Stoichiometrically Explicit Food Webs: Feedbacks between Resource Supply, Elemental Constraints, and Species Diversity

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Key Words

ecological stoichiometry, niche models, paradoxes of enrichment

Abstract

A stoichiometrically explicit approach to food web ecology yields new insight into promotion and degradation of diversity, changes in species composition along environmental gradients, biomass partitioning among trophic levels, and limitation of primary production. These revelations emerge from food web modules that incorporate fundamental constraints imposed by mass balance and a key trait, stoichiometric body composition, into a species' niche. These niche components involve a species' requirements from its environment and its own impacts on its environment. More specifically, stoichiometric composition influences minimal nutrient requirements of consumers (perhaps especially grazers); this component becomes pertinent because large imbalances often arise between nutrient:carbon content of consumers relative to prey. Furthermore, these imbalances then modulate the impact of consumers on their own resources through nutrient recycling. Once these niche components become synthesized, their implications in shaping food webs provide powerful mechanisms linking changes in environmental gradients with community structure and ecosystem function.

1. INTRODUCTION

Ecological stoichiometry formalizes what should seem obvious: Organisms interacting in food webs are composed of different elements, such as carbon, nitrogen, phosphorus. As a result, energy and nutrient flow through consumer-resource interactions obey fundamental constraints (e.g., mass balance of these elements). These constraints become interesting because chemical composition can differ greatly between consumers and resources (Elser et al. 2000a, Sterner & Elser 2002). When such imbalances arise, mass balance constraints can have immense implications for consumer-resource interactions: Elemental mismatches influence growth of consumers, nutrient recycling by them, their population dynamics, and decomposition. Sterner & Elser (2002) summarize these arguments and review origins of stoichiometric imbalances in species interactions. Their book (and Elser 2006) also elegantly reveals deep connections of stoichiometry to genetics, cellular biology, and physiology. Here, I take those concepts and focus them on issues pertinent to community ecology (see also Moe et al. 2005). Eco-stoichiometry can create opportunities for species to interact in manners unanticipated by more conventional theory: Embracing implications of mass balances constraints causes new insights to emerge into mechanisms that promote and degrade species diversity.

To make this argument, I use food web modules and the mechanistic niche concept. Modules focus on small sets of species interactions that provide building blocks of larger food webs. There is a long tradition of using modular approaches (Grover 1997, Holt 1977, Murdoch et al. 2003, Tilman 1982); they help us understand how pieces of food webs operate before we tackle the whole. Therefore, I focus on extant stoichiometrically explicit food web modules (**Figure 1**). They allow integration of stoichiometric traits of species with other traits in key influential community modules. To create this integration, I use the mechanistic niche concept (Chase & Leibold 2003; Leibold 1995, 1996), which involves characterizing a species by two interrelated components. First, each species has environment requirements, often for resources. For instance, minimal resource requirements (R^*) govern whether a species can replace itself. Second, species impact their environment; this aspect is often formalized using impact vectors. As shown below, species impact their resources in part via nutrient recycling, which intimately depends on stoichiometry. By integrating both aspects of a species' relationship with its environment and resources, stoichiometrically explicit niche models uncover linked sets of trade-offs that permit coexistence while obeying mass balance constraints.

