increase in $\overline{\frac{dm}{d\tau}} = B - C$ up to the point where uptake saturates for any additional transporters. In fact this sum gives rise to an optimal number of transporters which can be easily shown to be

$$n_{opt} = \frac{8\pi a^2 \left(\beta_n^{-1/2} \left(sYDS_\infty\right)^{1/2} - 1/2\right)}{s\left(4a - \pi s\right)} \tag{13}$$

It can be seen in **Figure 4B** that for a cell of $a = 10^{-6}$ m this optimal value occurs before the entire cell is covered in transporters. For a cell of this size the optimal solution is achievable. However, this may not be possible for all cell sizes. **Figure 4C** gives the scaling of n_{opt} with cell size (type-1 optima) and shows that there is a size, $a = 1.14 \times 10^{-6}$ (m), at which the total surface area is entirely covered in transporters. This represents a minimum cell size at which the optimal solution is feasible; any smaller cells would have fewer than the optimal number of transporters. In this example, the type-2 optimum for the number of transporters occurs at the largest possible cell size.

We could allow for smaller cells to have suboptimal performance by, for example, keeping a fixed fraction of the surface area covered in transporters. However, these suboptimal cells would run into another limitation, where the total surface area becomes less than the area of a single transporter. The point where the cell surface area is equal to the area of a single transporter is given by

$$4\pi a^2 = s \tag{14}$$

and occurs when $a = 1.95 \times 10^{-9}$ (m). There are other limitations facing the cell that we have not considered. For example, its entire surface area cannot be covered in transporters both for structural reasons and because other functions must be imbedded in the membrane (e.g., the machinery for ATP synthesis).

In general, this single trait optimization could be interacting with a variety of other traits. For example, we have only considered the requirement that uptake meets the costs of the transporters themselves, and in this scenario it is not the return on investment of a transporter that ultimately limits the cell. For all cell sizes we can determine the number of transporters beyond which uptake exceeds the cost of producing those transporters (until surface area limits at the small end). However, this analysis does not consider the internal metabolic requirements of the cell, where the volume to total surface area ratio is scaling proportional to a and we would expect the transporters, even if they cover the entire surface area, to be increasingly unable to support larger cells. These other limitations could be added to Equation (12) by, in the simplest case, adding a cost term proportional to overall volume. Consequently,

$$\overline{\frac{d\vec{m}}{d\tau}} = \frac{1}{E_m}\left(\begin{bmatrix} a\frac{ns}{ns+\pi a\left(1-\frac{ns^2}{4a^2}\right)} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} - \begin{bmatrix} 0 & n & 0 \\ 0 & 0 & a^3 \end{bmatrix}\right)\begin{bmatrix} Y4\pi S_\infty D \\ \beta_n \\ \frac{4}{3}\pi\beta_v \end{bmatrix} \tag{15}$$

$$= \frac{1}{E_m}\begin{bmatrix} a\frac{ns}{ns+\pi a\left(1-\frac{ns^2}{4a^2}\right)} & -n & 0 \\ 0 & 0 & -a^3 \end{bmatrix}\begin{bmatrix} Y4\pi S_\infty D \\ \beta_n \\ \frac{4}{3}\pi\beta_v \end{bmatrix}. \tag{16}$$

where β_v is the unit cost per volume of creating and maintaining an existing unit of biomass over a lifetime (see Kempes et al., 2016, 2017 for a more in depth accounting of cellular composition and the costs that would form β_v). In this example the first row represents the trait of uptake while the second row represents the trait of cytoplasmic volume.

This addition does not change the value of n_{opt}, but will shift the overall growth rate. In this case the added cost is negligible for small cell sizes but eventually becomes the dominant cost for large cells and sets an upper bound on cell size at $a = 2.67 \times 10^{-6}$ (m) (**Figure 4D**). This upper bound occurs because the cost of the cellular volume eventually outpaces uptake and growth goes to zero. It should be noted that in this example we have not considered the physiological and metabolic functions within the cellular volume that interact with the uptake of resources to provide the metabolic power available to the cell. Such considerations would add interconnections between the first and second rows (e.g., how the cellular volume produces energy given the uptake rate), adjust the structure of $\vec{p}$, and would require a more complicated optimization of $\overline{\frac{dm}{d\tau}}$. Similarly, we could add a consideration of the tradeoffs between two traits, say the investment in the number of transporters and investment in chemotaxis (see **Appendix A.2**). In this case the two traits, swimming velocity and the number of uptake sites, are fundamentally interconnected and must be co-optimized to maximize $\overline{\frac{dm}{d\tau}}$. However, the point is that ultimately we are trying to optimize the linear combination that makes up $\overline{\frac{dm}{d\tau}}$ even if individual terms in that sum are complicated and interrelated functions, which should at least be numerically achievable.

This single-cell case study demonstrates how our general framework can be applied to a specific context and explicitly illustrates the three main features that we are interested in, those being:

1. The change in optimal performance across many different sizes (e.g., the maximum growth rate per unit mass increases for larger cells **Figure 4D**).
2. The size at which optimal performance becomes impossible (e.g., the optimal number of transporters exceeds the total surface area of the cell **Figure 4C**).
3. The ultimate limit of size where any functionality is impossible (e.g., a single transporter covers the entire surface area of the cell Equation 14).

3.3. Independent Trait Optimization

The framework that we have proposed gives a general perspective for the co-optimization of physiological constraints, appearance of scaling relationships, and prediction of ultimate constraints. However, constructing the complete set of physiological traits and their interactions with physical constraints (the complete $\mathbf{g} = \mathbf{b} - \mathbf{c}$ and $\vec{p}$) is a daunting task and an important area of future effort. Yet it is important to note that within our general framework there can be traits that are unrelated to other traits. In such a case optimizing a trait's contribution to fitness can be done in isolation. Since $\overline{\frac{dm}{d\tau}}$ is a linear sum, optimizing one trait increases a portion of overall fitness so long as this trait is

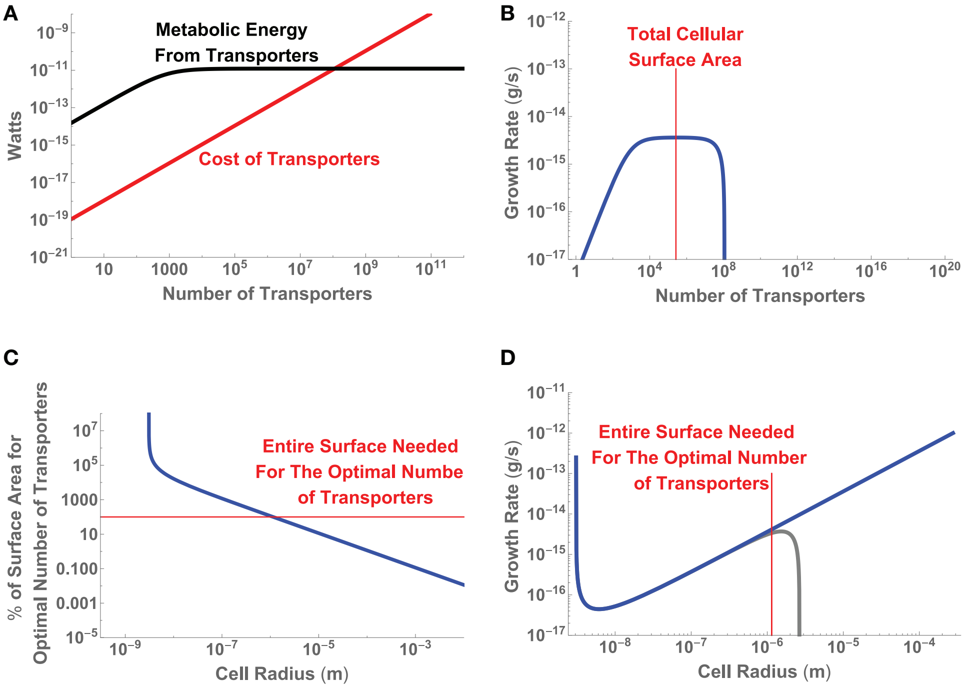

FIGURE 4 | (A) The relative energetic uptake and cost of transporters for a cell of size $a = 10^{-6}$ (m), along with **(B)** the inferred growth rate of that cell. **(C)** The percentage of cellular surface area devoted to n_{opt}, the optimal number transporters from Equation (13), as a function of cell size. **(D)** The inferred growth rate given the optimal number of transporters as a function of cell size. The blue curve considers only the cost of the transporters in the optimization, while the gray curve includes the cost of the cellular volume.

not connected to other traits and thus does not have competing consequences in the overall sum. It should also be noted that a trait can be effectively independent of all other traits if the contribution it makes to one $\frac{\overline{dm_i}}{d\tau} = (B_i - C_i)/E_m$ is much larger than its influence on all other $\frac{\overline{dm_j}}{d\tau} = (B_j - C_j)/E_m$ for $j \neq i$. In general, if all of the traits are independent we have that

$$\max\left(\frac{\overline{dm}}{d\tau}\right) = \max\sum_i \frac{\overline{dm_i}}{d\tau} = \sum_i \max\left(\frac{\overline{dm_i}}{d\tau}\right) \tag{17}$$

implying that each trait can be optimized individually. If we have a mix of independent traits and traits with complicated interdependencies, then we have that

$$\max\left(\frac{\overline{dm}}{d\tau}\right) = \max\sum \frac{\overline{dm_i}}{d\tau} = \sum_j \max\left(\frac{\overline{dm_j}}{d\tau}\right) + \max\sum_k \frac{\overline{dm_k}}{d\tau} \tag{18}$$

where j represents all of the traits that are effectively independent of other traits (and can be individually optimized), and k the set of traits which contain interdependencies. It should be noted that sums like $\sum_k \frac{\overline{dm_k}}{d\tau}$ amount to summing and combining rows in Equation A4 (see **Appendix**), which then form new "effective traits."

These representations make it clear that if enough trait independence exists, then single trait optimizations will accurately predict the observed scaling of a trait with body size. This helps explain past successes in deriving and predicting allometric relationships by focusing on a few dominant constraints and performing type-1 optimizations (e.g., West et al., 1997, 1999).

3.4. Simplified Metrics of Performance and Ultimate Limits

In light of the formalism above we can see why single-trait optimizations often predict allometric relationships and much past attention has already been given to these optimizations and scaling relationships. One of our primary interests here is to use these concepts to predict ultimate limitations, one of the main types of higher-order behavior that we can extract from a constraints-based perspective of evolution. These limits are important because they predict the range of body sizes achievable for a given body plan. We are also interested in how organism performance shifts across this range of body sizes as this informs aspects of selection.

In order to make these ideas more explicit we introduce several systematic metrics that capture the essence of our earlier framework but focus on a reduced set of traits and allow us to predict ultimate limits for particular categories of organisms. We introduce two types of common biological currency for assessing performance and for understanding the ultimate limits on a particular body plan, both of which were employed in our single-cell example in section 3.2.

For the ultimate limits of a particular body plan we are interested in the size where growth ceases ($dm/d\tau = 0$ in Equation 5), which is realized when the costs of all of the traits are equal to their metabolic return: $\sum_i B_i = \sum_i C_i$. In this context, a natural metric for performance is the ratio of costs to metabolic return, $\sum_i C_i / \sum_i B_i$. It is also natural to set the highest value of performance, P, to unity, and define $P = 1 - \sum_i C_i / \sum_i B_i$. If we are interested in considering the constraints imposed by a single trait, then we can simplify this metric to

$$P(m) = 1 - \frac{C_f(m)}{B(m)} \tag{19}$$

where $C_f(m)$ is the cost of a particular trait, $B(m)$ is the total metabolic rate of an organism ($\sum_i B_i$), and where we have made the dependence on organism mass, m, explicit for the metric and subcomponents. This metric will either determine when one trait would be limiting, even if other traits impose more serious limits on organisms, or will define the ultimate limit in the case where C_f is the most dominant constraint (e.g., $C_f \gg \sum_{i \neq f} C_i$). It should be noted that this equation could be parameterized in terms of other measures of organism size such as volume rather than mass.

It should also be noted that an evolutionary optimization to particular physical constraints at each scale may lead to a scaling in both $B(m)$ and $C_f(m)$, implying that $1 - P(m)$ scales allometrically. If $C_f(m)$ scales in the same way as $B(m)$, then $1 - P(m)$ will be a constant implying scale-independent performance. If $C_f(m)$ and $B(m)$ each scale as a power law with body size, but with different exponents, then $1 - P(m)$ will be defined by a positive or negative scaling exponent indicating decreasing or increasing performance, respectively, as body size increases (larger P indicates greater performance). In connection with our earlier and more general framework, the point at which $P(m^*) = 0$ corresponds to $f_i \rightarrow 0$ and represents the point where the type-1 optimum is infeasible. At this point m^* is either the maximum of minimum size for organisms with a particular body plan.

It is not always straightforward to calculate the energy consumption of a particular organismal trait $C_f(m)$, nor is this always the most relevant indication of a limit as features can fundamentally limit an organism without consuming much metabolic power. For example, the construction and maintenance of particular arteries is insubstantial compared to overall metabolic rate, but what does matter for arteries is the likelihood of rupture under expected forces, or the likelihood of blockage under the normal range of physiological conditions. While the metabolic cost of rupture could be converted into energetic terms (e.g., pumping energy becomes infinite once the vessel is no longer connected) it is often more meaningful and practical to simply recognize that a rupture causes death, and to calculate the requirements of rupture avoidance. These are direct physical limits, and are topics with rich histories in the biophysical literature (e.g., Currey, 1970; McMahon, 1973; McMahon and Kronauer, 1976; Wainwright et al., 1976; Peters, 1986; Berg, 1993; Alexander, 1996; Calder, 1996; West et al., 1999; Gere, 2003; Niklas and Spatz, 2004, 2006; Vogel, 2004; Niklas, 2007; Niklas and Hammond, 2013). Such constraints often manifest in the dimensional and morphological requirements of particular organism features, such as the ratios of thickness to surface area and volume or of lengths to radii. Instead of $P(m)$ a more useful dimensionless metric is to consider is $M(m)$, which is the ratio of the minimal requirements of the size of a feature, $S_f(m)$, compared with maximum allowable size $S(m)$,

$$M(m) = 1 - \frac{S_f(m)}{S(m)}. \tag{20}$$

More specifically, $S_f(m)$ is the size of a trait, such as a leg, that is required to work at all in performing a defined function (e.g., not breaking under the typical forces experienced over an organism's lifetime). $S(m)$ is the space allowable for that trait given other constraints of the physiology and geometry of the organism. For example, if the cross-section of the leg is completely filled by the skeleton, then this represents an extreme upper-bound as there would be no space for muscles. More realistically, we can define the space allowable for the skeleton based on the space needed to accommodate the muscles that operate the leg, which are defined by the force required to move the leg, all of which leads to a smaller value for $S(m)$ than the entire volume of the leg.

It is thus clear that $M(m)$ allows for choices in the dimensions of $S_f(m)$ and $S(m)$, which could be volumes or linear dimensions, and where $S(m)$ can be chosen at the feature or organism scale. As mentioned above for $P(m)$, when $S(m)$ is the volume of the entire organism, then $M(m^*)$ represents the extreme upper bound to an organism's size, which often gives us intuition about which constraints are most limiting for specific categories of organisms.

We apply these metrics to several examples for insects, bacteria, vascular plants, and mammals, as classes of organisms with extensive biophysical predictions for scaling relationships and well-developed perspectives on the ultimate limits of particular biophysical processes. Our goal is to understand how physical constraints have shaped the ultimate limits for particular classes of organisms. Within each class we take as a given the known body plan and do not consider how this architecture evolved, which is an interesting area for future research. Within each example our focus is on the point where type-1 optima become infeasible. In the context of the metrics that we have developed, for an upper bound on a particular body plan this is defined either as $M(m_{max}) = 0$, or $P(m_{max}) = 0$, and for a lower bound we are looking for $M(m_{min}) = 0$, or $P(m_{min}) = 0$. We will also discuss when there is a well-defined optimum body size for a class of organisms between the limiting sizes (e.g., a type-2 optimum), as for example at the large end of mammals (Yeakel et al., 2018). As mentioned above, in some cases P or M is more appropriate for highlighting limits. For bacteria, we are able to show that P and M occur at similar scales for particular features and the energy and dimensional requirements are interconnected. In arthropods we primarily rely on M in connection with the limits of exoskeletons. In vascular plants and mammals we rely on both P and M as metrics.

4. EXAMPLES WITHIN GROUPS OF ORGANISMS

4.1. Insect Biomechanics and the Interplay of Different Physical Constraints

Insect appendages provide an example of how the structure of a trait is phylogenetically constrained, and how the performance of different functions by that trait is determined by physical laws. A critical phylogenetic constraint on insects is that the body is surrounded by an exoskeleton. Therefore, all organs and muscles must operate inside a container of fixed dimensions. Exoskeletons are scratched and punctured as animals move around in natural habitats and interact with other organisms, unlike endoskeletons that are protected from such surface damage by the surrounding soft tissues. Furthermore, insects must shed their exoskeleton (molt) in order to grow to larger size. Another phylogenetic constraint that limits the mechanical performance of insects is that the exoskeleton is composed of chitin fibers in a protein matrix.

Insect appendages illustrate how the dimensions of a structure (in this case an appendage is the trait) can affect different aspects of mechanical performance (each of which is a column in Equation 1). The motions of and forces exerted by jointed appendages of insects (e.g., legs, wings, mouthparts, antennae, each being a row in Equation 1) can be analyzed by treating these structures as lever systems (Alexander, 2003). Appendages that are short are better at exerting large forces on the environment (e.g., for crushing prey or digging) for a given muscle force. In contrast, appendages that are long are better at rapid motions (e.g., running) for a given rate of muscle shortening. If we consider the exoskeleton of a stiff segment of an insect leg as a hollow, circular cylinder (**Figure 5A**), we can examine the consequences of changes in the cylinder's dimensions on other aspects of mechanical performance using standard beam theory (e.g., Currey, 1970), as described in biomechanics and engineering textbooks (e.g., Wainwright et al., 1976; Gere, 2003; Vogel, 2004). Some examples of how different aspects of leg performance depend on body and leg dimensions are given in **Table A2** (Appendix). The cost to produce and move the exoskeleton depends on its volume. However, the ability of the leg's exoskeleton to resist deformation (**Figures 5B,C**) and breakage also depend in different ways on its length (L) as well as its radius (R) and the radius (r) of the space inside the exoskeleton. A hollow exoskeleton can also fail by undergoing local buckling (kinking like a bent soda straw, **Figure 5D**), which can damage the tissue inside the exoskeleton. The critical local stress (σ_{Lcrit}) to cause a kink not only depends on the dimensions of a hollow cylinder (**Table A2** in Appendix), but is much lower if the surface is scratched, as exoskeletons are prone to be.

The mechanical properties of the material composing the exoskeleton of an insect appendage also constrain its performance. For example, resistance to bending, bowing, and kinking by the exoskeleton of an appendage depends on the stiffness (elastic modulus, E) of the material (**Table A2** in Appendix). Whether a stress (force per cross-sectional area of material bearing a load) in the exoskeleton will cause breakage depends on the strength (breaking stress, σ_{brk}) of that material. These mechanical properties of insect exoskeleton are determined by the amount and orientation of the chitin fibers, the degree of cross-linking (tanning) and of hydration of the protein matrix, and the relative thickness of the heavily-tanned outer layer (exocuticle) and the less-tanned inner layer (endocuticle) (e.g., Wigglesworth, 1948; Wainwright et al., 1976; Parle et al., 2017).

The radius (r) of the space within the exoskeleton limits the force production and shortening of the muscles it contains, and thus can limit the ability of the appendage to perform various functions. The force that a muscle can produce depends on its cross-sectional area normal to the long axis of the muscle fibers. Because the r of the exoskeleton constrains muscle cross-sectional area, r limits the maximum force that can be exerted by a muscle; r also limits how much a contracting muscle can bulge radially, thereby limiting the distance that the muscle can shorten. The force exerted by a contracting muscle is a complex function of its change in length (Rassier et al., 1999; Nishikawa et al., 2018), so by limiting muscle shortening, r also affects force production. These constraints are mitigated in insects because most of their muscles are pennate, with fibers that are oriented at an angle to the muscle's line of action (**Figure 5E**). Thus, a pennate muscle can exert higher forces, but also shortens less ($\Delta_{Lmuscle}$, **Figure 5E**) than a parallel-fibered muscle (Vogel, 2003). These constraints of the exoskeleton on muscle force and shortening can limit the performance of activities (e.g., running, pushing) that affect the competitive success and survival of insects in the environment, and can thus determine $S_f(m)$ of the trait (leg) in Equation (20).

Using these physical rules described above, the type-1 optimal morphology for a leg can be determined for an insect of a given size if the aspects of leg performance (e.g., rapid running, forceful digging) can be identified that are most likely to affect the insect's fitness in its ecological setting. By examining the type-1 optima for the legs of insects across a range of body sizes, the type-2 optimum can be determined, and the physical limits on body size can be explored.

The effect of body size on different aspects of appendage performance are illustrated in **Table A2** (Appendix). In this example, we assume for simplicity that the exoskeleton of a leg is a hollow circular cylinder, that the insect grows isometrically, and that the mechanical properties of the exoskeleton material and the behavior of the muscle (force production per area normal to muscle fibers, and maximum shortening velocity) do not change with size. The consequences to leg mechanics of an isometric doubling of body dimensions illustrate how different functions vary with size. The load that a leg must bear (F) and the cost of producing and moving the exoskeleton increase 8-fold, while the force produced by a muscle only increases 4-fold. Relative to the F's that must be resisted, the maximum force exerted by the appendage per muscle force exerted is only half of that at the smaller size. Resistance to bending and to breaking while bearing body weight or locomoting are also reduced by 50% if size doubles, whereas resistance to bowing is reduced by 75% and to kinking by 87.5%. This suggests that leg failure by kinking may determine the maximum allowable size, $S(m)$ in Equation (20), for a given insect body plan. This $S(m)$ can be increased

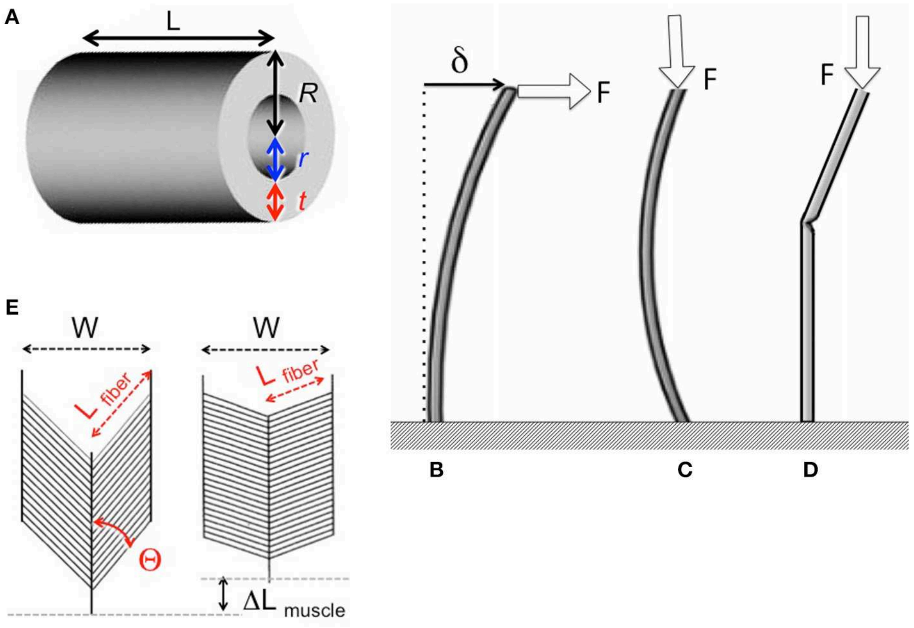

FIGURE 5 | (A) Dimensions of a hollow cylindrical exoskeletal element: L = length, R = outer radius, r = inner radius, t = wall thickness. **(B)** Diagram of the deflection (δ) of the free end of an exoskeletal element being bent like a cantilever by a force (F) acting laterally on the end of the of the cantilever. **(C)** Elastic Euler buckling of an exoskeletal element acting like a column bearing an axial load (F). **(D)** Local buckling (kinking) of an exoskeletal element acting like a column bearing an axial load (F). **(E)** Diagram of a pennate muscle when relaxed (left) and after the muscle fibers have contracted (right): θ = angle between muscle fibers and the line of action of the muscle, L_{fiber} = length of the muscle fibers, W = width of the muscle, ΔL_{muscle} = distance muscle shortened when fibers contracted. Muscle bulging is not in the radial direction, and a greater number of shorter muscle fibers can fit into the volume of a pennate muscle than into a parallel-fibered muscle of the same size. However, the component of the force produced by the contracting fibers (F_{fibers}) in a pennate muscle that acts parallel to the line of action of the muscle (F_{muscle}) depends on the angle (θ) of the fibers ($F_{muscle} = F_{fibers} \cos\theta$), so F_{muscle} decreases as the muscle shortens and θ becomes more oblique (Azizi et al., 2008).

by selection for allometric growth (e.g., smaller r relative to R) or for increased stiffness and strength of the material composing the exoskeleton.

Insects have to molt their exoskeleton to grow. The mechanical properties of the exoskeleton material change during this process (e.g., Wigglesworth, 1948; Parle et al., 2017). After the old exoskeleton is shed, the new exoskeleton is thinner (lower t) and less cross-linked (lower E and σ_{brk}) than the older shed exoskeleton. With time after molting, the new exoskeletal material becomes more cross-linked and the thickness of the wall of the exoskeleton increases as more endocuticle is secreted. Therefore, resistance to bending and resistance to failure (by breaking or kinking) are lower right after molting. This poor mechanical performance of the soft, thin exoskeleton right after molting might be the factor that limits the overall body size of insects. Furthermore, insects are more vulnerable to predators right after a molt because locomotory appendages may buckle and bend too easily for effective escape maneuvers, and the exoskeleton may be easier to break or puncture by the predator. Therefore, while vulnerability to the predators in the environment of an insect may set the $S_f(m)$ required for survival, molting reduces $S(m)$ and the performance metric $M(m)$.

In addition to the biomechanical constraints of an exoskelton and molting, other limits to the size of insects have been proposed and debated, including the supply of oxygen via the tracheal system, the power requirements for flight, and the effect of size on maneuverability of flying insects after bird and bat predators evolved (e.g., Kaiser et al., 2007; Kirkton, 2007; Okajima, 2008; Harrison et al., 2010; Clapham and Karr, 2012). We suggest that the approach illustrated in **Figure 1** would be a fruitful way to evaluate the body sizes at which the various proposed mechanisms are likely to be most important and to identify which are most likely to constrain the size of insects.

While the exoskeleton of an insect appendage provides an example of a trait that does a number of physical tasks whose performance varies with size (as illustrated in the top row of **Figure 1**), the physiology of bacteria provide an example of how several traits together affect the performance of an organism as a function of its size (bottom row of **Figure 1**).

4.2. Bacterial Physiology and Ultimate Limits

Prokaryotes represent the oldest and morphologically simplest forms of self-reproducing life, although their metabolic and genetic diversity far exceeds the eukaryotes. We can consider their morphology, in a first approximation, as a membrane with embedded protein complexes enclosing a solution of DNA, carbohydrates, RNA, and proteins of various complexity. We are interested in how this physiology and architecture inform the evolutionary possibilities for bacteria in terms of the physics of both internal physiology and interaction with an external environment.

Considering interactions with the external environment, bacteria live in a world characterized by a low Reynolds number. That is, in conditions where viscous forces dominate over inertial forces. Within this low-Reynolds world one of the most common forms of motility is run/tumble chemotaxis, in which bacteria swim linearly for a variable time and then perform a random reorientation before swimming again. This form of motility is an asymmetric process, and allows for both a random-walk search and gradient following through biasing the random walk by dynamically adjusting the probability of tumbling (Berg, 1993). Within the context of motility it is also possible to calculate our metric P. It has been shown that the minimum power required for run-tumble chemotaxis is approximately given by

$$B_{mot} = \frac{kTD}{a^2} + 3a^3 \tag{21}$$

where k is the Boltzmann constant, T is absolute temperature, a is again the cell radius, and D is the molecular diffusivity (Mitchell, 2002). This result follows from considerations of the rotational and translational diffusion of cells, combined with the required distance a cell must move to detect a change in the concentration of a resource (Purcell, 1977; Mitchell, 1991, 2002; Berg, 1993). This cost must be a fraction of the total metabolic power, which in bacteria is known to scale with cell volume, V, according to

$$B = y_0 V^{\alpha} \tag{22}$$

with $\alpha = 1.76$ and $y_0 = 3.76 \times 10^{14} (\mathrm{W\ m}^{-\alpha})$ (DeLong et al., 2010). The ultimate limit of motility is the point where its costs equal the total available metabolic energy, which can be found by setting Equation (22) equal to Equation (21) and substituting $a = (3V/4\pi)^{1/3}$. Taking $D = 5.19 \times 10^{-10}$ ($\mathrm{m}^2\ \mathrm{s}^{-1}$) and $T = 298.15\ K$, the numerical solution for this lower limit is $V_{min} = 2.72 \times 10^{-21}$ (m^3). This limit can also be defined in terms of our metric for performance, $P = 1 - B_{mot}/B$, where **Figure 6A** illustrates that for most of the range of bacterial sizes $P \approx 1$ and B_{mot} is a negligible fraction of total metabolic power. This calculation also illustrates that before reaching the ultimate limit described above ($P = 0$ at V_{min}), P decreases sharply (**Figure 6A**), thus defining an intermediate size at which motility costs become radically more expensive, and may become selected against. This precipitous decrease occurs as B_{mot} increases sharply, due to the increasing significance of overcoming molecular diffusion.

Turning to the internal constraints of the bacterial body plan, recent efforts have shown that there are significant changes in the physiological processes and composition of bacterial cells across the range of cell size (Kempes et al., 2016). Many of these follow power-law relationships with asymptotic behavior that arise at distinct scales. It has been shown that the partitioning of total metabolic power between growth and maintenance purposes predicts the scaling of population growth rate across bacteria, including a lower-bound on cell size where maintenance metabolism exceeds total metabolic rate. This lower bound on size also agrees with considerations of physical space, where the combined scaling of all cellular macromolecules entirely fills the cell at a similar size and further constrains this lower bound. The total macromolecular pool is dominated by DNA and protein content at the small end of bacteria due to a sub-linear scaling of both. This same scaling causes these two macromolecules to be diluted in concentration with increasing bacterial cell volume. However, other theory has shown that the requirements for ribosomes can be predicted to scale roughly linearly with cell volume over a large range of cell volumes, up to a point where the requirement for ribosomes increases rapidly and exceeds total cell volume, thus setting an upper limit of bacterial cell sizes. This limiting behavior occurs because there is finite-volume singularity—at a distinct cell volume an infinite number of ribosomes are required—caused by the point where the cell division time is faster than the time it takes a ribosome to replicate itself.

These set of space limitations can be easily translated into our metric M by taking S to be the total volume of a cell and S_f to be the known scaling of protein, DNA, and ribosome volumes (see **Appendix A.3** for the details of each of these scaling relationships). For example, given the total protein volume in the cell, V_p, the morphological metric is defined by $M_p = 1 - V_p/V$. **Figure 6B** provides the overlay of the performance curves for each of the three components, illustrating that at the small end of cell size proteins and DNA cause M to go to zero, and at the large end ribosomes have the same effect. Similar to our considerations of motility, we observe that over a wide range of intermediate cell sizes $M \approx 1$ for considerations of the proteins and ribosomes, up to, for example, the point where the previously described "ribosome catastrophe" occurs.

4.3. Vascular Organisms

4.3.1. Trees

Terrestrial vascular plants are defined by a body plan that couples photosynthesis in leaves suspended in the atmosphere to nutrient and water acquisition from the soil. As such, the vascular system—which transports sugars from the leaves and nutrients from the roots to the rest of the tissues—is of central importance. Trees are also characterized by the need to effectively fill the entire canopy space in order to collect as much sunlight as possible and consequently to be as tall as possible to outcompete other plants for sunlight and avoid being shaded. These various constraints have led to a variety of perspectives for understanding plant allometry together with an extensive set of theories, calculations, and measurements.

Given the competitive importance of tree height, there have been many proposed mechanisms for determining its ultimate limit. These mechanisms have focused on both mechanical and hydraulic constraints. The mechanical constraints were originally addressed quantitatively by McMahon (McMahon, 1973; McMahon and Kronauer, 1976) who pointed out that the maximum possible height of a tree was set by the buckling limit (small lateral displacements cause failure) of its trunk, and this could be calculated using a formula first derived by Greenhilll from the classic bending moment equations for solid materials:

$$h_{max} = C \left(\frac{E}{\rho} \right)^{1/3} d^{2/3} \tag{23}$$

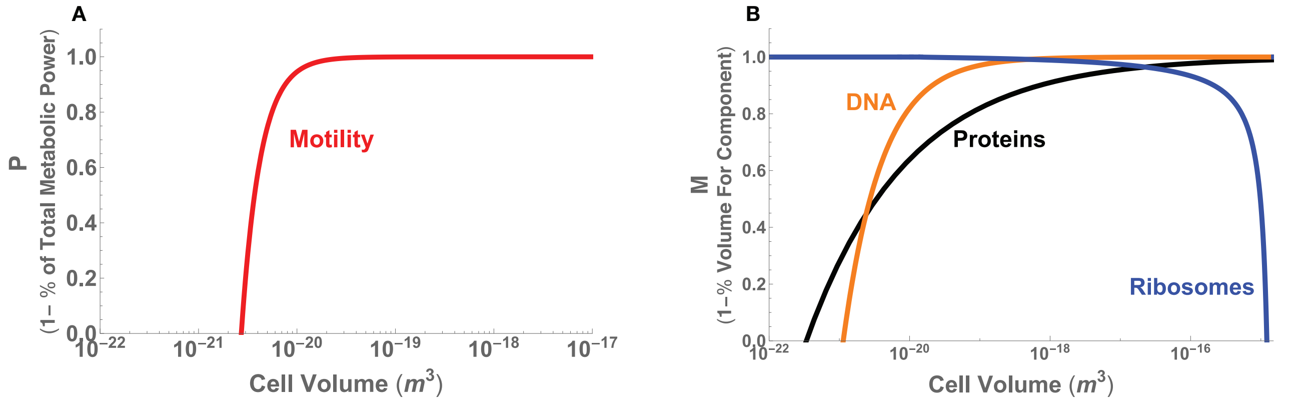

FIGURE 6 | (A) The minimal power requirements for motility in bacteria as a function of total cell volume and given as the metric P, which is 1 minus the percentage of total metabolic power. **(B)** The volume requirements for DNA, protein, and ribosomes in bacteria as a function of cell volume and given as the metric $M = 1 - V_C/V$, where V_C is the volume of each component.

where ρ (g m^{-3}) is the density of wood, E (g m^{-1} s^{-2}) is the elastic modulus, d (m) is the trunk diameter, and $C = 0.792$ (s$^{2/3}$ m$^{-1/3}$) when the force is distributed over the entire column (e.g., this model considers a single beam with a uniform radius over its height) (McMahon, 1973; McMahon and Kronauer, 1976). This relationship has the same scaling between height and radius, $h \propto d^{2/3}$, as that for trees across all sizes and is in good agreement with data. However, using measured value of E (g m^{-1} s^{-2}) $\approx 1.05 \times 10^5$ (McMahon, 1973; McMahon and Kronauer, 1976), this relationship leads to a critical height which is roughly 3 to 4 times larger than the observed scaling. Trees exist in a region of parameter space far below this upper bound and these mechanical constraints don't seem to limit the tallest possible trees at any size nor set an upper bound on the ultimate tallest possible vascular plant.

