



The Foundation for Building the Conservation Capacity of Community Ecology

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Ecology is a young discipline that needs to develop into a predictive science to confront the challenges of human population pressures and habitat degradation. Basic ecology has disproportionately focused on undisturbed, charismatic ecosystems, species and academic questions, leaving gaps in its ability to inform the conservation and management of degraded, threatened ecosystems. Foundation species-dependent organisms have been studied at the expense of the habitat-forming species that build and maintain communities. We used cobble beaches as a model system to discuss the consequences of this disparity on translational ecology. We suggest that the historic development of ecology has led to an academic discipline ill-suited for proactive conservation. We propose that the incorporation of foundation species and a hierarchical organization theory, into the conceptual framework of ecology, will improve its predictive ability and successful application in conservation and the restoration of degraded ecosystems.

Keywords: conservation biology, experimental ecology, foundation species, hierarchical organization, natural history

INTRODUCTION

Understanding the physical and biological forces that create patterns in biotic communities and ecosystems is the major goal of ecology. Community, evolutionary, and conservation ecology have grown from a common ancestry of natural history. In spite of this, ecology has been challenged in its ability to develop into a predictive science informing the management and restoration of threatened or damaged systems (Wallington et al., 2005). Due to the barriers created by the historic development of ecology, conservation practice has been piecemeal, differing across ecological systems, and has been predominantly reactive, rather than proactive (Brooks et al., 2006; Sutherland et al., 2011; Cook et al., 2013, 2014). A unified translational conceptual ecology framework based on the fundamental role of a hierarchical community organization is needed to confront the contemporary conservation crisis.

A BRIEF HISTORY OF ECOLOGY

Originating from the seminal science of natural history observation, ecology developed to explain processes and patterns in natural communities (Odum, 1953; Krebs, 1972). Contemporary ecology and evolutionary biology grew from global exploration voyages of the 19th and early 20th Centuries. Darwin and Wallace pioneered the study of evolution on these voyages (Darwin, 1859). Ecology pioneers like Tansley and Clements described species and studied spatial patterns to build the conceptual foundation of ecology (Tansley, 1935; Clements, 1936). Their work was correlative, assumed causation from correlation, and led to the quantification of species distributions relative to abiotic variables—a hallmark of ecology in the first half of the 20th century.

From this descriptive beginning, theoretical ecology focused on niches, competition, and trophic dynamics. Gause's (1934) "Struggle for Existence" painted an ecological framework echoing Darwin's work. Grinnell, Elton, and Hutchinson developed a niche theory based on distribution and abundance patterns, reflecting physical tolerances and competitive interactions among species (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). This era influenced ecological theories, such as Garret Hardin's competitive exclusion principle (Hardin, 1960) and Eugene Odum's ecosystem superorganism concept (Odum, 1969), which assumed ecosystem equilibrium but ignored the dynamic fluxes and disequilibrium that are conspicuous in the field.

Hypothesis-driven field experiments (Connell, 1961; Paine, 1966) led to recognition of disturbance (Dayton, 1971) and its role in structuring natural communities. Experimental ecology further demonstrated the limited ability of correlations to provide mechanistic answers in community ecology. Hutchinson's "Ecological Theater and the Evolutionary Play" (Hutchinson, 1969) metaphor captured our contemporary view of how natural evolutionary and ecological processes generate patterns in nature. But, this recognition of a unified theoretical framework of ecological pattern generation came shortly before recognition that all ecosystems on Earth were impacted by the unnatural human influences of overexploitation of resources, eutrophication, and climate change driven by our unchecked population growth (Vitousek, 1994; Steffen et al., 2007; Halpern et al., 2008; Estes et al., 2011). As these stressors have intensified in spatial extent, severity, and/or frequency, the conservation of natural systems has been affected by shifting baselines syndrome (Pauly, 1995) and "generational amnesia" (Alleway and Connell, 2015), where "healthy" baselines and expectations for ecosystem services are continuously shifted toward lower, more degraded states.

PROBLEMS UNITING CONCEPTUAL ECOLOGY AND CONSERVATION BIOLOGY

Attempts to apply ecological principles to conservation practice exposed inherent problems that limit the value of ecology as a predictive, applied science (Balmford and Cowling, 2006; Kareiva et al., 2017). One primary issue is that ecology is strongly habitat,

taxa, and community biased, and lacks a unified conceptual framework (Lawton, 1999; Meine et al., 2006). Animal and plant ecologists use different terminology, are commonly described by systems in which they work, and produce results that are often habitat-specific and not generalized. Even assembly rules and operational definitions of concepts differ among subfields, begging the question: can ecology become more than a collection of case studies?