Figure 1

The focal stoichiometrically explicit food chain and web modules examined in this review. Arrows point in the direction of nutrient or energy flow. (*a*) An autotroph with flexible nitrogen:phosphorus stoichiometry and its two nutrient resources. (*b*) A grazer consuming a producer with flexible phosphorus:carbon content, where primary production depends on phosphorus and light. (*c*) The classic resource ratio model: two autotrophs with fixed stoichiometry competing for two inorganic nitrogen and phosphorus. (*d*) The pentagon model, combining the resource ratio model with apparent competition. (*e*) Resource ratio for grazers: Two grazers compete for an autotroph with flexible stoichiometry with light and nutrient-dependent production. (*f*) Addition of an inedible producer that competes with stoichiometrically flexible producers for light and nutrients. (*g*) A stoichiometrically explicit model of intraguild predation. (*h*) A stoichiometrically explicit tritrophic model. (*i*) Interactions between an autotroph, a decomposer, and a grazer that may or may not eat the decomposer, and two nutrient resources. (*j*) Two decomposers compete for an inorganic and an organic resource. (*k*) The resource ratio model revisited, with a decomposer. (*l*) Stoichiometrically explicit disease. Key to symbols: A_j, autotroph (primary producer, plant) *j*; $A_{C,P}$, autotroph with flexible carbon:phosphorus stoichiometry; $A_{N,P}$, autotroph with flexible nitrogen:phosphorus stoichiometry; A_I, inedible autotroph; C, consumer (predator or parasite); D_j, decomposer *j*; G_j, grazer *j*; O, omnivore; R, resource; R_I, inorganic resource; R_N, nitrogen; R_o, organic resource; R_P, phosphorus.
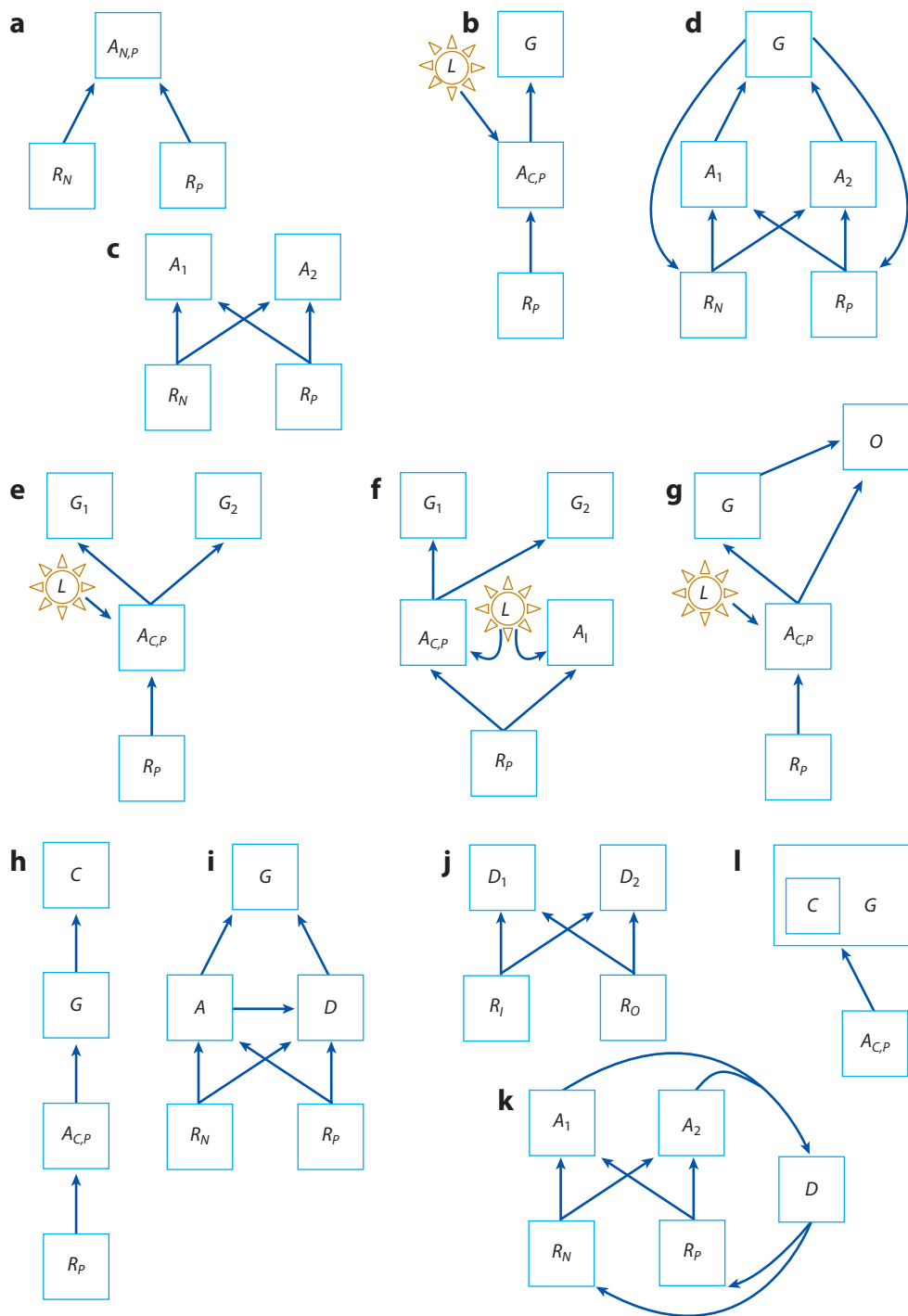
Because this review dives into several modules in detail, I should frontload core themes to avoid losing the proverbial forest for the trees. Eco-stoichiometry offers new insights into autotroph-grazer dynamics that arise from net interplay between requirements of grazers (which depend on stoichiometric mismatches between them and their prey) and their impacts on the stoichiometry of their prey. Furthermore, stoichiometric constraints open up the niches of species that can provide "stabilizing mechanisms" (sensu Chesson 2000) that promote diversity. However, the net interplay between stoichiometric constraints, consumption, and nutrient recycling reveal mechanisms that degrade diversity and provoke shifts in species composition across environmental gradients. Finally, eco-stoichiometry provides powerful approaches to understand how biomass and nutrients become allocated among trophic levels and into detritus. This enhanced understanding of food web structure and energy and material flow through food webs may eventually enhance predictions about the implications of global change for food webs and ecosystems.

