



From Elements to Function: Toward Unifying Ecological Stoichiometry and Trait-Based Ecology

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Specialty section:

This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: 26 January 2017

Accepted: 19 April 2017

Published: 08 May 2017

Citation:

Meunier CL, Boersma M, El-Sabaawi R, Halvorson HM, Herstoff EM, Van de Waal DB, Vogt RJ and Litchman E (2017) From Elements to Function: Toward Unifying Ecological Stoichiometry and Trait-Based Ecology. *Front. Environ. Sci.* 5:18. doi: 10.3389/fenvs.2017.00018

The theories developed in ecological stoichiometry (ES) are fundamentally based on traits. Traits directly linked to cell/body stoichiometry, such as nutrient uptake and storage, as well as the associated trade-offs, have the potential to shape ecological interactions such as competition and predation within ecosystems. Further, traits that indirectly influence and are influenced by nutritional requirements, such as cell/body size and growth rate, are tightly linked to organismal stoichiometry. Despite their physiological and ecological relevance, traits are rarely explicitly integrated in the framework of ES and, currently, the major challenge is to more closely inter-connect ES with trait-based ecology (TBE). Here, we highlight four interconnected nutrient trait groups, i.e., acquisition, body stoichiometry, storage, and excretion, which alter interspecific competition in autotrophs and heterotrophs. We also identify key differences between producer-consumer interactions in aquatic and terrestrial ecosystems. For instance, our synthesis shows that, in contrast to aquatic ecosystems, traits directly influencing herbivore stoichiometry in forested ecosystems should play only a minor role in the cycling of nutrients. We furthermore describe how linking ES and TBE can help predict the ecosystem consequences of global change. The concepts we highlight here allow us to predict that increasing N:P ratios in ecosystems should shift trait dominances in communities toward species with higher optimal N:P ratios and higher P uptake affinity, while decreasing N retention and increasing P storage.

Keywords: food web, biological stoichiometry, functional trait, fitness, trade-off, resource

INTRODUCTION

Ecological stoichiometry (ES) is a framework that links an organism's metabolic demands with the relative supply of elements in the environment (Sterner and Elser, 2002; Hessen et al., 2013). It postulates a crucial relationship between the balance of elements, typically but not limited to carbon (C), nitrogen (N), and phosphorus (P), and their role in determining growth and reproduction of organisms as well as in ecological interactions. The recognition of the importance of stoichiometric constraints between consumer needs and prey nutrient content has substantially increased our

understanding of trophic interactions. For example, high C:P food is often of low-quality for a variety of organisms including molluscs (Stelzer and Lamberti, 2002; Fink and Elert, 2006), crustaceans (Boersma and Kreutzer, 2002; Meunier et al., 2012, 2016a), insects (Perkins et al., 2004), fish (Borlongan and Satoh, 2001; Vrede et al., 2011), and birds (Grone et al., 1995). ES has therefore proven to be a highly suitable framework in community ecology, explaining consumer responses to prey food quality (food intake, growth, as well as competition between consumer species, and consumer effects on prey nutrient composition (Sternner, 1990; Sternner et al., 1992; Sternner and Hessen, 1994).

Trait-based ecology (TBE) focuses on functional traits expressed by an organism allowing its growth and survival under distinct environmental conditions (McGill et al., 2006). Functional traits are the morphological, physiological, phenological, and behavioral characteristics of an organism that influence its performance or fitness. As such, TBE couples biological function to the success of species in a food-web (Litchman and Klausmeier, 2008; Litchman et al., 2013; Kremer et al., 2016). More specifically, TBE focuses on traits rather than taxa, providing a functional approach to understanding ecological interactions. For example, it has been shown that trait diversity can provide a better predictor of primary production as compared to taxonomic diversity (Vogt et al., 2010). Numerous studies indicate that abiotic parameters, such as temperature, precipitation, and nutrient concentrations, can directly influence spatial and temporal trait patterns both at the population and at the community levels (Brun et al., 2016). TBE therefore constitutes a powerful tool linking species functional characteristics to their distributions along environmental gradients, as well as to community interactions and ecosystem function.