The information era has created new problems for developing a predictive, mechanistic, understanding of community ecology. The drift toward summaries and/or meta-analyses of databases and existing information, rather than field observations and experiments in natural systems has slowed progress in the discipline and prevents ecology from becoming a predictive science. Review papers can be useful as hypothesis generating tools and for identifying gaps in understanding but place a potentially detrimental focus on past research (Schmidt and Hunter, 2014). We argue that a hypothesis-driven, experimental path is needed to synthesize ecology, evolution and conservation into the predictive science needed to confront conservation challenges into the future.

Analogous to the recognition by molecular geneticists that not all gene sequences are equally important, experimental ecology has shown that not all species are equally important in structuring communities and provisioning ecosystem functionality. First described by Dayton (1972), foundation species are abundant organisms that provide habitat templates for communities. Across most ecosystems, foundation species significantly alter physical and biological stress regimes, promoting increases in biodiversity, function, and overall ecosystem development (Stachowicz, 2001; Angelini et al., 2015; Ramus et al., 2017). Most ecosystems can therefore be viewed as hierarchically organized, since the community of inhabitants and their network of ecological interactions are dependent on the setting created by foundation species. In contrast to the highly abundant foundation species, keystone species are those that have a disproportionately large impact despite their low abundance (Power et al., 1996) and their importance can become more apparent as human stressors amplify, interact, and alter the trophic structure of ecological communities (Jordán, 2009). There is an ongoing debate in the literature regarding exact definitions of these terms (Mills et al., 1993) and the context of if and when foundation species may have disproportionate, keystone effects (Coleman and Williams, 2002). Nonetheless, the breadth of their potential interactions and the depth of their reach into the community means that both foundation species and keystone species typically require hypothesis-driven field experiments to identify, rendering species lists and diversity metrics good descriptors, but largely useless as predictors without underlying mechanisms.

COBBLE BEACHES AS MODEL SYSTEMS FOR CONCEPTUAL ECOLOGY

We suggest that the conceptual development of modern ecology is in danger of becoming untethered from the natural history

field acumen of ecology's founders, and that the lack of this grounding will obscure the development of an inclusive, robust and predictive ecology. We explore this perspective using cobble beach community model systems. Most ecosystems are defined by foundation species and illustrate the importance of a hierarchical organization and the contribution of keystone species. We use cobble beaches because they are rare relative to the important role they have played in developing ecological theory, making them "keystone" in their contribution to the advancements of conceptual ecology.

Cobble beaches occur where glaciers from Pleistocene ice ages crushed and eroded bedrock into boulders, cobble, and sediment. In North America, the mass of the 2.5 km-thick Laurentide Ice Sheet covering an area exceeding 13,000,000 km² compacted, crushed, fractured, scoured and depressed underlying bedrock. The resulting dislodged rocks, sediment, and debris were pushed by advancing glaciers or deposited as the ice retreated. These processes created capes, coastal islands, and rocky and cobble beaches where shorelines were scoured, and rock debris was deposited (Packham and Willis, 1997).

While cobble beaches have recently attracted the attention of ecologists, they have played a pivotal role at important stages in the development of conceptual ecology. Cobble beaches harbor foundation species-dependent communities at experimentally manageable spatial scales and have disproportionately contributed to a mechanistic understanding of community assembly and dynamics directly applicable to management and conservation. In particular, the dependency of biological communities on substrate stability and positive species interactions was experimentally elucidated in this system (Bruno, 2000; Bruno and Bertness, 2001).