If no other physical constraints predicted this same scaling, then one could argue that trees have simply evolved to be a fixed safety factor from the mechanical limit and, provided that they conform to the $h \propto d^{2/3}$ scaling of height to diameter, there is no upper bound on tree height. However, arguments related to hydraulic limits and space-filling predict the same scaling relationship between height and radius as that from the mechanical constraints and, at the same time, set an upper bound on the tallest possible trees as discussed below (West et al., 1999; Niklas and Spatz, 2004, 2006; Niklas, 2007). Nevertheless, the buckling arguments are important in the broader space of all evolutionary possibilities. For example, these constraints could be relevant to vascular plants with alternate body plans, alternate evolutionary trajectories, or at earlier stages of vascular plant evolution compared with those that seem to conform to hydraulic limits.

There are several approaches to considering the hydraulic limits to tree height centered either on the requirements for conductive tissue or the feasibility of pumping fluid over the length of a single vascular tube. For the conductive tissues arguments there are two main perspectives. The first uses the observations and/or assumptions that (i) annual growth scales with leaf mass, (ii) annual growth scales with total plant mass to the 3/4 power, (iii) the flux of water through the leaves must match the flux through the conductive tissue so that leaf mass scales with the hydraulically functional cross-section, and (iv) the mass of the roots scales isometrically with the mass of the stems which in turn is proportional to the cross-sectional area times length. From these assumptions it can be shown that tree height, h, is related to diameter, d, as

$$h = k_1 d^{2/3} - k_2 \tag{24}$$

where a good fit to data is obtained with $k_1 = 34.64$ (m$^{1/3}$) and $k_2 = 0.475$ (m) (Niklas and Spatz, 2004, 2006; Niklas, 2007). For large trees this relationship parallels the Euler-Greenhill predictions, but also does a better job of capturing observed curvature in the data away from a power law at the small end of trees. While this relationship does not predict an upper bound on tree size it does predict a lower bound of $d_{min} = (k_2/k_1)^{3/2} = 0.0016(m)$ for $h = 0$, which is roughly the diameter of petioles (the segment of the plant that attaches leaves to the stem) suggesting that this smallest size agrees with the minimal vascular plant of a single leaf and stem. This limit can also be understood in terms of our metric M, where we can define $M\left(h\right) = 1 - d_{petiole}/d$. Here M is defined in terms of h as the overall measure of size, d is the required diameter, and its ratio to the petiole diameter, $d_{petiole}$, defines performance. Given the above relationships, $M\left(h\right) = 1 - \frac{k_1^{3/2} d_{petiole}}{(h+k_2)^{3/2}}$, which quickly approximates unity for $h > 0$. The above derivation of the equation for h shows that this lower bound is due to differences in the observed scaling of the leaf mass and trunk diameter with total plant mass, representing underlying hydraulic constraints. However, since this relationship relies on several empirical scaling relationships it is difficult to see exactly which physical constraints are being optimized.

The second perspective on hydraulic limits uses the assumptions of (i) canopy space filling, (ii) mechanical stability, and (iii) hydraulic resistance minimization within a fractal-like architecture to optimize the overall plant body plan (West et al.,

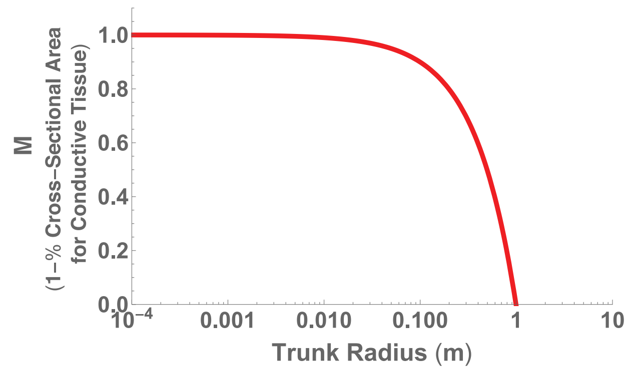

FIGURE 7 | The fraction of trunk cross sectional area required for conductive tissue as a function of trunk radius and represented as the metric *M*.

1999). The optimization is performed in terms of the various ratios of the vessel and branch sizes and a detailed calculation of the total resistance of the entire vascular network. Similar to the perspective above, the results predict that $h \propto d^{2/3}$, but also predict a maximum height where the entire trunk becomes conductive tissue. This can be seen by choosing $S_f = A_{ct} = \pi n_N a_N^2 r_N^{-7/3} r^{7/3}$, the total area of connective tissue in the trunk, where n_N is the total number of vascular tubes in a petiole, a_N is the radius of a petiole tube, and r_N is the radius of the entire petiole. If we take S to be the total area of the trunk, then we have that $M = 1 - A_{ct}/\left(\pi r^2\right)$ or

$$M = 1 - n_N a_N^2 r_N^{-7/3} r^{1/3} \tag{25}$$

which is plotted in **Figure 7** using the typical values of $n_N = 200$, $a_N = 1.0 \times 10^{-5}$ (m), and $r_N = 0.5 \times 10^{-3}$ (m) (West et al., 1999).

The maximum trunk radius and associated height is given by $M = 0$, which corresponds to $A_{ct}/\left(\pi r^2\right) = 1$,

$$r_{max} = n_N^{-3} a_N^{-6} r_N^7, \tag{26}$$

and

$$h_{max} = l_N n_N^{-2} a_N^{-4} r_N^4 (1 - n^{-1/3})^{-1} \tag{27}$$

where $n \approx 2$ is the number of branches at each generation and $l_N \approx 0.04$ (m) is the length of a petiole. Given the values listed above, these relationships predict $r_{max} \approx 1(m)$ and $h_{max} \approx 100(m)$ in good agreement with record trees. This approach thus predicts the fundamental limit on vascular plants, in addition to the cross-species scaling, by co-optimizing the dominant physical constraints of both hydraulic resistance and mechanical stability. This is a case where the accurate prediction of the limit corroborates that the dominant constraints of the system have been identified.

4.3.2. Mammals

Similar to vascular plants, a theory of fractal vascular networks regulating metabolic supply has been developed for the metabolic scaling of mammals and broadly predicts a variety of observed allometries and scaling relationships (West et al., 1997). This theory considers transport to be the rate-limiting step for metabolism and that optimizing the transport network by minimizing its cost predicts overall metabolic rate and a host of downstream effects. This theory is impressive not only in its ability to predict interspecific scaling relationships across a wide range of body sizes, but also for its ability to predict asymptotic limits to the mammalian body plan. This is possible because the theory provides a detailed description of the coupling of the body plan to the underlying physical and geometric constraints. For example, for very small mammals, the pulsatile waves emanating from the heart are unable to reach the capillaries because of the dissipation of energy due to hydraulic resistance along the path of the branching vascular tubes. Previous work has shown that in all mammalian vascular systems there is a point in the network where pulsatile flow becomes laminar flow, and this cross over occurs at $r_c^2/l_c \approx 8\nu/\rho c_0$, where r_c and l_c are the critical radius and length of a vascular segment at the branching generation in the network where the cross over occurs, $\nu = 4$ (g m^{-1} s^{-1}) is the viscosity of blood, $\rho = 10^6$ (g m^{-3}) is the density of blood, and $c_0 = (Ew/2\rho r_c)^{1/2} = 6$ (m s^{-1}), where E is the modulus of elasticity of the vessel with a wall of thickness w (West et al., 2002). As mammals become smaller the branching generation at which this cross-over occurs decreases and eventually becomes the aorta itself, and corresponding to a dramatic decrease in efficiency due to an overdamped vascular system. From this perspective, we can define the metric M in terms of the system damping by taking $M = 1 - \left(r_0^2/l_0\right)/\left(r_c^2/l_c\right)$, where r_0 and l_0 are the dimensions of the initial segment (aorta) of the vascular network. The lower limit of mammal size is given by $r_0^2/l_0 = r_c^2/l_c$. Noting that the aorta allometry of $r_0 = a_1 m^{3/8}$ and $l_0 = a_2 m^{1/4}$, where a_1 and a_2 are allometric normalization constants, the preceding equality is equivalent to $\frac{a_1^2 m^{3/4}}{a_2 m^{1/4}} = \frac{8\nu}{\rho c_0}$, which defines the minimum size as $m_{min} = \left(\frac{8\nu a_2}{\rho c_0 a_1^2}\right)^2$. Given that a mammal of $m = 10,000$ (g) has the vessel dimensions of $r_0 = 0.0075$ (m) and $l_0 = 0.2$ (m), then $a_2/a_1^2 = 355,556$ (g m^{-2}), and the minimum mammal size is predicted to be $m_{min} \approx 3.6$ (g) (West et al., 2002). This lower limit is close to observed sizes of several species of shrew which are the smallest mammals. Similar to many of the other analyses above, this example illustrates that even when a type-1 physiological optimization is performed at every body size, there will still be a body size where even optimal performance represents an impossible physiology.

5. DISCUSSION

We propose that it will eventually be possible to enhance our understanding of the complex selective factors involved in evolution by analyzing the overlay and co-optimization of physical constraints for a particular body plan at a given size scale. Here we have suggested that the first step is to understand the limits of a body plan that is optimized to a particular set of dominant constraints. Moving forward we need theories that establish a hierarchy of physical constraints for identified types of body plans of organisms. We also need theories that can predict the interconnected temporal evolution of physiology, body size, and physical constraints.

Implicit in a full theory of evolution under constraints is the need to identify and integrate the ecological constraints that organisms face in addition to the phylogenetic and physical constraints discussed above. Ecological constraints emerge, for instance, from interactions among the set of coexisting organisms through predator-prey dynamics, competition for overlapping resources, and via more complicated symbioses, coevolution, and niche construction. For example, recent theoretical work on the population dynamics of foragers using a single shared resource has connected basic allometric physiology with the dynamics of resource consumption, as well as consumer starvation, growth, and reproduction (Yeakel et al., 2018). This work shows that Damuth's law—the observation that the population density (Individuals m^{-2}) of a species is proportional to body mass to the $-3/4$ power (Damuth, 1987)—is predicted as the natural steady state of the complicated dynamics of reproduction, starvation, and mortality, where the rate of each of these processes is based on the underlying energetics of allometric metabolism. More importantly for our considerations here, this model of interacting foragers also shows that larger mammals should outcompete smaller mammals up to a maximum mammalian size. This maximum mammalian size occurs at a point where the population consumes all available resources and perishes. This limit is supported by data, where the predicted maximum size of a mammal is roughly 3.5 times larger than the largest observed terrestrial mammals, which are in the fossil record (Yeakel et al., 2018). In contrast to our analyses here of single-organism physiology, this maximum size limit emerges as an ecological-scale interaction between an entire population and available resources.

Environments may also introduce additional constraints through the expected variation of conditions. For example, one would expect selection on breaking resistance (e.g., **Table A2** in Appendix) in trees to depend not on typical wind speeds, but rather on the probability of unusually high wind speeds over the lifetime of a tree. Earlier we introduced the formalism presented by McNeil Alexander in which the evolution of safety factors is dictated by the equation $\phi(s) = l(s)F + U(s)$ (Alexander, 1996). As noted earlier, trees seem to have a safety factor of roughly four which has also been directly verified in detailed analyses of bending under wind stress. A broader literature on the economy of wood density has quantified the variation of safety factor in response to a variety of competing evolutionary considerations including life-history strategies for resource acquisition (e.g., quick growth for sunlight), adult stature, wood production cost, and wood resistance to decay and herbivores. The effect of decay and herbivory on the strength of the wood in trees also varies during the lifetime of a tree. The formalism of Alexander can thus be expanded to encapsulate all of these limits, which goes beyond our focus on the physiology and biomechanics of individual organisms. An important challenge of such an approach is defining $l(s)$ and $U(s)$ under a complex set of species interactions and distributions that occur under various changing environmental conditions and stresses. In our formalism, the challenge becomes defining the matrix $\mathbf{g}$ in such a way that each entry represents an entire life-cycle value that integrates the probabilities of various environmental and competitive effects. Future efforts should focus on developing new, and expanding existing, compendia of constraints for particular body plans and integrating these into detailed evolutionary models. If this is done, it may be possible to make ever more specific evolutionary and ecological predictions from physical constraints.

Finally, since the framework presented here only requires the specification of organism structure and physical constraints, it is amenable to general considerations of life for origins of life and astrobiology research.

AUTHOR CONTRIBUTIONS

CK: conceived of the project. CK, GW, and MK: developed mathematical formalisms, conducted analyses, and wrote the paper.

ACKNOWLEDGMENTS

CK and GW thank CAF Canada for generously supporting this work. We also are also grateful for grants from the National Aeronautics Space Administration, 80NSSC18K1140 (supporting CK), the National Science Foundation, IOS-1655318 (to MK) and PHY1838420 (to GW), and from the Gene & Clare Thaw Charitable Trust (to GW). We also thank the 4 reviewers of this paper whose feedback greatly improved the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

A. APPENDIX

A.1. Connection to Ecological Constraints

The full treatment of fitness considers how all traits are constrained by the interaction of both physiological and ecological factors with physical constraints. Ecological effects consist of all of the features affecting the effective number of offspring such as predation, likelihood of diseases, or starvation risk. From this perspective fitness can be written as

$$\begin{bmatrix} t_1 \\ t_2 \\ \vdots \\ t_T \end{bmatrix} = \begin{bmatrix} g_{1,1} & g_{1,2} & \dots & g_{1,P} \\ g_{2,1} & g_{2,2} & \dots & g_{2,P} \\ \vdots & \vdots & \ddots & \vdots \\ g_{T,1} & g_{T,2} & \dots & g_{T,P} \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \\ \vdots \\ p_P \end{bmatrix} + \begin{bmatrix} e_{1,1} & e_{1,2} & \dots & e_{1,P} \\ e_{2,1} & e_{2,2} & \dots & e_{2,P} \\ \vdots & \vdots & \ddots & \vdots \\ e_{T,1} & e_{T,2} & \dots & e_{T,P} \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \\ \vdots \\ p_P \end{bmatrix} \tag{A1}$$

which can be rewritten as

$$\vec{t} = \mathbf{g}\vec{p} + \mathbf{e}\vec{p} \tag{A2}$$

where p_p is a particular physical constraint, $g_{t,p}$ is a term representing the net benefit attributed to a particular trait due an organism's physiology interacting with a physical constraint, and $e_{t,p}$ is the net benefit attributed to a particular trait due to an ecological interaction with a physical constraint. It should be noted that $e_{t,p}$ will generally depend on complicated ecological quantities such as the density of predators. In all of these cases, lowercase subscripts refer to to an arbitrary element of a matrix or vector, such that t_t is an arbitrary element of $\vec{t}$, and uppercase subscripts refer to the last element where P is the length of $\vec{p}$, T is the length of $\vec{t}$, and $\mathbf{g}$ is a $T \times P$ matrix.

It should be noted that the sort of linear separation performed in Equation (A2) is only possible if there are not traits that can only be described in terms of functions of both $g_{t,p}$ and $e_{t,p}$ together. In addition, an implicit assumption in optimizing a particular trait according to maximizing only $\sum_{p=1}^{P} g_{t,p}p_p$ is that the physiological effects on fitness are larger than the ecological effects, or that $\sum_{p=1}^{P} g_{t,p}p_p \gg \sum_{p=1}^{P} e_{t,p}p_p$, for a particular trait t. It could be the case that for some other trait, t', the fitness effects are determined by $\sum_{p=1}^{P} e_{t',p}p_p \gg \sum_{p=1}^{P} g_{t',p}p_p$, in which case the ecological optimization would be most relevant for understanding the trait and overall fitness. In some cases, considering both terms may be required for understanding a trait. Here we mostly focus on traits where the physiological effects dominate.

TABLE A1 | Definitions for the physical constraints framework.

	Definition	Notes
t_t	Contribution of a particular trait to overall fitness	$\vec{t} = g\vec{p}$
p_p	A particular physical constraint	
$g_{t,p}$	Net benefit attributed to a particular trait due to a physical constraint	
f	Fitness	$= \sum_{t=1}^{T} t_t$
B_i	Contribution of trait i to overall metabolic energy	
C_i	Metabolic cost of trait i	
$\frac{dm}{d\tau}$	Growth rate of an individual	$= \left[\sum_i B_i(\tau) - \sum_i C_i(\tau)\right]/E_m$
$P(m)$	Metabolic metric of performance	$= 1 - C_f(m)/B(m)$ where $C_f(m)$ is the cost of a particular trait, $B(m)$ is the total metabolic rate of an organism
$M(m)$	Morphological metric of performance	$= 1 - S_f(m)/S(m)$, where $S_f(m)$ is the size of a trait, and $S(m)$ is the maximum allowable size

A.2. Detailed Example of Trait Co-optimization

The ultimate goal of the general framework is to consider the tradeoffs amongst multiple traits in optimizing growth rate. To illustrate this procedure we can analyze the tradeoffs between two traits within our single-cell example. Consider the investment in the number of transporters and investment in chemotaxis and competing and complementary ways to increase total resource uptake to the cell. In such a situation, we would have that

$$\frac{\vec{dm}}{d\tau} = \frac{1}{E_m}\left(\begin{bmatrix} g\left(a, v_s, n, S_\infty, D\right)\frac{ns}{ns+\pi a} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} - \begin{bmatrix} 0 & n & 0 & 0 \\ 0 & 0 & a^3 & 0 \\ 0 & 0 & 0 & av_s^2 \end{bmatrix}\right)\begin{bmatrix} 4\pi S_\infty Da \\ \beta_n \\ \frac{4}{3}\pi\beta_v \\ 6\pi\eta \end{bmatrix} \tag{A3}$$

$$= \frac{1}{E_m}\begin{bmatrix} g\left(a, v_s, n, S_\infty, D\right)\frac{ns}{ns+\pi a} & -n & 0 & 0 \\ 0 & 0 & -a^3 & 0 \\ 0 & 0 & 0 & -av_s^2 \end{bmatrix} \begin{bmatrix} 4\pi S_\infty Da \\ \beta_n \\ \frac{4}{3}\pi\beta_v \\ 6\pi\eta \end{bmatrix}. \tag{A4}$$

where $g\left(a, v_s, n, S_\infty, D\right)$ is a complicated function parameterizing diffusion through a boundary layer and the characteristics of the fluid. The power output required for swimming at a particular speed is given by $6\pi\eta av_s^2$ where v_s is the swimming speed and η is the viscosity of the fluid. In this example the first row represents the trait of uptake through transporters and the third row the trait of swimming. However, since these two traits must be co-optimized given the mutual dependence on swimming speed, v_s, we could combine them into a single row representing the combined trait of resource uptake:

$$\frac{\vec{dm}}{d\tau} = \frac{1}{E_m}\begin{bmatrix} g\left(a, v_s, n, S_\infty, D\right)\frac{ns}{ns+\pi a} & -n & 0 & -av_s^2 \\ 0 & 0 & -a^3 & 0 \end{bmatrix}\begin{bmatrix} 4\pi S_\infty Da \\ \beta_n \\ \frac{4}{3}\pi\beta_v \\ 6\pi\eta \end{bmatrix}. \tag{A5}$$

TABLE A2 | Various mechanical features are proportional to body and leg dimensions.

Mechanical feature	Proportionality to body or leg dimensions	Factor by which feature changes if body length doubles	Factor by which weight-bearing performance changes if body length doubles
Force on leg due to body weight, or when landing during locomotion (F)	L_B^3	8	–
Maximum force exerted by a muscle (F_{max})	d^2	4	–
Cost to produce skeleton for leg	$L(R^2 - r^2)$	8	–
Weight of skeleton of leg (and thus cost to move leg)	$L(R^2 - r^2)$	8	–
Force exerted by end of leg when muscle contracts with force F_{max}	L_m/L	4	0.5
Velocity of foot when muscle shortens at V_{max}	L/L_m	1	–
Resistance to bending (minimize deflection, **Figure 5B**)	$E(R^2 - r^2)/L^3$	2	0.25
Resistance to Euler buckling (maximize force required to cause elastic bowing, **Figure 5C**)	$E(R^2 - r^2)/L^2$	4	0.5
Resistance to local buckling (maximize critical local stress, σ_{Lcrit} required to cause kinking, **Figure 5D**)	$E(R^2 - r^2)/R$	1	0.125
Resistance to breaking (minimize maximum stress, σ_{max} in skeleton)	$(R^2 - r^2)/LR$	4	0.5

*The mechanical performance of the exoskeleton of an insect leg is shown for the simple case of a hollow circular cylinder. The factors by which those mechanical features change if the body of an insect doubles in length are shown in column 3. For simplicity, we assume that growth is isometric, that the mechanical properties of the material of the exoskeleton do not change, and that the muscle properties (physiology, force production per area normal to muscle fibers, and maximum shortening velocity, V_{max}) are the same at both sizes. The factor by which weight-bearing performance changes if body length doubles (column 4) is the ratio of the factor by which the load that the leg has to bear increases (F, row 1) to the factor by which that feature changes. This is only calculated for aspects of performance that affect load-bearing by a leg, either when standing or during locomotion. L_B = length of insect body, d = diameter of muscle perpendicular to axis of muscle fibers, F_{max} = maximum force muscle can produce, and E = elastic modulus (stiffness) and σ_{brk} = breaking stress (strength) of the exoskeleton material. Stress (σ) is force per cross-sectional area of material bearing that force. All other symbols are shown in **Figure 5**.*

The trait of resource uptake could then be optimized independently to find the ideal combinations of n and v_s across a range of cell sizes. The cost of the cellular volume would only matter again in terms of solving for an upper bound on cell size where $dm/d\tau = 0$.

It should be noted that in all of our illustrative examples, the matrices involved can be condensed into a single row where the summation of costs and benefits is simply the dot product of vectors. This scenario would not be the case for more complicated trait optimizations, and, in general, summations of the form of Equation (5) will allow for optimizations where constructing the matrices is not simple or useful.

A.3. Bacterial Composition

Previous efforts have characterized the scaling of the major macromolecular components of bacteria (Kempes et al., 2016), where the volume of the DNA follows

$$V_{DNA} = d_0 V_c^{\beta_D} \tag{A6}$$

where $d_0 = 3.0 \times 10^{-17}$ $(\mathrm{m^3\ DNA} \cdot (\mathrm{m^3\ Cell})^{-\beta_D})$ and $\beta_D = 0.21 \pm 0.03$, while the volume of expressed proteins scales more steeply with cell size following

$$V_p = P_0 V^{\beta_p}, \tag{A7}$$

where $P_0 = 3.42 \times 10^{-7}$ $(\mathrm{m^3\ Protein} \cdot (\mathrm{m^3\ Cell})^{-\beta_p})$, and $\beta_p = 0.70 \pm 0.06$. Taken together with the known scaling of growth rate, defined by $\mu \approx \mu_0 V^{\beta_\mu}$, the volume of expressed proteins determines the required volume of ribosomes which follow

$$V_r \geq \frac{\nu_r P_0 V^{\beta_p} \bar{l}_p}{\bar{\nu}_p \left(\ln(2)\left(\mu_0 V^{\beta_\mu}\right)^{-1} r_r - \bar{l}_r\right)}. \tag{A8}$$

TABLE A3 | Description of parameters for bacteria.

Param.	Definition	Value	Notes
BACTERIA			
S_∞	Background concentration of a resource in a fluid	0.0005 (mol m^{-3})	Value for glucose
n	The number of uptake sites on the cell surface		
a	Radius of the cell (m)		
s	Radius of an uptake site	3.91×10^{-9} (m) (Szenk et al., 2017)	
D	Molecular diffusivity	6.73×10^{-10} (m^2 s^{-1}) (Koch, 1996)	Value for glucose
Y	Yield coefficient for a limiting resource	2.87×10^6 (J mol^{-1}) (Tran and Unden, 1998)	Value for glucose
β_n	Cost to produce one transporter	1.09×10^{-19} (W transporter^{-1}) (Kempes et al., 2017)	Found over a lifetime
β_v	The cost of creating and maintaining an existing unit of biomass over a lifetime	4.09×10^5 (W m^{-3}) (Kempes et al., 2012, 2016, 2017)	
VASCULAR PLANTS			
ρ	Wood density	6.18×10^5 (g m^{-3}) (McMahon, 1973)	
E	Elastic modulus of wood	1.05×10^8 (g m^{-2}) (McMahon, 1973; McMahon and Kronauer, 1976)	
A_{ct}	Area of conductive tissue		
n_N	Number of vascular tubes in a petiole	200 (West et al., 1999)	
a_N	Radius of a petiole tube	1.0×10^{-5} (m) (West et al., 1999)	
r_N	Radius of the entire petiole	$r_N = 0.5 \times 10^{-3}$ (m) (West et al., 1999)	
n	Number of branches at each generation	2 (West et al., 1999)	
l_N	Length of a petiole	0.04 (m) (West et al., 1999)	
MAMMALS			
ν	Viscosity of blood	4 (g m^{-1} s^{-1}) (West et al., 2002)	
ρ	Density of blood	10^6 (g m^{-3}) (West et al., 2002)	

where $\beta_\mu \approx 0.64$, $\mu_0 = 4 \times 10^7$ $(\mathrm{s}^{-1} \cdot \left(\mathrm{m}^3\,\mathrm{Cell}\right)^{-\beta_\mu})$, $v_r = 3.04 \times 10^{-24}$ m^{-3} is the average volume of a ribosome (Zhu et al., 1997; Gabashvili et al., 2000), $\bar{v}_p = 4.24 \times 10^{-26}$ is the average volume of a protein (Neidhardt et al., 1996; Erickson, 2009; Phillips et al., 2012), $\bar{l}_r = 4566$ bp is the average length of a the combined ribosomal protein transcripts (Bremer et al., 1996), and $r_r = 63$ $bp\ s^{-1}$ is the transcript processing rate (Bremer et al., 1996), and $\bar{l}_p = 975$ bp is the average length of a protein transcript (Dill et al., 2011).

A.4. Definitions and Parameter Values

Table A1 provides a list of definitions for the main features of our general framework, **Table A2** provides definitions for insects, and **Table A3** provides parameter definitions and values for bacteria, trees, and mammals.

frontiers
in Ecology and Evolution

REVIEW
published: 13 August 2019
doi: 10.3389/fevo.2019.00293

Scaling and Complexity in Landscape Ecology

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Landscapes and the ecological processes they support are inherently complex systems, in that they have large numbers of heterogeneous components that interact in multiple ways, and exhibit scale dependence, non-linear dynamics, and emergent properties. The emergent properties of landscapes encompass a broad range of processes that influence biodiversity and human environments. These properties, such as hydrologic and biogeochemical cycling, dispersal, evolutionary adaptation of organisms to their environments, and the focus of this article, ecological disturbance regimes (including wildfire), operate at scales that are relevant to human societies. These scales often tend to be the ones at which ecosystem dynamics are most difficult to understand and predict. We identify three intrinsic limitations to progress in landscape ecology, and ecology in general: (1) the problem of coarse-graining, or how to aggregate fine-scale information to larger scales in a statistically unbiased manner; (2) the middle-number problem, which describes systems with elements that are too few and too varied to be amenable to global averaging, but too numerous and varied to be computationally tractable; and (3) non-stationarity, in which modeled relationships or parameter choices are valid in one environment but may not hold when projected onto future environments, such as a warming climate. Modeling processes and interactions at the landscape scale, including future states of biological communities and their interactions with each other and with processes such as landscape fire, requires quantitative metrics and algorithms that minimize error propagation across scales. We illustrate these challenges with examples drawn from the context of landscape ecology and wildfire, and review recent progress and paths to developing scaling laws in landscape ecology, and relatedly, macroecology. We incorporate concepts of compression of state spaces from complexity theory to suggest ways to overcome the problems presented by coarse-graining, the middle-number domain, and non-stationarity.

Keywords: coarse-graining, complex systems, complexity, hierarchical organization, macroecology, middle-number problem, non-stationarity, scaling relationships

OPEN ACCESS

Edited by:
Angelica L. Gonzalez,
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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *06 March 2019*
Accepted: *23 July 2019*
Published: *13 August 2019*

Citation:
Newman EA, Kennedy MC, Falk DA and McKenzie D (2019) Scaling and Complexity in Landscape Ecology. Front. Ecol. Evol. 7:293. doi: 10.3389/fevo.2019.00293

INTRODUCTION

Landscapes and their associated ecosystems are often treated as "complex systems" (Allen and Starr, 1982; Odum, 1983; Schreiber, 1990; Brown et al., 2002; Maurer, 2005; Moritz et al., 2005; Falk et al., 2007; McKenzie and Kennedy, 2011; McKenzie and Perera, 2015; Littell et al., 2018). Landscapes—and the ecological processes they support—share properties with other complex systems in that they contain large numbers of heterogeneous components that interact in multiple ways, exhibit non-linear dynamics, and have emergent properties (hereafter, "**emergence**"). Ecological landscapes have feedbacks and interactions across scales, and show scale dependence, whether they appear to be simple or complex (Wu and David, 2002; **Figure 1**). Indeed, properties such as scale dependence and emergence are not simply features that complex systems share; they are diagnostic attributes of them.

Although "complex" and "complicated" are often used interchangeably in the vernacular, complex systems have a number of important properties that go beyond mere complication. Various definitions for complexity have been proposed in different contexts (Kolmogorov, 1963; Gell-Mann and Lloyd, 1996; Bialek et al., 2001; Ladyman et al., 2013), but in general, more complex systems require more information to describe any given **state** of that system (**Table 1** defines and explains bolded terms). Models of a complex system may also be complex (Kolmogorov, 1963; Edmonds, 2000), or have simple rules generating complexity, as in the case of **fractals**; and model complexity is sometimes used as an overall measure of relative complexity. In these ways, complexity and information theory (Shannon, 1948) are fundamentally linked. Complexity is sometimes associated with the physical **entropy**, rather than **information entropy** of a system (**Figure 2**), and quantitative relationships between complexity and both types of entropy have been proposed (Wolpert, 2013).

As landscape ecology continues to develop as a field, it will be productive to engage the knowledge and terminology that have been developed in complexity science to define avenues of progress. In this paper, we approach landscapes as complex systems, and give examples of phenomena associated with landscape-level complexity that are challenges to defining models that cross scales of patterns and processes. We do not address complexity *per se*, which is itself a subject of much theoretical work (see Gell-Mann and Lloyd, 1996). Instead, we focus on three features of complexity that are intrinsic limitations, or challenges, to progress in landscape ecology. These features are: (1) **coarse-graining**, or how to optimally aggregate fine-scale processes to larger scales in a robust manner that minimizes error (Levitt and Warshel, 1975; Turner et al., 1989; Gorban, 2006); (2) the **middle-number problem**, which affects systems with enough elements to be computationally intractable, but with elements that are too few or too varied to be amenable to global averaging (Weinberg, 1975; O'Neill et al., 1986; Kay and Schneider, 1995; McKenzie et al., 2011a); and (3) **non-stationarity**, which refers to relationships or parameter choices that are valid in one environment in one domain (such as species distribution models), that no longer hold when projected onto other environments (Cooper et al., 2014), such as future scenarios of altered climate (Turco et al., 2018; Yates et al., 2018). Even with expected ongoing improvements in modeling, data collection, and data processing, these limitations are less **tractable** than other types of ecological modeling problems, such as missing data or variables. These limitations therefore represent underlying conceptual challenges in the field of landscape ecology. We describe different conceptual approaches that have been applied to modeling of scaling and complexity for landscapes, review their limitations and potential, and suggest potentially fruitful directions for future research in landscape ecology.

PHENOMENA ASSOCIATED WITH COMPLEX LANDSCAPES

The study of landscapes, disturbance processes and disturbance regimes, and anthropogenic forcing of climate change occupies a domain in **parameter space** in which phenomena and the models that describe them become "complex" (Kolmogorov, 1963; Edmonds, 2000). When a system is described as "complex," it means that observed phenomena are intrinsically difficult to model due to the dependencies or interactions between their parts (which has been referred to as "bottom-up" control on outcomes and system variables) or between a given system and its environment (also known as "top-down" controls on relationships among outcomes and system variables) (Reuter et al., 2010). Complex systems such as landscapes or general ecological systems have characteristics such as non-linearity, scale dependence, and emergence that make physical and ecological phenomena difficult to parse into independent variables, and prevent easy transference across space or time, or to different physical scales (Wiens, 1989; Yates et al., 2018). Simplifying assumptions about complex systems, such as not accounting for basic physical constraints (e.g., mass balance) in food web models, or modeling ecosystems as closed systems will lead to unrealistic results (Loreau and Holt, 2004).

In a complex system, emergent dynamics are not explained completely by simple reducible components, future states of the system may be deterministic and chaotic, or may contain stochastic components, and causal mechanisms are challenging to identify because any given component can act as both a driver and a response due to feedback mechanisms. Furthermore, the issue of prediction in complex systems poses a major challenge, because many future outcomes are possible, and these systems have high sensitivity to initial states of the system. The global climate system is a well-known example of a complex system with these properties. Because outcomes will be sensitive to initial conditions and may not be entirely deterministic, predictions about emergent behavior will never be perfectly accurate, even with increasing amounts of data and better computational resources (e.g., Lorenz, 1963; **Figure 2**). However, despite these limitations, reliable predictions are possible over short time horizons and for well-delimited questions where appropriate empirical data are available.

Landscape ecology, and particularly issues related to wildfire (a major focus of this manuscript), exemplifies many of these properties of complex systems. For example, in landscape fire, we often study the interplay and feedbacks between large-scale, top-down drivers of wildfire, such as climate and human land-use (Gill and Taylor, 2009), and more mechanistic and smaller-scale bottom-up drivers, such as ignitions, fuel patterns, and local topography (Falk et al., 2011; McKenzie et al., 2011b; Parks et al., 2012). Landscape ecology seeks to describe the dynamic relationships between ecological patterns and processes across spatial scales, from plot or forest-stand level to watersheds, from local regions to ecosections, or globally.