The framework of ES is essentially, although not explicitly, based on traits such as homeostasis, growth rate, and nutrient uptake. For instance, the relationship between organism size and stoichiometry has been well studied (see below for more detail) but connecting these ES traits with more traditional TBE traits still remains a major challenge. Combining the framework of ES with TBE furthers the coupling of elements to functional traits from subcellular processes to species interactions and ultimately ecosystem dynamics. For example, linking ES with TBE could help studying how variation in traits related to elemental body composition influences organismal fitness (Leal et al., 2016). The focus of this paper is to explore and synthesize existing insights, and to develop novel connections between ES and TBE. We first review key traits and their elemental requirements, highlighting differences between trophic levels as well as ecosystems. Next, we describe trade-offs between traits that directly or indirectly affect the elemental composition or requirements of organisms. We also develop hypotheses on how different traits could be linked to life history trade-offs, and we outline community and ecosystem consequences of variation in ES traits and identify limitations and opportunities for future research further connecting TBE and ES. This framework will foster collaboration between scientists of different disciplines (freshwater, marine, and terrestrial ecologists) and enhance our understanding of fundamental ecological issues.

TRAITS AND ELEMENTAL BALANCES

Four interconnected major trait groups affect the balance of energy and elements in organisms: acquisition, cell/body stoichiometry, storage, and excretion. These traits define how organisms interact with their environment as well as with one another, and are, therefore, among the key determinants of ecological niches. This elemental trait framework has already been successfully used to identify how resource imbalances affect basic physiological processes (Frost et al., 2005). In the following sections, we describe different strategies utilized by autotrophs and heterotrophs to acquire and use C and nutrients, and we explain how these traits directly influence organismal stoichiometry. While traditional stoichiometric approaches are implicitly trait-based, we here aim to fully place life history trade-offs in a stoichiometric context. This conceptual framework should enhance our ability to predict how communities will respond to changes in nutrient conditions in the environment.

Autotrophs

Autotrophs obtain energy (mostly sunlight) and material from different, uncoupled sources within their environment. Therefore, plants needed to develop strategies to store these resources, as the availability of one resource does not guarantee another one. Nutrient uptake strategies are often linked to storage capacity and therefore to plasticity in cellular stoichiometry. When C or nutrients are taken up and fixed by autotrophs, they may be used immediately for growth or accumulate as storage pools for later use (Chapin, 1980; Reynolds, 2006). Due to their need and hence capacity to store nutrients, autotroph C:N:P ratios greatly vary with available nutrient ratios, indicating a high flexibility in chemical composition and a lack of homeostasis (Sternner and Elser, 2002; Meunier et al., 2014). This can result in different competitive strategies between various autotroph species. For instance, for phytoplankton, three major nutrient acquisition strategies have been proposed (Sommer, 1984): (1) velocity-adapted species, or r-strategists, with high maximum nutrient uptake rates and high maximum growth rates that are able to directly utilize nutrient pulses for growth, (2) storage-adapted species, with high rates of nutrient uptake but lower maximum growth rates that have the ability to store excess nutrients, and (3) affinity-adapted species, or K-strategists, with the ability to effectively take up and assimilate growth-limiting nutrients even at low concentrations, a strategy that is advantageous in oligotrophic environments. Comparable nutrient-acquisition strategies exist in terrestrial systems, and nutrient availability strongly influences interspecific plant interactions and community composition (Zemunik et al., 2015). For instance, tall-growing species with high growth rates are generally favored by high nutrient inputs at the expense of species with conservative growth strategies (Diekmann and Falkengren-Grerup, 2002). Physiological traits such as nutrient requirements also alter interspecific competition, giving a competitive advantage to species with high-nutrient affinity (Price and Morgan, 2007).

Such different strategies may affect the stoichiometry of autotrophs. For instance, high growth rates may lead

to higher demands for P (see below), storage will increase cellular quota of distinct elements, while high affinities will reduce the minimum nutrient requirements (**Figure 1**). Stoichiometric plasticity will furthermore be determined by physiological limits, as was shown for phytoplankton N:P ratios that increased non-linearly with increasing N:P supply ratios (Rhee, 1978; Persson et al., 2010). In other words, the upper limit of nutrient quota is determined by storage capabilities, while the lower limits are determined by minimal structural and functional requirements, as well as the affinity for a nutrient. These boundaries within which the organism's stoichiometry can fluctuate represent the "homeostatic capacity" parameter defined by Meunier et al. (2014). This parameter corresponds to the boundaries within which the organism's body stoichiometry can fluctuate and therefore characterizes storage capacity. Consequently, storage- and affinity-adapted species will be generally characterized by variable stoichiometric composition while velocity-adapted species with high P demands will have low cellular N:P ratios (Hillebrand et al., 2013).