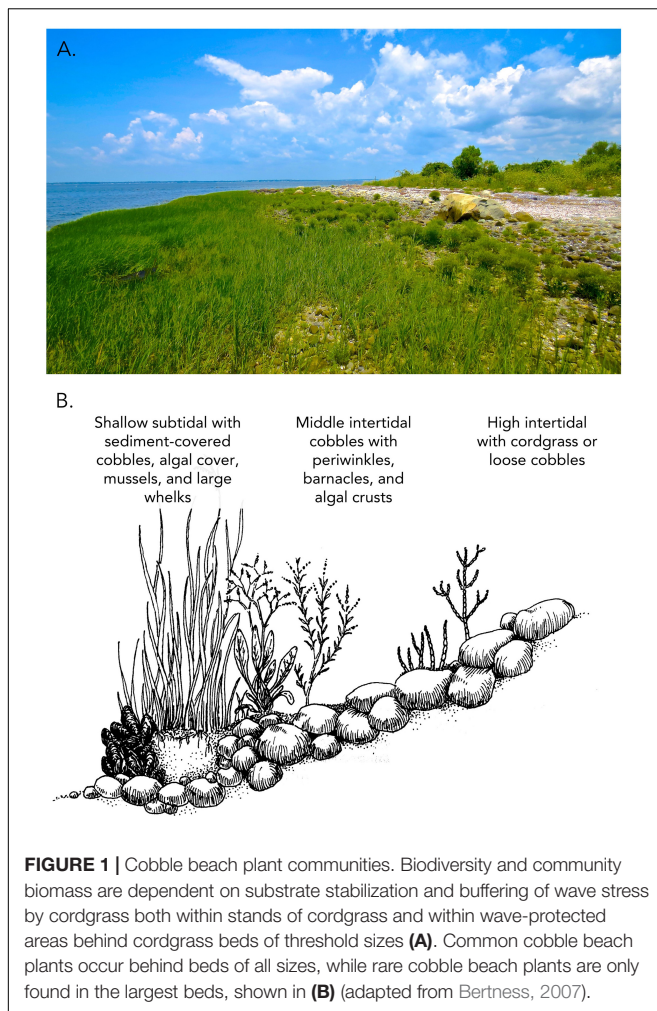
The first general idea that grew from cobble beaches featured the consequences of disequilibrium rather than stability and equilibrium – the intermediate disturbance hypothesis (IDH). Early ecologists avoided disturbed habitats, leading to the assumption that communities existed in equilibrium, a problematic belief for conservation ecology as nearly all are disturbed from their natural state due to human impacts (Watson et al., 2016). This bias became fixed in early ecological theory until Dayton (1971) and Platt's (1975) work in rocky intertidal and grassland ecosystems, respectively, pointed to the role of disturbance in structuring communities. This work inspired cobble beach studies by Sousa (1979) showing that maximum species diversity and richness occur on intermediately sized rocks large enough to prevent constant disturbance and colonization by weedy species, but small enough so they were disturbed occasionally which limited the emergence of a competitive dominant. The development of the IDH (Connell, 1978; Sousa, 1979) freed ecologists from the constraint of equilibrium and was exported and extrapolated extensively to virtually all communities. Future insights were based on the transitional nature of cobble beaches lying between muddy beaches and boulder fields, their interaction with the physical forces that cause stress and instability, and the dependency on positive biotic interactions for structuring the communities that inhabit them (van Wesenbeeck et al., 2007).

FOUNDATION SPECIES AND ECOSYSTEM ENGINEERS

Foundation species are abundant organisms that provide habitat and infrastructure templates for communities (Dayton, 1972). Ahead of its time, Dayton's foundation species work did not fit into the food web-based conceptual ecology developing at the time and contradicted Paine's (1966) idea that keystone species were the most important drivers of species diversity by suggesting that habit-forming organisms were the primary determinant of biodiversity patterns, rather than the species that ate them. Dayton (1972) coined the term foundation species working with sponges in Antarctica, and then popularized the term through his work with intertidal algal canopy communities that provided shading, water retention, and thermal stability during low tide exposure to physically stressful terrestrial conditions, and acted as a refuge from consumers during high tide foraging (Dayton, 1975). Without the stress amelioration provided by the algal canopy, the understory organisms suffered increased mortality from physical and biological stressors. Foundation species structure ecological communities by providing physical structure and stress amelioration across most ecological systems, whether they are algal canopy, forest canopy, coral reefs, mussel or oyster beds or seagrass meadows (Bruno and Bertness, 2001; Ellison et al., 2005; Angelini et al., 2011; Altieri and van de Koppel, 2013).