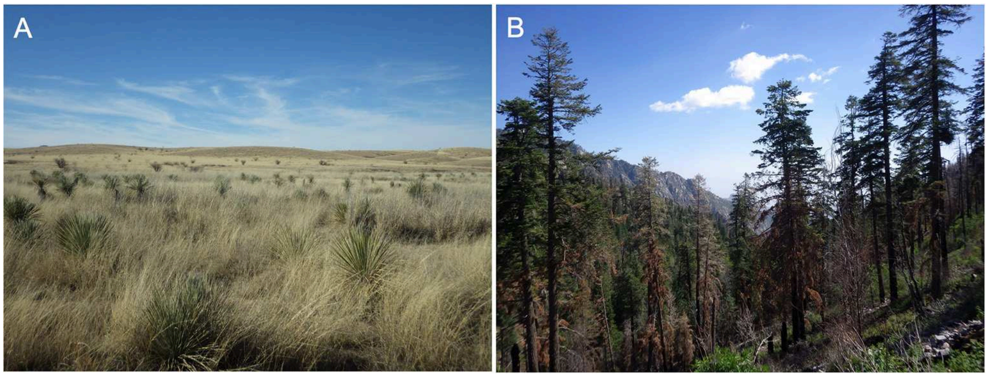

FIGURE 1 | Landscapes vary in complexity. Panel **(A)** shows a southern Arizona grassland at Las Cienegas National Conservation Area, illustrating a landscape with low taxonomic diversity, plant functional trait diversity, and topographic complexity. Panel **(B)** by comparison, has higher complexity, with a clear legacy of disturbance by wildfire, high plant functional diversity and topographic complexity, and more interactions among a higher number of species. Photo from Mount Graham, in the Pinaleño Mountains of Arizona. Ecosystems and ecology are shaped dynamically by bottom-up factors such as local topography, spatial clustering of resources, and stochastic events such as ignitions, as well as top-down processes and controls such as temperature, precipitation, and other climatic factors. Disturbances such as wildfire and insect outbreaks are influenced by these factors and others, including phylogenetic history of organisms and their disturbance adaptations, physical structure and demography of organisms, and landscape history. However, knowing all of this information perfectly is not sufficient to predict fire behavior, initial ignition points, or extent of insect-caused mortality, because the features of emergent phenomena (such as disturbance regimes) are highly sensitive to initial conditions and may not be deterministic. Photo credits: E.A. Newman.

Properties common to all complex systems, including self-organization, non-linearity, feedbacks, and robustness (including lack of central control) are reviewed in Ladyman et al. (2013) and elsewhere (Reuter et al., 2010). In studying the landscape ecology of wildfire, complexity is particularly expressed as emergence (section Emergence), landscape memory (section Landscape Memory), landscape resistance (section Landscape Resistance), and contagion (section Contagion). As a consequence, landscape fire ecologists inevitably confront modeling complexity, and must grapple with these problems through choice of variables, scale, and delimitation of a system that lacks closed boundaries.

Emergence

Emergence refers to new patterns, processes, or structures that appear at higher levels of organization in the observation of phenomena that are not present at lower levels of organization. Emergent phenomena are the products of causal mechanisms at lower levels of organization, but they are expressed primarily in behavior of high-order components. For example, many individual mechanical parts of a watch, when organized correctly, can track time together, but the individual parts cannot do this by themselves. Similarly, the functioning of social insect colonies results from the actions of individual worker insects with different tasks, and vehicle traffic patterns are the emergent result of individual drivers' choices about travel. The property of life in organisms is itself an emergent property of the organization of molecules and biochemical pathways. Emergent processes must be consistent with finer-scale laws and cannot violate them; for example, biological processes have independent dynamics not fully explained by the laws of physics, but they are nonetheless subject to them.

Many phenomena of landscapes result from emergence, including community-level structure and function, disturbance regimes, physiognomy of vegetation (forested landscapes vs. savannas, for example) and patch formation and dynamics (White and Pickett, 1985; Wu and Loucks, 1995; Bormann and Likens, 2012). Landscape patch patterns are often a legacy of many disturbance events (Cuddington, 2011; **Figure 3**). Landscape patches are identifiably distinct areas of any size in the spatial pattern of a landscape, such as the mosaic of burned and unburned areas in a large landscape wildfire. Burn-severity patches are the emergent result of the landscape distribution of fuels and fuel conditions, individual plant susceptibility to heat damage to living tissues, topographic influences on fire spread, fine-scale patterns of wind, and combustion physics at the submeter scale. The size distribution and spatial structure of the post-fire patches are primary drivers of finer-scale landscape-ecological processes such as tree regeneration, which is constrained by seed availability and suitable recruitment environment, and future fire spread, which can either be constrained or accelerated by fuel availability (Collins et al., 2017; Davis et al., 2019). Such outcomes have led to the ideas of *downward causation* (Campbell, 1974), in which processes at lower levels (here regeneration and fire spread) appear to be responding to emergent forcings, and *contextual emergence* (Atmanspacher and beim Graben, 2009), or how contingencies at more complex, higher levels of description provide the "context" for outcomes at lower levels (Flack, 2017).

Landscape Memory

Landscape memory or ecological memory, is a generic term for the legacies of landscape process and pattern, including their longevity and the strength of their influence on current landscape dynamics (Peterson, 2002; Turner, 2005; Johnstone et al., 2016). It also includes concepts of legacy effects of prior disturbances and use of the landscape (Cuddington, 2011). Johnstone et al.

TABLE 1 | Common terms in complexity science, as related to landscape complexity.

Term	Explanation
Coarse-graining	Any method for aggregating finer-scale processes or patterns to larger-scale summaries.
Emergence	New patterns, processes, or structures that appear at higher levels of organization in the observation of phenomena that are not present at lower levels of organization. Emergence of patterns in data is produced by *coarse-graining*.
Fractal	A geometric relationship or mathematical curve that can be characterized by a fractional dimension. Fractals may or may not be strictly self-similar, in which key elements will appear exactly the same when viewed at multiple scales.
Hierarchical organization	A multi-level structure of entities (e.g., ecosystems or landscapes) in which higher-level structures act as constraints on those below them, and lower-level structures act as forcings on those above them.
Information entropy	Information entropy is a way of quantifying how much uncertainty there is in associating with a particular outcome with an underlying probability distribution (Shannon, 1948).
Lacunarity	An algorithmic way of characterizing the spatial configuration of gaps in the dominant components of a spatial pattern (such as asymmetry or size variation of gaps). Lacunarity relies on a box-counting procedure and the results of the analysis are therefore dependent on the scale chosen. Lacunarity analyses that produce power-law type relationships are indicative of power-law (fractal) properties.
Middle-number problem	Any analysis or computation for which the individual elements are too numerous to be treated singly, but too varied to be characterized sufficiently by statistical summaries such as averages.
Non-stationarity	Formally, this is a property of any stochastic process whose moments are different if sampled at different points in the process. More broadly, and as we use it here, it refers to the defining parameters of a process or a quantitative relationship being non-constant over space or time. An example is the coefficients of a regression fit, which may vary with new predictor and response variables.
NP-hard problems	Non-deterministic polynomial time, or NP, problems are those for which the time taken to solve them increases exponentially (i.e., not in polynomial time) with the number of instances. NP problems belong to a complexity class of their own. NP hard problems contain all the computational problems whose difficulty has the lower bound of at least as hard as the hardest problems that are "in NP." An example is the famous "Traveling Salesman" problem, whose computational time increases exponentially with the number of cities visited. NP problems are peculiar, however, in that if a specific solution is proposed, it can be checked for accuracy in polynomial time.
Parameter space	The domain of values in which includes all possible combinations of all variables or parameters in any given mathematical model. This domain can be represented as a multi-dimensional space. Realized values of the parameter space will often be only a subset of the possible combinations available. This concept is distinct from phase space, which describes only the possible initial conditions of the system.
Physical entropy	A statistical measure of the disorder in a physical system. The more likely a physical state is for a given system, the higher the physical entropy associated with that state is. This concept is distinct from information entropy, but shares mathematical similarities.
Self-organization	A process in which spontaneous order arises from a heterogeneous system, in which elements of a system interact in a way that increases their structure or complexity. Self-organization refers to more than just the formation of patterns (and the term may be overused in the ecological literature to characterize patterns). True self-organization requires a repeatable cumulative process; for example, an "auto-catalytic set" of molecules whose repeated interactions build more complex structures (Kauffman, 1986). There are few true cases of self-organization in landscape ecology (McKenzie and Kennedy, 2012), with the possible exception of the formation of termite mounds, fairy circles, and mima mounds (e.g., Griffon et al., 2015).
State	The condition of a system at a particular moment or time, as described by all of the parameters that contain information about that system. The state of a system does not contain information about rates, or about previous states of that system. A snapshot will produce an estimate of a state, whereas at least two measurements are needed for a rate. States of a system can be very difficult to estimate.
Tractable (i.e., computationally tractable)	Informally, tractable problems are those which can be solved. More technically, "computationally tractable" problems are solvable in exponential time, rather that polynomial time. That is, tractable problems are not NP-hard problems. When fine-scale calculations are intractable, *coarse-graining* may sometimes be used to lower the complexity of the problem from NP to not NP.

These terms are used throughout this paper (appearing in ***bold****) and are discussed in more detail here.*

(2016) decompose ecological memory into two forms of legacies: informational, which derives from species life-history traits and adaptive potential; and material, which encompasses physical legacies such as soil and seed banks. In the context of fire regimes, landscape memory can be short-lived and "ephemeral"; or long-lived and "persistent," depending on the frequency and severity of disturbances (van Mantgem et al., 2018). A grassland with frequent fire and rapid regrowth may have a relatively short-term landscape memory for any particular fire event, whereas the legacy of wildfire in a forest with long-lived tree species may persist for multiple centuries (**Figure 3**). McKenzie et al. (2011b) propose a spatio-temporal domain of landscape memory as a function of scalable elements of fire regimes (section Energy and Regulation Across Scales).

In wildland fire, the legacy of individual fire events and the properties of the dominant plant community form a dynamic system in space and time. For example, the behavior of a wildfire (rate of spread, flame length, heat output per unit area and time) is conditioned at each moment of combustion by multiple properties of topography (slope,

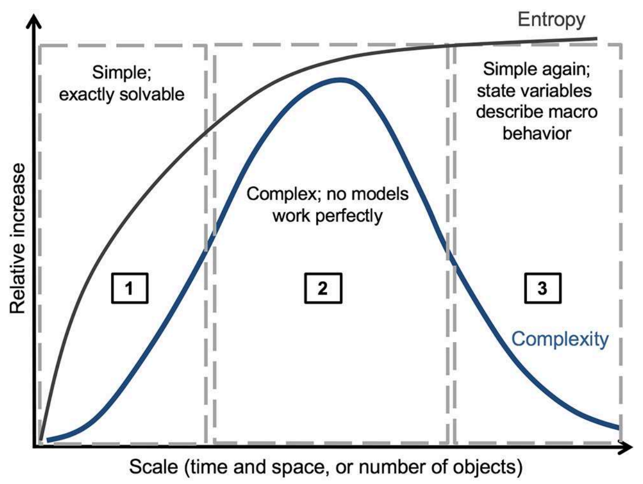

FIGURE 2 | Schematic relationship between entropy and complexity. Entropy increases monotonically with increasing scales of physical systems, whereas complexity increases from (1) the region of fundamental physical models, (2) to the "middle-number domain," but then decreases (3) as large systems are described adequately by aggregate properties. In region (1), models are deterministic and exactly solvable. In region (2), complex behavior of the system is controlled by interacting top-down and bottom-up processes, and models therefore will not provide perfect predictions of data. In region (3), statistics are highly aggregated for large numbers of interacting elements, and general laws emerge (for example, the Ideal Gas Law, the species area relationship in macroecology, or annual wildfire burned area at subcontinental scales).

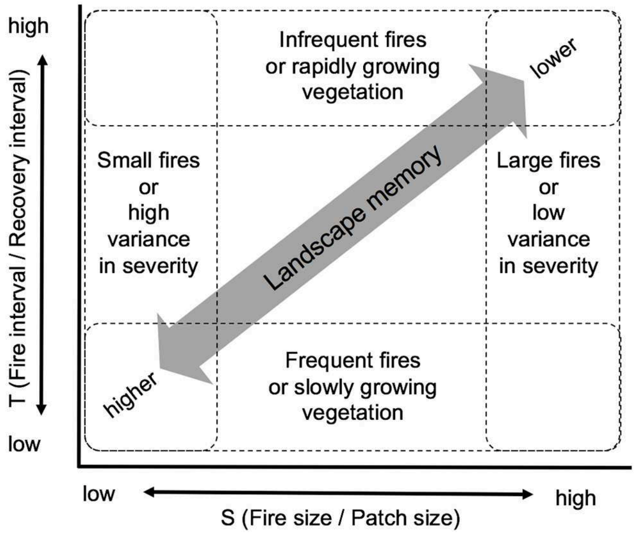

FIGURE 3 | Relationships between landscape memory and scales of time (T) and space (S) of landscape disturbances. The "landscape memory" of a disturbance decreases as the ratio of disturbance interval to recovery interval increases, and the ratio of disturbance size to patch size of the affected landscape increases. Revised, with permission, from McKenzie et al. (2011b).

aspect, topographic position), weather (wind direction, air temperature and humidity, precipitation, ignition sources such as lightning), and vegetation (woody and herbaceous biomass, three-dimensional spatial distribution, water content of live and dead fuels). Fire behavior interacts with species' life-history traits and effects on soils to constrain individual survivorship and mortality, the primary metrics of fire severity (Keeley, 2009). Plant condition and prior fire exposure also influences post-fire mortality (van Mantgem et al., 2013, 2018).

The behavior and effects of wildfire then set the stage for post-fire ecological and hydrologic processes. Soil stability and permeability strongly regulate the speed with which vegetation can become re-established; severely burned hydrophobic soils take longer to become plant-suitable, and some plant guilds may be excluded initially by soil properties alone. The landscape mosaic of burn-severity patches and residual vegetation governs the post-fire trajectory, especially in large ($>10^3$ ha) patches with few or no surviving trees. These areas must be recolonized by dispersing seeds from relict tree islands or adjacent surviving trees, which is a strongly scale-regulated process because the effective seed dispersal radius of many species is 250 m or less, and successful seedling establishment can be limited by the availability of safe sites and suitable climate (Stevens-Rumann and Morgan, 2016; Davis et al., 2019; Law et al., 2019). Recolonization of large high-severity patches can take decades or even centuries, leaving a persistent legacy of plant age classes, forest physiognomy, and species distributions that create the conditions that will regulate the next fire event (Collins et al., 2009, 2017).

Landscape Resistance

Landscape resistance is a spatially structured characteristic of landscapes, quantifying resistance to movement with respect to a particular agent or process. Typically, this concept is applied to animal movement (Keeley et al., 2016), but it can also be applied to disturbances. In the former, it is often a function of variation in habitat suitability or topography; with fire, it is a function of barriers or pathways to fire spread, such as steep topography or rivers and other non-flammable elements. Landscape resistance controls the optimal paths of fire spread and the minimum travel time of a disturbance between locations, primarily through the influence of topography and fuels over landscape space (Finney, 2002). For example, Conver et al. (2018) mapped the most parsimonious fire spread pathways in a forest-grassland ecotone in northern New Mexico, and showed that fire followed pathways of optimal fuel mass, moisture, and tree cover, reflecting the physics of a spreading fire. The inverse of resistance is connectivity, which is a combined effect of various landscape properties that facilitates the flow of mass or energy, and is related to contagion. Resistance (connectivity) is an emergent landscape property resulting from the condition and spatial distribution of large number of individual plants, as well as their associated soils and topographic position.

Contagion

Contagion is a property of disturbances that propagate within a conducive medium. Contagion requires two elements: connectivity and inertia (or "momentum"). Connectivity allows the spread of a disturbance from one part of the medium to another, whereas inertia represents the ability of the disturbance to overcome some threshold and be passed from one unit to another. Without enough inertia or momentum, the contagion will eventually end; but with enough momentum, a contagious disturbance will "percolate" and affect the majority of the elements of the community (Balcan and Vespignani, 2011). Contagion is sometimes modeled as connectivity of networks, with the nodes in a network representing actors in the network, and edges representing the connections between them as the specific interaction being modeled. Nodes may be species, individuals, or locations; edges may represent disease or bark beetle outbreaks. For example, infectious disease, such as root rot in trees, is a contagious disturbance that be modeled as an interaction network (Delmas et al., 2019). The two nodes representing hosts or potential hosts of the disease would have one edge between them, representing an interaction of passing an infectious agent, if one party has infected another. Inertia in this case may represent the disease having to overcome a host's immune response. Networks may also be modeled with latency, to mimic dynamics and time-dependence of infection and spread.

Contagion can alternately be modeled without the network paradigm (Peterson, 2002). For example, wildfire spreads through the medium of flammable vegetation and must cross the threshold of ignition temperatures to initiate fuel pre-heating and pyrolysis, which ultimately set up the chain reaction that allows fire to spread from one flammable element to another in space and time. Similarly, insect outbreaks propagate through vulnerable host species of the correct age or size, overcoming the defensive mechanisms of trees to make use of the individual tree. In these cases, contagion is often modeled as a function of proximity of one grid cell, representing either an area or an agent, to another. Such disturbances are "contagious" disturbances, whereas hurricanes, tornadoes, and other storms are not.

With wildfire, both contagion and landscape resistance are relevant primarily within at medium spatial and temporal scales that have high complexity (region 2 in **Figure 2**), ranging from submeter scales to tens of kilometers. For example, models of fire spread at the degree or half-degree grid spacing of global climate models are extrapolated outside the domain of contagion, as the spatial variation that controls fire spread is much more finely scaled (McKenzie et al., 2014) and the physical process of spread, coarse-grained to that level, is unrealistic compared to fine-scale physical models of combustion (Parsons et al., 2017). This middle domain of spatial scales has the greatest complexity (section The Middle-Number Problem).

CHALLENGES TO PROGRESS IN MODELING COMPLEX LANDSCAPES

Coarse-Graining

Coarse-graining refers to processes in both the real world and in scientific methodology, that is, both physical and statistical processes. In both cases, coarse-graining is defined as the way in which processes, structures, and states aggregate and are combined into fewer larger entities to reduce modeling complexity (Levitt and Warshel, 1975; Gorban, 2006). In the physical world, coarse-graining produces emergence (section Landscape Resistance), as physical systems combine progressively, for example, from atoms, into molecular, chemical, biological, and then ecological systems. At each level, processes and patterns are observable that cannot necessarily be inferred from those below or above. Classic examples in the physical world includes the coarse-graining of statistical mechanics to classical thermodynamics (Jaynes, 1957), and the development of global-scale climate dynamic general circulation models (Meehl, 1990). In ecology, classic examples are the coarse-graining of individuals to populations, species to communities, and the combination of biological organisms interacting with abiotic conditions to well-defined ecosystems. In ecological modeling specifically, we aggregate discrete processes like predation to population cycles, sub-daily processes like photosynthesis to annual productivity, and fine-scale processes such as fire and bark-beetle behavior to landscape modeling of disturbance. This results in the emergence of aggregate patterns (of patch sizes, for example; Povak et al., 2018), that are scale specific (**Figure 4**).

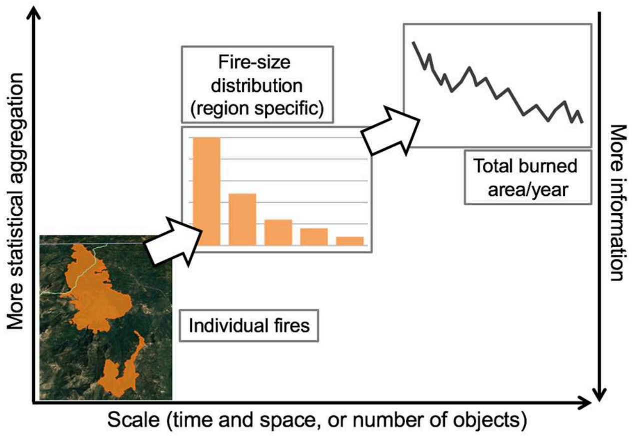

FIGURE 4 | Coarse-graining leads to useful metrics at the largest scales, but reduces the amount of event-specific information retained in each step of statistical aggregation. In this schematic example, coarse-graining applies to individual fires, where information such as location, perimeter, point of ignition, severity, topography, local temperatures, and other information are known. One first step of coarse-graining produces a fire-size distribution, where information on number of fires and area burned are known for some time period. At this level of coarse-graining, trends in aggregate properties of multiple fires are detectable, but still scale-dependent. A fire-size distribution emerges from a second step in coarse-graining, which maintains information about area burned for comparison over large time scales or large regions, but loses information about number of fires. The observed pattern in this second step will also depend on the spatial extent of the data. Other forms of coarse-graining, such as those employed in macroecology, will result in other emergent properties, some of which may be independent of scale.

Many coarse-graining methods in the physical sciences draw on the availability of state variables at fine and coarse scales, i.e., *microstates* and *macrostates*. For these cases, coarse-graining has been termed "state-space compression" (Wolpert et al., 2017) and produces canonical algorithms to optimize its accuracy and

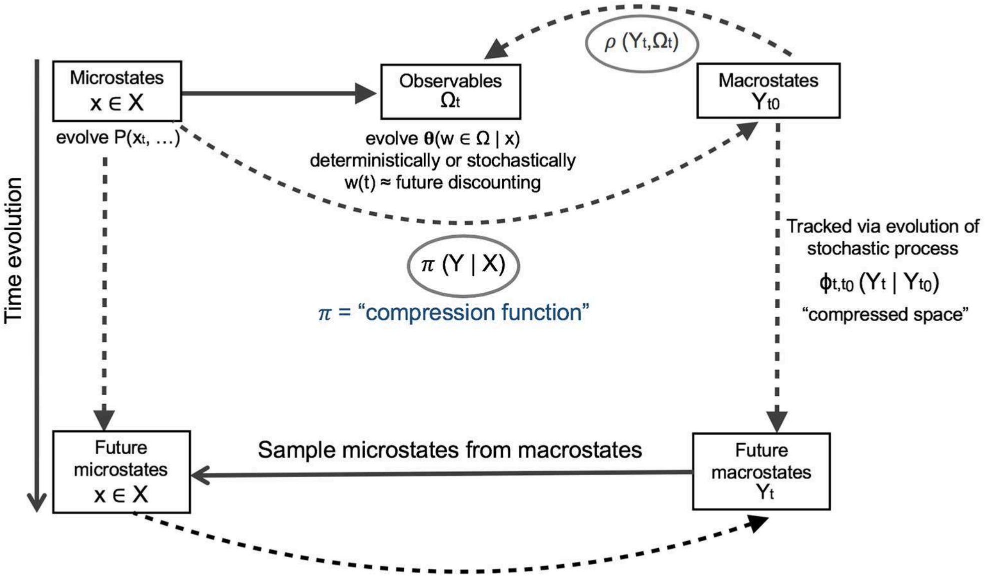

FIGURE 5 | A roadmap for a rigorous approach to coarse-graining in complex systems, from Wolpert et al. (2017). The key to optimized coarse-graining is a "compression function," here designated as $\pi(Y|X)$, which translates microstates (fine-scale information X) into macrostates (broad-scale or "landscape scale" information Y). To ensure that the choice of compression function is optimal, we model the time evolution of the macrostates identified by $\pi(Y|X)$ in parallel with evolution of the original microstates. Some combination of $\pi(Y|X)$, the computed macrostates of the system "Y," the time evolution of macrostates by a stochastic process φ, and the mapping of macrostates onto observables by some empirical relationship ρ will be optimized by a multivariate objective function. Our focus here is on $\pi(Y|X)$, to address the coarse-graining challenge, for which some choices include simple adding up, regression, simulation, and maximization of information entropy.

minimize computational costs. Wolpert et al. (2017) provide a roadmap for this (**Figure 5**), which we draw on below.

Building models to analyze data requires two forms of scaling: choosing the grain size of the data, which is the coarse-graining procedure, and then choosing an extent that the data represent. Grain and extent are two primary properties of scale (Turner et al., 1989; Palmer and White, 1994; Wu, 2004). Models of a process or structure are usually specified at a scale that is optimal, or at least convenient, for analysis that is informative and tractable to solve a particular problem (Levin, 1992). For example, in GIS work, units of data may be observations and climatic variables may be aggregated to a grain size of 1 km^2, and analyzed across an extent of a watershed, or some other landscape unit where the extent is much larger than the grain size. As noted by Turner et al. (1989), tracking the loss of information with changes in grain size and extent of data explicitly may be key to predicting and correcting for that lost information. Investigating scaling relationships in this manner may make it possible to correct for statistical biases introduced by coarse-graining.

We can aggregate measurements of finer-scale processes and models to summarize measures of central tendency and higher moments (such as variance) of their distribution. We may also need to transform variables qualitatively while trying to minimize error propagation across scales. With fire, for example, heat transfer in physics-based models at sub-meter scale (Mell et al., 2007) becomes fireline intensity at the fire front at the meter scale, producing fire spread that depends on external kinetic energy, such as from wind and solar heating, and landscape connectivity at the scale of tens to hundreds of meters. At even coarser scales in space and time, we reach annual area burned, fire size distributions, and fire regimes, whose nature and complexity are the domain of landscape ecology.

In this sense, coarse-graining is a method that is used to reduce modeling complexity by side-stepping the middle-number problem, but the use of coarse-graining poses its own challenges. In complex systems, coarse-graining is never a perfect solution to the middle-number problem, because, as demonstrated by Essex et al. (2007), "systematic modeling errors might survive averaging over an ensemble of initial conditions," which can lead to the introduction of an unknown amount of bias into any prediction, and to unpredictable "surprises." These surprises might consist of sudden state shifts (in the climate system, for example) due to undetected internal dynamics. However, in the case of mechanistic models using coarse-grained variables, predictions that can be validated over short time horizons or when models using these variables are transferred to similar environments can also be used to judge the validity of that model (Houlahan et al., 2017) (though the same may not be true of entropy-based models; see Dewar, 2009).

With particular relevance to landscape ecology, challenges imposed by coarse-graining include:

- Loss of important information. Physics is realized at sub-millimeter to meter scales, and the processes of interest are often non-linear rather than additive. In fire behavior, this is a large source of uncertainty (Mell et al., 2007).
- Regression to the mean removes information about heterogeneity, and may introduce statistical bias (Essex et al., 2007). We lose measures of variability, and estimates of

the mean, variance, and higher moments of the distributions of random variables being measured. This is a particularly difficult source of error when there is spatial or temporal autocovariance (Kennedy and Prichard, 2017).

- Underrepresenting the influence of extreme events, because aggregating controls variability (see Levin, 1992 on the relationship between variance and window size). More technically, because we are often forced to implement coarse-grained processes stochastically, we can arrive at arbitrary realizations that are difficult to validate against observations (Lertzman and Fall, 1998; Deser et al., 2012).

The Middle-Number Problem

The *middle-number problem* refers to the domain of data complexity in which neither local mechanistic models nor generalized global relationships holds exactly, although both local and global processes exert influence on observed patterns. As we move from small numbers of objects or events (e.g., local datasets) to larger numbers (e.g., regional or global datasets), we cross a zone of complexity known as the "middle-number domain" (**Figure 2**). In this domain, systems contain enough elements to be computationally intractable, but too few elements, or elements that are too heterogeneous, to be amenable to global averaging (Weaver, 1948; O'Neill et al., 1986). The basic problem of predicting species richness in a local region from larger averages falls into this category, as richness may be known at the ecosystem scale, but controlled by a huge variety of factors at smaller scales, ranging from moisture availability and soil type, to the presence of predators or pollution. Similarly, weather is famously hard to predict in the long term, because of the small-scale factors that influence it (Lorenz, 1963).

In the middle-number domain, fundamental physical models that apply at fine scales are no longer adequate because the systems are driven by both "lower-order" (mechanistic and physical) and "higher-order" (context) processes. These medium-scale processes and heterogeneity prevent global models from making completely accurate predictions over subsets of their domains. This region is one in which **self-organization** occurs, in which elements of a system interact in a way that increases their structure or complexity, sometimes resulting in pattern formation. Predictions about future states of a system, or relationships between elements, are computationally intractable in this region, in the sense that they may correspond to what are known in computational complexity theory as **NP-hard** (Non-deterministic Polynomial-time) problems (Papadimitriou, 2003).

A classic example of the middle number domain in physics is "in between" statistical mechanics descriptions of individual molecular motion, and classical thermodynamics, which characterizes systems by their pressure, volume, and temperature, which are averages of the properties of large numbers of particles in motion. In ecological systems, individual organisms are the analog of molecules and are described by individual interactions and physiology models, whereas regions or continents of ecosystems are the analog of aggregate thermodynamics, and are well-described, for example, by macroecology (section Macroecology). In between, on the landscape, or watershed, there are too many elements to constrain individually, but not enough (with manageable heterogeneity and variance) to model with high precision in the aggregate.

Simplifying assumptions may reduce computational complexity, but these assumptions can backfire. Even with the best possible information, uncertainty and bias can survive averaging and aggregation through long-term forecasting (a modeling error that it may or may not be possible to detect), leading to unpredictable state changes (Essex et al., 2007). In a fascinating report that takes on complexity issues in ecological prediction without a specific system, Cooper et al. (2014) show that excluded variables and interactions (or small perturbations within the training region) can lead to *arbitrarily large forecasting errors* in complex systems outside the training domain. This reinforces how important the selection of appropriate models is, and in the case of mechanistic models, correct predictions provide a necessary form of validation (Houlahan et al., 2017). This logic can be extended to better understand which environments are suitable for model transfer, rather than approaching the question from the side of which model may best be used for all environments and time periods.

In landscape fire, we extend the ideas of McKenzie et al. (2011a), from the scale at which the middle-number domain begins (i.e., smallest spatial scale or smallest number of interacting elements), to scales at which explicitly spatial interactions become both numerous and relevant. For example, post-fire recovery is dependent on the interactions among the individual-level processes of survivorship, reproduction, and growth, and the equivalent interactions of competition, mutualism, and dispersal. These individual-level processes aggregate to produce the legacy of past fires, watershed-scale topography, and the weather associated with the subject fire. Analogously, the middle-number domain ends (largest spatial scale) where connectivity, or contagion, and landscape resistance cease to be important proximate controls on fire-scale processes. For instance, our understanding of fire regimes at the scale of ecosections (variable in size but at least 100s of square kilometers) comes in terms of area burned and top-down climatic regulation (e.g., Parisien and Moritz, 2009; Moritz et al., 2011; Littell et al., 2018), which unlike fuel models, is no longer dependent on the characteristics of individual organisms. We can predict fire regimes (emergent properties of multiple events in space and time) at the scale of ecosections, and fire behavior at scales of centimeters to tens of meters, but when we try to follow how fires initiate and spreads contagiously over large landscapes, we have a coarse-graining problem, and a middle-number problem, up to the limit of the extents of the largest fires. In theory, an error-free coarse-graining would resolve the middle-number problem for its specific case, but error propagation with increasing scale and level of organization is an inherent challenge.

In summary, with reference to landscape ecology, the middle-number problem can be characterized as the following:

- Outcomes are sensitive to many variables, each of which is distributed non-uniformly in both time and space.

- The relative importance of variables (drivers) changes with scale. Lower- and higher-level processes change in both strength and heterogeneity with the scale being examined.
- We observe and measure what is emergent (observations are the results of these interactions), but we may not witness the process of the interactions themselves. More specifically, we cannot compute the outcomes of fine-scale mechanisms at large scales and temporal extents without simplifying assumptions.
- Important outcomes, including those most relevant for management and policy, are often desired within the parameter space in which complexity is greatest, and where variation occurs at multiple scales.
- Projections of models from one region of training (one part of the middle-number domain) to another can lead to unbounded, or arbitrarily large errors (Cooper et al., 2014).

Non-stationarity

Non-stationarity refers to the limitations of using models with adjustable parameters to predict future states (Wolkovich et al., 2014; McKenzie and Littell, 2017; Turco et al., 2018). These include most empirical statistical models and many "process-based" models: those that use mathematical relationships involving parameters that have been estimated from data, even when the model is said to represent a physical or biological mechanism. In time series and spatial statistics, *stationarity* is the property that the generating function for a stochastic process is constant. This means that the underlying probability distribution of an observable (a physical quantity that can be measured), typically its mean or variance but also including its autocorrelation function, is not spatially or temporally dependent. When we model relationships using empirical data from current and past observations, we estimate a particular distribution (mean model and variance/covariance matrix) from a discrete environmental domain, such as the relationship of tree growth to soil moisture or the relationship of soil respiration rates to temperature. When these empirical models are used to project into the future, it is implicitly assumed that the distributions are stationary. That is, the mean value (or model, and associated variance/covariance matrix) we estimate currently for the relationship among variables, e.g., a regression coefficient, will be the same mean value (or model) in the future, or in a different place.

In the context of landscape fire, stationarity is often implied with use of the *historical range of variation* (HRV) in fire regimes (Morgan et al., 1994; Keane et al., 2009). Stationarity in the HRV sense implies stability over space and time in the statistical distribution of a variable (such as fire frequency or fire-size distribution), including central tendency, but each of these variables may exceed its historical distribution when the underlying drivers go outside their historical range (Elith and Leathwick, 2009). A more robust definition of stationarity is stability in relationships among variables, even when a driving variable exceeds its historical range; for example, the relationship between maximum annual temperature and annual area burned at large scales. In the context of current and projected environmental change, the best practice in statistical models is to make predictions only within the domain of the data used to estimate the model; where the driver is projected to fall outside the historical envelope, statistical models may be unreliable (McKenzie and Littell, 2017; Turco et al., 2018). In that case, other types of models, such as purely mechanistic models, or models that rely on the functional traits of organisms (Dobrowski et al., 2011; McDowell and Allen, 2015) must be employed.

By definition, we cannot expect stationarity to hold uniformly in the context of current and near-future climate change, where the distributions of climatic drivers of ecological dynamics are and will be departing from their historical means and ranges. For example, the strength and direction of the correlation between annual area burned and water-balance deficit varies across the western USA, depending on the distribution of the water deficit (McKenzie and Littell, 2017; Littell et al., 2018). In ecophysiology, the strength of climate-growth relationships of trees (e.g., the correlation between annual increment and precipitation) varies over time and broader climatic cycles, also depending on the distribution of the climatic driver (Marcinkowski et al., 2015). In both these cases, the adjustable parameters, or specifically the regression coefficients in a statistical model, vary over the spatial domain of the data, and will certainly also vary over time in a non-constant climate.

In summary, with reference to landscape ecology, the non-stationarity problem is that:

- Most mathematical relationships used in models include adjustable parameters.
- In empirical studies, these parameters, and the relationships between the parameters, change across both space and time (Dobrowski et al., 2011).
- Projections for the future that rely on models fit from observations therefore are fragile to expected changes in these parameters (Yates et al., 2018).
- Important examples for fire, relevant to management and policy, are statistical relationships between climatic drivers and fire effects at the level of individual organisms and associated soils, with implications for aggregate properties such as annual area burned (Littell et al., 2018), fire-size distributions (Reed and McKelvey, 2002), occurrence of extreme events (Stavros et al., 2014), and spatial patterns of fire severity (Cansler and McKenzie, 2014).

Interactions Among These Challenges

These challenges do not arise in isolation; interactions among them will confound proposed solutions to one or more of the challenges. For example, it has been argued that fully mechanistic models should be a goal in landscape simulations because they optimize adjustable parameters to be most able to be projected into new environments (Keane et al., 2015). In theory, fully mechanistic models avoid the non-stationarity problem because the model will be perfectly transferable as long as it includes all the mechanisms that affect the observables (see Gustafson, 2013 for a landscape modeling example). There are two problems with this claim: first, many so-called "mechanistic" mathematical models include parameters that are fitted from data that do not sample the full range of conditions and therefore cannot determine exact mechanisms. Second and perhaps more importantly, extrapolating fine-scale computations (which mechanistic models invariably are, e.g., physics-based fire models) to larger scales of interest runs into the middle-number problem. Computations become intractable (because they are NP-hard; for a useful discussion of this topic relevant to biology; see Felsenstein, 2004), and the demands of data and associated data input uncertainty increase (Kennedy and McKenzie, 2017). A solution to this middle-number problem therefore may lie in coarse-graining both model processes and associated input data in a way that minimizes error, but this encounters problems imposed by non-stationarity. In this sense, solving the middle number problem may be possible only in stationary systems; solving problems in non-stationary systems will require inventive applications of coarse-graining to avoid the middle-number problem. In landscape ecology, joint solutions to these challenges are uncharted territory. Below, we describe some potential paths to solutions that have particular relevance to cross-scale analysis of landscapes as complex systems.