Variation in N:P ratios between organisms often reflect functional differences, such as the ones that have been described for optimal N:P ratios (Güsewell, 2004; Hillebrand et al., 2013), i.e., the N:P ratio at which growth is maximized. In aquatic environment for example, a recent meta-analysis identified a scaling relationship between maximum growth rate and phytoplankton nutrient demand (Hillebrand et al.,

2013). Phytoplankton N:P ratios decrease with increasing growth rates and simultaneously display decreasing variance, particularly driven by P limitation, which follows predictions of the Growth Rate Hypothesis (Sterner, 1995a; Elser et al., 1996; Sterner and Elser, 2002). This suggests that fast growing phytoplankton species, or within a species under less severe limiting conditions, phytoplankton are relatively more P-rich. Using a trait-based eco-evolutionary model, Klausmeier et al. (2004) showed that different environmental conditions select for species with different N:P ratios: P-rich conditions select for fast growers with low N:P, while P-limited conditions select for better P competitors with higher N:P ratios (due to their investment in resource acquisition proteins, **Figure 1**). Not only the N:P ratio itself but the form of N and P available to phytoplankton matters. While we may expect higher biomass of small phytoplankton at lower N:P supply due to their generally fast growth (and thus high P requirements), higher picophytoplankton densities are only observed under high N:P conditions (**Figure 1**; Glibert, 2016) which is likely caused by changes in N redox and relative proportions of reduced relative to oxidized N (Glibert et al., 2016). A review of interspecific differences in N:P ratios of terrestrial plants concluded that N:P ratios correlate negatively with maximum relative growth rate in herbaceous and woody plants (Güsewell, 2004). Species with inherently low N:P ratios are predicted to dominate N-limited communities and should be favored during P fertilization (**Figure 2**; Tilman, 1997). Therefore, nutrient supply and composition often shape terrestrial and aquatic autotroph community composition by species sorting as well as by dynamic shifts in species' C:N:P stoichiometry (Sterner and Elser, 2002; Persson et al., 2010; Meunier et al., 2014).

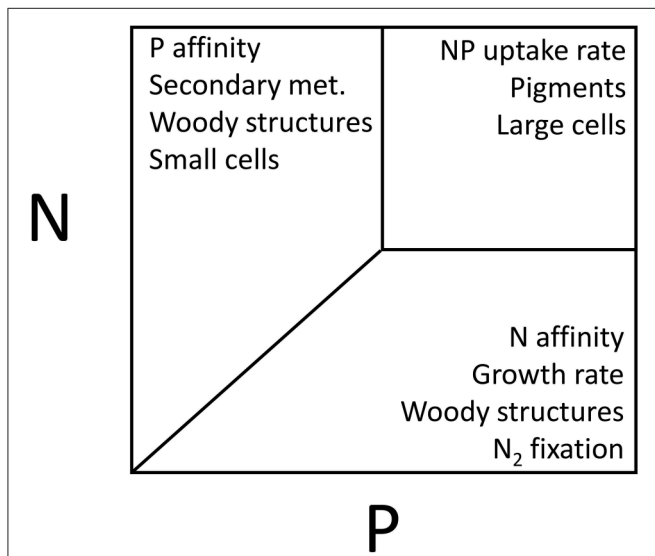


FIGURE 1 | Influence of N and P availabilities on trait dominance in autotrophs. Low N and P supplies will favor species with high affinities and may also facilitate synthesis of C-rich woody structures. Furthermore, species with C-rich woody structures may be facilitated by low N and P supplies. Relatively high N supplies may selectively favor synthesis of N-rich secondary metabolites, while relatively high P supplies may selectively favor faster growth, and N₂ fixation (in cyanobacteria). Both high N and P supplies may facilitate large species not limited by nutrients, and favor high maximum uptake rates. Furthermore, high N and P supplies will promote autotroph biomass and consequently self-shading, and thus may favor species with high pigment contents and/or species with accessory pigments.

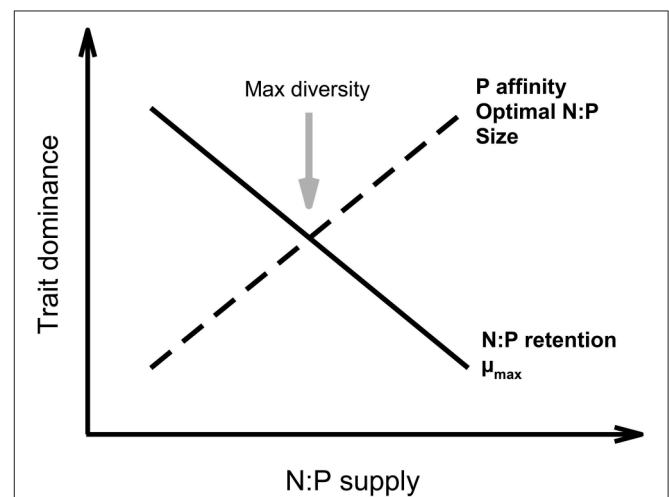


FIGURE 2 | Influence of N:P supply on trait dominance. With increasing N:P supply, an organism's optimal N:P ratio, P uptake affinity, and size are expected to increase, and organisms that selectively retain P over N should have higher maximal growth rates than those which do not, as predicted by the Growth Rate Hypothesis (Sterner, 1995b; Elser et al., 2000c). Further, Tilman's resource-ratio based theory of competition predicts that biodiversity should be maximal (gray arrow) at balanced supply ratios (Tilman, 1982).