Despite early development of the foundation species concept, the general importance of foundation species in biological communities was not recognized until the critical role of positive feedbacks for community persistence and stability became apparent in plant communities (Wilson and Agnew, 1992). Positive feedback switches were proposed to be common in community assembly, occurring when species ameliorated physically stressful habitats, and improved growth and survival conditions for themselves and others. One of the first experimental examples was the foundational role of cordgrass colonization of cobble beaches. Foundational cordgrass was shown to transform areas characterized by low-diversity, high disturbance, mobile, rolling rocks to biodiverse, stabilized habitats that hosted a guild of plants that could develop into fringing salt marshes replete with the plant zonation, interspecific competition, facultative plant-animal mutualisms and ecosystem services that characterize salt marshes (Bruno, 2000). This positive feedback switch is evident in New England salt marshes in sheltered bays where centuries of compact peat accretion often overlay cobble beach foundations (Coverdale et al., 2014). Whole system facilitation of cobble beach plant communities is a long process initiated when cordgrass gains a foothold on barren cobble beaches. Successful cordgrass establishment and lateral expansion leads to development of compacted organic root debris and sediment, and, if not disturbed in early stages, develops a peat foundation. This peat foundation buffers cobble shorelines from wave energy, limits cobble movement by binding cobbles to the beach, and dissipates wave energy, creating low wave energy refugia among cobbles at higher elevations (**Figure 1**).

As cobble beach cordgrass stands increase in size and robustness through clonal growth, their ability to buffer wave



energy increases non-linearly, triggering positive feedbacks through increased sedimentation and the recruitment of commensal and facultative mutualists. This further stabilizes the cobble beach plant communities and associated animals. Increasing bed size also leads to the recruitment of rare plant and animal species unable to recruit to or persist in smaller beds with less habitat amelioration. This hierarchical development leads to a strong positive relationship between bed size and plant community species richness, recruitment, and persistence (Bruno, 2002).

In addition to foundation species, the role of allogenic ecosystem engineers, or organisms that transform resources from one state to another (Jones et al., 1994; Coleman and Williams, 2002), in driving community pattern formation was identified in cobble beach communities. Experimental examination of the impact of the invasive European Periwinkle, *Littorina littorea* (hereafter *Littorina*), to North American shorelines revealed dramatic habitat change mediated by snail engineering (Bertness, 1984). This herbivorous snail was introduced to Nova Scotia in the mid-19th century, but quickly invaded south to Chesapeake Bay where it filled an apparently empty niche created by the retreat of Pleistocene glaciers, frequent winter icing, and the

industrial revolution that had eradicated all but the weedy, fast growing and early reproducing species (Wetthey, 1985). As a result, *Littorina* quickly became the most abundant grazer on New England rocky shores.

On southern New England cobble beaches, *Littorina* removal experiments revealed their role as keystone grazers because their activity and feeding behavior engineered the structure of the shoreline, mediating whether cobble beaches remained bare or transitioned to cordgrass stands on muddy beaches with abundant associated fauna and flora. Within a month, snail removal cages had a lush canopy of ephemeral green algae and were blanketed with sediment that buried and suffocated sessile organisms. Cages with snails remained entirely free of algae and sediment. Three months after the snail removal, control cages remained sediment and algal free, while infaunal worm and mud crab larvae recruited to the sediment and algal covered ungrazed cobble. The following year cordgrass rhizomes invaded muddy snail removal areas along with their facultative mutualist mussels and fiddler crabs (Supplementary Figure S1). When the experiment ended and snails were allowed to return to all plots, this process reversed as sediment and cordgrass retreated. The experimental evidence was clear; Narragansett Bay cobble beaches were on an ecological tipping point and the presence or absence of invasive snails engineered whether shorelines were sediment-free with barnacles, or biodiverse muddy, incipient salt marshes (Bertness, 1984).

HIERARCHICAL ORGANIZATION AND FACILITATION CASCADES

Foundation species have particularly powerful effects when they overlap in facilitation cascades. These indirect positive interactions occur when a primary foundation species alleviates stress to facilitate a secondary foundation species and together, they support a larger, more diverse community with increased ecosystem functionality than either foundation species alone (Altieri et al., 2007; Gedan et al., 2014; Thomsen et al., 2018). Facilitation cascades are another emergent trait of cobble beach communities. On southern New England cobble beaches, the secondary foundation species and mutualist ribbed mussel, *Geukensia demissa*, settles gregariously on cordgrass roots. Once established, mussel shells provide hard substrate for the recruitment of barnacles and seaweed and crevice space for mobile organisms. This hierarchical organization of foundation species leads to a facilitation cascade of marine organisms and cobble beach vascular plant communities (Altieri et al., 2007). Additional studies revealed that secondary foundation species consistently increase the abundance and richness of associated communities across spatial scales, latitudes, and ecosystems including wetlands, coral, mussel and oyster reefs, terrestrial forests and sand dunes—a finding that has implications for robust community assembly rules and the conceptual core and basic assumptions of community ecology theory (Supplementary Table S1) (Bell and Westoby, 1987; Hall and Bell, 1988; Pettersson et al.,