APPROACHES TO UNDERSTANDING COMPLEX LANDSCAPE PHENOMENA ACROSS SCALES

Models in landscape ecology that work well across scales, solving the above challenges, will involve quantitative scaling laws that combine top-down and bottom-up perspectives. Multiple disciplines, such as physics, biology, and ecology, have incorporated quantitative scaling relationships in an attempt to model phenomena that cross physical scales. In landscape ecology, the following concepts and paradigms show promise for solving the coarse-graining, middle-number, and non-stationarity problems. The first, Hierarchical Patch Dynamics, involves **hierarchical organization** applied to discrete spatial scales thought to be most important, whereas the next three (**lacunarity**, Energy and Regulation across Scales, and Macroecology) invoke quantitative scaling laws that are or are nearly continuous in large systems.

Hierarchical Patch Dynamics

Hierarchical Patch Dynamics (HPD) is a proposed paradigm shift, or new framework, for ecology, espoused by Wu and Loucks (1995). Its goal is to resolve problems of scale and non-equilibrium in ecological systems. This idea is similar to contextual emergence, in the sense that the framework contains levels of complexity, in which larger scales are more complex than the smaller scale items that they contain. In HPD, patches of ecosystems interact at multiple scales, and hierarchy theory provides a means for quantifying and ordering phenomena at multiple scales.

The major elements of HPD (Wu and Loucks, 1995) are that (1) *Ecological systems can be modeled as nested discontinuous hierarchies of patch mosaics* (see also Holling, 1992). Patches are structural and functional units, and they are nested, meaning larger patches contain smaller ones. A defining assumption is that patches can be nested perfectly, and that the highest level of organization is not contained by any of the smaller ones. (2) *System dynamics are a composite of patch dynamics*. This simplifying assumption states that individual patch changes can be aggregated meaningfully such that overall system dynamics are recoverable from their composite. (3) *The pattern-process scale perspective*. This restates the landscape ecology paradigm that pattern and process interact mutually and recursively at multiple scales. (4) *Non-equilibrium*. Transient dynamics can dominate at small scales, but this leads to: (5) *Incorporation and metastability*. With the etymological meaning of "incorporate," fine-scale transient dynamics are literally swallowed up by stabilizing forces at "meta" scales (implying the middle-number domain), whereas at very broad scales stochastic processes dominate again. Note that this is opposite to our view of the middle-number problem and its domain as being the least stable, at least in the sense of predictability.

A limitation of this paradigm is that it assumes that coarse-graining is a straightforward outcome of aggregating the dynamics of nested patches. We have seen (section Landscape Resistance) that emergent properties at coarser scales are not necessarily direct outcomes of fine-scale dynamics, and that additive processes are only a subset of coarse-graining, whether observed or modeled (Wolpert et al., 2017). This conceptual framing does not directly map onto a unique way to aggregate, or coarse-grain the middle number domain. Although some problems of the middle number domain may be solved through this aggregation of patches (Wu and Loucks, 1995), the framework of HPD may simply not be mathematically rigorous enough to solve all problems associated with the middle number domain; indeed, not all such problems may be solvable. It is now known that uncertainty and bias can survive averaging and aggregation through long-term forecasting (a modeling error that it may or may not be possible to detect) (Essex et al., 2007), and that small perturbations or "unimportant" missing variables in a training region of a model can lead to predictions where there is no meaningful bound that can be placed on the error of the model outside of its original training data (Cooper et al., 2014). That said, HPD does offer an important framework for modeling discrete scales in landscape dynamics, especially in the context of non-equilibrium states.

To address our three challenges, HPD would, in theory, assume that discrete scales in space are metastable, extending upward through the middle-number domain. These scales are the domain of ecosystem dynamics, *sensu* Holling (1992). There is an implicit link to hierarchy theory (O'Neill et al., 1986), in which cross-scale dynamics are clearly defined and directional. This means that processes increasing in scale are driving, whereas processes decreasing in scale are constraining. In theory, this hierarchical structure entails the optimal degree of coarse-graining. Analogously, non-stationary dynamics are subsumed into the hierarchical patch structure.

Lacunarity

Lacunarity is way of characterizing the spatial configuration of points or other components of a spatial pattern, such as patches or pixels. The lacunarity algorithm is a "box counting" procedure that specifies a grain size over a region of interest, and quantifies the presence or absence of a phenomenon in each "box" (Allain and Cloitre, 1991). Specifically, lacunarity is a dimensionless metric that estimates the roughness of a pattern as a fractal dimension, and identifies gaps in the overall patterns (Plotnick et al., 1996). Highly heterogeneous patterns with low rotational and translational symmetry have high lacunarity (and high complexity), whereas mostly homogeneous patterns that have high rotational and translational similarity are considered to have low lacunarity (and low complexity; Karperien, 2013). With this metric, we can obtain a form of the variance-to-mean ratio that is calculable and directly comparable across scales. Lacunarity estimates may complement estimates of fractal dimension, but provide further information in that the shape of lacunarity curves (with increasing window size) can illustrate departures from a self-similar or isometric character at identifiable scales (Dale, 2000).

Lacunarity is a static property of patterns, and is generally used to quantify properties of self-similar fractal-like patterns to determine the fractal power that describes them. Lacunarity has been adopted in landscape ecology for data sets that are not necessarily self-similar, such as seedling counts along transects and other two-dimensional patterns, like landscape patches (Plotnick et al., 1993, 1996; Swetnam et al., 2015). In landscape ecology, lacunarity can be seen as an aggregate expression of processes, such as disturbance and competition, that create *landscape memory*. With respect to landscape fire, the lacunarity index at a broad scale is computed directly, and consistently, from spatial patterns of fuels and topography. This is demonstrated in Kennedy and McKenzie (2017), where lacunarity is used to compare simulated and observed patterns of fire spread in a forested landscape to evaluate a stochastic fire model whose objective is to replicate fire-regime properties, rather than individual fire perimeters. Lacunarity also captures scale automatically through the specification of a grain size and extent, which leads the way into investigations of spatial heterogeneity and spatial statistics in landscapes (Wagner and Fortin, 2005).

With reference to the three challenges we have posed, lacunarity collapses scale-specific metrics into one that is especially robust across scales, thereby using a form of coarse-graining with minimal error. In theory, this avoids the numerosity associated with the middle-number problem and the need for adjustable parameters. An obvious limitation of lacunarity is the reliance on one metric to capture what are often noncommensurate aspects of complexity, which are measured in different units (for example, landscape complexity associated with succession and demography is measured in different units than phylogenetic information). Whereas lacunarity can adequately represent an aggregate of processes, it is not possible to recover the ecological information lost in the aggregation process, and it would be difficult to track error propagation associated with this extreme level of coarse-graining.

Energy and Regulation Across Scales

Energy and Regulation across Scales (ERS) is a conceptual framework for understanding contagious disturbance on landscapes (McKenzie et al., 2011a), developed specifically for modeling landscape fire. ERS aims to identify scaling relationships that accomplish coarse-graining without some of its most error-prone components: (1) aggregating elements that have substantial uncertainty associated with them, and (2) changing variables across scales with *ad hoc* methods. ERS separates the important drivers of contagious disturbances on landscapes into their fundamental elements, *Energy,* and *Regulation.* With suitable metrics for each, they can be applied across both spatial and temporal *Scales* in a way that minimizes the coarse-graining errors associated with changes of variables.

Energy is the fundamental "currency" of wildland fire, in that it can be measured and tracked across scales with no change of variables. Although vegetation on a landscape is often described in terms of stored mass or carbon, the fundamental nature of wildfire reminds us that vegetation can also be described in terms of its embodied energy. All biomass consists of both atomic mass and molecular bond energy. The atomic constituents of photosynthesis and carbon fixation (C, H, O) are organized into more complex molecules with higher energy content. The bond energy in these more complex molecules thus reflects the net energy captured during photosynthesis and subsequent carbohydrate synthesis. Energy storage on the landscape scale is regulated by factors that govern net primary productivity (Rasmussen et al., 2011; O'Connor et al., 2017).

Energy can be measured and calculated in the same units (joules) at any scale. The cycling of kinetic and potential energy (*sensu* Figure 1.4, McKenzie et al., 2011a) subsumes the variety of ecological dynamics imputed to the "fire landscape," including fire behavior, fire effects, and vegetation succession. These latter are fragile to changes in scales of measurement and modeling, and have different units. *Energy* can be represented by a scalar quantity, but in the landscape context it can be vectorized, for example, as a vector field of wind containing a certain amount of energy, that drives fire behavior.

Regulation is an umbrella concept representing constraints on kinetic energy, and may be represented as a scalar, vector, or even a tensor quantity. For example, humidity can be represented as a scalar quantity, and will regulate combustion and fire spread. Humidity could therefore be expressed theoretically in units of reduced kinetic energy of the system. Another type of *regulation* is anisotropic topographic complexity, made up of a scalar element, representing a magnitude, and a tensor element, incorporating direction and directional response to interactions. If regulation can be represented as a dimensionless and normalized scalar quantity, it could be robust to spatial scaling. As a vector or tensor, the directional component may be an additive quantity, scaling linearly with area. A scalable representation of *regulation* in ERS will produce landscape resistance, or reduce contagion. Its spatial variation will produce lacunarity. Ideally, these complex attributes of the middle-number domain can be realized with minimal error propagation across scales.

As proposed, two problems need to be solved in order to implement an ERS framework. First, *Energy* and *Regulation* need to be reconciled in a way that is computationally tractable by appropriate choices of the scales at which their interactions are calculated. The scaling laws that we seek will be "grounded" at regions in scale space at which there is the most "action" (*sensu* Holling, 1992). For example, in complex topography, the obvious scales of variation of kinetic energy (e.g., wind), potential energy (e.g., fuels for fire or hosts for insects), and the two types of *regulation* will all be different. Second, the mathematical representation of coarse-graining of some aspects of *regulation* (e.g., topographic complexity) remains to be articulated so as to avoid a middle-number problem (e.g., being overwhelmed by numerosity).

ERS would, in theory, address all three of the fundamental scaling challenges by (1) adoption of the two canonical variables, *Energy* and *Regulation*, and (2) estimating the shape of universal scaling laws, as in macroecology (Wilber et al., 2015) by explicitly taking into account the scale of the processes under consideration. Whether these scaling laws would be "stationary" has not yet been addressed. It is likely that ERS would need a "meta-stationary" framework to approximate complex landscapes, where in the aggregate, landscapes would have approximately stationary, non-ergodic realms that produce aggregate patterns.

Macroecology

Macroecology is a subdiscipline of ecology that seeks to find and be able to predict universal patterns and explicit scaling laws in systems that are organized across multiple orders of magnitude of space and time. Brown (1999) characterized macroecology as "an approach to studying a certain class of complex ecological systems" and "as a way of investigating the empirical patterns and mechanistic processes by which the particulate components of complex ecological systems generate emergent structures and dynamics." Macroecologists have long sought to explain and predict patterns of biodiversity, including species richness over area, abundances of species, and allometric scaling relationships (West et al., 1997; Enquist et al., 1998; Niklas and Enquist, 2001). By investigating patterns explicitly while controlling for the effect of scale, macroecology becomes a form of statistical aggregation that is a method of coarse-graining (Maurer, 2005; Storch et al., 2008; Bertram et al., 2019). For patterns in ecosystems that consider organisms and their physical characteristics, diversity, and spatial distribution, macroecology may offer the most reliable coarse-graining approach, in that it side-steps the middle number problem (**Figure 2**) by not trying to model mechanisms that lead to pattern formation at all scales; focusing instead on aggregate properties of large numbers of elements. Often in ecology, these elements are individuals, populations, or species. This idea of macroecology as a meaningful form of statistical aggregation is consistent with McGill's proposed definition for macroecology (McGill, 2019): "the study at the aggregate level of aggregate ecological entities made up of large numbers of particles for the purposes of pursuing generality."

In attempting to characterize universal ecological patterns, such as the species area relationship, the species abundance distribution, and various metabolic relationships, some modern forms of macroecology embrace the complex nature of information underlying these patterns, and their predictions are based on maximizing the **information entropy** of the system. Information entropy is a way of quantifying the uncertainty associated with a particular outcome drawn from an underlying probability distribution (Shannon, 1948). Maximizing information entropy (the maxent approach) is the least biased way of determining an underlying probability distribution, given known outcomes (Jaynes, 1957). This approach has been applied to macroecological questions, beginning with Shipley's maxent (Shipley et al., 2006; Shipley, 2010). More recently, the Maximum Entropy Theory of Ecology (METE) has used maxent in a constraint-based approach to predicting interrelated macroecological metrics, which requires information from the ecosystem in the form of state variables (Harte, 2011; Harte and Newman, 2014; Brummer and Newman, 2019). These state variables include energy embodied in the organisms in communities being modeled (Niklas and Enquist, 2001; Newman et al., 2014; Harte et al., 2017; Bertram et al., 2019). Energy is therefore a uniting factor among models, because it is irreducible and fundamental to ecosystems. Macroecological models sometimes include area (a 2-dimensional measure of the space being modeled), which is also fundamental to landscape ecology models. The potential to use macroecology in concert with other types of landscape ecology models is obvious but not well-developed (Newman et al., 2018).

Although various forms of macroecology are successful in describing and predicting metrics at highest level of statistical aggregation, not all ecological questions can be addressed through this framework, including questions of fine-scale processes and unusual dynamics. However, "failures" of general macroecological patterns to describe particular data sets are actually useful for identifying the scales at which mechanism influences observed patterns (Wilber et al., 2017; Newman et al., 2018). Constraint-based approaches, such as METE, have the potential to reveal the scale at which mechanism becomes important, and also which mechanisms matter at the highest level of statistical aggregation. These approaches have been applied successfully in testing mechanisms in disease ecology (Wilber et al., 2017), and could be extended to other systems.

Macroecological theory currently deals with all of the three challenges posed above:

- Macroecological metrics can provide solutions to coarse-graining and middle-number issues, because they can contain explicit scaling laws (in the case of maxent-based macroecology, these solutions are least-biased estimators of the distributions in question).
- Macroecology relies on variables like area and energy, that are fundamental to ecosystems, and landscape models.
- Non-stationarity is not a problem in predictions of a single state of the plot or ecosystem, because scaling parameters and state variables are non-adjustable, but macroecology is not yet a dynamic theory (i.e., it does not model changes in ecological systems over time), and there have been limited attempts to incorporate predictions of disturbed and successional systems into the theory (Supp and Ernest, 2014; Newman et al., 2018).

CONCLUDING REMARKS

In this paper, we discuss key properties of landscape complexity. We identify four phenomena of complex systems that are common to ecological landscapes: emergence (section Emergence), landscape memory (section Landscape Memory), landscape resistance (section Landscape Resistance), and contagion (section Contagion). We also review three intrinsic problems associated with modeling complex systems, including coarse-graining (section Coarse-graining), the middle number problem (section The Middle-Number Problem), non-stationarity (section Non-stationarity) and interactions among these challenges (section Interactions Among these Challenges). We discuss why these particular challenges and their interactions need to be addressed in designing general models of landscapes (Yates et al., 2018). We codify these specific challenges as outstanding hard problems for scaling in landscape ecology.

Complex biophysical systems present fundamental challenges to ecological modeling and analysis. In order to make reliable predictions with credible uncertainty bounds and acceptable levels of precision for the complex problems of environmental management and planning, we require methods that simultaneously do two things. These are (1) coarse-graining across scales without introduction of statistical bias and without loss of relevant information, while also (2) contending with the problems of non-stationarity and lack of transferability.

To avoid the middle-number problem we require a method of coarse-graining that retains key information across scales, but that adds as little additional information as possible (Jaynes, 1957). This also necessitates the identification of important system metrics (e.g., *Energy* in the ERS system) for which scaling laws are informative to those underlying dynamics (Gorban, 2006). When considering a coarse-graining method, summary statistics applied to any quantity in a complex system should be by default expected to be scale-dependent. Choosing a variable that itself does not need to change over scales, such as energy or information, may be a first step to simplifying the overall complexity of a model, and being able to compare direction and magnitude of statistical biases between models.

In general, a model that incorporates mechanisms (i.e., is process-based) would be expected to be robust to problems of non-stationarity, but a fully mechanistic cross-scale model is not feasible for complex systems due to the middle-number problem and associated coarse-graining challenges. Models used to simulate complex systems should incorporate uncertainty and variation, and avoid false precision in model prediction. Models of ecological processes should by default have the null expectation of non-stationarity, and scale dependence both in the grain size and the extent of prediction (Levin, 1992). Although perfectly accurate forecasts of ecosystem dynamics and emergent behavior are not possible in complex systems, better models may lead to a better understanding of thresholds and interactions (Turner, 2005).

Given these challenges, we identify four potential approaches at various stages of development that may improve our ability to model complex landscapes: Hierarchical Patch Dynamics (section Hierarchical Patch Dynamics), lacunarity (section Lacunarity), Energy and Regulation across Scales (section Energy and Regulation across Scales), and macroecology (section Macroecology), where lacunarity is a metric, and the remaining three approaches are theoretical frameworks. Each of these approaches either identifies metrics that are potentially scalable, or quantifies structure and relationships across scales. Although all of these strategies have started from different conceptualizations of the landscape in ecology, each has engaged the problems of complexity, specifically scale dependence and the middle-number problem, in their own ways. Some insight can be derived from what each lacks; more mechanistic forms of macroecology may be able to overcome some part of the non-stationarity problem, for example, and lacunarity might be effectively incorporated to Hierarchical Patch Dynamics or Energy and Regulation across Scales as an effective form of coarse-graining.

These approaches are not the only ones available to scientists working in complex systems. A number of recent advances from different fields may offer ways forward for similar problems in landscape ecology. For example, problems in protein folding have been solved via the use of coarse-graining applied to atomic to molecular interactions (Levitt and Warshel, 1975). Evolutionary biologists have been able to use what is termed “branch and bound” methods to reduce the amount of probability space that must be searched in order to infer phylogenetic trees, some of which constitute NP-hard problems (Felsenstein, 2004). This successful technique is a way of reducing the computational complexity of problem solving in the middle-number domain. Some solutions for long-term forecasting and non-stationarity may come from recognizing the mathematical symmetries of proposed models (Essex et al., 2007) in dealing with undetected biases in ensemble averages. Large scale predictions with biodiversity and disturbance models might see advances from the field of information entropy-based macroecology, which employs constraint-based methods and ecological state variables (Shipley et al., 2006; Harte, 2011) to make predictions about community structure in equilibrium conditions. As Wolpert et al. (2017) suggest, new approaches to state-space compression, which optimize the efficiency of a coarse-graining procedure from microstates to macrostates, but allow for time evolution, may be a way forward for all complex models.

The challenges imposed by coarse-graining, the middle number problem, and non-stationarity in landscape ecology are also handles on the overall problem of complex systems. They may similarly be solved with innovative computational techniques, or at least see progress on those fronts in the coming years. However, a cross-disciplinary approach may be required, in that many of the successes of modeling complex systems have been developed independently in different fields, but the fastest progress in classifying the complexity classes and computational tractability of complex problems has been made in physics and computational science (Arora and Barak, 2009).

We present these concepts of complex systems and their intrinsic challenges as they apply to ecological disturbance dynamics to highlight their important attributes, while illustrating the limitations of our common methods of analysis. With this review, we hope to inspire progress in the development of quantitative methods that meet these challenges. Improvements to our understanding and prediction of complex ecological systems may enable better theory development, and in turn, better decisions in land management that meet the needs of conservation, biodiversity, and resource management.

AUTHOR CONTRIBUTIONS

EN and DM created the figures. All authors contributed to the conceptualization and writing of this manuscript, and approved the final version of the manuscript.

FUNDING

Funding for this work was provided in part by the Bridging Biodiversity and Conservation Science program to EN, by the USDA Forest Service to EN and DM.

ACKNOWLEDGMENTS

We thank David Hembry for discussion and edits to the manuscript, and Carol Miller and David Wolpert for comments and contributions to figures in the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

REVIEW
published: 08 November 2019
doi: 10.3389/fevo.2019.00424

Where the Ecological Gaps Remain, a Modelers' Perspective

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Humans have observed the natural world and how people interact with it for millennia. Over the past century, synthesis and expansion of that understanding has occurred under the banner of the "new" discipline of ecology. The mechanisms considered operate in and between many different scales—from the individual and short time frames, up through populations, communities, land/seascapes and ecosystems. Whereas, some of these scales have been more readily studied than others—particularly the population to regional landscape scales—over the course of the past 20 years new unifying insights have been possible via the application of ideas from new perspectives, such as the fields of complexity and network theory. At any sufficiently large gathering (and with sufficient lubrication) discussions over whether ecologists will ever uncover unifying laws and what they may look like still persist. Any pessimism expressed tends to grow from acknowledgment that gaping holes still exist in our understanding of the natural world and its functioning, especially at the smallest and grandest scales. Conceptualization of some fundamental ideas, such as evolution, are also undergoing review as global change presents levels of directional pressure on ecosystems not previously seen in recorded history. New sensor and monitoring technologies are opening up new data streams at volumes that can seem overwhelming but also provide an opportunity for a profusion of new discoveries by marrying data across scales in volumes hitherto infeasible. As with so many aspects of science and life, now is an exciting time to be an ecologist.

Keywords: ecology, scale, modeling, anthropocene, challenges

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University of Exeter, United Kingdom

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Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *11 February 2019*
Accepted: *21 October 2019*
Published: *08 November 2019*

Citation:
Fulton EA, Blanchard JL, Melbourne-Thomas J, Plagányi ÉE and Tulloch VJD (2019) Where the Ecological Gaps Remain, a Modelers' Perspective. Front. Ecol. Evol. 7:424. doi: 10.3389/fevo.2019.00424

ECOLOGICAL MODELS AND GAP FILLING

Models have many roles in ecology—from explanatory (conceptual) exploration of theoretical hypotheses, to anticipatory predictions to guide short-term tactical decision making, or longer-term projections to inform strategic direction setting (FAO, 2008; Mouquet et al., 2015). While predictive capacity is important when models are being used to guide explicit decision making, models are useful conversation starters to generate interest and discussion around a topic. Indeed, it is the authors' experience that more breakthrough learnings about system function have eventuated when a model has been wrong than when it has been right (as all involved are keen to know why it was wrong, fewer people ask when a model matches observations or expectations). All of these roles continue a long tradition of synthesizing knowledge in generalisable and useful forms.

Humanity has been codifying its theories about the function of the world since the earliest story tellers and religious practices, although the discipline of ecology was not formally recognized until

TABLE 1 | Summary of the strengths, gaps and drivers for change in empirical and theoretical ecology and modeling as perceived by the authors.

Research domain	Strengths	Gaps	New driver	Next steps
Empirical ecological studies	Direct connection to the observable phenomena	• Tactical integrated statistical models: empirical validation but minimal mechanistic understanding • Historical observations may become irrelevant as climate change introduces new dynamics; evolutionary changes; gaps in data on previously unimportant species, parasites etc.	Rapid, continuous, automated data collection possible	• New methods (e.g.. machine learning) to make best use of the new volumes of data available (extracting patterns that could not be seen in small datasets). • Contributing to hybrid approaches
Theoretical and mathematical ecology	Synthesize and generalize understanding	• Theoretical ecological models: provide basis for general understanding and testing mechanisms, often limited testing • Equilibrium based theoretical underpinnings increasingly starting to fail under changing climate and changing distributions. • Eco-evolutionary feedbacks demonstrating need for further testing. • Cross-scale contributions of diversity to functional resilience of ecosystems not well-understood	Advances in ecological theory. Dramatic improvements in computing power.	• Focusing on dynamic theoretical equations rather than equilibrium formulations • Building theories on larger scales • Improved frameworks to compare terrestrial and marine systems and understand connections • Contributing to hybrid approaches • Expanded retrospective assessment of existing model projections • New (including as yet unrealised) approaches.
System level hybrid models	Bring together the strengths of different modeling methods, representing each facet in the way that best captures that component or process. Can be made explicitly multi-scale and allows for more dynamic representations.	• Tropho-dynamic species and trait-based models: gaps in both empirical & theoretical underpinnings (e.g., density dependence, biodiversity, evolution) • Whole of ecosystem models: modeling gaps confounded by need to capture broader and more complex ecological interactions. • Socio-economic ecosystem models: gaps due to two-way feedbacks between ecological, social & economic systems	Integrating ideas and models from different research fields	• Move beyond fixed parameterisations, fixed functional relationships and formulations. • Adopt dynamic model structures. • Develop multi-scale hybrid models, cross validate with empirical statistical models and test emergent properties against general theory and patterns

the late nineteenth century (Egerton, 1977) and is often still seen as a relatively "young" science. Throughout that long history and up to the present day ecologists have drawn upon observations to try to summarize the world around us and the complex interrelations contained therein (Haeckel in Egerton, 1977), to elucidate the underlying mechanisms that shape the patterns we see (Levin, 1992). In some instances, they have combined forces with mathematicians to provide a more theoretical standpoint or to create synthesis via model construction, which explicitly involves abstracting away unnecessary detail and retaining only the essentials required to produce observed patterns (Costanza and Sklar, 1985; Levin, 1992; Håkanson, 1997; Fulton et al., 2003a; Plagányi et al., 2014).

As mechanisms often occur on different scales to the patterns they shape, this makes scale the key conceptual problem in ecology (Levin, 1992). Ecological studies began at small scales (Melbourne-Thomas et al., 2017), but more recently, is grappling with more data streams, from more disciplines, new technologies and across broader scales, particularly as global change has become such a dominant consideration (Chave, 2013). As understanding has accumulated there have been numerous attempts to unify the threads into a common framework (e.g., Scheiner and Willig, 2005, 2008). These exercises have had mixed success and significant gaps remain—particularly at the largest and smallest scales. This "modelers' perspective" provides a summary motivated by the authors' experience with those gaps, assessing which have been filled and which loom largest on the horizon.

Our starting point was to reflect on our experience, its dead ends as much as its successes, the persistent trials along with more recently emerging challenges. Our observations are summarized in **Table 1**, which captures our collective view of the strengths, gaps, and drivers of change across the broad research domains of empirical ecological studies, theoretical and mathematical ecology, and system-level hybrid models. In pondering how scale plays into these issues we developed a set of "Stommel diagrams" (Stommel, 1963) to frame our thinking. This series of schematic diagrams (**Figure 1**) reflects the scales and dimensions that characterize key system components and processes (terrestrial, marine, and anthropogenic), as well as the reach of observational methods and models in representing those features. The shading on the diagrams highlights the extent of understanding drawn

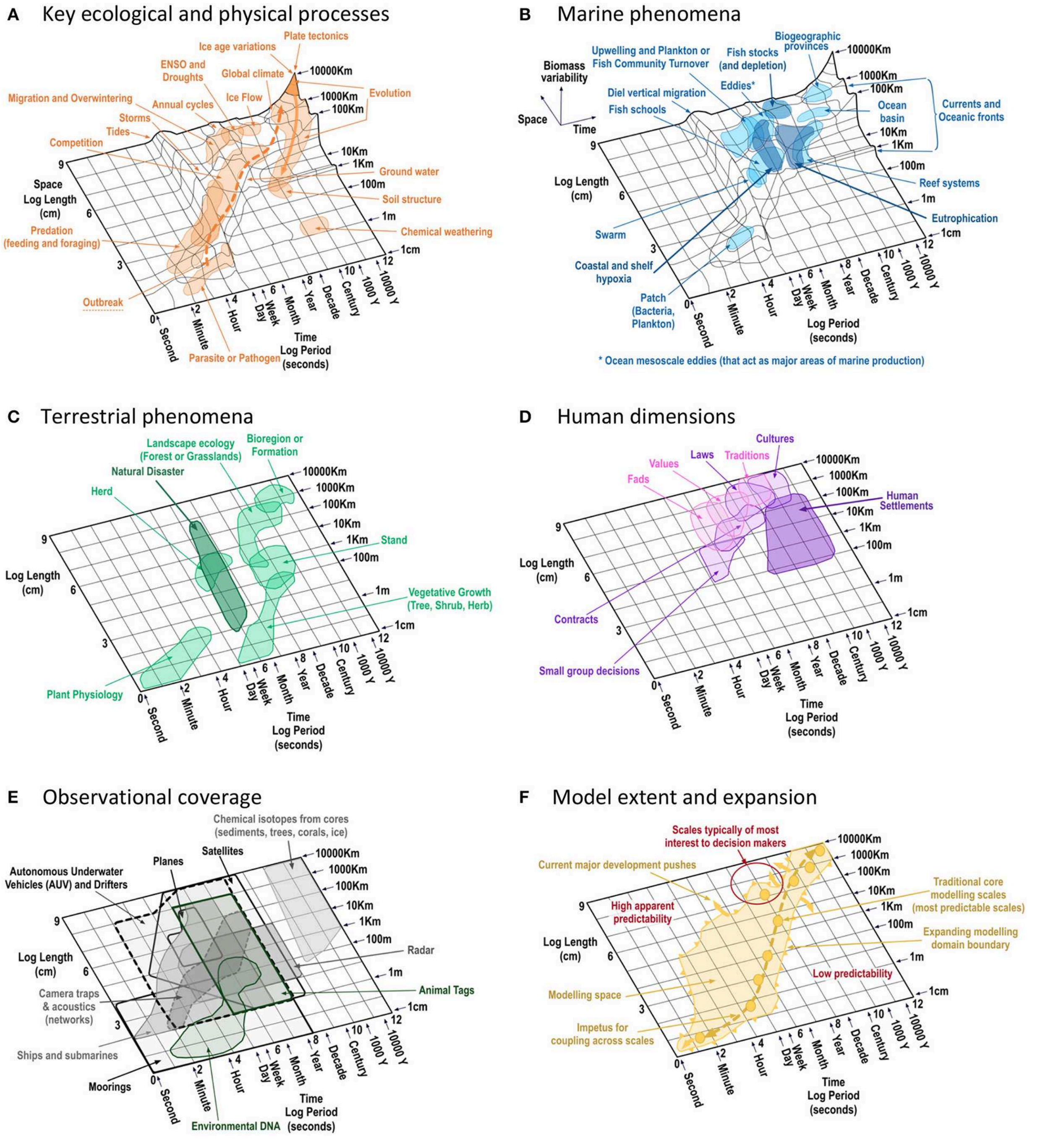

FIGURE 1 | Set of schematic Stommel diagrams showing: **(A)** key ecological processes (with the solid arrow indicating the new understanding about the scales of action of evolution and the dashed line showing the cross scale connection ecology is realizing stems from linking processes at different scales such as parasitism, ecosystem structure and function and large scale nutrient cycles); **(B)** marine phenomena (components and processes); **(C)** terrestrial phenomena (including the scale of natural disasters such as fire, flood, earthquakes, and volcanoes); **(D)** human dimensions (including the scale of human settlements and decision making processes and influences); **(E)** observational scales from illustrative major sensor platform types (noting that citizen science is significantly extending data collection beyond the scales of the platforms shown); and **(F)** the scales most reliably captured by models (the solid dots indicate scales well-captured by traditional approaches, the shaded area the growing extent of models, the small and large arrows the push for continuing development and the dashed line the push for coupling across scales; there may be additional model types that already sit outside the shaded domain, but it is largely indicative of the scope of scales covered). Together these diagrams create a conceptual figure highlighting the scales and disciplinary dimensions that characterize reality. The base figure for the key ecological process and marine components is redrawn and updated from Vance and Doel (2010). For the other diagrams the scales of the key phenomena and system features also drawn from Clark (1985b), Marquet et al. (1993), Peterson et al. (1998), Westley et al. (2002), Scholes et al. (2013), Kavanaugh et al. (2016), and Rose et al. (2017). Note for these other diagrams **(C–F)**, we have chosen to draw them on a flat two dimensional space as the original Stommel diagram's third dimension may not be as relevant for these other dimensions (but there was insufficient information to reliably try to replicate this third axis for the other properties).

from historical ecological and modeling studies, with the arrows in **Figures 1C,F** showing the likely directions of expansion for ecological knowledge and model representations of ecological processes (some of which has already begun).

Modern ecological modeling (represented by the shaded area in **Figure 1F**) has been underpinned by both empirical studies and mathematical explorations (**Table 1**). The early efforts of observational, theoretical and mathematical ecology were relatively simple and often confined to "local" (small) scales (the phenomena on scales of <1–100 km and from a few months to a few years in extent shown in **Figure 1**). However, the strong relationship between time and space scales (the diagonal patterns seen across **Figures 1A–C,F**) also allowed for some researchers (e.g., Clements, 1916) to conceptualize processes on large (landscape) scales over very large time periods (the top right corner of **Figure 1B**). Since then there has been a coevolution of empirical and conceptual/theoretical ecology. Accumulating data streams, technological improvements (e.g., increased computing power) and a growing understanding of the interconnected and nested nature of ecological systems has seen all ecological fields, but perhaps particularly modeling, which simultaneously come under pressure to become increasingly complex while appreciating the extensive list of things they still do not know (continuously pushing out the shaded areas of understanding in **Figure 1**). Our experience of this pressure over the past 2 decades motivates this perspective piece, which briefly explains the historical trajectory of (theoretical and mathematical) ecology, then summarizes more recent realizations for the field (including insights from models and implications for their ongoing development) and finally concludes with our thoughts on what the future holds and what may be fruitful pathways of enquiry. While we have tried to be even handed in our discussion, much of our experience stems from marine ecosystems and we acknowledge that bias. We hope that any of our unintentional omissions are not so grievous as to detract from our intent to start a conversation about how the scientific community can go about broadening the cloth of modeling and ecology.

HISTORICAL TRAJECTORY OF ECOLOGY

The broad concepts that underpin ecology have been accepted for decades—e.g., species have heterogeneous distributions contingent on interactions with their experienced abiotic and biotic environments; resources and life spans are finite and realized ecological properties are shaped by a mix of behavior and evolution (Scheiner and Willig, 2008). Nevertheless, finding a "simple" set of rules that can be used predictively to describe those concepts has proved more challenging. There have been many contenders—either for a "grand unifying" concept or at least theories that synthesize significant chunks of ecological thought, including: island biogeography theory (MacArthur and Wilson, 1967), succession theory (Pickett et al., 1987), metapopulation theory (Hanski, 1999), food web theory (Pimm, 1982), unified neutral theory of biodiversity and biogeography (Hubbell, 2001), metabolic theory of ecology (Brown et al., 2004), biodiversity via emergent neutrality (Scheffer and van Nes, 2006), theories of macroecosystem ecology (Rose et al., 2017), and the many other theories listed in publications such as Marquet et al. (2015). Indeed, so many unified theories have been proposed that there are now pushes to unify the unified theories (McGill, 2010). Of these many ecological concepts, cross-scale macroecological theories (McGill and Collins, 2003) are one of the few that explicitly address multi-scale processes—from local interactions to large scale dynamics.