Heterotrophs

Autotrophs' stoichiometry also reflects their quality as food for herbivores. Since autotrophs are usually more C-rich than animals, herbivores typically ingest a diet rich in C but deficient in nutrients (Sterner and Elser, 2002), which has implications for herbivore and detritivore performance and subsequent trophic dynamics (Elser et al., 2000b; Hessen et al., 2013). Grazers however possess a large range of adaptations that allow them to minimize the consequences of these nutrient imbalances. Besides selective feeding (e.g., Kagata and Ohgushi, 2011; Meunier et al., 2012, 2016a) and habitat choice (Winder et al., 2004; Reichwaldt, 2008), consumers may handle poor food quality by selectively retaining and excreting nutrients (Elser and Urabe, 1999; Knoll et al., 2009). These physiological adjustments are tightly linked with the stoichiometry of traits such as elemental ratios of recycled materials and body stoichiometric homeostasis.

Nutrient storage capacity is a much more confined trait in heterotrophs than in autotrophs resulting in more constrained body composition (Persson et al., 2010; Meunier et al., 2014). While the lack of homeostasis allows organisms to store nutrients (see above), the advantages of stoichiometric homeostasis remain unclear. It can be argued that the ability to store nutrients, which results in flexible body stoichiometry, is the more advantageous strategy, especially where food supply or food quality fluctuates (Meunier et al., 2014). It has been hypothesized that homeostasis is the optimal response strategy to fluctuations in food quality, as it should minimize the cost of adjusting to new conditions (e.g., selective nutrient retention and excretion) while maximizing growth rate (Giordano, 2013). Indeed, when feeding conditions are relatively stable within an organism's life span, homeostasis minimizes noise in physiological channels and establishes a stable environment for cellular processes (Woods and Wilson, 2013).

Stoichiometric homeostasis also results from adjustments in the elemental ratios of recycled material. The stoichiometry of excreted material is influenced by both the consumer's stoichiometry, e.g., low N:P consumers will have high N:P excretion, as well as by the resource stoichiometry, e.g., the excreted N:P ratio will increase with increasing resource N:P ratio (Vanni, 2002). However, several studies question the link between body stoichiometry and elemental ratios of excreted material (Allgeier et al., 2015; Vanni and McIntyre, 2016). The lack of evidence for the relationship between resource stoichiometry and consumer nutrient excretion is likely due to the fact that, in these studies, bulk stoichiometry was measured instead of the stoichiometry of assimilated materials (e.g., Dodds et al., 2014).

Interspecific variations in recycling traits will also have consequences at the ecosystem scale. For instance, experiments in lakes provided evidence that the replacement of the high body N:P copepods with low N:P *Daphnia* caused a transition from N to P limitation for primary producers (Sterner, 1990; Elser et al., 1996), likely driven by the higher N:P ratio of recycled material (Elser et al., 1988). In addition, intraspecific variation in nutrient recycling traits during copepod ontogeny has been suggested to influence biogeochemical cycling within marine systems (Meunier et al., 2016a). Like zooplankton, aquatic vertebrates such as fish and amphibians can also

have important stoichiometric impacts on nutrient cycling and trophic dynamics (Vanni et al., 2002). Similarly, in terrestrial systems, consumers' body stoichiometry and nutrient recycling traits are expected to shape limitation patterns (Cherif and Loreau, 2009, 2013). However, it is important to consider the intrinsic differences between producer-consumer interactions in aquatic and terrestrial ecosystems. While planktonic herbivores may eat a very large percentage (70–80%) of the daily primary production (Calbet, 2008; Löder et al., 2011), in terrestrial ecosystems, plants are less nutritional and lose lower percentages of production to herbivores, and a higher level of C is channeled as detritus (Cebrian, 1999). Traits directly influencing herbivore stoichiometry should therefore play only a small role in the cycling of nutrients in forested ecosystems, with decomposers and detritivores playing a more important role (Cherif and Loreau, 2009, 2013). Given the importance of homeostasis for biogeochemical cycling in food webs, quantifying the contribution of this trait to ecosystem services related to biogeochemical cycles (i.e., C sequestration, water quality) represents a promising avenue for future research. The consequences of differences in homeostasis between autotrophic and heterotrophic microbes for nutrient cycling have been explored in a number of studies (e.g., Cross et al., 2005; Cotner et al., 2010). Further, exploring the importance of the stoichiometry of traits as both drivers of, and responses to, ecosystem changes will result in datasets that will advance our understanding of how biological communities will perform under different environmental conditions, including the changing climate. This approach could in turn be used to explore traits that both directly and indirectly affect a given ecosystem function or service.