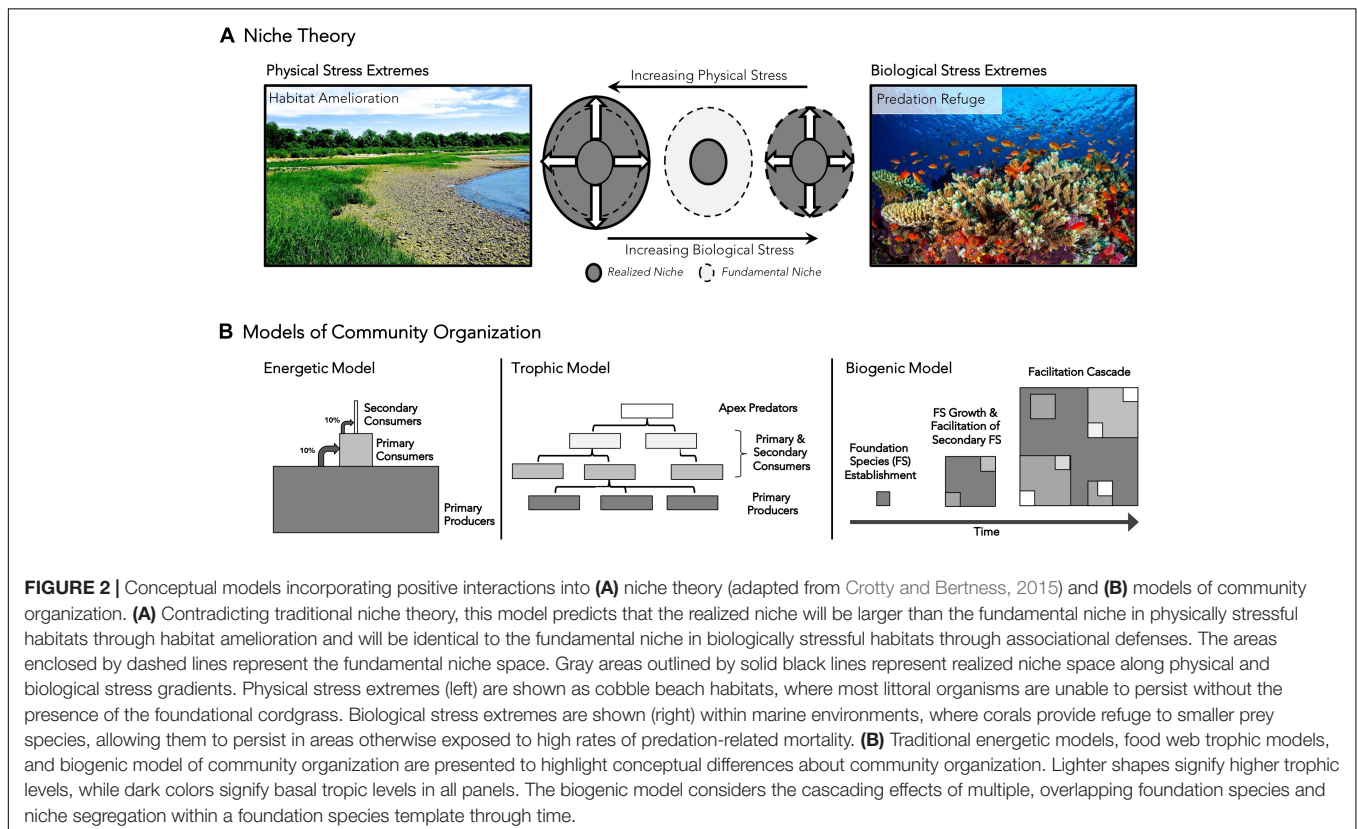
1995; Castro et al., 2004; Ellwood and Foster, 2004; MacDonald et al., 2008; Thomsen, 2010; Angelini and Silliman, 2014; Thomsen et al., 2016).