Drawing on our modeling experience, our sympathies lie with those who see strength in diversity and see "a monolithic unified theory of ecology is neither feasible nor desirable" (Loreau, 2010a,b); preferring instead to deploy the wide range of competing ideas in addressing applied ecological problems such as resource management, conservation, or restoration (Palmer et al., 2008). Much as with the debates over "top-down vs. bottom-up" control of food webs (Lynam et al., 2017), "density dependent vs. density independent" control factors (Turchin, 1995), or the relative importance of birth-death vs. movement related processes (Kondoh et al., 2016), it has been our experience that reproducing real world dynamics often involves a mix of most of the concepts, with what is/isn't important changing with the system, the dominant conditions and most importantly the question being asked. Reflecting on experiences from studying multiple ecosystems has seen us realize that there are some common features (a common "skeleton" if you will), but that, unlike physics and chemistry, each ecological system will have its particular idiosyncrasies (the "flesh" of the detail). General principles and patterns do of course exist and more remain to be found, but while we wait for those theoretical principles to be tested, as scientists servicing applied management needs, we have chosen to pragmatically combine concepts and tools as needed—i.e., the hybrid approach that is beginning to gain traction in the modeling world. This approach, highlighted in **Table 1** as a strong direction of future model development, appears to be the best means (in terms of practicality of implementation and level of model skill) of achieving the linking across scales shown by the dashed arrow in **Figure 1F**. It has certainly been the only means we have found of capturing or anticipating the emergent properties that have posed the greatest challenges to coastal resource managers. For instance, to correctly capture the responses of reef-associated fish communities to interacting environmental and fishing pressures along the northwest coast of Australia, we needed to tie mean field representations of advectable larval patches to age structured metapopulatons of settled juveniles to individual-based representations of the adult stages of key large fish species (Gray et al., 2006). Similarly, in producing models of developed coastal margins (for the purposes of envisaging potential alternative future development and management pathways) it has been necessary to combine a multitude of modeling methods to successfully represent the many ecosystem components and human uses present in these systems. For example, in a model of Patagonia developed to assist with planning for sustainable aquaculture (Fulton et al., 2018), it was necessary to couple time series (for environment drivers and economic demand) with qualitative networks (of social and ethnic aspects), statistical models (to represent the epidemiology of farmed fish), process-based analytical models (e.g., age structured metapopulation models for wild fish stocks), agent-based representations (of large marine mammals), cellular automata (for land uses such as agriculture, forestry and urban settlements) and stocks and flow representations of industrial production (e.g., mining, energy production, and manufacturing).

As the scope of the models have grown from populations to communities to ecosystems and finally socioecological systems (the central arc of points in **Figure 1F**) it has been necessary and important to draw upon an expanding range of disciplines—not just for directly relevant information on the processes to be considered (expanding from ecology to biology, chemistry, geology through to human oriented sciences like economics, sociology, psychology, etc.), but also for the new perspectives they bring. Without this expansion of perspective, we have found it impossible to successfully reproduce the history of exploited ecosystems (e.g., in south eastern Australia; Fulton et al., 2005, Fulton and Gorton, 2014).

The value of considering the world from new points of view is something ecology has struggled to achieve (with some notable exceptions, such as the interchange of ideas around game theory with economics; e.g., Riechert and Hammerstein, 1983; Brown, 2016). Ecological observation, particularly before the invention of modern remote or autonomous monitoring systems was logistically difficult. Technological advances have also not negated that observations can also be costly or protracted. These realities led to an accidental bias in the formative ecological studies, with the majority of the most influential tending to come from more accessible locations—i.e., terrestrial forests and grasslands (Elton, 1924), freshwater lakes (Tilman, 1977; Carpenter et al., 1987), or the marine intertidal (Paine, 1969); and were often situated in the northern hemisphere. While the importance of scale in ecology was appreciated on similar time scales in the marine (Smith, 1978; Steele, 1978) and terrestrial realms (Allen and Starr, 1982), the sharing and transference of ecological concepts between landscapes and seascapes has often lagged. Metapopulation theory, for example, began its development on land more than 30 years before it was considered in marine systems (Sale et al., 2016). There has also been a substantial separation in the focus of work done by practically focused ecologists working on resource management (e.g., for forestry, fisheries or pest control), who typically began from a population stand point (e.g., Russell, 1931; Hjort et al., 1933), and academic ecology which had a much earlier focus on complexity and community dynamics (e.g., Clements, 1916). Access bias also means that critical ecological processes that structure the harder to access marine systems may be under-appreciated (or unrealized).The hemispherical bias has meant that our understanding of southern hemisphere ecosystems (e.g., in the Southern Ocean) has faced challenges because aspects of the ecosystem functioning are substantially different (the northern hemisphere is dominated by continental land masses, the southern by ocean, this influences large scale current patterns, climate, temperature patterns, life histories, ecology (Chown et al., 2004), as well as levels of human occupation, exploitation and pollution (FAO, 2005; World Health Organization air pollution database available from https://www.who.int).

There are a few common ecological principles such as source-sink dynamics (Pulliam, 1988), that hold equally well in marine and terrestrial realms; whereas other processes are more obviously prominent in one context than another (e.g., habitat selection is clearly important in terrestrial forests or coral reefs, but its role in pelagic systems, while important, is not as well-appreciated). Given the different properties of the essentially two-dimensional nature of many terrestrial ecosystems vs. the three-dimensional reality of open ocean ecosystems, it is likely that theories developed in one perspective may not easily equate in the other (Steele, 1985). As highlighted by Webb (2012) some comparisons are straightforward—the same taxa in different environments, or the same process (e.g., predation) in different environments, consideration of community structure in similar environments (soils and marine sediments)—while others are less obvious [e.g., when taxa as different as whales and trees have a similar biogeochemical role, such as carbon storage and nutrient cycling (Ratnarajah et al., 2016)]. This need for creative equivalence has delayed appreciation of how some ecological properties do port between systems—as demonstrated by the importance of size as a structuring mechanism on land and sea (Yvon-Durocher et al., 2011) and the related fact that the biomass equivalence rule popularized by Sheldon et al. (1972) in the pelagic marine realm holds equally well in the 3D interstitial realm inhabited by soil communities, something registered by Ghilarov (1944) but not effectively recognized, even by size spectra specialists, until recently (Polishchuk and Blanchard, 2019).

THE MODELING TRAJECTORY

Models have played a beneficial role in taking ideas between the different realms; they have also built off ecological observations and theory to provide feedback that helps advance all the disciplines. Early mathematical analyses of ecological systems established many of the basic concepts that underlie ecology (Pacala, 1994)—such as competition (Ekschmitt and Breckling, 1994)—even when empirical evidence has been hard to source (e.g., Allee effects; Courchamp et al., 2008). Anderson and May (1979), for instance, not only used models to describe phenomena such as disease outbreaks but to emphasize how these analyses could function as a test bed for theories of spatial ecology (Ferguson et al., 1997). Marine (typically fisheries inspired) modeling has played a significant role in advancing population (e.g., as summarized in Allen, 1975) and ecosystem modeling (see review in Fulton, 2010) as well as bio-economic modeling (e.g., Clark, 1985a). Marine work has also inspired inclusion of socio-cultural aspects in models (van Putten et al., 2013) and contributed to some of the earliest work on epidemiological modeling (e.g., Anderson and May, 1978).

Initial simplistic concepts such as the Lotka-Volterra representation of interactions (Volterra, 1926; Lotka, 1932) have been refined—for example via the foraging arena concept (Ahrens et al., 2012) or the explicit relation of physiological/metabolic processes to body size. Allometric approaches, now widely used to explain ecological processes on land and sea, grew from early attempts to find simple relationships using mean body size (Yodzis and Innes, 1992). Attempts to push ecological models to new scales and embed them in larger models representing entire socioecological systems (linking with social, economic and climate components) has highlighted entirely new gaps in our understanding of system connections and feedbacks (Levin et al., 2013). Examples include how human exploitation can influence evolutionary processes on ecologically relevant timeframes (Audzijonyte et al., 2013) and how changing social-ecological conditions need to be accounted for to understand and manage regional resilience of terrestrial protected areas (Cumming et al., 2015). This has helped drive the desire to share ideas from other research fields, to help close some of these gaps—for example bringing together ecologists, economists and others to capture iterative interactions between human actions and natural system responses in fisheries (e.g., Fulton et al., 2014; Weber et al., 2019), catchments (e.g., Voinov et al., 1999) and agricultural landscapes (e.g., Münier et al., 2004; Crepin and Lindahl, 2009).

Different Modeling Focus for Land and Sea

Marine modeling has maintained a relatively steady focus on population modeling (as discussed in 2015 special issue of ICES Journal of Marine Science), biogeochemical modeling (e.g., Franks, 2002), multispecies or ecosystem modeling (e.g., Plagányi et al., 2014), as well as habitat, species, and community distributions (e.g., Cheung et al., 2009; Dunstan and Foster, 2011; Pitcher et al., 2018). Terrestrial modelers have similar interests and some shared methods, but have tended to have a different methodological focus to their efforts. For instance, statistical methods appear to have played a much larger role in some areas of terrestrial ecology, perhaps due to access to larger data sets than are often available in the ocean. Structural equation modeling, a multivariate technique useful for evaluating multivariate causal relationships, has been used to explore ecosystem responses (e.g., to climate change or human disturbance) and processes (Fan et al., 2016). Bayesian hierarchical models have also been used to great effect, not only to look at species distributions (e.g., Diez and Pulliam, 2007; Stewart-Koster et al., 2013), but also to look at ecological impacts and responses to human activities (such as to altered environmental flows; de Little et al., 2013) and to allow for the integration of experimental ecology and mechanistic (or process-based) modeling (e.g., Ogle, 2009). Bayesian Belief Networks (BBNs) have been used in both marine and terrestrial circumstances, but have perhaps had more attention in terrestrial systems. These models graphically represent probabilistic influence networks and correlative and causal relationships among variables and have been used to look at the implications of alternative management approaches (McCann et al., 2006). Some of the most substantial efforts in terrestrial ecological modeling have gone into the modeling of terrestrial biosphere (Fisher et al., 2014), including biogeochemical cycles, soil and vegetation (e.g., Rastetter et al., 1991), or landcover and associated properties—such as state and transition models of rangeland management (Bestelmeyer et al., 2017) and semi-mechanistic models of community-level biodiversity and its responses to climate shifts (Mokany and Ferrier, 2011). More recently there have been a growing number of efforts to breach the divide and share lessons between the terrestrial and marine domains (Milner-Gulland et al., 2010).

Complexity Theory Has Helped Structure Crossing Scales

Looking across both land and sea over the last 20 years, as the scope and the number of scales included in ecological studies and models expanded, two particularly useful additions to the ecological lexicon were complexity theory and network theory. Complexity theory is an interdisciplinary approach that integrates concepts from a broad range of disciplines (including chaos theory, computer science, mathematics, fuzzy logic, statistical physics information theory, non-linear dynamics, evolutionary biology, cognitive psychology, behavioral economics, anthropology, and general systems theory) which attempts to explain the behavior and evolution of common properties of complex systems such as embedding, the importance of diversity and interconnections, contextual dependence, emergent properties, and distributed control. Complexity theory brings together methods to tackle the behavior of systems (e.g., ecosystems displaying non-linear and dynamically adaptive responses) that had eluded more traditional, often equilibrium, approaches (Hastings et al., 2018). We have found this to be a particularly useful framework for dealing with the hierarchy of interactions within and across the 14 orders of magnitude in spatial scales (and the similarly large number of temporal scales) that contribute to ecosystems—from the bacterial to basin and global scales (**Figure 1**). Metapopulation concepts took the first step, recognizing within and between patch processes (Levin, 1992), but complexity theory went further and ecosystems are now clearly seen to be complex adaptive systems characterized by: feedbacks between processes occurring at different scales, amplification of responses to minor (noisy) variations, and emergent patterns (Levin, 1998; Anand et al., 2010). A powerful example of this is ecosystem patterns that are driven by ecological interactions that are themselves mediated by metabolically determined chemical signaling (Chave, 2013). The value of complexity theory as a means of solving issues of mismatches in scales of modeling biophysical systems, anthropogenic drivers, and socio-economic dynamics has been given considerable attention in the terrestrial modeling literature. For example, Parker et al. (2008) summarized the complexity of modeling land-use systems due to direct and indirect interactions and the mismatch of scales of human actions and their impacts, specifically dealing with: harmonizing models and data sets with vastly different resolutions in space and time; using expert knowledge to constrain modeled transitions; and carefully considering the level of coupling required of the biophysical and socioeconomic components—whether it is "one-way" or "fully coupled" and whether it considers only direct or also indirect links.

Network Theory—Finding Patterns and Connections

Network theory (whereby key system components and their interactions are represented by a set of "nodes" connected by "links" of varying strength) has also been particularly useful for understanding ecology from local to regional scales—allowing for characterization of trophic and habitat interactions and key player identification (Jordán et al., 2006; Bascompte, 2009; Thébault and Fontaine, 2010), as well as to predict management outcomes for interacting threats (Marzloff et al., 2016b; Baker et al., 2018; Tulloch et al., 2018), or distributed patches, such as networks of aquaculture leases (Mardones et al., 2011). Network theory has also supplied science with a powerful means of integrating information sources (e.g., by allowing for explicit connection of observations from different disciplines and with traditional knowledge) to provide new insights into system functioning (e.g., Dambacher et al., 2003). Furthermore, network theory has provided the capacity to deal with multilayer networks (spanning multiple spatiotemporal scales and other forms of ecological complexity such as ontogenetic shifts). This, in turn, has enabled analysis of interactions between the processes that operate within and between scales and the evolution of networks through space and time (Pilosof et al., 2017). Network analysis is also allowing for the identification of universal properties that govern multi-scale system behavior. Gao et al. (2016) demonstrate that the resilience of multi-dimensional complex systems are strongly influenced by the topological properties of density, heterogeneity and symmetry. This capacity to highlight common properties of multi-scale behaviors, integrating ecological and management aspects and their associated feedbacks, means that network theory is helping to fill the gaps in the diagonal spine of the diagrams in **Figure 1**. We have found network-based representations of systems (using loop analysis) such a useful means of characterizing conceptual understanding of ecosystem form and function that it is now routinely used as the first step in our modeling work.

RECENT ECOLOGICAL REALIZATIONS

The Significance of System Specificity

Whereas, finding universal (cross-scale) properties of structure and function is a comforting anchor for those trying to understand, conserve or manage the world around us, the reality is that contingent dynamics of complex systems is the recurrent theme and challenge of the new generation of ecological problems. The first step in tackling this situation has been to accept the system specificity (contextual dependence) of the outcome of some processes (e.g., evolution and food web structure; Eklöf and Stouffer, 2016) and the resulting implications for human use and management—such as the performance of ecological indicators (e.g., Dale and Beyeler, 2001; Shin et al., 2018) or natural vs. artificial marine substrata (Ferrario et al., 2016). This has also led to the realization that whereas there are core ecological properties that are universal (and codified in general modeling frameworks), system idiosyncrasies will often demand bespoke model modifications if the applied models are to faithfully capture the observed dynamics of the system in question (Fulton et al., 2004). Care must be taken to restrict this to necessary processes and guard against unnecessary over-fitting, but experience has shown that the extent to which this is an issue depends on the use of the model (whether it is for strategic or tactical questions) and the interpretation of outputs.

Systems Are Moving Beyond the Immediate Observation Record

Another step in improving the veracity of ecological models in our rapidly changing world is to understand the limitation of the observational record. One of the most commonly discussed reasons for the patchy reliability of projections based on statistical relationships is that empirical correlations often fail when moving into conditions outside the observed range (Levin, 1992; Mokany et al., 2016). Even when using increasingly sophisticated statistical approaches to ease computation demands there is still the need to build from assumptions (or preferably robust mechanistic understanding) of the phenomena being considered (Mouquet et al., 2015). Taking a theory-based approach can extend the envelope of reliability, while simultaneously assisting in the accumulation of knowledge and the reduction of uncertainty (Thuiller et al., 2013). In principle, ecology could draw on historical analogs to inform ideas and models of future change. Unfortunately, such efforts are sparse, particularly in the marine realm, as they often draw on paleontological time frames rather than simply observations from recorded history, as the degree of future environmental change may shift ecosystems into states that are governed by previously unobserved variables and interactions. Where available, fossil records have already given insights into the changing role of functional diversity, species composition and network structure with shifting pressures on ancient ecosystems and how a weakening of functional diversity exacerbated responses to later pressures (e.g., Yasuhara et al., 2008; Mitchell et al., 2012; Dunne et al., 2014; Roopnarine and Angielczyk, 2015; Pimiento et al., 2017; Lowery et al., 2018). Work on paleontological patterns of extinction underline that areas with high intrinsic risk of extinction (due the geographic range and taxonomic identity of species found there) coincide today with areas of rapid climate shifts and elevated human impacts (Finnegan et al., 2015; Pimiento et al., 2017). Paleoecological proxies—such as the examination of pollen patterns or tree ring records (Birks and Birks, 2003), or diatoms in seabed cores (Mackay et al., 2003)—can allow for reconstruction of the dynamics of ecosystems beyond the immediate observational record on to scales of 1000s of years (in particular over the Holocene), meaning they include a greater overlap with the species alive today. Models can then be tested against these proxies to see the veracity of the model's capacity to effectively capture dynamics of these species and ecosystems beyond the modern period. Iglesias et al. (2015), for example, describe how linking sedimentary charcoal data and ecological models has been used to reconstruct past fire regimes and the implications of climate-vegetation-fire linkages and drivers at different spatial and temporal scales. While such proxy-based data sets are typically sparser than modern observations, they are a lot less sparse than the fossil record.

The field of ecology will be faced with a fast-paced race to update models and understanding in an attempt to keep pace with rapid observational corrections to prior predictions. In attempting to anticipate this modeling arms race, modelers have begun to look at the inclusion of fine scale processes that influence species' responses and adaptation. Unfortunately, this is where ecological modelers encounter a number of significant challenges. It is not a simple process to incorporate sub-grid scale processes, fine-scale behaviors and phenology into ecological models; particularly those models attempting to capture the dynamics of entire ecosystems (Griffith and Fulton, 2014). It is computationally infeasible to explicitly represent the small spatial and short time scales involved (Hastings et al., 2018). Advances can be made by clever use of statistical characterizations or abstractions which influence the mechanistic model dynamics and modify outcomes on the explicitly modeled scales (Ellis and Pantus, 2001; Moorcroft et al., 2001) or to use agent-based approaches which see the "emergence" of the desired phenomena (DeAngelis and Mooij, 2005). However, even then ecology can fall short in terms of providing suitable mechanistic understanding. Environmental data is currently too coarsely resolved to support fine-grained processes (Mouquet et al., 2015). Moreover, not all ecological processes have received equal attention—mutualism, amensalism, and facilitation have received a tiny fraction of the attention garnered by predator-prey interactions (Martorell and Freckleton, 2014); and mixotrophy, which has an important part to play in marine planktonic systems, has rarely been included in models to date (Berge et al., 2017).

Both macroecological relationships (Brown et al., 2004; Cabral et al., 2017) and trait based approaches (McGill et al., 2006) appear to have strong potential as means of connecting the arrows along the spines of **Figures 1C,F**—simultaneously synthesizing cross scale processes, helping bridge the divide between models of ecosystem composition and function, and delivering larger scale patterns without requiring crippling complexity, or unreasonable computational and data loads (Blanchard et al., 2017). Even then, caution is required due to the scale-dependent role of traits (Suárez-Castro et al., 2018), the significant variation that exists around macroecological relationships (Gaston and Blackburn, 1999) and knowledge that the relationships can change dynamically (Supp et al., 2012). These very factors may help explain phenotypic responses and range edge effects (Chuang and Peterson, 2016), as well as species-specific responses to processes such as ocean acidification (Vargas et al., 2017) and localized variation in adaptation and adaptive capacity (Bennett et al., 2015). Nonetheless, they are also likely to have important implications for spatiotemporal patterns in the diversity and functioning of ecosystems and our capacity to model those patterns (Mokany et al., 2016).

Gaps in Fundamental Ecological Understanding

All of these issues act to highlight additional ecological gaps. There is still limited understanding of how ecosystem structure changes through time and space—and how the processes concur or differ between land and sea (e.g., many of the well-studied features at smaller spatial scales appear to span longer time periods on land than at sea—compare **Figure 1A** and **Figure 1B**). Nevertheless, recent advances in process-based macroecology (Cabral et al., 2017; Connolly et al., 2017) and trait-based approaches (Kiørboe et al., 2018) are making advances in terms of dynamic prediction of macroecological patterns, including across scales. Isotopic methods are helping bridge the trophic gaps at larger spatial and temporal scales (Hobson et al., 2010; Quillfeldt et al., 2010) and new metagenomic methods are being used to generate new ecosystem scale maps of active processes and biodiversity (Raes et al., 2018). As we outline above, nested network approaches are also helping to link understanding of interactions and connectivity across processes, space, and time (Pilosof et al., 2017). As an example, to support management of the deleterious impacts of crown of thorns starfish on Australia's Great Barrier Reef coral communities, ecological models are being integrated across a range of scales accounting for fine-scale Allee effects (Rogers et al., 2017) through to embedding an ecological model in a meta-community reef network model incorporating large scale processes such as cyclone and terrestrial runoff from agriculture practices (Condie et al., 2018).

Unfortunately, it remains the case that there is little empirical understanding of the true natural structure and interactions in many systems (Griffith and Fulton, 2014). Science often likes to begin from a "no effects" case and then build incrementally from there, but in ecology that is proving exceptionally difficult to do given humanity's pervasive footprint (Halpern et al., 2015). Palaeoecological studies (that aim to reconstruct ancient webs prior to human influence) are making advances (Mitchell et al., 2012; Yeakel et al., 2013), but few systems have survived a human signature (Yeakel et al., 2014). This means we are starting from partial information when trying to decipher what are healthy system structures, how humans may impact those and what to expect as we either degrade or endeavor to recover ecosystems.

Socioecology Makes Ecology Look Straightforward in Comparison

The challenges above are compounded further when we move from strict ecological to socio-ecological responses. Many key processes in socioecological systems, such as those driving institutional change, have gone unrecorded and the footprint of human activities and settlements push into the combinations of time and space scales with low predictability (see the area marking out the scale of settlements in **Figure 1D**). This creates new challenges for ecology and modeling. For instance, the question of how to manage the novel ecosystems arising as a result of climate associated range shifts now bedevils resource managers, especially where valuable stocks move from one country's jurisdiction to another or where new interaction effects emerge (Pinksy et al., 2018). Recovering marine mammal stocks are causing significant issues in a number of marine systems. This is via predation pressure that may be beyond what the current human perturbed ecosystem states can support (Estes et al., 2009; Chasco et al., 2017), or are at least beyond what human users are used to or (in some cases) willing to accept, leading to tensions with local fisheries and other users (as reported in the popular media of Australia, Canada, USA, and

Chile). Moreover, contextual dependency of complex systems also means we cannot simply rewind the clock—reintroductions fail (e.g., Barkai and McQuaid, 1988) or strong hysteresis create blockages (Marzloff et al., 2016a). Key to addressing these challenges are quantitative modeling methods that can predict the consequences for the recipient ecosystem. Fortunately, significant advances have already been made on these issues in terrestrial systems (e.g., Baker et al., 2017).

Processes and Interactions—At New Scales and Cross Scale

Work with more complex and dynamic systems has also allowed ecologists to appreciate that some of the ideas fundamental to ecology, such as evolution, need expansion or revision to correctly connect their expression at the scales now being observed (see the arrow pushing to smaller scales in **Figure 1C**). For example, 20–30 years ago it was standard practice to teach evolution as a process that was irrelevant on less than effectively geological scales (disease resistance dynamics being one of the few exceptions). Ecological modelers were comfortable ignoring evolutionary drivers (i.e., those developing models for the bottom left of the diagrams in **Figure 1** typically did not bother with processes in the upper right). Suggestions that processes on ecological scales could drive observable change were strongly contested (e.g., the debate around fisheries induced evolution; Audzijonyte et al., 2013; Eikeset et al., 2016). Now, as human activity provides strong directional pressure at multiple scales, variants of Gould and Eldredge's (1977) idea of punctuated equilibrium seem to be a dynamically experienced event and there is frequent discussion of phenotypic variation, eco-evolutionary processes (Pelletier et al., 2009; Chave, 2013; Gillman and Wright, 2014; Laland et al., 2015; Watson et al., 2016; Weiss-Lehman et al., 2016), and epigenetic effects (Danchin et al., 2011; Bonduriansky, 2012; Ryu et al., 2018). Hence ecologists are realizing that their models are missing key processes. Fulton and Gorton (2014) found that to reliably reproduce recent observed ecosystem shifts in their models of south east Australia, evolution and acclimation processes (along with modification of coastlines by human activities) were needed. When those models were projected forward they led to vastly different projections of future system state than models that used only fixed parameters. In trying to validate the rate of expression of these additional approaches it was soon clear that this is one of many cases illustrating that our understanding of how the natural world operates is not as complete as we had thought. We may have had a credible grasp of the functioning of systems within certain limits and configurations, but the Anthropocene is moving our world beyond those limits, which is highlighting new or underappreciated processes and species roles (Hobbs et al., 2009). This new reality drives home that ecology lacks a universally solid foundation from which to extend existing theories and modeling approaches to easily absorb the many interacting components and scales. Moreover, for modelers it is highlighting how many of the abstractions that underpin the representation of the more complex ecological interactions and processes are unvalidated, impossible to measure directly and based on equilibrium concepts that are not compatible with the dynamically transient nature of changing ecosystems influenced by both human use and environmental shifts.

A good example of where this realization hits home is in our capacity to reliably model the changing distribution of species. There is no denying that the science has come a long way and can capture large scale observable patterns on land and in the oceans (Follows et al., 2009; Olsen et al., 2016). This has been made possible in part because modern tracking technology means we can now track animal movements to a degree unheard of only 5 years ago (Kays et al., 2015; Klein et al., 2019; Lowerre-Barbieri et al., 2019). However, research is still struggling to link physiological tolerances to multivariate habitat dependencies (Bozinovic and Naya, 2015), life-history and ecological traits (dispersal capability; Bates et al., 2014) and species co-occurrence (Cazelles et al., 2016) in order to reliably predict range shifts, habitat contraction or expansion and the role of adaptation in these processes. For example, while zooplankton assemblages in the North Atlantic have conserved their thermal niches and tracked isotherms poleward (e.g., Chust et al., 2013), spatial distributions of Southern Ocean mesozooplankton communities have not advanced polewards, despite surface layer warming in the Atlantic sector over at least the past six decades (Tarling et al., 2017), contrary to the assumptions of species distribution models (e.g., Mackey et al., 2012). In addition, global models often do not perform well for the poles in particular, but can also require tailoring (in downscaling efforts) to particular regions—where the system specificity proves particularly strong (e.g., Bryndum-Buchholz et al., 2018).

Some issues of scale mismatch and interconnection have been solved within terrestrial environments, with methods developed that scale-up individual-based models of fine-scale physiological and ecological processes and dynamics to global ecosystem scales (Moorcroft et al., 2001), including embedding fine-scale vegetation demography within Earth Systems Models (e.g., Fisher et al., 2018) to account for changing climatic conditions. Integral projection models (e.g., those developed by Coulson, 2012) actively try to address the interplay of population ecology and evolution (quantitative genetics). These models clearly show that phenotypes and life histories (and thus parameters in ecological models) will change as adaptation occurs, leading in turn to changing population dynamics (Coulson et al., 2015) and likely ecosystem interactions (Forestier et al., in press). The modeling approach is being extended to cope with novel environmental conditions by linking it with dynamic energy budget models (Smallegange et al., 2017).

Advancing ecological modeling means acknowledging the gap in understanding around cross-scale processes and interactions (represented by the dashed line in **Figure 1C**), which are only beginning to be appreciated (e.g., Donadi et al., 2017). Traditionally, ecological questions tackled by experimentation have gained tractability by simplifying the circumstances, focusing on single taxa or functional roles, or limited spatial scales. However, recent studies are finding multitrophic richness and abundance strongly influence ecosystem functioning (Soliveres et al., 2016; Ushio et al., 2018). This has likely meant there has been an under-appreciation of the role of diversity in ecosystem functioning (Soliveres et al., 2016), slowing the merging of the composition and functional modeling communities. Similarly, there has been an under-appreciation of the functional role of cross-scale contributions of diversity to functional resilience of ecosystems. For example, there has been much discussion around algal-coral dynamics and resilience to disturbance in tropical reefs (e.g., Hughes et al., 2007), but it wasn't until 2016 that cross-scale processes were considered explicitly (Nash et al., 2015). That study provided empirical support for resilience as a result of the combined effects of cross-scale and functional redundancy—whereby multiple species within a functional group perform a functional role at different spatial scales (cross-scale redundancy) and respond to disturbance in different ways (i.e., functional redundancy via response diversity). Appreciating this involves understanding the contributions of trait diversity (e.g., in dispersal at different life history stages), the implications for the species scale of operation, and how that affects ecosystem properties (Massol et al., 2016). Furthermore, when trying to understand the outcomes of perturbations and predict ecosystem responses there is the simultaneous need to consider the spatial and temporal dimensions of disturbances (i.e., what scales they cross) and how that interacts with these multifaceted forms of redundancy—e.g., can dispersal act as a rescue mechanism or does patch fragmentation or even a regime shift occur (Zelnik et al., 2018)? Bartlett et al. (2016), for example, found that ecosystem responses (both in terms of abundance and compositional structure) were mediated by synergistic interactions between habitat loss and fragmentation; the relative sensitivity of fauna (e.g., large-sized animals) to fragmentation (as this influenced top-down processes within the trophic webs) also played in an important role.

If the contributions of such cross-scale process are to be understood, however, there is the need to be collecting data at the appropriate scales to understand what is going on (and at scales appropriate for addressing the management needs). Unfortunately, as highlighted by a number of recent meta-analyses, many ecological studies have not included a wide enough range of scales to accurately estimate the true scales of effect for particular processes and the resulting inferred ecological-environmental relationships (Jackson and Fahrig, 2015; Martin, 2018). Coming to terms with all of this complexity and avoiding mis-steps due to misplaced focus would likely benefit from a healthier marriage of experimental, theoretical, applied and model-based studies (Essington et al., 2017; see also **Table 1**). This is particularly important as ecology is not so much about identifying "one true scale" of operation, but recognizing dynamic change is occurring simultaneously across multiple scales due to multiple interacting phenomena (Levin, 1992), thus requiring multiple approaches to elucidate the true dynamics. While integration of multiple lines of evidence (e.g., field studies and ecosystem modeling) is becoming more common there is still a tendency (often due to logistical constraints) for one or the other to feel an unequal partner—ultimately short changing the effective value that can be gained from an even handed combination of the constituent players; such as where field data could provide models with information on how the relationship between predators and prey varies with environmental conditions through space and time (Griffith and Fulton, 2014).

Having worked on a number of large multi-faceted projects over the last 20 years, it is a common pattern in our experience that models are seen as an integrating factor, but that time to develop and deliver that work is concertinaed in terms of time and available resources due to delays in delivery of data or logistical hiccups. This is not about laying blame, but recognizing the plans/intent vs. reality of execution. In areas with greater funding streams, later projects can alleviate this outcome by allowing time to be made up in subsequent rounds of research. This is not the case in economically constrained nations (including Australia in terms of being able to service its entire marine estate given its relatively small human population). This means modelers have to rely on rapid and easily deployable "starting steps" (e.g., loop analysis) so that they can make the most of data as it comes along and have much of the preparatory work done ahead of polishing the final product during later stages of the project work. It also means that integration of input from multiple disciplines must be a very intentional action or "later steps" will be lost. This is often the case if human dimensions are addressed sequentially after biophysical aspects have been addressed and a model includes very simplistic representations that fall short of the dynamic richness seen in the other facets of the model. If these pitfalls can be avoided via intentional efforts to integrate "early and often" then model potential is maximized (as has been the experience in oceanographic models or earth system models, e.g., Medlyn et al., 2016), and it becomes more of an issue of sharing learnings back out to the broader group interested in that system. It is often the case that a modeler more than any other ends up with the completest view of system content, structure and function.

IMPLICATIONS AND CHALLENGES FOR ECOLOGICAL MODELING

While recognizing these shortfalls is important for going forward from an informed position, to target future steps to reduce uncertainty and improve reliability of predictions, we are not advocating a blanket increase in model complexity. There are many circumstances where building complex models is simply infeasible. Moreover, there is a significant body of work indicating that increasingly complex models are not immediately more reliable (and can often degrade in performance; Ludwig and Walters, 1985; Fulton et al., 2003a; Evans et al., 2013; Collie et al., 2016). Overly simplistic models are error prone (due to the omission of key dynamics), but highly complex models typically lead to poorer decision making—due to accumulated biases, errors and difficulty in interpreting outputs (Ludwig and Walters, 1985; Fulton et al., 2003a). A lot of intuitive insight is sacrificed when models become too complicated. Model performance is often greatest when using a minimum realistic (Butterworth and Harwood, 1991), intermediate level of complexity (Plagányi et al., 2014) that captures the essence of the main interactions (this philosophy holds even when building system models, and including or excluding components with care). In practice this means it is important to think about how we might go about capturing the essence of the cross scale connections without adding undue complexity; how to modify existing approaches or take entirely new model development directions to address the identified shortcomings of existing modeling platforms and successfully tackle cross-scale issues (**Table 1**).

Creating Credible Operational Scale Models

Operational (tactical) scale models face some of the steepest hurdles when it comes to cross-scale considerations. These models need to be tractably and transparently executed on short time scales and often with limited data sets consistent with what is available to management bodies. Yet they are being increasingly asked to address ecosystem considerations (Plagányi et al., 2014, 2018), such as the implications of the exploitation of prey species for predators or competitors (e.g., Punt et al., 2016). In terrestrial systems there have been some successes in automated near real time process-based models, but the experience in the marine realm (which typically deals with substantially more trophic levels and processes) has been quite different. Growing from the concept of including only the key interactions and processes needed to reproduce the dynamics of the phenomena of interest (Levin, 1992), "Models of Intermediate Complexity for Ecosystem assessments" (MICE) have tackled this marine systems operational challenge by employing simple formulations that are statistically fit to available data, but applied across ecological-environmental-anthropogenic dimensions, to explain the dynamics of small groups of interconnected species (Plagányi et al., 2014). This approach advances tactical management efforts to incorporate and address considerations such as climate effects (Tulloch et al., 2019), moving the modeling more and more into the scales most relevant to resource management interests (**Figure 1F**). However, hurdles remain around how to provide guidance on ecosystem structural concerns rather than stock status. The ecological and spatiotemporal coverage of these kinds of models is also being expanded by new ways of approaching ecological modeling—such as moving away from population oriented representations to size and trait based models (Blanchard et al., 2017) or equation-free mechanistic empirical dynamic models (Sugihara et al., 2012; Yea et al., 2015; Ye and Sugihara, 2016; Ushio et al., 2018).