TRAIT CONNECTIONS

Correlative Relationships

Several studies have linked elemental stoichiometry to distinct species traits in order to explain ecosystem structure (for an overview see **Table 1**). As we previously mentioned, the tight relationship between the body N:P ratio and organismal growth rate is formulated in the Growth Rate Hypothesis (**Table 1**), a central hypothesis in ES. It postulates that species with high growth rates have more ribosomal RNA content for rapid protein synthesis than slow-growing species (Sterner and Elser, 2002). Because ribosomal RNA is rich in P, faster growing species should have a higher P content and lower body N:P ratios (Sterner, 1995a; Elser et al., 1996; Sterner and Elser, 2002). Although the Growth Rate Hypothesis is supported for a large range of organisms, several studies have questioned its generality (Sardans et al., 2012, and reference therein). For instance, mass-balance modeling demonstrated that maintenance costs for high biomass P content can drive the relationship between P content and growth rate (Shimizu and Urabe, 2008). This has been confirmed in experiments showing that consumers release P at a substantial rate, even when fed high C:P food (Demott et al., 1998; Shimizu and Urabe, 2008). Despite these limitations associated with P losses, e.g., through molting (Shimizu and Urabe, 2008), a large body of literature points toward a negative relationship between

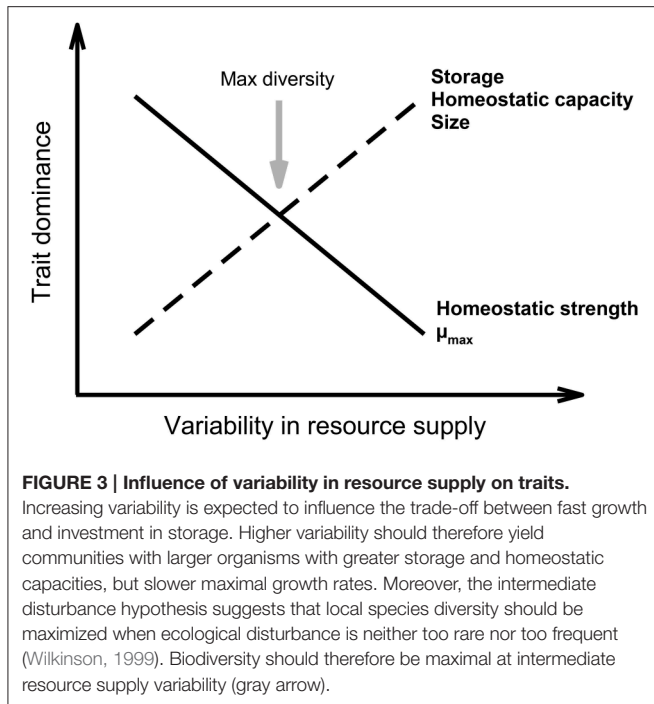
TABLE 1 | Relationships between elemental stoichiometry characteristics and physiological traits among autotrophs and heterotrophs, with abbreviated description of the linkage and associated citations.