INCORPORATING FACILITATION THEORY INTO CONSERVATION BIOLOGY

Textbook ecology and its extrapolation to conservation continue to be based on niche theory and the competitive exclusion principle. But the use of niche theory to predict species distributions has been questioned by findings on cobble beach ecosystems. The prevailing theory predicts that the spatial and temporal space that a species can survive in allopatry, the fundamental niche, is larger than the realized niche that a species occupies with biotic interactions or in sympatry, particularly owing to competition (Chase and Leibold, 2003). Experimental studies on cobble beaches, however, have shown that by ameliorating physical and biological stresses, foundation species not only impose hierarchical organization on communities, but dramatically increase the size of realized niche space at biological and physical stress extremes. Inclusion of positive interactions, by altering the predictions of niche theory, can more accurately predict distribution patterns in nature (Figure 2A; Crotty and Bertness, 2015). Evidence for this revised niche theory is apparent in a variety of ecosystems, including corals that generate physical structure and productivity on oligotrophic reef habitats

(Knowlton and Jackson, 2001), trees that provide structure, trophic resources, and habitat amelioration to understory food webs (Ellison et al., 2005), and beavers that engineer temperate forests into habitat for wetland plants (Naiman et al., 1988). Seagrass meadows, mangroves, and mussel and oyster reefs provide additional examples of foundation species extending the range of associated organisms beyond their predicted area through amelioration of physically and/or biologically stressful environments.

Human impacts on foundation species and ecosystem engineers have illustrated the inadequacy of competition-based niche theory. The great dust bowl of the American plains, desertification of over-harvested forests, and the ongoing die-off of oyster and coral reefs, salt marshes, seagrasses, and mangroves forests all have unique proximate causes. However, the common denominator among all of these examples is the loss of foundation species leading to system collapse (Intergovernmental Panel on Climate Change [IPCC], 2014). The general lessons from these events—that facilitation is as ubiquitous an interaction as competition and that the hierarchical overlap of foundation species is often responsible for ecosystem structure, function, resilience, and recovery potential—needs to be incorporated into mainstream conservation biology and associated proactive management prescriptions (Gedan and Silliman, 2009; Thurstan et al., 2013; Fariñas-Franco et al., 2018). Where ecological systems are already perturbed, restoration ecology can and should become the experimental testing ground for predictive community ecology based on



this new understanding. In the few instances where facilitation theory has begun to inform restoration design, the results have been overwhelmingly positive—providing support for the idea that utilizing the hierarchical organization perspective of foundation species, and the associated positive feedbacks, will be critically important for enhancing the recovery and resilience of ecological systems as anthropogenic stressors intensify and degrade ecosystems (Silliman et al., 2015; Derksen-Hooijberg et al., 2017; **Supplementary Box S1**).

BUILDING A PREDICTIVE PRACTICAL COMMUNITY ECOLOGY

To date, community ecology has largely been an academic exercise that has not reached its potential as a predictive applied science. It has produced an intellectually satisfying body of literature and theory that explains the pattern and dynamics of biotic communities but has generally been reactive when challenged with large local and global anthropogenic threats. It is commonly believed that the failures of ecology as a translational science are a communication problem (Sutherland et al., 2006; Jacobson et al., 2015). We disagree. While communication is important, it needs a clear intuitive message to succeed. We suggest that these failures are instead a conceptual problem based on the inability to apply traditional niche, energetic, and trophic models to solve problems in the conservation, management, and restoration of threatened ecosystems. These models are valuable metrics for evaluating ecosystem health and understanding the functional and dysfunctional dynamics

of biological communities, but do not address the system ontogeny that is key to the resilience and recovery of damaged ecosystems (**Figure 2B**). The solution is a simpler biogenic model of a community structure based on the fundamental importance of foundation species and ecosystem engineers, the hierarchical organization generated by these critical species, and the role of facilitation cascades in driving the structure, function, and positive feedbacks that underpin the resilience of biotic communities. Adopting this perspective will allow ecology to develop into a predictive applied science needed for the future success of conservation, management and restoration.

AUTHOR CONTRIBUTIONS

MB and SC wrote the first draft of the manuscript. All authors revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00238/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.

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