Model Fitting and Model Performance (Skill)

As ecological models mature there has been a greater focus on the inter-related topics of parameter fitting (Kramer-Schadt et al., 2007), sensitivity analysis and model uncertainty (Pantus, 2006), model-data fusion (Kuppel et al., 2014), model skill reporting (Olsen et al., 2016), and statistical ensemble modeling (Spence et al., 2018). It is now routinely expected that at least some, if not all, of these will be provided or discussed when documenting model content and outcomes. This is however raising the issue of having sufficient data available to follow through on all aspects of the model. More typically the model is fit to the limited number of available time series (usually only available for exploited or conservation species and often patchy spatially), meaning that model reliability varies across components; which may become problematic if the relative role of the more uncertain components increases under the kinds of disturbance of interest. One underutilized means of checking ecological model skill is retrospective assessment of performance, where model projections are revisited and checked against how the system actually evolved. Given the hundreds of published and applied models it is surprising how rarely this is done (often due to the dictates of shifting funding and focus which does not provide for revisiting old sites and topics). If more is to be made of this potential reservoir of model learning—whether it is used directly to improve mechanistic models or simply to help train machine learning-based emulators—then more needs to be done in terms of having standardized protocols and making models publicly available in repositories (Melbourne-Thomas et al., 2017), much like the push for large publicly available data stores for observational data (Mouquet et al., 2015).

A closer evaluation of model skill will no doubt highlight some model shortcomings. However, when addressing cross-scale issues modelers have already identified and begun to act on some pressing issues. One long-standing aspect of multi-scale effects that has been of prime concern to modelers is the issue of appropriately capturing lags and inertia in ecological and ecosystem models (Fulton et al., 2003a). This has become even more challenging as models have grown to couple physical and socioecological processes (Österblom et al., 2013; Plagányi et al., 2014; Fulton et al., 2015). Even when just constraining the focus to lags in the ecological components, success requires considerable effort. This is because the many interacting processes within ecosystems that dictate biodiversity and ecosystem function operate on and feedback across different scales; necessitating frameworks that explicitly allow for elucidation of the mechanisms and circumstances contributing to cumulative lagged responses (Essl et al., 2015). The need for clear conceptual frameworks to support clear thinking around cumulative, non-linear and interacting effects grows larger once the dimensions (and scales) of the cumulative effects are expanded. This is evident in the growing interest in a pragmatic means of assessing cumulative impacts of human activities and other stressors on ecosystems (Giakoumi et al., 2015; Holsman et al., 2017; Jones et al., 2018; Stelzenmüller et al., 2018). Despite these limitations, the importance of linking human and ecological processes to predict future dynamics has been recognized for some time—e.g., in urban and agricultural systems (Alberti, 2008)—with advances achieved using agent-based models that couple socio-demographic, ecological, and biophysical models (e.g., Filatova et al., 2013; Fulton et al., 2015).

Non-static Model Representations

Another aspect of models that is getting much more explicit consideration is dynamic change and variability. In the past the available data and ambient conditions most often meant simplification to single parameterizations were sufficient rather than recognizing individual-level variability (such as the pioneering work by Clark et al., 2003). The directed pressures that characterize our world and expanded available observational data sets mean we now appreciate that heterogeneity is often important and can no longer be safely abstracted away. The resulting move to represent variability and dynamic change in models has come in multiple forms—from recognition of intraspecific variation within existing modeling frameworks (Moran et al., 2006; Melbourne-Thomas et al., 2011; Fulton et al., 2019), to the explicit representation of functional influences of biodiversity, acclimation, adaptation, and eco-evolutionary feedbacks (**Table 1**). In their simplest forms these processes may be included via allowing for dynamic parameterisations (Jørgensen et al., 2016). In contrast, in terrestrial dynamic global vegetation models fundamental adaptive processes (e.g., acclimation, plasticity, migration, selection, and evolution), are now being accounted for to allow for an exploration of their potential to mitigate effects of climate extremes (Scheiter et al., 2013). Some modeling frameworks are also beginning to explicitly represent evolution and its implications for ecological processes (Grimm and Berger, 2016), such as predation pressure and trait expression (Forestier et al., in press; Romero-Mujalli et al., 2019). This can create new tensions in modeling—what is the effective benefit of replacing one set of fixed parameters (e.g., around growth) with others (e.g., around rates of evolution). Modelers will, most likely, need to ponder this on a case by case basis, at least until alternative means of dealing with the representation of dynamic ecological processes are more mainstream (e.g., potentially leveraging off the model morphing approaches of Gray and Wotherspoon, 2015 discussed more below).

New Approaches to Modeling Ecosystem Structure and Function

There have also been calls to find a new form of ecosystem modeling that explicitly combines species/functional composition properties with ecosystem process representation (Griffith and Fulton, 2014; Mokany et al., 2016). The intent is to better capture how simultaneous alterations to environmental drivers and compositional diversity (e.g., via exploitation) could interact with significant consequences for ecosystem function (Loreau, 2010a; Durance et al., 2016). Existing composition- and function-based modeling approaches are individually inadequate for a number of reasons (as outlined in Mokany et al., 2016): (i) correlative compositional (biodiversity) models fail to reflect the dynamic outcome of key ecological processes; (ii) trait-based methods are hampered by insufficient information; and (iii) hybrid models that are functionally oriented (i.e., that combine models of key individual species with coarser functional groups) are incapable of tractably representing the high biodiversity present in the majority of systems (Mokany et al., 2016). How to tractably address all of these shortfalls is not yet clear as it will involve developing methods that allow for emergence of the desired phenomena, not all of which are well-understood. Some steps down this road may well have been taken—witness the number of ecological properties related to size (metabolic rate, clearance rate, swimming speed, sensory range, trophic strategy, sensory mode, body shape, and reproductive strategy), feeding mode and "jellyness" (Andersen et al., 2016). Avoiding hardwiring desired behaviors is important however. This is a hard learnt lesson by many marine trophic modelers and is why current food web models allow for the expression of shifts in dominant pathways (Shin et al., 2010). Successfully representing the interactions between system function, fine scale species composition and the implications of different forms of biodiversity within dynamic frameworks will likely involve a fresh take on ecosystem modeling and the development of customized models that integrate processes and scales relevant to both ecosystem composition and function (Mokany et al., 2016; Grimm et al., 2017). In turn, this is likely to require cross fertilization from across many modeling lineages and scientific disciplines. The value of such cross discipline inspiration is being realized in many complex system relevant domains currently, witness the burgeoning of interdisciplinary science (Nature's 2015 special volume, 525, on interdisciplinarity; McDonald et al., 2018).

WHERE TO FROM HERE

Dealing With New Sources of Data

As we have discussed above some of the key challenges facing modeling and ecology are embracing new modeling approaches, spanning more dimensions (covering more and more of the grid in **Figure 1E**) and allowing for dynamic and evolving model parameterizations and structures. Multiple nagging concerns are associated with all of these, specifically: (a) how to achieve valuable improvements without being overwhelmed with additional complexity and (b) having sufficient data at multiple scales to usefully inform and constrain the models (Mouquet et al., 2015), with the handling of uncertainty a part of this conundrum. This latter concern, of insufficient data, is not new when looking at barriers to advancing ecology—being expressed for instance by the early ecosystem modelers in the 1970s (Gurney et al., 1994; Pacala, 1994; Scheffer and Beets, 1994). In the first instance the use of cross scale models themselves will help ease the data burden. Where data are unavailable at one scale (e.g., the individual or regional scale), data can be used to assess model performance at another scale (e.g., global). This approach is being exploited in global models (e.g., see Harfoot et al., 2014 or Fisher et al., 2018).

New data sources will also help, though they will come with their own challenges. Technological advances—in terms of automation, sensor capacity, and new monitoring methods (from biochemical tracers, genomics and environmental DNA through to high resolution remote sensing)—are providing data in quantities that can overwhelm traditional methods, driving searches for new approaches that maximize utilization of these valuable resources. Learning to use this data wealth well is a key step (Durden et al., 2017), continuing the demand for the development of new methods. The ecological value of taking the time to do this cannot be overemphasized, as evidenced by the blossoming of discoveries derived from having sufficient volumes of data to deconstruct complex patterns and by marrying data across scales (Chave, 2013; Mouquet et al., 2015). Examples such as the development of close-kin mark recapture methods

(Bravington et al., 2016) showcase how new data streams can revolutionize ecological data collection on large scales and provide precision far beyond what was possible for earlier generations of ecologists. The complementary use of multiple data sources—gut contents, biochemical and isotopic tracers, and DNA—are also revolutionizing our understanding of foodweb connections (Pethybridge et al., 2018; McCormack et al., 2019) and changes through time (Young et al., 2015). This kind of utilization is important, as models (conceptual or mathematical) play a key role in bringing many data streams together; the emergence of frameworks to facilitate access and synthesis (e.g., statistical methods, data portals etc.) is beneficial to ecology more broadly.

Expanding the Scope of Models

The broader range of available datasets is also expanding the scales and processes modelers can consider (pushing out the boundary of the area marked in **Figure 1F**). Due to data constraints models have typically been constructed and tested at levels where the most detailed information exists—an approach known as the "middle-out" (Noble, 2003) or rhomboid approach (deYoung et al., 2004). Whereas this modeling approach can be an intentional developmental decision it is also often an accident of available information—meaning models have focused on the more well-understood scales and processes and missed components at the extremes (see the location of the solid dots in **Figure 1F**). In the last few years, there has been a growing appreciation of the true influence of pathogens and parasites on ecosystems (e.g., Weitz et al., 2015; Guerrero and Berlanga, 2016; Jephcott et al., 2016; Mischler et al., 2016; Preston et al., 2016; Médoc et al., 2017; Trivedi et al., 2017). It is now understood that predation and parasitism have non-additive effects within food webs (Banerji et al., 2015) and that the collective actions of metabolic processes within aggregate biofilms can have a profound influence on individual, community and ecosystem properties (Guerrero and Berlanga, 2016). Fungal and microbial communities (e.g., in soils) can interactively shape ecosystems at regional to continental scales and mediate energy and material flows at multiple temporal scales (Dighton, 2016; Trivedi et al., 2017). This means that (along with other flora and fauna) microbes play essential roles within biogeochemical cycles of water, carbon, nutrients (Schmitz et al., 2010, 2018), and trace elements (Weitz et al., 2015; Preston et al., 2016); and influence fluxes of both biomass and energy (Mischler et al., 2016), ultimately influencing temporal ecosystem dynamics and disturbance, succession, and stability relevant processes (Preston et al., 2016). Appropriately recognizing the role of the smallest denizens of ecosystems, which also have the most rapid expression of adaptive capacity, will likely be extremely important as we consider the implications of global change for ecosystems.

Bringing together the disparate fields necessary to realize these and other mechanisms behind ecological feedbacks in the earth system is likely to be a key focus of the activities of Earth system groups over the next few years and of the coming UN Decade of Ocean Science. The effort to link changes in energy flow through food webs to carbon uptake and climate regulation will likely involve giving more consideration to mechanisms previously accorded marginal attention—such as the role of consumers, including top predators, in mediating productivity (Estes et al., 2011), either directly via contributions to nutrient cycles (Pastor et al., 2006; Nicol et al., 2010) and physical mixing in the ocean (Katija and Dabiri, 2009), or indirectly via the "ecology of fear" (where signs of predators in an area can modify prey behavior even in the absence of direct attacks; Wirsing and Ripple, 2011). It may even involve the exploration of small scale interactions between seemingly unconnected processes—such as the potential for fisheries (which can have cascading effects down to the plankton, Reid et al., 2000) to influence local atmospheric processes via plankton-mediated processes. Examples include dimethyl sulfide production and the influence on cloud formation (Malin et al., 1992), or the carbon cycle (Monroe et al., 2018). Model coupling—interactively joining models of different types and scales (physical, biogeochemical, trophic, habitat, human use)—will likely also be a strong feature of the coordinated work across disciplines, as already seen in some terrestrial modeling (e.g., Alberti, 2008) and in earth system modeling efforts to date (Prinn, 2012; Fisher et al., 2014, 2018).The evolution of ecosystem modeling has already been marked with a shift from one-way coupled drivers influencing small groups of species to more systematic representations of interaction networks characterized by multiple pathways and processes (Shin et al., 2010), allowing for significant growth in modeling capacity.

Handling Uncertainty

This increase in capacity has seen models used in an increasing number of roles—not just academic, but as decision support (Condie et al., 2005; Plagányi et al., 2014) and as a means of inputting advice to international initiatives, such as the IPCC (e.g., Hartmann et al., 2013). This has put the effective handling of uncertainty front and center. A full review of how that field is developing is beyond the scope of this paper, but it is worth noting that recognition of structural uncertainty (i.e., uncertainty pertaining to the model assumptions, formulation, and internal connections) has been a key part of these modeling efforts. The use of Bayesian approaches and model ensembles to provide ranges of possible outcomes across model types is now becoming more common (e.g., Gharbia et al., 2016). The first use of model ensembles was in economics (Bates and Granger, 1969) but has now become a staple of many fields—economics, systematics, meteorology, and climatology—and is often now used when considering shifting species distributions (e.g., Araújo and New, 2007) or terrestrial ecosystem impacts (Baker et al., 2019). Model intercomparison projects (MIPs; e.g., Warszawski et al., 2014; Lotze et al., 2019) are also bringing together the world's modeling community to share outcomes, lessons and understanding, accelerating model improvements and rigor. This kind of multi-model approach has been relatively easily accepted, as it is a logical outgrowth of the even more familiar parameter variation form of sensitivity testing and uncertainty analysis.

New Dynamic and Hybrid Modeling Approaches

By comparison, the future development of multi-scale and hybrid approaches (**Table 1**) will require ecology to move well beyond its current "comfort zone." Most disciplines begin with simplifying assumptions as a foundation to build from and ecology has been no exception—note the simplicity of the Lotka-Volterra assumptions for predators and prey. Indeed, the vast majority of extant ecological and ecosystem models still assume fixed parameterisations and even for those that don't (e.g., Jørgensen, 2012) they most often assume fixed functional relationships and formulations. This means, as touched on above, that more remains to be done in terms of representing appropriate levels of variability and dynamic change. Under perturbation, ecological systems can exhibit significant structural reorganization and shifts in the dominance of species and processes. Modeling techniques attempting to appropriately represent this magnitude of response may well require not just changing parameters but dynamically changing structural components (the network connections) and process expression (e.g., functional forms), and potentially even shifting model scales as the simulated systems evolve.

In terms of the approaches that can facilitate the representation of fully dynamic structural properties of models and ecosystems, both allometric food web models (Curtsdotter et al., 2017; Reum et al., 2019) and network approaches show promise. Experimentation with dynamic network approaches is allowing for the representation of dynamic restructuring behavior (Bryden et al., 2012), reflecting changes in the properties of system components (e.g., individuals or species) and the effect that has on interactions. These approaches (and other model types that allow for shifting food web links) have the potential to capture some of the ecological surprises that arise in changing ecosystems; such as context-dependent reversal of predator-prey roles, as has occurred between sprat and cod in the Baltic (Köster and Möllmann, 2000) as well as lobsters and whelks on Marcus Island in South Africa (Barkai and McQuaid, 1988).

One approach to spanning ecological scales is to explicitly link models that resolve processes and function at different resolutions (Walpole et al., 2013). A number of ecosystem models already do this to differing degrees and the approach has significant potential—at least up to a point. While it is possible to follow a common formulation regime to resolve neighboring scales, it becomes more difficult as the number of scales grows. The kinds of challenges to continuing those approaches as we move to the smallest and largest scales have already been touched on in previous sections. A promising alternative approach for tackling multiple scales and dynamic ecological phenomena is the hybrid modeling approach (**Table 1**). This modeling method sees modelers create ecological systems models by combining multiple modeling approaches from multiple disciplines (e.g., system models, process-based representations, Markov chains, Bayesian networks, cellular automata or other agent/individual based approaches, statistical models (including multivariate and Bayesian methods discussed previously), partial differential equation based physical or biogeochemical models, geographic information systems and approaches from artificial intelligence, or machine learning algorithms). This approach has been a very useful step toward grappling with multi-scale complexity of ecosystems or broader socioecological systems (McDonald et al., 2008; Parrott, 2011). Use of such mixed model formulations has matured over the past 20 years, where it started from the humble beginnings of using empirically derived functional forms or correlative statistical approaches to represent more poorly known system components or ecological processes (Fulton et al., 2003a). This combined approach is being advocated strongly as additional scales and processes are embraced in ecological models—for example in implementing integrated models of ecosystem composition and function (Mokany et al., 2016) or considering socioecological systems (Melbourne-Thomas et al., 2017). Taking a hybrid approach allows for the synthesis of many kinds of data from many different sources (Cressie et al., 2009), thereby fostering greater understanding (Mouquet et al., 2015) by providing an interface across disparate scales, phenomena and disciplines (Levin, 1992).

This flexible hybrid approach allows for the selective representation of each component of a system in the "currency" (spatiotemporal scales, units, complexity of detail) that best captures that component and maximizes the overall model utility (Gray and Wotherspoon, 2015). New mathematical breakthroughs have shown that it is possible to go still further, to allow for truly dynamic model structures that shift in representational form as the dominant components and processes operating in the system change (Gray and Wotherspoon, 2015). These new approaches allow sub-models to change their form (e.g., from differential equations to individual based) conditional on their own state and the states of the other system components that they are directly or indirectly interacting with. For example, moving from a population level representation to an individual-based model and back as migrating animals encounter a contaminant plume (Gray and Wotherspoon, 2012), or any other event where heterogeneity in a process may be important for the system level outcome. The results of these early efforts indicate that allowing for such switching forms is not only feasible but beneficial in terms of fidelity to observed real world dynamics and the computational efficiency. Fine scale detail is only retained when it is needed, when fine scale phenomena dominate, with the statistical summaries saving that detail in a useful state during periods when coarser representations are sufficient as dominant processes are occurring at higher scales. While the tree-based mathematics and coding languages required to develop such models are still under active development, the potential seems vast for addressing more scales while keeping model complexity tractable. In addition, marrying such methods with the growing fields of artificial intelligence and neurocomputing could see fluidly self-mutating model structures that allow ecologists to delve seamlessly into and across all the spatiotemporal scales. This push for new methods is not to say simpler models should be universally abandoned, but that new approaches should be added to the suite of tools available to expand our capacity to look at questions from all relevant angles.

CONCLUSIONS

All of the roles that models have traditionally had in ecology—explanatory and predictive—will be just as important going forward. The utility of models as thinking tools will be needed for interpreting new and novel situations, where the magnitude of disturbance potentially highlights how strong the links between scales can really be. In addition, it is already clear that models will be central aids for navigating adaptation and equitable, sustainable societal outcomes. In our experience, the changing tenor of the questions being asked of (socio)ecological models over the course of the last 20–30 years clearly shows that global change is already presenting decision makers with increasingly complex and fraught decisions. The volume of the safe operating space is being squeezed (Steffen et al., 2015) and models are needed to help understand how to navigate a world where transient dynamics rather than equilibrium assumptions are most relevant. Hence, we posit that some of the key challenges facing modeling and ecology involve embracing new modeling approaches and data streams, spanning more dimensions, filling the gaps at the smallest and grandest scales, and allowing for dynamic and evolving model parameterizations and structures (**Table 1**).

Ecology has been built by generations of scientists concerned with the dynamics of ecosystems and the mechanisms shaping the spatial and temporal patterns that characterize them (Levin, 1992). Now the scales considered are expanding, complementing traditional foci with an interest in new scales (large and small), new processes, and new analytical and modeling methods, may also require rethinking the goalposts of progress in ecological science (Currie, 2019). We've come a long way, but as we outline in the sub-sections above, there is still a long way to go, especially given growing anthropogenic pressures and the resultant rates of change in socioecological systems. We summarize gaps in fundamental ecological understanding that widen further when considering socio-ecological responses as well as emerging needs to handle uncertainty. Moreover, large gaps are evident in ecological understanding of entire fields of research, such as the influence of pathogens and parasites on ecosystems. Most of the competing extant model formulations overlap and equally explain the bulk of conditions, but the devil has been in the detail at the extremes (Fulton et al., 2003b). Unfortunately, we are increasingly living in a world where we are pushing toward extremes. Closing the gaps in future ecological work will necessitate understanding mechanisms behind ecological feedbacks in the earth system. Consequently, in the coming decades, ecology will be spending a lot of time weaving those new scales and new lessons into its lexicon of understanding.

AUTHOR CONTRIBUTIONS

EF conceived of the paper. All authors contributed to writing it (agreeing on content of what became **Table 1**, concepts included in what ultimately became **Figure 1**). While VT did bring in extra terrestrial content, in actuality all authors contributed to the ideas, writing and links to broader literature contained in the revised text.

ACKNOWLEDGMENTS

Thanks are due to the many mentors and collaborators who have discussed modeling concepts and fixes with us through the years. In particular the contributions by Tony Smith, John Parslow, Carl Walters, Simon Ferrier, Karel Mokany, Asta Audzijonyte, George Branch, Doug Butterworth, and John G. Field. In particular, we would like to sincerely thank E. J. Milner-Gulland for some very insightful comments on a draft of this paper.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

REVIEW
published: 27 May 2020
doi: 10.3389/fevo.2020.00092

Allometric Trophic Networks From Individuals to Socio-Ecosystems: Consumer–Resource Theory of the Ecological Elephant in the Room

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A well-known parable is that of the blind men studying an elephant each of which assert the elephant is the part they first hold in their hands, e.g., "rope!" says the tail holder while the leg holder asserts "tree!" The various subdisciplines of ecology appear similar in that we each engage in our enthusiastic but at least somewhat myopic study with remarkably limited agreement or even discussion about the overall system which we all study. Allometric trophic network (ATN) theory offers a path out of this dilemma by integrating across scales, taxa, habitats and organizational levels from physiology to ecosystems based on consumer-resource interactions among co-existing organisms. The network architecture and the metabolic and behavioral processes that determine the structure and dynamics of these interactions form the first principles of ATN theory, which in turn provides a synthetic overview and powerfully predictive framework for ecology from organisms to ecosystems. Beyond ecology, ATN theory also synthesizes eco-evolutionary and socio-ecological research still largely based on consumer-resource mechanisms but respectively integrated with different processes including natural selection and market mechanisms. This paper briefly describes foundations, advances, and future directions of ATN theory including predicting an ecosystem's phenotype from its community's genotype in order to accelerate more predictive and unified understanding of the complex systems studied by ecologists and other environmental scientists.

Keywords: ecological networks, synthesis, prediction, consumer resource dynamics, allometry, food webs, mutualistic networks, stability

Edited by:
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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *28 March 2019*
Accepted: *20 March 2020*
Published: *27 May 2020*

Citation:
Martinez ND (2020) Allometric
Trophic Networks From Individuals
to Socio-Ecosystems:
Consumer–Resource Theory of the
Ecological Elephant in the Room.
Front. Ecol. Evol. 8:92.
doi: 10.3389/fevo.2020.00092

INTRODUCTION

The parable of the blind men and the elephant (Saxe, 2016) describes one of the most compelling and widely known metaphors for scientific unification (e.g., Himmelfarb et al., 2002; Cohen et al., 2003). The millennia-old parable ridicules the different religions that adamantly maintained disparate theologies about a single god on the Indian subcontinent. Probably the most famous English version of the parable is the poem written by J. G. Sax in the mid 1800's (**Figure 1**) that concludes "And so these men of Indostan disputed loud and long, . . .though each was partly in the right, and all were in the wrong!" Ecology and its many subdisciplines share disconcertingly many similarities with this parable. Perhaps most strikingly is the lack of explicit discussion among

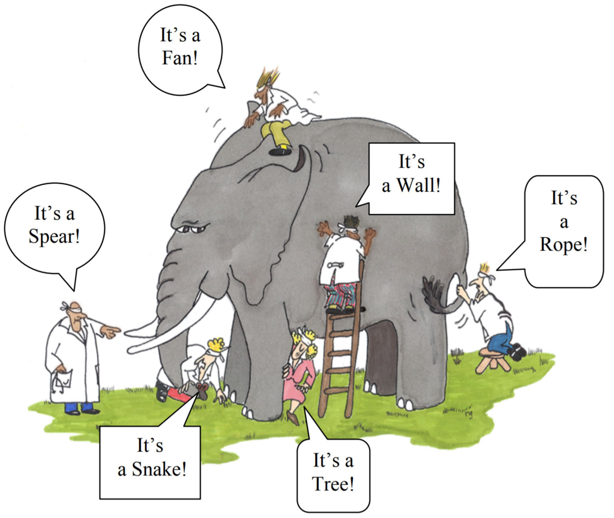

FIGURE 1 | Blind people "seeing" the elephant (reproduced with permission from Himmelfarb et al., 2002).

subdisciplines of how different subdomains of ecology fit together to form a more unified concept of ecological systems. Allometric Trophic Network (ATN) theory (Brose et al., 2006b; Martinez et al., 2006; Otto et al., 2007; Berlow et al., 2009; Boit et al., 2012) helps fill this void by providing a synthetic mechanistic description of ecological systems that integrates the physiology and behavior of organisms with their interactions among other organisms scaled up to the many species and interactions that determine the behavior of complex communities and ecosystems (**Figure 2**).

ATN theory (**Figure 3** and **Box A**) pursues such advances by building upon the metabolic theory of ecology and its emphasis on unification across scales (Brown et al., 2004). ATN theory does this by integrating metabolic theory with a theory of trophic networks comprised of organisms consuming resources produced by other organisms (e.g., food) and, in case of autotrophs, the environment (e.g., sunlight, water and inorganic chemicals). This theory holds that organisms' existence, abundance and dynamics critically depend on these same properties of their consumers and resources. ATN theory also embraces the importance of metabolic rates in determining the rates of organismal activity and the central tendency of mass-specific metabolic and production rates to consistently scale with body size over 20 orders of magnitude (Brown et al., 2004). This range includes practically all the organisms disparately studied by subdisciplines separated according to taxonomy (e.g., microbial, plant, animal etc.), habitat (terrestrial, freshwater, marine, etc.) and geography (temperate, tropical, montane, etc.). However, in contrast to its name, the metabolic theory of ecology appears to be primarily a theory of organismal physiology controversially based on how nutrients and waste are transported within organisms (Price et al., 2012). Though metabolism closely relates to many phenomena from organismal locomotion to the global carbon cycle (Marquet et al., 2004; Allen et al., 2005; Schramski et al., 2015), the role of the metabolic theory of ecology in the 'elephant' (**Figure 1**) that is ecology (**Figure 2**) deserves more active and explicit attention. A description of what the science of ecology is and its need for scientific unification provides important context for such attention.

ECOLOGY AND SCIENTIFIC UNIFICATION

A straightforward definition of ecology is a biological science focused on the study of organisms interacting within their environment (Odum, 1969). This defines ecology and its focus on interacting organisms much like cellular and molecular biologists define their discipline as the study of biological cells and their molecules and physiology defines itself as the study of organisms and their parts. While including environment in definitions of ecology may seem gratuitous, such inclusion emphasizes that ecology's focal entities, i.e., organisms, appear more exposed to, and driven by, the spatial and temporal variation in their abiotic environment than are organisms' physiological and molecular components whose biotic environment helps buffer these components from such variation. The influential Cary Institute extends ecology's focus to this abiotic variability by defining ecology as: "The scientific study of the processes influencing the distribution and abundance of organisms, the interactions among organisms, and the interactions between organisms and the transformation and flux of energy and matter" (Cary Institute Definition of Ecology, 2019). While this broad definition usefully emphasizes abiotic processes such as climate and hydrological mechanisms, ATN theory focuses on the biological core of ecology involving interacting organisms and then considers abiotic and other mechanisms beyond simple forcing functions as interdisciplinary extensions beyond this core.

However defined, few see ecology as scientifically unified (Scheiner and Willig, 2008) and instead many see ecology as "a mess" (Lawton, 1999; Vellend, 2010) with only a "few fuzzy generalizations" (Simberloff, 2004). To some, this suggests that ecologists should embrace the "elegant chaos" of ecological systems along with the "non-predictive side of their science" (Anonymous, 2014) that purportedly achieves understanding without the power to successfully predict (Pickett et al., 2010). Such perspectives effectively set ecology, especially community ecology, not only apart from other biological disciplines but also apart from natural sciences in general and what distinguishes science from other social activities (Evans et al., 2012). Eschewing such exceptionalism, ecology needs scientific synthesis and predictive success simply because it is our mission as scientists to create and test generally predictive theory about the entities we study (Evans et al., 2013; Marquet et al., 2014). Physics achieved it with Newton's laws of motion. Chemistry achieved it with the periodic table of elements. Molecular biology achieved it with the transcription and translation paradigm. Evolutionary biology achieved it with Darwin's theory of natural selection.

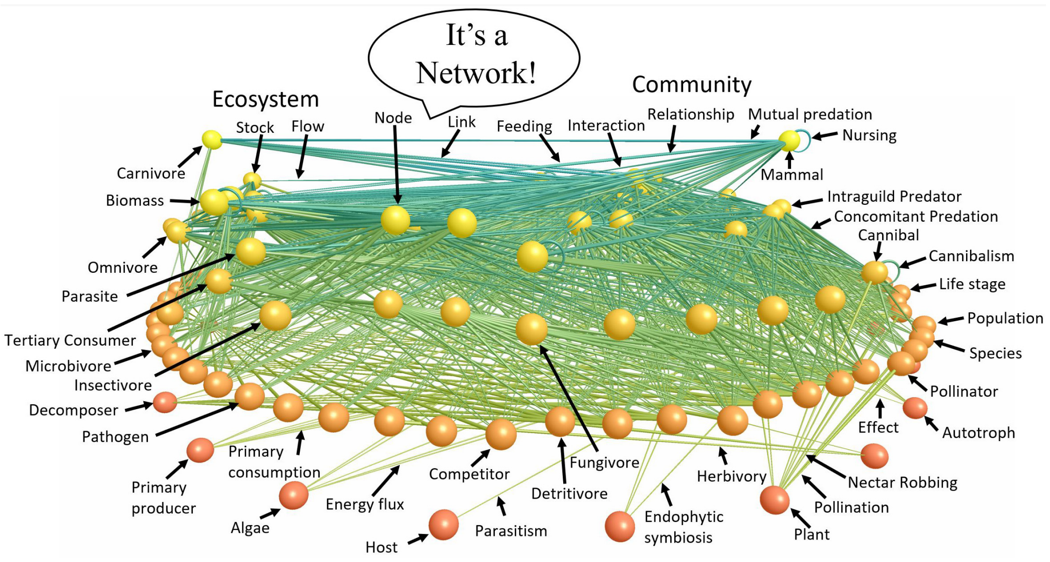

FIGURE 2 | A food web labeled with terms describing different components and aspects of the network. Nodes of the network are vertically arranged according to trophic level with autotrophs at the bottom and upper level carnivores at the top. Links between nodes represent feeding relationships. The various terms characteristic of ecology's various subdisciplines that point to the parts of the ecological network emphasize that ecological subdisciplines study very similar entities from different perspectives. ATN theory helps synthesize these subdisciplines by focusing on the structure (**Figure 3**) and dynamics (**Box A**) of ecological networks such as that of Little Rock Lake (Martinez, 1991) visualized (Yoon et al., 2004) and figuratively labeled here.

In each of these cases, an evolving theoretical core has been identified that synthesizes and clarifies the nature of vast swaths of the entities each discipline studies and the mechanisms responsible for the behavior of these entities. Such rigor and understanding allows these disciplines to generally understand and precisely predict phenomena within their domains from the creation of the universe to healing humans from inherited diseases. Few would claim that ecology has achieved such scientific success but a good first step may be more fully acknowledging the success it has achieved (Scheiner and Willig, 2008).

Scientific unification is perhaps best indicated by theory that achieves both broad and precise predictive power within a discipline's domain (Kitcher, 1989). Given this perspective, humans have already achieved much ecological understanding as indicated by the incredible success of humans in becoming the most abundant and widely distributed animal species on the planet (Bar-On et al., 2018). We have achieved this by developing an increasingly powerful theory of consumer-resource interactions among organisms within many different environments. Indeed, we define our earliest societies in terms of these interactions as hunter-gatherers. These societies developed sophisticated understanding of interactions among organisms and the environment that determine the distribution and abundance of organisms that they consumed and were consumed by. This understanding critically included creating and manipulating fire as a means of increasing the variety and palatability of humans' food and of protecting humans from predation. Early human societies also used fire as a means of increasing the abundance of their food by burning forests and grasslands in order to provide more resources for our prey and clear habitats of hiding places for our predators. Our understanding of consumer-resource theory continued to progress through the development of agriculture and the green revolution through to current advances in epidemiology, vaccines and other medicines that help prevent our microbial consumers from decimating our populations.

This is all to say that purported limits to ecological understanding appear unduly limited (Scheiner and Willig, 2008) by a myopic and somewhat narcissistic focus on the last century or less of what western science explicitly labels as "ecology" but exclusive of much of that within its defined domain of organisms interacting within the environment. While our understanding lacks much of the rigor and general precision that theory has achieved in other physical and biological sciences, our perhaps excessive fitness suggests that what ecology may not lack is basic understanding of which mechanisms are responsible for the structure and function of ecological systems including the distribution and abundance of organisms. Such basic understanding of physics was held by farmers before Newton who knew the force of two horses could carry a cart up a hill faster than one horse. Similarly, humans centuries ago knew well how interacting organisms maintain themselves within their environment and accurately predicted the behavior of organisms based on mechanistic understanding of consumers and their resources. Beyond this broad and somewhat imprecise yet powerful understanding of the critical need for organisms to consume essential resources, the lack of a rigorous theory that formalizes consumer-resource or other mechanisms into a more general and precisely predictive framework is what distinguishes ecology from more unified sciences.