ES characteristics	Physiological trait	Description	Citations
AUTOTROPHS			
Organismal C:P and N:P contents	Growth rate	Autotrophs of lower C:P and N:P contents exhibit greater maximum growth rates	Güsewell, 2004; Hillebrand et al., 2013
	Structure (wood investment)	Investment in woody structures reduces plant tissue N and P contents	Han et al., 2005
Homeostasis	Temporal stability	Homeostatic plant species show reduced temporal variation in grassland communities	Yu et al., 2015
	Maximum growth rate	Homeostatic phytoplankton exhibit faster growth rates	Hillebrand et al., 2013
Nutrient uptake	Cell size	Phytoplankton nutrient uptake affinities decline with increased cell size	Irwin et al., 2006; Edwards et al., 2012
	Growth rate	Higher phytoplankton maximum growth rates with greater nutrient uptake affinity	Edwards et al., 2012
	Resistance to grazing	Phytoplankton resistant to grazing may be poor competitors for limiting nutrients	Litchman and Klausmeier, 2008
	Symbioses (mycorrhizae)	Mycorrhizal symbionts increase host plant nutrient acquisition	Brundrett, 2009
HETEROTROPHS			
Organismal C:P and N:P contents	Growth rate	Heterotrophs of lower C:P and N:P exhibit greater maximum growth rates	Elser et al., 2003; Hood and Sterner, 2014
	Defense (bone investment)	Investment in bone decreases vertebrate body C:P contents	El-Sabaawi et al., 2016
	Ontogeny	Vertebrate C:P and N:P decline during development, whereas invertebrate C:P and N:P increase during development	Pilati and Vanni, 2007; González et al., 2011; Back and King, 2013; Tiegs et al., 2016
	Sex	Divergent P contents between males and females	Back and King, 2013
Homeostasis	Maximum growth rate	Species of flexible homeostasis tend to have high maximum growth rates	Hood and Sterner, 2014
	Sex	Divergent flexibility in body P contents between males and females	Goos et al., 2014
	Generalism vs. specialism?	Homeostatic consumers may exhibit greater nutritional specialism	Sperfeld et al., 2017
Nutrient assimilation	Gut residence time or gut length	Increased gut length confers increased nutrient assimilation efficiencies	Liess et al., 2015
Consumer-resource elemental imbalance	Trophic level	Higher trophic levels exhibit reduced consumer-resource elemental imbalances	Lemoine et al., 2014
	Omnivory	Selective feeding may reduce imbalances between consumers and resources	Snyder et al., 2015; Meunier et al., 2016a
Nutrient recycling	Growth rate	Faster-growing animals recycle less P	Elser et al., 2000a
	Body size	Higher mass-specific nutrient recycling by organisms of smaller body size	Allgeier et al., 2015; Vanni and McIntyre, 2016
	Phylogeny	Taxonomic identity affects size scaling and rates of N and P excretion	Allgeier et al., 2015

growth rate and body C:P or N:P (e.g., Carrillo et al., 2001; Meunier et al., 2016a).

Interestingly, organisms' size and growth rate are usually negatively correlated (Table 1), which implies that, based on the growth rate hypothesis, smaller heterotrophic organisms might generally have lower N:P ratios (Figure 2). These explicit connections between body size, ontogeny, and N:P stoichiometry

have been well documented (Elser et al., 1996; Gillooly et al., 2005; Méndez and Karlsson, 2005; Meunier et al., 2016a). Further, larger cells have higher biomass-specific storage capacity due to smaller surface/volume ratios and higher minimum cellular metabolic requirement that selectively allows them to provide them with a competitive advantage over smaller cells under higher resource concentrations (Figure 3; Irwin et al., 2006).



Experiments in lakes showed that the interaction between top-down and bottom-up controls can lead to the replacement of small zooplankton with high N:P by larger species with low N:P (Sterner et al., 1992; Hall et al., 2004). This community shift also causes a transition from N to P limitation for primary producers, likely caused by the higher N:P ratio of recycled material (Elser et al., 1988). However, the relationship between size and stoichiometry is expected to be opposite in vertebrates (i.e., decreasing N:P ratios with increasing body size) due to relatively higher P needs for bones (Elser et al., 1996; González et al., 2011). The interplay between traits and elemental requirements hence influences the success of an organism in response to different environmental conditions (Table 1), which, in turn, will shape community structure.

Changes in environmental conditions can also lead to evolutionary changes in traits. The mutual interactions between the evolved functional traits and environment characteristics therefore have gained increasing interest over the past two decades. In particular, understanding how genome and proteome adaptations are shaped by selection on growth-related traits and the parameters determining the extent of stoichiometrically relevant variation in genomes across taxa are increasingly studied (Kay et al., 2005). For example, genes that respond to changes in P availability have received much attention, and variation in the environmental supply of P has been associated with the expression of highly conserved genes (Jeyasingh and Weider, 2007; Frisch et al., 2014). Rotifer populations with a P limitation selection history yielded higher biomass and reduced food to lower levels when fed with P limited food (Declerck et al., 2015). Although this adaptation of populations did not involve changes in elemental composition, it did alter important population traits, including birth and death rates, population structure and

grazing pressure. Both TBE and ES are at the intersection of evolution and ecology, and their integration will thus greatly help understanding eco-evolutionary dynamics (Jeyasingh et al., 2014; Declerck et al., 2015).

Trade-Offs

Natural selection balances traits associated with the three main missions of any organism, i.e., to eat, survive, and reproduce in order to maximize fitness. However, it is generally not possible to maximize all traits simultaneously, particularly as resources are often limiting. Trade-offs are therefore inevitable and different organisms specialize in various aspects of their life history. Such trade-offs are typically enabled by trait specialization and plasticity. For example, consumers with lower P requirements and higher body N:P ratios should be abundant in low P environments despite having reduced maximum growth rates (Sterner, 1995b; Elser et al., 2000c). The quantification of trade-offs associated with key traits will therefore yield a set of comparisons allowing the prediction of physiological, morphological, and behavioral responses of communities to environmental changes (Litchman and Klausmeier, 2008; Litchman et al., 2013). Particularly regarding stoichiometry, Montecchiario and Giordano (2010) discussed the conditions influencing the trade-off between stoichiometric homeostasis and maximal growth rate. Generally, when enduring periods of nutrient limitation, an organism should adopt a strategy that lessens the cost of adjusting to the new conditions (degree of homeostasis) and maximizes growth rate. This trade-off has been observed in experiments where phytoplankton were grown at different growth rates and subjected to a stress (Fanesi et al., 2014). The authors observed that, when the duration of the perturbation was long enough, cells with lower growth rate were more elementally homeostatic after a change in nutrient supply, which indicates that the trade-off between acclimation and homeostasis depends on the duration of the perturbation relative to cellular division rate (Fanesi et al., 2014). Based on these results, we hypothesize that homeostatic strength should decrease with increasing variability in resource supply (Figure 3). Similar patterns are expected in heterotrophs (Meunier et al., 2014) but, to our knowledge, no experiment has yet been conducted to test this prediction.

Similarly, low nutrient availability in the environment forces plants to adopt different strategies. For example, they can invest in storage traits and preferentially accumulate N rather than P (Chapin et al., 1990; Yu et al., 2015). Experimental work in freshwater (e.g., Sommer, 1984; Li and Stevens, 2012), marine (e.g., Smayda, 1997), and terrestrial systems (for review see Chapin et al., 1990) has shown that investing in storage traits provides a competitive advantage under highly variable and unpredictable nutrient availabilities (Figure 3). For example, organisms with high N affinity and storage capacity relative to other nutrients should have a competitive advantage under low N supply, as is often observed in N-limited terrestrial systems (Meunier et al., 2016b). These results indicate that the trade-offs between size, rapid growth, and storage capacity are strongly regulated by nutrient availability as well as the frequency and duration of nutrient pulses

relative to organismal growth rates (**Figure 3**). Thus, if nutrient pulses are regular, small velocity-adapted species should prosper due to their high maximum nutrient uptake rates and high maximum growth rates (**Figure 3**; Sommer, 1984). Along similar lines of reasoning, the intermediate disturbance hypothesis suggests that local species diversity should be maximized when ecological disturbance is neither too rare nor too frequent (Wilkinson, 1999), although the theoretical underpinnings of this hypothesis have been increasingly questioned (Fox, 2013). This implies that biodiversity is maximized when the resource supply is intermediately variable (**Figure 3**). Indeed, N pulses of intermediate frequencies may lead to coexistence of different strategies, i.e., velocity and storage specialists (Grover, 1991; Litchman et al., 2009).

In their review of phytoplankton traits and trade-offs, Litchman and Klausmeier (2008) suggest that the trade-off between nutrient competitive abilities and grazer resistance is key among phytoplankton. One strategy to obtain resistance to grazing is through a large cell size, which is associated with lower growth rate and reduced nutrient uptake abilities because of the decreased surface area to volume ratios (Reynolds, 1988) but increases the cell's storage capacity (Litchman et al., 2009; Wirtz, 2013). However, small size also offers several advantages to phytoplankton, including a more efficient acquisition of limiting nutrients (Sherwood et al., 1975; Ploug et al., 1999) and higher maximum growth rates (Banse, 1976), although it can increase susceptibility to grazing (Thingstad et al., 2005). This trade-off is one of the drivers for species succession during phytoplankton blooms as well as annual changes in community composition (Reynolds, 1984; Sommer et al., 1986). Organismal replacement along nutrient gradients can also be driven by this trade-off (Leibold, 1996), which ultimately has consequences for biodiversity within communities (Kneitel and Chase, 2004). The trade-off between cell size and competitive ability for limiting nutrients is therefore a key determinant of species dominance in phytoplankton communities. In addition to pairwise trade-offs, traits can be linked via multidimensional trade-offs. For example, Edwards et al. (2011) identified a three-way trade-off between N vs. P competitive abilities and cell size as a proxy for grazer resistance.