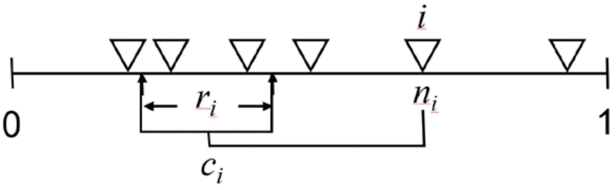

FIGURE 3 | Diagram of the niche model from Williams and Martinez (2000). This model formalizes the theory that the primary mechanisms responsible for food-web structure are the bioenergetic processes that create a trophic hierarchy based on autotrophs from herbivory through omnivory and carnivory and biophysical processes that constrain consumers to feed on species within a contiguous section of this hierarchical niche space. The one-dimensional axis from 0 to 1 represents this community niche space. The model's two input parameters are the number of species (S) and complexity in terms of directed connectance (C = # of links/S^2). Each of S species (e.g., S = 6, each shown as ∇) is assigned a random "niche value" (n_i) drawn uniformly from the interval [0,1]. Species higher on axis tend to be at higher trophic levels than species lower on the axis because species i consumes all species within a range (r_i) that is placed by uniformly drawing the center of the range (c_i) from $r_i/2$ to the lesser of n_i or 1- $r_i/2$. This placement keeps all of r_i on the niche axis and permits looping and cannibalism by allowing up to half r_i to include values $\geq n_i$. Species lower (higher) on the axis tend to be more specialized (general) because the size of r_i is assigned by using a beta function to randomly draw values from [0,1] whose expected value is 2C and then multiplying that value by n_i, expected E(n_i) = 0.5, to obtain the desired C. A beta distribution with $\alpha = 1$ has the form $f(x|\ 1,\beta) = \beta(1-x)^{\beta-1}$, $0 < x < 1$, 0 otherwise, and $E(X) = 1/(1+\beta)$. In this case, $x = 1-(1-y)^{1/\beta}$ is a random variable from the beta distribution if y is a uniform random variable and β is chosen to obtain the desired expected value. This form was chosen for of its simplicity and ease of calculation and it provides for a large number of different network structures similar to the number expected due to maximizing entropy (Williams, 2010). The fundamental generality of species i is measured by r_i. The number of species falling within r_i measures realized generality. The species with the lowest niche value and other species who happen to have no species that fall within their feeding range are assigned to the first trophic level. Assuming species tend to be larger than their resource species, the niche model gives rise to allometric degree distributions where larger bodied species tend to be at higher trophic levels, more generalized, and have fewer consumer species than species at lower trophic levels. Such degree distributions have been found to be highly stabilizing which allows for coexistence for many more species than food webs without such degree distributions (Brose et al., 2006b; Otto et al., 2007; Kartascheff et al., 2010; Digel et al., 2011; Yan et al., 2017). Overall, the niche model has been widely used to generate realistically structured and dynamically stable food webs while developing and testing allometric trophic network theory.

ALLOMETRIC TROPHIC NETWORK THEORY TO THE RESCUE?

Allometric trophic network (ATN) theory pursues such rigor and synthesis by asserting that the mechanisms responsible for the basic structure (**Figures 2**, **3**) and dynamics (**Box A**) of ecological networks concerning trophic hierarchy from plants through carnivores and their feeding niches can be described in terms of "simple rules [that] yield complex food webs" (Williams and Martinez, 2000). A theory of network dynamics was built upon this simple theory of network architecture (Williams and Martinez, 2004b) by pursuing the strategy of a relatively simple bioenergetic theory whose "ultimate goal is to use these consumer-resource models as building blocks . . . for more complicated systems involving many interacting species" (Yodzis and Innes, 1992, p. 1152). This strategy was pursued both theoretically (Williams and Martinez, 2000; Brose et al., 2006b; Martinez et al., 2006; Otto et al., 2007; Schneider et al., 2016) and empirically (Dunne et al., 2008, 2013; Berlow et al., 2009; Boit et al., 2012; Banks et al., 2017; Jonsson et al., 2018; Curtsdotter et al., 2019). Theoretically, it built upon broader mechanistic consumer-resource theory of few interacting populations (Rosenzweig and MacArthur, 1963; Yodzis and Innes, 1992; Holland and DeAngelis, 2010; Lafferty et al., 2015) by scaling up such interactions to many species within whole systems represented as complex networks (Pascual and Dunne, 2006; Thompson et al., 2012). This formalizes relationships among diverse populations and different ecological subdisciplines while describing an overall vision of the 'elephant' that unifies the different parts studied by different ecologists (**Figure 2**). This vision is, given the essential metabolic requirements for life, that a network of the consumer-resource relationships forms a more general and precisely predictive framework for understanding organisms interacting within their environment. Philosophically, this vision holds that "The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns" (Levin, 1992, p. 1943). Conceptually, ATN mechanisms involve networks with more or less contiguous diets hierarchically structured according to trophic level (Williams and Martinez, 2008) and body-size (Dunne et al., 2013; Brose et al., 2019a) whose consumer-resource interactions proceed largely at metabolically determined rates with consumption rates saturating at high levels of resource abundance (Yodzis and Innes, 1992; Williams et al., 2007). The tractability and empirical base of this vision rests on the major efforts ecologists focus on identifying organisms along with their body sizes and interactions within practically all habitats ecologists study. Broad agreement among ecologists about organisms and their interactions facilitates frequent and relatively consistent collection of these data. For example, ecologists generally aggregate organisms into functionally or taxonomically identified populations (Martinez, 1991), record their body size and type (e.g., vascular plant, vertebrate endotherm, etc.), and typically link these aggregates according to their consumer-resource interactions. The links most often document direct feeding interactions (McCann, 2011) between prey and their predators, plants and their herbivores and mutualistic partners (Bascompte and Jordano, 2013), and other biophysical consumer-resource interactions responsible for negative (Tilman, 1982; McPeek, 2019) and positive (Bruno et al., 2003; Holland and DeAngelis, 2010) effects species have on one another. Such general agreement about the nodes and links increases the rigor of quantitative comparison of ecological networks among almost all habitats (**Figure 2**) by increasing methodological consistency among the data compared. A major challenge to the completeness of such data involves the "dark matter" of biodiversity comprised of microbes that are invisible to the naked eye and feed without engulfing (Purdy et al., 2010; Weitz et al., 2015). Still, this is a unifying challenge, at least methodologically, due to the presence of microbes in all habitat types and the ability of tools such as protein sequencers to similarly address the challenges among

BOX A | Allometric trophic network (ATN) theory's master equations.

ATN theory asserts that population size is primarily determined by balancing losses to consumers and metabolic costs with gains from autotrophic production and heterotrophic food consumption. As such, the architecture of consumer-resource interactions among species and their rates of resource consumption and production are the central focus of ATN theory. This core theory is formalized as a set of ordinary differential equations (ODEs) originally developed and applied to a 2-species food chain (Yodzis and Innes, 1992), and later extended to *n*-species (Williams and Martinez, 2004a; Williams et al., 2007), plant nutrient dynamics (Brose et al., 2005a,b), and then further extended to include age-structured populations (Kuparinen et al., 2016), nutrient recycling through detritus (Boit et al., 2012), growth inefficiencies (Boit et al., 2012; Kath et al., 2018), and pollinator's reproductive services to plants (Hale et al., 2020). The following ATN equations and description was developed for fisheries applications (Kuparinen et al., 2016) and lacks the explicit dynamics of plant nutrients. These equations and several key parameter values are presented to describe their basic structure as well as their flexibility in being developed for different applications e.g., the addition of population structure needed for modeling fishing pressure on adults within populations. These three ODEs model the dynamics of (1) producers, (2) consumers, and (3) detritus:

$$\frac{dB_i}{dt'} = \overbrace{r_i B_i G_i\,(\boldsymbol{B})\,(1 - s_i)}^{\text{gain from producer growth}} - \sum_j \frac{\overbrace{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}^{\text{loss to consumer } j}}{e_{ji}} \tag{1}$$

$$\frac{dB_i}{dt'} = -\overbrace{f_m x_i B_i}^{\text{maintenace loss}} + \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B})}^{\text{gain from resource } j} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}{e_{ji}}}^{\text{loss to consumer } j} - \overbrace{F_{max} S_{age} B_i}^{\text{loss to fishing}} \tag{2}$$

$$\frac{dD}{dt'} = \sum_{\mathrm{i}} \Big[\overbrace{\sum_j \frac{x_i y_{ij} B_i \mathrm{F}_{ij}\,(\boldsymbol{B})}{e_{ij}}}^{\text{ingestion of resource } j \text{ by consumer } i} \overbrace{(1 - e_{ij})}^{\text{egestion}} \Big] + \sum_i \overbrace{r_i B_i \mathrm{G}_i\,(\boldsymbol{B})\,s_i}^{\text{exudation by producer } i} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}\,(\boldsymbol{B})}{e_{ji}}}^{\text{loss to detritivore } j} \tag{3}$$

where ***B*** refers to the matrix of all biomasses, B_i is the biomass of species *i*; r_i is intrinsic growth rate of producer *i*, $G_i(\boldsymbol{B})$ is logistic growth $[1 - (\sum_{j=producers} B_{\mathrm{j}})/K]$ where carrying capacity *K* is shared by all autotrophs; s_i is the fraction of exudation and/or exfoliation; x_i is the mass-specific metabolic rate of consumer *i* usually estimated by allometric scaling; y_{ij} is the maximum consumption rate of species *i* feeding on *j*; and e_{ji} is the assimilation efficiency describing the fraction of ingested biomass that is actually assimilated; f_m is the fraction of assimilated carbon respired for the maintenance of basic bodily functions; and f_a is the fraction of assimilated carbon that comprises consumers' net biomass production (1- f_a is respired). F_{ij} (***B***) in Eqn. 3 is the consumers' normalized functional response

$$F_{ij}(\boldsymbol{B}) = \frac{\omega_{ij} B_j^{q_{ij}}}{B0_{ij}^{q_{ij}} + \sum_{k=consumers} d_{kj} p_{ik} B_k B0_{kj} + \sum_{l=resources} \omega_{il} B_l{}^{q_{il}}} \tag{4}$$

where ω_{ij} is the relative prey preference of consumer species *i* feeding on resource species *j*; q_{ij} = 1.2 which forms a relatively stable functional response intermediate between the Holling Type-II and Type-III functional responses (Williams and Martinez, 2004b); $B0_{ij}$ is the half saturation constant of resource species *j* at which consumer species *i* achieves half its maximum feeding rate on species *j*; d_{kj} is the coefficient of feeding interference of species *k* with *i* while feeding on species *j*; p_{ik} = the fraction of resource species shared between species *i* and *k*. d_{kj} also accounts for prey resistance to consumption that may increase with increasing abundance of consumers of species *j*.

The fishing mortality of the fully selected individuals (F_{max}) depends on age-specific fishing selectivity (S_{age}). For fish juveniles (age = 1) and larvae (age = 0) as well as all the organisms that are not fished, S_{age} = 0. For fish 2 years or older (age > 1), selectivity varies logistically according to $S_{age} = 1/[1 + \text{e-}2(\text{age-age}_{F50})]$ (S_{age} is 0.12, 0.50, and 0.88 for age-classes 2, 3, and 4 years and older, respectively), where age_{F50} is the age at which 50% of individuals each year are caught and was set to 3 years for two fish species (Kuparinen et al., 2016). This selectivity scenario was chosen to mimic the standard attempt of fisheries management (and gear regulations) to set targets for fishing pressure so that fish may adequately reproduce prior to being caught. See Kuparinen et al. (2016) and Bland et al. (2019) for treatment of intraspecific variation among different life stages of fishes.

these different environments (Purdy et al., 2010; Pompanon et al., 2012; Nielsen et al., 2018).

Based on such broad insights and consistencies among ecologists and ecological systems, food webs, the most iconic of ecological networks which depict organisms' roles within the architecture of feeding relationships relative to primary producers, have long formed a fundamental cornerstone of ecological thought (Dunne, 2006). From their embrace in one of the first texts in ecology (Elton, 1927) which emphasized trophic levels and pyramids throughout the development of ecology including its current resurgence as complex ecological networks integrated with metabolic ecology (Humphries and McCann, 2014) and engagement with network science (Dunne et al., 2002a; Newman, 2010; Barabási, 2012), the trophic relationships that comprise food webs have been central to addressing major ecological questions. These questions addressed diversity and stability (May, 1973; McCann, 2000; Brose et al., 2006b; Stouffer and Bascompte, 2010, Stouffer and Bascompte, 2011), top–down vs. bottom–up control (Power, 1992; Schneider et al., 2016), trophic levels (Cousins, 1987; Williams and Martinez, 2004a), trophic cascades (Polis and Strong, 1996; Wang and Brose, 2018), keystone species (Paine, 1966; Power et al., 1996; Brose et al., 2005b), biodiversity-ecosystem function (Naeem et al., 1994; Martinez, 1996; Loreau, 2010; Cardinale et al., 2012; Thompson et al., 2012; Miele et al., 2019), and tipping points (Barnosky et al., 2012).

Food webs play such central roles largely because the first principles and foci embraced by food-web research are also central to the major subdisciplines of ecology (**Box B**). Two of these principles are: (1) organisms require energetic and other resources to live, grow and reproduce and, in fulfillment of these needs, (2) organisms consume other organisms and

BOX B | Organizational levels integrated with ecological networks.

Levels and their associated subdiscipline of ecology	Subdisciplinary foci quantitatively integrated by Allometric Trophic Network Theory
Physiological Ecology	Metabolic rates, assimilation efficiency, diet, heat effects, prey defense
Behavioral Ecology	Search and handling times, adaptive and optimal foraging, functional responses, predator interference and avoidance, heat-dependent movement, interference competition
Population Ecology	Growth and reproduction rates, carrying capacity, non-linear dynamics, age and size structure, loss to starvation, predation, parasites and biotic diseases
Community Ecology	Intra- and inter-specific interactions, diversity-complexity-stability, coexistence, consumer-resource interactions, mutualism, resource and apparent competition
Ecosystem Ecology	Energy and nutrient stocks and flows and cycling among producers, consumers and decomposers, biodiversity and ecosystem function, carbon dynamics and sequestration, energetic processing and efficiency

their products. Organisms' physiology, behavior, and abundance largely determine rates of consumption and population growth. In order to specify these rates, the metabolic theory of ecology (Brown et al., 2004; Humphries and McCann, 2014) has been integrated with trophic network theory by using body size to assign metabolic maintenance costs and maximum consumption and production rates to populations within the networks. ATN theory multiplies these rates by the biomass (Brose et al., 2006b) or numerical abundance (Schneider et al., 2016) of species' populations processing and interacting at these rates in order to generate a systems-level predictive understanding of population, energetic, and nutrient dynamics within ecosystems (Lindeman, 1942; Chapin et al., 2011; Boit et al., 2012).

The central concepts and principles involving feeding interactions and food webs have motivated a synthesis of network and consumer-resource theory (Martinez, 1995; Thompson et al., 2012) that integrates organismal (Holland and Deangelis, 2009), population (Turchin, 2003), community (Bascompte, 2009) and ecosystem ecology (Getz, 2011, **Box B**). The synthesis also integrates subdisciplines focused on trophic interactions within different aquatic and terrestrial habitats and among different organisms involving plant-animal, predator-prey, parasite-host, and pathogen-host interactions and also involving symbiotic relationships such as those between plants and fungi and between plants and pollinators (Martinez, 1995; Hale et al., 2020). Such synthetic integration is achieved in no small part by quantitative comparison of the architecture of trophic interactions in terms of network properties (e.g., Cohen, 1978; Bascompte et al., 2003; Dunne et al., 2013) that describe distributions of specialists and generalists, food chain lengths, degrees of separation, relative prevalence of motifs, along with the flows within this network structure (Shurin et al., 2006) that can be surprisingly well estimated from network structure alone (Williams and Martinez, 2004b; Carscallen et al., 2012). Beyond this pervasive core including virtually all types of organisms within all types of habitats, research on ecological networks extends consideration of consumer-resource interactions to evolutionary scales (Martinez, 2006; Dunne et al., 2008; Allhoff and Drossel, 2013, 2016; Allhoff et al., 2015a; Edger et al., 2015; Romanuk et al., 2019) and plant-nutrient (Brose et al., 2005a), reproductive (Hale et al., 2020), and other non-feeding interactions (Kéfi et al., 2012).

ATN theory builds upon major advances in ecology over the last half century that, in contrast to much of that progress that has led to increasingly disparate subdisciplines (Martinez, 1995; Loreau, 2010), weaves the disparate threads back together into a more coherent fabric (Thompson et al., 2012). This fabric illustrates, for example, how fisheries dynamics, infectious disease epidemics, competition and mutualism among plants and animals may be understood as different parameterizations and functional forms of consumer-resource interactions (Holland and DeAngelis, 2010; Lafferty et al., 2015) that comprise food webs and their more broadly powerful offspring; ecological networks (Pascual and Dunne, 2006) that also include non-feeding interactions such as plant nutrient consumption (Brose et al., 2005b), ecosystem engineering (Kéfi et al., 2012), and reproductive services (Hale et al., 2020). Such research has shown how scientific feats once thought difficult or impossible have been achieved (**Box C**). For example, the unlikely stability of many species coexisting within complex ecosystems appears largely due to allometric degree distributions (Brose et al., 2006b; Otto et al., 2007; Gross et al., 2009) where species' generality (number of species eaten) increases and vulnerability (number of consumer species) decreases with increasing body size and trophic level (**Figure 3**) combined with non-linearities in feeding behavior (Williams and Martinez, 2004a; Hale et al., 2020) from which increases in highly stabilizing intraspecific competition (Chesson, 2000; Chesson and Kuang, 2008) emerge (Kartascheff et al., 2010). Also, while ecologists have argued that even a field guide to which species may strongly interact with others may be permanently out of reach (Power et al., 1996), ATN theory has gone much further by accurately predicting interaction strength (Paine, 1992) including how much the experimental removal of a species alters the abundance of other species in field (Berlow et al., 2009) and lab (Jonsson et al., 2018; Curtsdotter et al., 2019) experiments. For example, ATN theory accurately predicted that the effects of removing a species on the abundance of a species remaining a field experiment is a simple function of biomass of the two species and the body mass of the removed species (Berlow et al., 2009). ATN theory has also shown how verbal theory describing the classic seasonal population dynamics of complex lake ecosystems as well as their component populations (Sommer et al., 2012) may be surprisingly well quantified and forecasted (Boit et al., 2012). This paves the way for direct application to ecosystem management of fisheries (Martinez et al., 2012; Gilarranz et al., 2016; Kuparinen et al., 2016). Important steps in this direction includes disentangling different ecological, evolutionary and economic causes of the destabilization of

BOX B | Allometric trophic network milestones.

Year	Milestones
1992	Transformed established scaling of complexity with diversity (Martinez, 1992, 1993b)
	Allometrically scaled bioenergetic theory of two species established (Yodzis and Innes, 1992)
1993	Scale-dependent food webs overturn "scale-invariant" webs (Martinez, 1993a,b, 1994)
1998	Bioenergetic theory of two species extended to three species and omnivory (McCann et al., 1998)
2000	Widely accepted theory of food web structure established (Williams and Martinez, 2000, 2008; Stouffer et al., 2005)
2002	Structural robustness of food webs to species loss elucidated (Dunne et al., 2002b)
2004	Bioenergetics of few interacting species scaled up to complex networks (Williams and Martinez, 2004a; Williams, 2008)
	Unified theory of spatial scaling of species and trophic links developed (Brose et al., 2004)
2005	Plant nutrients integrated with food-web dynamics (Brose et al., 2005b)
2006	Allometric trophic network (ATN) theory introduced (Brose et al., 2006b)
2008	Architecture of Cambrian food webs successfully predicted (Dunne et al., 2008)
2009	Experimentally determined interaction strengths successfully predicted (Berlow et al., 2009) Corroborated patterns in invasion success predicted (Romanuk et al., 2009, 2017)
2010	Stabilizing influences of empirically prevalent feeding motifs illuminated (Stouffer and Bascompte, 2010)
2011	Stabilizing influences of compartmentalization illuminated (Stouffer and Bascompte, 2011)
2012	Seasonal dynamics of a complex ecosystem simulated (Boit et al., 2012), Nutrient recycling through detritus integrated (Boit et al., 2012), anabolic costs of biomass production incorporated (Boit et al., 2012; Kath et al., 2018), and economic supply and demand mechanisms integrated (Martinez et al., 2012)
2013	Inclusion of parasites found consistent food-web theory (Dunne et al., 2013)
2015	Evolutionary processes construct realistic food webs (Allhoff et al., 2015a)
2016	Dynamics and degradation of fisheries elucidated (Gilarranz et al., 2016; Kuparinen et al., 2016)
	Intraspecific variation and ontogenetic niche shifts integrated (Kuparinen et al., 2016; Bland et al., 2019)
	Mechanisms linking multi-trophic biodiversity to ecosystem function elucidated (Schneider et al., 2016; Wang and Brose, 2018)
	Impacts of warming and eutrophication elucidated (Binzer et al., 2016)
	Humans explicitly integrated into food webs (Dunne et al., 2016; Kuparinen et al., 2016)
2019	Big data on consumer-resource body-size ratios and patterns published (Brose et al., 2019a)
2020	Mutualistic consumer-resource interactions enhance ecosystem stability and function (Hale et al., 2020)

fished populations and their ecosystems by fishing (Gilarranz et al., 2016; Kuparinen et al., 2016) as well has how thermal stress and (Gilarranz et al., 2016) and environmental noise (Kuparinen et al., 2018) affects fishery and other ecosystems. Finally, consumer-resource network theory has helped resolve prominent debates regarding the implications of observed network architecture for the stability of mutualistic networks (Valdovinos et al., 2016) and ecosystems (Hale et al., 2020) while successfully predicting novel foraging behavior of pollinators in the field (Valdovinos et al., 2016). This suggests that, well beyond agreement about the centrality of a conceptual framework, a substantial body of evolving theory is steadily advancing toward a simultaneously general, accurate and precise understanding and prediction of the structure and function of complex ecological systems. The following discussion of the foundations, current status, and future directions of ATN theory helps illuminate these claims further and the basis for making them.

ALLOMETRIC TROPHIC NETWORK THEORY, PAST AND PRESENT

Conceptual Foundations

Allometric trophic network (ATN) theory asserts that that the behavior of ecological systems is primarily determined by the organismal production and consumption of resources that provide the energy organisms require to live, grow and reproduce. Central to this theory is the network structure of consumer-resource interactions, especially the feeding interactions needed to supply organisms' metabolic requirements, that form food webs. This focus on the production and consumption of food forms a more narrow conceptual core than do other broad theories of ecology (Reiners, 1986; Scheiner and Willig, 2008; Vellend, 2010) while also answering Reiners's (1986) call for a theory of causal networks of population interactions to complement energy and matter theories of ecosystems. Extending beyond this core are other often limiting resources such as various services that organisms produce. These include services consumed by plants such as the reproductive services of pollinators and seed dispersers as well as nutrient provisioning services produced by mycorrhizal fungi and other detritivores (Hale et al., 2020). Other services consumed by a fuller range of organisms include habitat provisioning services produced by ecosystem engineers such as beavers, coral, and trees (Jones et al., 1994; Kéfi et al., 2012). The emerging broad interest in multiplex networks in the general field of network science may contribute much to understanding how diversity types of links affect ecological networks (Kéfi et al., 2017; Pilosof et al., 2017; Barner et al., 2018) and continue the practice of network science (Barabási, 2012) of contributing to, and benefiting from, research on ecological networks (Dunne et al., 2002a; Williams et al., 2002) including their controllability (Liu et al., 2011; Li et al., 2017; Jiang and Lai, 2019) and resilience (Gao et al., 2016).

Whereas the network architecture of consumer-resource interactions constitutes much of the *structure* of ecological systems formalized by ATN theory (**Figure 3**), the *function* of these networks is largely determined by the dynamics of the closely related rates of metabolism, production and consumption of organisms engaged in the consumer-resource interactions depicted by the network's structure (**Figures 2**, **3**). Given the diversity and complexity of these networks, 'allometric' merely refers to role of body size in constraining feeding relations such as those among predators and prey (Brose et al., 2019a) and hosts and parasites (Dunne et al., 2013) and the tactical decision to embrace the metabolic theory of ecology (Brown et al., 2004) by using organismal traits including body size and type (e.g., invertebrate) as the most general, powerful, and efficient way of estimating metabolic rates in lieu of more direct measurements when unavailable or inconvenient. Similarly, the niche model (**Figure 3**) is typically used to estimate realistic food web architectures (e.g., Domínguez-García et al., 2019) in lieu of more direct observations of particular food webs (Boit et al., 2012) and food web patterns (Riede et al., 2010). Several prominent variants of the niche model with different strengths and weaknesses (Martinez and Cushing, 2006; Williams and Martinez, 2008) have also been created that elucidate roles of body size (Beckerman et al., 2006; Petchey et al., 2008; Williams et al., 2010; Allhoff et al., 2015a; Schneider et al., 2016), phylogeny (Cattin et al., 2004; Stouffer et al., 2012; Allhoff et al., 2015a) and the contiguity of feeding niches (Stouffer et al., 2005, 2011; Allesina et al., 2008; Williams and Martinez, 2008; Williams et al., 2010) in generating empirically observed food webs. While the genesis of ATN theory began with allometrically scaled metabolism and feeding operating within networks structured according to the niche model, ATN theory is not restricted to these simple origins and continues to develop well beyond them.

Key to such development is the basis of ATN theory on the two previously mentioned principles of biology that provide a mechanistic foundation for integrating the several scales and organizational levels from organisms to ecosystems. Those principles include organisms' need for energy and other resources and the production of those resources by organisms. These two principles locate a basic foundation of ATN theory primarily at the physiological level of metabolism as determined by fundamental biochemical reactions such as photosynthesis and the Krebs cycle which create biochemical energy and controls the ability of organisms to live and the rates that they can function. These functions include consumption, production, movement, and reproduction. While the physiology of metabolism both enables and constrains the basic ability for these functions to occur, organismal behavior mediates this potential by largely determining how much of the potential is realized. Compared to physiology, behavior also more clearly drives the production of services such as reproductive services performed by pollinators (Hale et al., 2020) and habitat modification performed by ecosystem engineers (Jones et al., 1994). By aggregating organismal behaviors among organisms, ATN theory scales up physiological and organismal behaviors to the population level in order to determine population dynamics and abundance. By focusing on consumer-resource relationships between populations coexisting within a habitat, ATN theory scales up populations and their interactions to the community and ecosystem levels. Whereas community ecology often focuses on the diversity and nature of interactions among populations, ecosystem ecology focuses on the stocks and flows of energy and nutrients involved in these interactions (Loreau, 2010). ATN theory scales up population ecology to both community and ecosystem levels by focusing on the biomass of populations typically measured in units of carbon that can be simply converted into the number of organisms in a population using the distribution of body sizes of organisms within a population (Thompson et al., 2012). While these distributions are typically characterized by the mean body size of adults, more sophisticated measures that account for the abundance of immature individuals may also be used. Populations of different organisms may be aggregated or otherwise summed at will to match the functional foci of ecosystem ecologists (e.g., plant, herbivore, omnivore, carnivore, decomposer, etc.) and phylogenetic foci of community ecologists (e.g., species, family, order, etc.) as well as combinations of these foci (e.g., bacterial decomposers, insect pollinators, fungal symbionts, etc.). The seamless integration of community and ecosystem ecology based on physiological, behavioral, and population mechanisms forms one of the most powerful contributions of ATN theory (Reiners, 1986; Thompson et al., 2012).

Antecedents and Chronology of ATN Theory

ATN theory has its beginning over a half century ago in theory about the structure and dynamics of food webs that were first described at least a century ago (Dunne, 2006). Early theory held that more links stabilized these networks by providing more options for resources to reach consumers if a particular species within a food chain was disrupted by drastically decreasing in abundance or going extinct (MacArthur, 1955). Later theory held that additional links increases the probability of positive feedback loops which would destabilize ecological networks such as food webs (May, 1972). Key to such considerations is the scaling of links with species diversity within such networks. Large increases of links with increased diversity increases niche overlap in consumer-resource networks. As Darwin (1859) and then Gause (Hardin, 1960) articulated, increased overlap could increase resource competition which could cause less fit species to go extinct. Such theory motivated the search for how linkage patterns in food webs within compilations of food webs from different habitats might alleviate such risks (Cohen, 1978). A key finding among these data was a constant "scale-invariant" ratio of the number of links per species in terms of feeding links per network node (Pimm et al., 1991). Such constancy causes network complexity in terms of the faction of all possible links or directed "connectance" (links per species^2, Martinez, 1992) to hyperbolically decrease as the number of species increases. This decrease helps to avoid destabilizing effects of increasing links with the number of species on ecological networks (May, 1972). This pattern also inspired an elegant theory of food web structure that proposed a trophic hierarchy of species where species on average ate a fixed number of species below them on the hierarchy (Cohen et al., 1990). As such, a first generation (Dunne, 2006) of mechanistic theory was established by which the dynamic processes of population variability and trophic energy transfer led to a food-web pattern that avoided destabilizing effects of positive feedbacks and competitive exclusion and allowed complex ecosystems with many species to persist (Pimm et al., 1991).

This initial generation of food-web research led to a new generation first of food-web data and then of food-web theory (Dunne, 2006). The new and improved data exhibited more complexity with new "scale-dependent" theory being generated to better explain and predict this complexity (Martinez, 1994). Perhaps most significantly, the second generation data exhibited much more rapid increases of links as species richness increases leading to the "constant connectance hypothesis" (Martinez, 1992) which challenged the first generation's "link-species scaling law" (Pimm et al., 1991) by asserting links increased approximately as the square of species diversity. This new pattern and others motivated new generation of theory asserting a trophic hierarchy that was more relaxed than the earlier one (Cohen et al., 1990) where species on average ate a fixed fraction of species within a contiguous range (Cohen, 1978) of the hierarchy that were on average below the consumer (Williams and Martinez, 2000). The relaxation accommodated previously excluded processes such as cannibalism and loops in food chains while the contiguity added mechanisms associated with physiological constraints such as digestive capabilities or gape size which forces species to consume resources within a contiguous range of trophic levels or body sizes, respectively (**Figure 3**). This second generation "niche model" (**Figure 3**) much more precisely predicted a much wider range of network properties in improved second generation food-web data (Dunne, 2006; Williams and Martinez, 2008). These data include ancient food webs over a half billion years old back in the Cambrian (Dunne et al., 2008) and other food webs including the many parasite species typically excluded from earlier data (Dunne et al., 2013). While this second-generation theory based on the mechanisms of trophic transfer and physiological constraints greatly increased the precision and generality over that of the first generation, the conflict between the dynamical considerations of the first-generation theory and the complexity of second-generation data had yet to be addressed.

Much of the first generation theory of ecological network dynamics (May, 1973) was based on representing direct and indirect interactions between two species as interspecific effects. For example, direct effects of a predator on a prey are typically negative and that of a prey on a predator are positive while indirect interactions such as competition between two species consuming a common resource are often considered direct negative effects both species have on each other (McPeek, 2019). A second generation of network dynamics emerged from avoiding such phenomenological representations and instead focusing on more easily measured and estimated processes such as consumer-resource interactions (Yodzis and Innes, 1992) between predators and prey from which intraspecific and interspecific effects emerge. This later generation scaled up these consumer-resource interactions into complex networks to discover the stabilizing effects of realistic foraging behaviors (Williams and Martinez, 2004a), network structure (Martinez et al., 2006), and body-size ratios between consumer and resource species (Brose et al., 2006a, 2019a). Rather than stability emerging from limiting niche overlap by decreasing connectance while increasing diversity (Pimm et al., 1991), second generation theory found that allometric degree distributions stabilized networks with high niche overlap (Williams and Martinez, 2000, 2008), complexity, and diversity (Brose et al., 2006b; Otto et al., 2007). These large overlaps in trophic niches and degree distributions where larger bodied species at higher trophic levels had fewer consumer species and more resource species than smaller bodied species at lower trophic levels (Cohen et al., 2003) emerge (**Figure 3**) from the constraints of hierarchy and contiguity in the niche model (Williams and Martinez, 2000, Williams and Martinez, 2008; Stouffer et al., 2011). Highly but not completely contiguous feeding niches that enhance overlap also enhance stability (Yan et al., 2017; Romanuk et al., 2019). Rather than achieving stability by simply limiting the number of interactions, ATN theory arranges many more interactions in more precisely described locations among species with varying body sizes which explains the remarkable stability of realistically structured networks over more randomly structured networks (Brose et al., 2006b; Martinez et al., 2006; Kartascheff et al., 2010).

Compared to the difficulty of measuring competition coefficients (Hart et al., 2018; Ellner et al., 2019), the relative ease of measuring consumer-resource interactions such as metabolic and consumption rates (Brose et al., 2008; Vucic-Pestic et al., 2010; Marx et al., 2019) and the even easier estimation of the rates of these interactions based on body size (Brose et al., 2006b, 2019a; Otto et al., 2007) opened up a wide range of ecological research to be addressed by ATN theory (**Box C**). Key to this increased breadth is parameterizing maximum feeding rates as a multiple of metabolic rate which appears surprisingly constant among organisms within metabolic groups such as invertebrates and ectotherm and endotherm vertebrates (Yodzis and Innes, 1992; Williams et al., 2007). Such rates indicate, e.g., that invertebrates may generally consume a maximum of eight times their metabolic rate over the long term while ectotherm vertebrates are limited to consuming only four times their metabolic rate (Brose et al., 2006b). Basing ATN theory on metabolic rates enables ATN theory to leverage the chief focus of the metabolic theory of ecology (Brown et al., 2004) i.e., the relationship between body size and metabolic rate, to vastly reduce the parameter space and focus it more specifically on complex networks of consumer-resource interactions found in nature (Hudson and Reuman, 2013). A key fulcrum of this lever is the observed body-size ratios between consumer and resource species (Brose et al., 2019a) broadly suggesting regularities such as invertebrate predators being an order of magnitude larger than their prey while vertebrates tend to be two orders of magnitude larger (Brose et al., 2006a,b, 2019a). Once the body size and type and therefore the metabolic rate of species at the base of the food web are set, combining these ratios and their huge variability (Brose et al., 2019a) with the structure of the food web generates fully and realistically parameterized networks for further research. Computational experiments that removed species from these networks enabled ATN theory to elucidate how traits of species generally affect the impacts of their loss (Brose et al., 2017), and more specifically predict the population dynamics (Curtsdotter et al., 2019) and quantitative effects of species removal experiments observed in the field (Berlow et al., 2009) and the lab (Jonsson et al., 2018) as well as help develop less empirically demanding methods for predicting such effects (Eklöf et al., 2013). Similarly, ATN species-invasion experiments helped generate empirically corroborated theory predicting generalists with few predators more effectively invade ecological networks and that low-connectance networks are more susceptible to species invasions while high-connectance networks experience larger extinction cascades resulting from the invasions (Romanuk et al., 2009, 2017) as well as other predictions of how temperature and species' traits affect food web assembly (Gounand et al., 2016).

Other key advances in ecological theory build upon ATN theory's synthesis of community and ecosystem ecology by elucidating effects of biodiversity on ecosystem function (Schneider et al., 2016; Miele et al., 2019). Having largely been confined to a single trophic level in terrestrial systems, primarily vascular plants (Hector and Bagchi, 2007), ATN theory has advanced such early research on biodiversity and ecosystem function to a much fuller range of organisms at many trophic levels (Schneider et al., 2016; Miele et al., 2019). Such advances emphasize that the way ecological systems function is determined much more by how their parts interact than the number of types of parts they have. That is, while many correlations between the number of nodes in a network and the network's function are evident, the mechanisms responsible for the correlation intimately involve the interactions among the nodes rather than the mere existence of the nodes (Cardinale et al., 2012).

Early biodiversity and ecosystem function research embraced this mechanistic premise by explaining positive biodiversity-ecosystem function correlations as a result of the complementarity of resource use that may occur when more plant species with different resource needs and consumption strategies inhabit an ecosystem (Cardinale et al., 2012). However, such interactions involve a very limited albeit critical part of the much larger networks that comprise complex natural ecosystems. Classic theory about plant communities asserts the species best able to consume the most limiting shared resource out competes other species and therefore excludes them from the community (Tilman, 1982). Higher trophic levels could prevent such loses of biodiversity by preferentially feeding on competitive dominants (Paine, 1969) or, more generally, if the dominants exchanged their high growth rates for increased vulnerability to consumers (Chase et al., 2002). However, such preferences and tradeoffs proved unnecessary to maintain coexistence in ATN networks (Brose, 2008). Instead, preference-free consumers of resource species free of growth-vulnerability tradeoffs are sufficient to maintain coexistence within realistically structured food webs (Brose, 2008). A broad density-dependent dynamic emerges whereby abundance is its own enemy and rarity is its own refuge respectively due to "kill-the-winner" dynamics among abundant organisms (Thingstad, 2000) and "ignore-the-scraps" dynamics among consumers of rare species very few of which are single species specialists (Srinivasan et al., 2007). Such insights and dynamics allow ATN theory to more simply and rigorously address biodiversity and ecosystem function of a much larger proportion of ecological diversity without parameterizing or even asserting preferences or tradeoffs (Schneider et al., 2016). Recent advances in ATN theory employing these insights find support for a "vertical diversity hypothesis" that asserts increasing the trophic levels of species along with maximum body sizes given observed consumer-resource body-size ratios increases primary productivity within ecological networks subjected to constant inputs of plant nutrients (Wang and Brose, 2018). Such research suggests that broadly focusing on energy flux across trophic levels illuminates general consumer-resource mechanisms by which biodiversity may determine ecosystem function (Barnes et al., 2018).

Other more applied advances of ATN theory involve the structure, function, and ecosystem management of fisheries. These advances build upon some of the firmest foundations of ATN theory, especially aquatic food-web structure (Martinez, 1991, 1993b) that appears more tightly constrained by size structure due to gape limited feeding than above-ground terrestrial systems (Cohen et al., 2003, 2005; Brose, 2010; Brose et al., 2019a). Another important contribution to such work is the sociological factor of aquatic ecologists synergistically focusing on particular systems such as certain lakes or ocean areas explored by large research vessels. Terrestrial researchers appear more able and willing to diffuse their focus among many geographically dispersed systems due to their relative ease of access. This distinction results in more holistic empirical and theoretical research on particular aquatic ecosystems including viruses to vertebrates compared to terrestrial research. Systems such as Lake Constance north of the European Alps illustrate this phenomenon well. For example, study by the lake's phytoplankton, zooplankton, and fish ecologists have resulted in multiple decade-long time series of the population abundances of dozens of these species observed every 2 weeks or less (Boit and Gaedke, 2014). An ATN model parameterized by the observed network structure and allometrically estimated metabolic rates of the organisms successfully simulates the overall seasonal dynamics of species' abundance and production within the lake's complex food web (Boit et al., 2012). Further development of this model to include ontogenetic size structure of fishes enabled ATN theory to illuminate how evolutionary and other mechanisms may be responsible for the increased variability of fished populations as well as the destabilization and degradation of fishery ecosystems due to fishing (Kuparinen et al., 2016; Bland et al., 2019) and how food webs buffer environmental variability (Kuparinen et al., 2018). This work shows how widely observed decreases in body size of fished populations may cause losses of ecosystem function and services that persist centuries after fishing has ceased (Kuparinen et al., 2016). Similar findings emerged from other similarly parameterized ATN analyses where fishing pressure and thermal stress decrease persistence among hundreds of simulated fisheries throughout the Caribbean (Gilarranz et al., 2016).

Extensions of ATN theory to fishery ecosystems is one of several approaches that incorporate humans into complex ecological networks. Research on a fuller range of species consumed by indigenous humans found that humans were "super generalists" in that they consumed more species than almost any other species within their food web (Dunne et al., 2016). Simulated invasions of ecological networks found that generalists were especially successful invaders that caused the most extinctions in food webs (Romanuk et al., 2009). Similar ATN studies of human-like species found reducing the fraction of super generalists' many links to resource species that were strong links greatly reduced the number of extinctions caused by their presence in the food web (Dunne et al., 2016). This may explain traditions of seasonally restricting harvests to few of the many species that indigenous peoples consume as a management strategy to prevent such destructive extinction cascades to occur (Dunne et al., 2016). Given that current consumption of species is often driven much more by economics than human demographics, work has begun to incorporate market mechanisms into ATN models in order to better understand human effects on ecological networks and how economic policies can better manage extractive exploitation of coupled human-natural networks (Martinez et al., 2012). Initial results suggest that fished populations go extinct beyond tipping points at levels of fishing effort near levels predicted to be optimal by the logistic growth theory underlying most fisheries management and that increasing costs of fishing could cause much higher yields and revenue than predicted by logistic theory to be realized with much lower effort (Martinez et al., 2012).

Such integration of social sciences including anthropology and economics extends ATN theory to the socio-ecosystem level. This extension empowers ATN theory to mechanistically address the sustainability of socio-ecosystems where their dynamics critically depend on how human consumption and other human behaviors depend on price and the price elasticity that indicates how readily people substitute one item, e.g., hamburger, for another, e.g., salmon (Martinez et al., 2012). While ATN theory emerged from a focus on mechanisms involving biotic and abiotic material and energy, this extension to socio-ecosystems firmly integrates mechanisms involving price, capital and markets which represents information (O'Connor et al., 2019) much more than these quantities represent material or energy. As such, ATN theory incorporates a full breath of processes from biochemical reactions within cells to information about cultural predilections of human societies. Formalization of these mechanisms as complex dynamic networks enables ATN theory to effectively advance our ability to understand, predict, and potentially manage a full range of ecological phenomenon determining the ability of species including humans to thrive or whither or, more dramatically, persist or perish.

Changes in the global environment involve less direct anthropogenic impacts than the extirpation and exploitation of species due to habitat loss and fishing but these changes form perhaps the most significant threat to the sustainability of humans and other species on the planet. This threat includes both early and more recently recognized changes such as eutrophication caused by the deposition of plant nutrients in aquatic and terrestrial ecosystems and warming caused by the deposition of greenhouse gasses into the atmosphere. One of the more powerful applications of ATN theory has been to examine how these two changes, both separate and in combination, impact ecosystems. The first of such applications leveraged ATN theory's explicit consideration of nutrient dynamics to find that eutrophication may increase interaction strength by increasing the maximum abundances of species responding to the loss of keystone predators from simple and complex food webs (Brose et al., 2005b). Higher maximum abundances enable larger changes in abundance to occur due to disturbances which often extirpate species. Later research leveraged the acceleration of metabolism by heat (Gillooly et al., 2001; Brown et al., 2004; Vasseur and McCann, 2005) to find that, while warming could conceivably just accelerate metabolism and behavior and largely leave ecosystems otherwise unaffected (Zhou et al., 2011), warming may instead decrease the efficiency of predation by increasing metabolism more than consumption (Vucic-Pestic et al., 2011) and stabilize population dynamics by increasing intraspecific interference (Lang et al., 2012). This leads to a rich range of predictions on the combined effects of eutrophication and warming depending on nutrient status and organisms involved (Binzer et al., 2016). For example, Binzer et al. (2016) found that warming may increase diversity in eutrophic systems while decreasing diversity in oligotrophic systems. They also found that body-size effects can cause warming to stabilize parasitoid-host systems while destabilizing predator-prey networks (Fussmann et al., 2014; Binzer et al., 2016). The sophistication and mechanistic bases of such ATN predictions of responses to novel environments greatly benefit from theoretically and empirically robust estimates of the effects of warming on network complexity (Petchey et al., 2010), body size (Sheridan and Bickford, 2011; Forster et al., 2012) and interactions of different rates such as nutrient supply and plant growth (Marx et al., 2019) and heat supply and feeding rates (Rall et al., 2012; Fussmann et al., 2014).

Beyond elucidating effects of separate and combined perturbations of biotic and abiotic components of ecosystems, ATN theory has elucidated system-level effects of perturbations more generally. For example, dozens of widely used measures of stability against episodic and sustained disturbances of ecosystems were recently found to map onto three largely independent dimensions of stability including "early response to pulse, sensitivities to press, and distance to threshold" dimensions (Domínguez-García et al., 2019). Such work illuminates a more integrated notion of ecological stability in general that articulates how different stability measures complement and contrast with each other when describing broader and more focused aspects of ecological responses to change. Combined with earlier investigations of how the more inherent stability of ecological networks' ability to maintain their integrity in the absence of disturbance depends on their architecture (Brose et al., 2006b; Martinez et al., 2006), functional responses (Williams and Martinez, 2004b) and body sizes (Brose et al., 2006b; Otto et al., 2007), ATN theory provides a relatively comprehensive overview of how complex ecosystems manage to dynamically persist or not in constant and more variable environments.

One of the most significant recent advances in ATN theory has been the integration of evolutionary mechanisms into the structure and dynamics of ecological networks (Martinez, 2006; Dunne et al., 2008; Brännström et al., 2012; Ritterskamp et al., 2016b). Early work in this area employed somewhat arbitrary network structures that emerged from stochastically adding species to communities and focused on which dynamical equations and rules resulted more realistic networks structures (McKane, 2004; McKane and Drossel, 2005; Rossberg et al., 2006). More recent work (Allhoff et al., 2015a) employed ATN theory by structuring food webs according to body size and rules of the niche model (Williams and Martinez, 2000, 2008) and simulating the non-linear dynamics of the network using allometrically parameterized differential equations to calculate bioenergetic stocks and flows within the network (Brose et al., 2006b). This work formalizes phylogenetic niche conservation of trophic interactions (Cattin et al., 2004; Stouffer et al., 2012) by stochastically varying or "mutating" each species' location and diet represented by the niche model's three parameters describing each species' fundamental trophic niche (**Figure 3**). Such work found that speciation events representing evolving species traits such as body size, metabolic rate and diet results in large realistically structured networks (Romanuk et al., 2019) with continuous turnover of species (Allhoff et al., 2015a) but little long-term changes in ecosystem function despite larger changes in functional diversity (Allhoff and Drossel, 2016). More specifically, ATN investigations (Romanuk et al., 2019) recently found that speciation results in surprisingly stable and complex networks with species sharing tightly packed feeding niches similar to empirical observations (Morlon et al., 2014; Romanuk et al., 2019) but unexpected based on competition (Ponisio et al., 2019) and more neutral (Morlon et al., 2014) theory.

Explorations of more subtle eco-evolutionary dynamics found fishing-induced evolution toward smaller and earlier maturing fishes degrades fishery yields and destabilize fished populations and their ecosystems (Kuparinen et al., 2016). Other explorations attempting to look for more dramatic changes in food webs over deep time found that food-web architecture changed relatively little over the half billion years recognizably complex ecosystems have been present on Earth (Dunne et al., 2008, 2014). Such research demonstrates the ability of ATN theory to integrate a range of evolutionary mechanisms including natural selection from seasonal (Yoshida et al., 2003; Boit et al., 2012; Hiltunen et al., 2014) to decadal (Kuparinen et al., 2016, 2018) to geologic (Dunne et al., 2008, 2014) time scales into the structure and dynamics of ecological networks.

FUTURE DIRECTIONS

While ATN theory has developed a relatively comprehensive framework for addressing complex ecological systems, much research needs to further test its predictions in order to understand and extend the limits of the framework along with its applications to pressing issues such as ecosystem management and the sustainability of human-natural systems. Key to these advances is a rich dialogue between theory and empiricism to better understand: (1) fundamental factors such as levels of network complexity (Petchey et al., 2010), metabolic rates (Kath et al., 2018; Quévreux and Brose, 2019), and consumer-resource body-size ratios (Brose et al., 2019a), (2) more nuanced behaviors such as migration and functional responses (Williams and Martinez, 2004a; Martinez et al., 2006; Williams, 2008; Heckmann et al., 2012; Rall et al., 2012; Pawar et al., 2019), and (3) more holistic comparisons between ATN models of ecosystems in computers and biological models of ecosystems in the lab (Jonsson et al., 2018; Blasius et al., 2020) and field (Berlow et al., 2009; Boit et al., 2012; Curtsdotter et al., 2019). Longer term observations of food web dynamics in the lab (Yoshida et al., 2003, 2007; Meyer et al., 2006; Blasius et al., 2020), mesocosms, and the field (Boit and Gaedke, 2014) are particularly needed. Such work helps illuminate whether and how ATN theory can effectively forecast ecosystem behaviors further into the future (Petchey et al., 2015; Brose et al., 2019b). Other important work includes refining the representation of the physiology of metabolism (Kath et al., 2018) and its sensitivity to abiotic and biotic environmental variation such as that in temperature (Vucic-Pestic et al., 2010, 2011; Rall et al., 2012) associated with climate change or the presence of predators associated with the ecology of fear (Sih, 1980; Ho et al., 2019). For example, accounting for anabolic efficiencies of biomass production appear critical to the ability to forecast complex ecological dynamics (Boit et al., 2012; Kath et al., 2018) and to predict positive effects of mutualism on the diversity, stability and functions of complex ecosystems (Hale et al., 2020). A particularly fascinating opportunity to study this may be to apply the systems biology of seagrass metabolism and production (Kumar and Ralph, 2017; Malandrakis et al., 2017) toward understanding the costs and benefits of rewarding animal pollinators (Hale et al., 2020) within these critically important marine ecosystems (Van Tussenbroek et al., 2016).

The important frontier of functional responses includes developing and testing models of how consumptive behaviors vary with the densities of resources (Gentleman et al., 2003; Vallina et al., 2014; Flynn and Mitra, 2016; Rosenbaum and Rall, 2018) and consumers of those resources (Skalski and Gilliam, 2001) as well as predators of the consumers (Sih, 1980; Schmitz and Suttle, 2001; Skalski and Gilliam, 2002) against individual based models (Katz et al., 2011) and empirical observations (Rall et al., 2009, 2012) of such behaviors. Such work helps to ensure the critically important functional responses within ATN models (Williams and Martinez, 2004b) accurately scale up the consumptive behaviors of individuals to behaviors of populations. This scaling would strongly benefit from incorporating recent advances in the allometry of organismal movement (Hirt et al., 2017, 2018) along with the preference for (Williams, 2008; Heckmann et al., 2012), searching for (Pawar et al., 2012, 2019), and handling of prey (Pawar et al., 2012, 2019) and other resources (Brose, 2010). Key to improving ATN theory in general and functional responses in specific is discovering when processes are better represented as functions, such as those representing adaptive foraging (Valdovinos et al., 2010, 2016; Heckmann et al., 2012), rather than constants. For example, ATN theory typically employs functional responses that assume constant search efficiency and handling times relative to metabolic rate whereas each process depends on temperature (Vasseur and McCann, 2005), allometry (Kalinkat et al., 2013) and whether the interactions occur in 3D environments such as pelagic and aerial habitats or 2D environments such as benthic habitats (Pawar et al., 2012, 2019). Such improvements may be unnecessary where e.g., temperature varies little, or critical e.g., when considering responses to climate warming (Binzer et al., 2016). For example, much ATN research employs logistically growing plants with a community level carrying capacity (**Box A**) due to its simplicity and qualitatively similar behavior to networks based on more sophisticated models of plant growth based on dynamically varying nutrient pools (Huisman and Welssing, 1999; Brose et al., 2005b). Deciding between simpler and more sophisticated theoretical treatments critically depends on the specific goal of applying all theory (e.g., Bauer et al., 2015) and ATN theory is no exception.

Further work scaling populations to communities involves the inclusion of more species and interactions in the architecture of consumer-resource interactions (Williams and Martinez, 2008). While earlier work has advanced the empirical basis of these networks from inclusion of tens of species to including hundreds of species (Jacob et al., 2011), molecular analyses of DNA in the environment and within organisms are leading to even more dramatic increases of biodiversity within food-web data (Pompanon et al., 2012; Roslin et al., 2016; Nielsen et al., 2018). A vast number of cryptic species and interactions including parasitic, symbiotic, and other interactions within organisms' microbiomes are sure to challenge ATN and food-web theory in the near future. Initial progress in this direction includes research on incidental predation upon parasites by predators of their hosts which appears to mount relatively subtle challenges to structural food-web theory (Dunne et al., 2013). More dramatic challenges may emerge from including incidental predation on species' entire microbiomes (Dunne et al., 2013) and the function of microbiomes within species. For example, a substantial amount of biomass consumed by purportedly herbivorous ungulates is produced by microbes within their multi-chambered gut system (Russell and Rychlik, 2001). Recognition of these ungulates as omnivores and quantification of their consumption of plant and microbial biomass could significantly revise understanding of major energy fluxes through food webs. Further attention on nursing by mammals including ungulates elucidates cannibalistic interactions, the feeding upon biomass of other individuals belonging to one's own species, among all mammals. Cannibalistic, predatory, and mutualistic feeding among plants emerge from the increasing realization that plant individuals exchange energetic resources through their roots with other plants (Klein et al., 2016). The recognition of such feeding among plants challenges the long-assumed generalization that the base of food webs is composed of autotrophic species that do not feed upon other species. The recognition of more widely occurring cannibalism among many more species suggests pursuing further research on how cannibalism generally affects the structure and dynamics of ecological networks (Holt and Polis, 1997). For example, density-dependent cannibalism could buffer population oscillations and increase cannibals' persistence by converting biomass from an energy sink into an energy supply when cannibals are abundant and their other resources are rare.

Another key frontier in ecological network research at the community level is the continued addition of non-feeding interactions to food webs (Kéfi et al., 2012). Early advances in this area involve the consumption of abiotic nutrients by plants (Brose et al., 2005b; Brose, 2008), nutrient recycling (Boit et al., 2012), bioaccumulation of toxics (Garay-Narváez et al., 2013, 2014), and the effects of environmental variability on the productivity of autotrophs (Boit et al., 2012; Kuparinen et al., 2018). More recent progress includes intraspecific variation addressed via links between age classes representing maturation and ontogenetic niche shifts in structured populations (Kuparinen et al., 2016, 2018; Bland et al., 2019). Other recent advances involve explicit consideration of facilitation (Kéfi et al., 2012; Valdovinos et al., 2016; Hale et al., 2020) and habitat modification also known as ecosystem engineering (Jones et al., 1994; Kéfi et al., 2012). Initial results show that the structure of these non-feeding interactions is highly predictable in terms of the overall architecture of these networks (Thébault and Fontaine, 2010) and more specifically, which subset of species within a community are involved different types of interactions (Kéfi et al., 2015). Further research shows how these non-feeding consumer-resource interactions can help stabilize the dynamics (Kéfi et al., 2016) and increase the positive effect of species diversity on ecosystem function (Miele et al., 2019) within ATN models of multiplex networks containing both feeding and non-feeding relationships. A key consideration in such extensions involves distinguishing feeding from non-feeding mechanisms occurring within an interspecific link. For example, pollination involves pollinators feeding on floral rewards produced by plants and plants consuming reproductive services produced by pollinators (Valdovinos et al., 2013). Explicit consideration of both interaction types as consumer-resource processes enabled ecological network theory to help resolve debate regarding whether the nestedness of mutualistic networks stabilizes (Bascompte et al., 2006) or destabilizes (James et al., 2012; Staniczenko et al., 2013) pollination networks (Valdovinos et al., 2016). The resolution holds that nestedness alone appears to destabilize mutualistic networks while also stabilizing these networks in the presence of adaptive foraging by pollinators who prefer partners with more floral rewards. The power of this resolution is perhaps best evidenced by its prediction that generalist pollinators prefer feeding on plants with fewer pollinator species to the same degree as such differential preferences are observed in the field (Valdovinos et al., 2016). Further progress in ATN theory involves incorporating such mutualistic mechanisms more broadly by including the production of plant rewards (floral rewards, nectaries, root exudate, etc.) and products of plant partners such as pollinators, seed dispersers, and mycorrhizal fungi providing reproductive and nutrient transport services in exchange for those rewards (Hale et al., 2020). Even broader advances may incorporate mutualistic and non-mutualistic facilitation such as those provided by coral polyps, shade plants, and barnacles that maintain the diversity and function of ecosystems as different as deserts are from the marine benthos.

In each of these advances, classic notions of antagonistic, competitive, mutualistic, etc. *effects* species have on each other would be replaced by focusing on more empirically tractable and successfully predictive *mechanisms* that dynamically generate these effects (Hale et al., 2020).

A final frontier of ATN theory discussed here involves more explicit consideration of space (Holt, 1996, 2002). Early considerations addressed effects of spatial extent on food web architecture in terms of connectance and found this measure of network complexity decreases as area increases such that populations' spatial niches within habitats do not all overlap (Brose et al., 2004). This reduction in spatial co-occurrence prevents some species from directly interacting. Adding a spatial dimension (Ritterskamp et al., 2016a) to the trophic dimension of niche space (Williams and Martinez, 2000, Williams and Martinez, 2008) can address such effects on food-web architecture. Further research has incorporated environmental gradients (Tylianakis and Morris, 2017; Pellissier et al., 2018; Baiser et al., 2019; Gravel et al., 2019) along with experimental (Piechnik et al., 2008; Piechnik, 2013) and theoretical (Holt et al., 1999; Gravel et al., 2019) effects of island biogeography on food-web structure. While such work elucidates key aspects (e.g., species-area relationships, community assembly, etc.) of the architectural framework for ATN theory, dynamical aspects have also been explored examining effects of spatial configurations of ATN models coupled by migration between the models (Allhoff et al., 2015b). This research paves the way for ATN-based meta-ecosystem models (Loreau et al., 2003; Gravel et al., 2010) of large landscapes with many interacting species analogous to global circulation models where the dynamics within a bounded area are determined by ATN theory coupled to neighboring areas by migration either due to random or bounded diffusion (Allhoff et al., 2015b; Ritterskamp et al., 2016a) or more realistic considerations of higher migration rates of relatively large-bodied species at high trophic levels due to resource quality and quantity (Hawn et al., 2018) that help stabilize coupled networks (McCann et al., 2005; Rooney et al., 2006, 2008). Global circulation models of atmospheric (e.g., weather) and aquatic (e.g., ocean circulation) dynamics similarly contain highly parameterized cells representing particular geographic areas where thermodynamic and other forces determine dynamics within each cell and Navier-Stokes equations model the migration of air and water among neighboring cells (Chassignet et al., 2014; Bauer et al., 2015). Navier-Stokes equations may also model plankton movement in aquatic systems supplemented by models of more mobile organisms migrating among neighboring ecological networks (McCann et al., 2005; Rooney et al., 2006, 2008) whose internal dynamics behave according to the bioenergetic equations of ATN theory (Yodzis and Innes, 1992; Williams and Martinez, 2004a; Williams et al., 2007). Such similarities suggest that research on spatial network ecology in aquatic and terrestrial systems could gain much from similar but much more advanced research in the earth sciences (Chassignet et al., 2014; Bauer et al., 2015).

An exciting and perhaps more immediate alternative to extending ATN theory by coupling networks in a spatially explicit manner is coupling ATN and macroecological theory. Whether assembled by evolution, migration or invasion (Rominger et al., 2016) or disassembled by eliminating certain species (Dunne et al., 2002b; Srinivasan et al., 2007) or simply failing to maintain densities above an extinction threshold (Brose et al., 2006b), ATN theory predicts the numbers, biomass, and metabolism of coexisting organisms and species within complex ecosystems. These outputs (e.g., total amounts of biomass and metabolism of all organisms and the total numbers of organisms and species) of ATN theory are the input or "state" variables for the recently developed Maximum Entropy theory of ecology (METE). METE successfully predicts a remarkable variety of empirically observed spatial and non-spatial macroecological patterns such as species-area and species-abundance relationships based on asserting that that organisms will be distributed in space and among species in the least biased way possible (Harte et al., 2008; Harte, 2011). Highly biased distributions occur, for example, when organisms are perfectly evenly distributed in space and among all species and if all but one species had only one organism with all remaining organisms belonging to one species restricted to one small area within a landscape. Instead of these biased distributions, METE predicts organisms are arranged into the distributions that are most likely given the constraints defined the theory's input variables. By analogy, if one rolls two six-sided dice, Max-Ent predicts from these inputs that the most likely sum of a roll is 7 because the largest number of combinations (6) out of the 36 possible combinations add to 7 compared to, for example, only 1 combination that adds to 2 or 12, the least likely sums to be observed. Of course, calculating the number of combinations that a certain number of organisms or amount of metabolism are distributed among a certain number of species and within a certain amount of area is much more involved, but it is still conceptually quite similar to the dice example. The remarkable ability of METE to unify and successfully predict patterns as different as species-area relationships are from species-abundance distributions based on constraints provided by the values of its state variables could extend local ATN predictions to macroecological scales from regions to continents. In contrast to the biological mechanisms underpinning ATN theory, this extension would be based on statistical and information theory (O'Connor et al., 2019) that essentially describes the most probable macroecological patterns to be observed given the constraints provided by ATN theory (Harte, 2011). Beyond enabling the predictions of spatial patterns based on ATN model outputs, the species-abundance distributions emerging from both theories can be tested against each other and the data such as those from simulating Lake Constance (Boit et al., 2012; Boit and Gaedke, 2014). Similar to testing ATN theory's functional responses of feeding against individual-based models of resource consumption, such tests of ATN theory's species-abundance distributions could help build and improve bridges among ecological subdisciplines as well as improve the subdisciplines themselves.

Predicting Ecosystem Phenotype From Community Genotype: A Grand Challenge for Network Ecology

To the skeptic, the many directions described here could suggest a Quixotic pursuit of scientific exactitude as parodied by Jorge Luis Borges' "life size map" subsequently reprised by Lewis Carroll as a cartographer's fantasy that was built but abandoned because the map was too big to ever be unfolded. Despite the freedom of computational science from such spatial constraints, the cautionary tale deserves consideration. Systems biology faced similar skepticism when proposing the simulation of the overall behavior of a whole cell involving the detailed functioning of the genome, proteome, transcriptome and metabolome as a grand challenge of the 21st century (Tomita, 2001). This grand challenge was largely met a decade later with a computational model that predicted phenotype from genotype of a human pathogen (Karr et al., 2012). This achievement not only illustrates the tractability of a highly complex project based on computationally synthesizing different types of biological networks (Palsson, 2006), it also provides strategies and tactics for meeting similar challenges (Palsson, 2015). Central among these strategies are "the enumeration of network components, the reconstruction of networks, the mathematical representation of networks and their mathematical interrogation to assess their properties, and experiments to verify or refute computational predictions" (Palsson, 2004). Tactics to achieve this include developing software standards (Hucka et al., 2003; Waltemath et al., 2016) and integrating Boolean network modeling and constraint-based modeling with ordinary differential equations to reduce the need for parameter estimation (Karr et al., 2012). ATN researchers have already started adopting such tactics by developing software packages to make ATN research easier to conduct and reproduce (Delmas et al., 2017; Gauzens et al., 2017).

Continuing further on a similar path could embrace predicting ecosystem phenotype from community genotype as a grand challenge to advance environmental biology. Meeting this grand challenge would develop the understanding of how the overall behavior of a complex ecological system emerges from the genetic potential of organisms within nominal environments in the lab and eventually less controlled environments in the field. Such work would extend research on biodiversity and ecosystem function to a more comprehensive assessment of diversity for which all taxa surveys (Lawton et al., 1998) and population diversity (Luck et al., 2003) form important starts toward more comprehensive metagenomes of specific habitats (Leray et al., 2012; McCliment et al., 2012). This challenge also integrates the study of ecosystem function beyond material and energy flows to include quantitative effects of species loss (Brose et al., 2005b; Berlow et al., 2009; Brose, 2011) and invasions (Romanuk et al., 2009, 2017) as well and environmental and anthropogenic impacts (Kuparinen et al., 2016) on much finer measures of function such as the ecological and evolutionary fates of individual populations. ATN theory embraces much of the conceptual foundation of systems biology including mechanistic first principles scaled up into data driven networks formalized as empirically parameterized ordinary differential equations empowered by ecoinformatics and computation. ATN theory bases research at different scales upon such foundations (**Box A**). Instead of metabolic networks linking different biochemical species, ATN theory links metabolic energy exchanged among taxonomic species (Brose et al., 2006b). And instead of biochemical species emerging from signaling among networks of genes, ecological species emerge from evolution among phylogenetic networks of taxa (Allhoff et al., 2015a). Integrating a full range of empirically informed ecological and evolutionary processes and interactions in this way could do much to advance a more comprehensive and predictive understanding of environmental biology focused on the structure, function, and evolution of multi-organismic systems in nature (Martinez, 1995, 1996).

Many less grand but no less scientifically important challenges to ATN theory need to be addressed to more broadly test and extend ATN theory. For example, more generic forms of stochasticity often employed in ATN studies need to better focus on specific forms known to greatly affect the structure, functional and evolution of ecological systems. The generic forms mimic the variability among systems found in nature and the disturbances they experience (Domínguez-García et al., 2019) such as species loss (Dunne and Williams, 2009) and invasion (Romanuk et al., 2009, 2017). More specific forms of stochasticity include prominent cases such as marine larval dispersal (Cowen and Sponaugle, 2009) and tree masting (Koenig and Knops, 2005). Initial advances in this direction integrated environmental stochasticity into ATN's deterministic equations via primary producers' carrying capacity and found that such stochasticity is dampened in realistically parameterized ecological networks, especially at higher trophic levels (Kuparinen et al., 2018). Further progress may be achieved similarly by characterizing the magnitudes and frequencies of the specific forms of stochasticity and applying it to the components directly affected in order to evaluate how such stochasticity propagates through ecological systems and determine its ecological consequences. In contrast to such specificity, ATN studies more often deemphasize stochasticity by focusing on mean behaviors among replicates of experiments conducted within restricted time periods (Berlow et al., 2009) or temporal replicates within long time periods (Boit et al., 2012). For example, Boit et al. (2012) averaged decades of time series to create a mean seasonal progression of a temperate lake for ATN forecasts to be tested against. Such averaging helps minimize effects such as stochastic year-to-year variations in weather. A straightforward extension toward focusing on individual years would help illuminate how ATN theory could integrate annual stochasticity in temperature, light, and wind in order to better forecast complex dynamics for individual years. Another broad challenge is more precisely parameterizing ATN equations (Banks et al., 2017). While strong systematic trends and variability about these trends in metabolic rates with body size enable ATN theory to elucidate broad generalities that can be applied to specific systems, more precise parameterization would enable ATN theory to be more specifically and powerfully tested. While this could be achieved by more directly measuring rather than estimating metabolic and functional response parameters, for example in laboratory feeding trials of relatively few species (Rall et al., 2011), the discovery of systematic variations among different taxa (Rall et al., 2011), interaction types (Dunne et al., 2013), and habitat types (Digel et al., 2011) could provide more precise estimates of key parameters with much less effort (Brose et al., 2019a). Such efforts need to be expanded to better understand the capabilities of ATN theory and its limits (Williams and Martinez, 2008).

CONCLUSION

Food-web theory has been developing at least as long as ecology has formally developed as science and forms a key conceptual core of ecology. ATN theory (Brose et al., 2006b; Otto et al., 2007; Berlow et al., 2009) has emerged out of that core based on the architecture (Williams and Martinez, 2000, 2008) and non-linear dynamics (Yodzis and Innes, 1992; Williams and Martinez, 2004a) of organisms consuming primarily food but also other critical resources such as abiotic nutrients (Brose et al., 2005a,b) and services (Kéfi et al., 2012; Hale et al., 2020) produced by other organisms. Metabolism controls the rates of these dynamics by determining the costs of maintaining and building biomass and speed at which resources can be produced and consumed. While ATN theory often embraces the niche model (**Figure 3**) and the metabolic theory of ecology (Brown et al., 2004) to generally explore the consequences of the structure and rates of these interactions, more direct measures of structure and rates can facilitate application of ATN theory, especially with respect to specific ecosystems (Boit et al., 2012) and types of ecosystems (Digel et al., 2014; Brose et al., 2019a). ATN theory has advanced well beyond answering broad qualitative questions about stability (Dunne et al., 2005; Martinez et al., 2006; Stouffer and Bascompte, 2010, 2011), species coexistence (Brose, 2008; Kartascheff et al., 2010), and functioning (Kuparinen et al., 2016; Schneider et al., 2016; Miele et al., 2019) of complex ecosystems to the accurate and detailed quantitative prediction (Dunne et al., 2008; Berlow et al., 2009) and forecasting (Boit et al., 2012) of the structure and dynamics of specific systems in nature. Mechanisms other than consumer-resource interactions such as evolution, migration, maturation, and economics are increasingly integrated into ATN research. As such, this body of theory forms a rigorous example and mechanistic framework for multi-scale predictive understanding of ecological systems from physiological to socio-ecological scales. A particularly intriguing example is the ability to mechanistically bridge the physiological and behavioral understanding of organisms to continental scales of macroecological species-area and species-abundance distributions. Such sub-disciplinary and disciplinary bridge building combines detailed mechanistic understanding and a holistic vision of the proverbial elephant (**Figure 1**), parts of which are studied by ecological subdisciplines in specific (**Figure 2**) and even more parts of which are studied by sustainability scientists in general.

Overall, ATN theory helps unify ecology by integrating diverse perspectives into a successfully predictive whole that ecologists from virtually all subdisciplines studying all organisms in all habitats at all scales from molecules to the biosphere have contributed to (**Figure 2**). The many active frontiers of ecology in general and ATN theory in specific ensure that these synergisms will continue well into the future. Much ATN research pursues a data-rich form of theory more similar to systems biology (Purdy et al., 2010; Evans et al., 2013) than to physics from which several of the most prominent theoretical ecologists have emerged. This suggests that future ATN research may be more like Darwin's extensive natural history expeditions and systems biologists' expansive characterization of DNA, genetic signaling networks, and kinetic coefficients of enzymes than Netwon's contemplation of a falling apple or Einstein imagining riding on a beam of light. In contrast to such brilliant advances in the physical sciences, the biological focus of ATN theory suggests ecologists attend more to spectacular advances and grand challenges of systems biology achieved by computational approaches (Holland, 2012) to integrating big data and diverse mechanisms using networks as a central organizing principle (Palsson, 2006) as have many other non-biological sciences (Barabási, 2012). Such work could well transform the theoretical core of ecology concerned with effects species have on one another to formalizing the mechanisms from which such effects emerge (Hale et al., 2020). Such a paradigm shift could result in future ecologists viewing our current preoccupation with antagonism, competition, mutualism and facilitation similar to alchemists' preoccupation with earth, air, fire, and water. Ecologist's ability to explain much but predict relatively little invoking these effects may share remarkably many similarities with the alchemists of old. Most hopefully, moving to a more mechanistic and data-rich focus would provide a much firmer foundation for sustainability science to help solve several of humanity's most pressing problems.

AUTHOR CONTRIBUTIONS

NM conceived of and wrote the manuscript.

FUNDING

This work was funded by the USA Department of Energy grant DE-SC0016247 and National Science Foundation grants 1241253, 1313830, 1642894, 1754207, and 1934817 to NM.

ACKNOWLEDGMENTS

This work was made possible by collaborations with many individuals most importantly lab members and visitors including B. Feifarek, D. Piechnik, R. Williams, U. Brose, J. Dunne, E. Berlow, K. Harrison, B. Harvey, C. Puleston, E. Vaccaro, I. Yoon, P. Yoon, R. Rael, T. Romanuk, L. Cushing, T. Srinivasan, H. Morlon, P. Tonin, A. Boit, B. Bauer, A. Kuparinen, A. Martín González, H. Ko, K. Salau, F. Valdovinos, K. Sale-Hale, K. Allhoff, and N. Kappler. Special thanks to the reviewers and Lelu Musick for artistic advice.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer, DG, declared a past collaboration with the author to the handling Editor.

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