IMPLICATIONS

Understanding the link between nutrient stoichiometry and organismal traits can help predict how human-induced changes in biogeochemical cycles will alter the interaction between producers' stoichiometry and consumer elemental requirements. Human activities have altered the C, N, and P biogeochemical cycles on a global scale (Peñuelas et al., 2012). These changes are apparent from increasing atmospheric CO₂ concentrations and the large amounts of nutrients applied on land, subsequently also enriching lakes, rivers, and marine coastal waters. More specifically, the use of agricultural fertilizers has tremendously disturbed global biogeochemical cycles and increased the amount of N and P available to plants and animals (Bobbink et al., 2010). Not only do the C, N, and P supplies increase, also their relative abundances are changing both in aquatic and terrestrial

environments (Grizzetti et al., 2012; Peñuelas et al., 2012; Sardans et al., 2012). Such shifts in the relative abundances of elements will alter autotroph stoichiometry and thereby their quality as food for herbivores (Van De Waal et al., 2010). For example, the N:P ratio available to plants has risen over the past decades in both terrestrial and aquatic systems (Sardans et al., 2012). The concepts we highlight here allow us to predict that such changes in nutrient availability should lead to communities dominated by species with higher optimal N:P ratios and higher P uptake affinity, while decreasing N retention and increasing P storage (**Figure 2**). The Growth Rate Hypothesis allows us to predict slower maximal growth rates at higher N:P supply and decreasing organismal size with increasing N:P supply, because body size is generally negatively correlated with growth rate (**Figure 2**). Linking TBE with ES therefore enables us to make predictions regarding the impact of human activities on both community structure and functioning. For example, it has been observed that communities dominated by species with higher optimal N:P ratios will substantially influence biogeochemical cycles by preferentially recycling N over P (Vanni et al., 2002; Knoll et al., 2009; El-Sabaawi et al., 2016).

CONCLUSION

Coupling functional traits to the stoichiometry of organisms allows a more general understanding of ecological interactions. Specifically, optimal body N:P ratios, nutrient uptake and storage traits, as well as their associated trade-offs, have the potential to drive species competition and thereby influence food web interactions and ecosystem dynamics. Quantifying the contribution of these traits to ecosystem services (i.e., C sequestration, water quality) represents a promising avenue for research into changes in biogeochemical cycling associated with global environmental change. At the same time, traits indirectly coupled to elemental demands, such as cell/body size and growth rate have a strong influence on, and are affected by, organismal stoichiometry. Therefore, combining observations and ideas from ES and TBE offers a unified framework that enables answering a wide array of complex ecological questions, for instance how biological communities will perform under changing environmental conditions. Linking and applying multiple ecological frameworks allows crosstalk between the various scientific disciplines, fostering the exchange of comparable efforts in understanding the complexity of ecosystem structure and functioning.

AUTHOR CONTRIBUTIONS

The manuscript was written by CM. **Table 1** was created by HH. **Figure 1** was created by DW. **Figures 2, 3** were created by CM. All co-authors helped to evaluate and edit the manuscript.

ACKNOWLEDGMENTS

This article summarizes the work done in the "Workshop on Biological Stoichiometry and Trait-Based Ecology" that took

place during the Conference On Biological Stoichiometry (2015, Trent, Canada). This conference was supported by the David Schindler Professorship of Aquatic Sciences at Trent University and by Trent University. The workshop was supported by the Canadian Institute of Ecology and Evolution. We thank all workshop participants for their input into the discussions: Claudia Acquisti, Thomas Anderson, Jeff Back, Stephen Baines, Esteban Balseiro, Gergely Boros, Krista Capps, Sarah Collins, Richard Connon, James Cotner, Michael Danger, Sanatan Das Gupta, Steven Declerck, Lenore Dumas, Dan Durston, Jonathan Ebel, James Elser, Michelle Evans-White, Carolyn Faithfull, Isabel Fernandes, Laura Fidalgo, Michał Filipiak,

Stephanie Fong, Paul Frost, Andrea Gall, Pat Glibert, Casey Godwin, Angelica L. Gonzalez, Jared Goos, Jin-Sheng He, Puni Jeyasingh, Susan Kilham, Ryan King, Jude Kong, James Larson, Cecilia Laspoumaderes, Kimberley Lemmen, Shawn Leroux, Patrick Lind, Paloma Lopes, Keeley MacNeill, Adam Martiny, Peter B. McIntyre, Katie Miller, Eric Moody, David Ott, Rachel Paseka, Angela Peace, Amber Rock, Anna Rožen, Amanda Rugenski, Andrew Sanders, Jennifer Schmitt, Kimberly Schulz, Ryan Sherman, Robert Sterner, Maren Striebel, Caroline Turner, Jotaro Urabe, Michael Vanni, Stoycho Velkovsky, Mandy Velthuis, Nicole Wagner, Wei Wang, Tanner Williamson, and Donald Yee.

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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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