2. STOICHIOMETRICALLY EXPLICIT FOOD WEB MODULES

### 2.1 Components of Stoichiometrically Explicit Food Webs

To appreciate the conceptual advances that eco-stoichiometry offers, we must first focus on its foundation (Sterner & Elser 2002). Here, I summarize two building blocks that establish the causes and consequences of elemental mismatches in consumer-resource interactions. The review then considers implications of these mismatches for species interactions.

2.1.1. Autotrophs can be stoichiometrically plastic. In contrast to many grazers, autotrophs can be stoichiometrically plastic (Ågren 2004, 2008; Droop 1974; Vitousek 1982). This plasticity stems from autotrophs' ability to store nutrients supplied in excess of optimal ratios via luxury consumption (Klausmeier et al. 2004a,b, 2008). The drivers of this variation in carbon:nitrogen:phosphorus ratios in particular depend on many factors (Ågren 2008, McGroddy et al. 2004, Urabe et al. 2003, Woods et al. 2003), including variation in light and nutrients. Two resource gradients have emerged most prominently. First, variation in nitrogen:phosphorus supply (Downing & McCauley 1992, Hall et al. 2005) drives large variability in the nitrogen:phosphorus

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Figure 2

Key building blocks of stoichiometry food web theory. (*a*) Producers, such as Rhee's (1978) *Scenedesmus*, can be quite stoichiometrically plastic: the nitrogen:phosphorus ratio of this alga's tissues can closely match the nitrogen:phosphorus ratio of nutrients supplied to them (yielding an H of 0.98). (*b*) However, nitrogen:phosphorus content of producers in a variety of systems seems much less flexible than Rhee's *Scenedesmus*. Key: a, marine seston; b, terrestrial plants; c, algal cultures; d, lake seston; e, lake mesocosms; f, benthic algae; g, pond seston. H values are given on the figure (from Hall et al. 2005). (*c*) Variation in producer stoichiometry in aquatic systems can also be driven, in part, by light:nutrients supplied to them (e.g., one to three regressions derived from data from Sterner et al. 1997; four stems from data of Diehl 2002, 2005). (*d*) A pond mesocosm experiment reveals that this light:nutrient-seston carbon:phosphorus relationship involves grazing (*A* + *G*), because treatments without zooplankton grazers (*A*) yielded no relationship (from Hall et al. 2007a). (*e*) This variation in nutrient content of producer tissues is closely linked to producer physiology, especially growth rate (following the Droop equation). Growth rate increases, at a decelerating rate, with increase of nutrient quota (*Q*, its nutrient:carbon content) from its minimum (Q_{min}). (*f*) Stoichiometric ratios become important for autotroph (*A*)-grazer (*G*) interactions if major imbalances arise. These imbalances are commonly seen, for example, in carbon:phosphorus ratios in terrestrial and freshwater ecosystems. Boxplots are from Elser et al. 2000a. (*g*) Although grazers typically appear much more homeostatic in their tissue stoichiometry than their producer-prey, tissue stoichiometry can vary interspecifically among grazers, as seen in Elser et al.'s (2000a) compilation of zooplankton grazers. (*h*) Because of imbalances between autotrophs and grazers, grazer populations can become limited by the amount of carbon and/or nutrient in their food resources. Hall (2004) graphically depicted the implications of carbon limitation (CL) versus nutrient limitation (NL) of grazers (*G*) using the nullcline-impact vector approach with the addition of a system nutritional constraint (SNC; see text for details).

content of producers. Ecologists obsess about these two resources and their ratio because autotrophs are often limited by one, the other, or both (Downing et al. 1999, Elser et al. 2007, Hecky & Kilham 1988). Facing large variation in nitrogen:phosphorus supply, a classic study (Rhee 1978) demonstrates an almost 1:1 matching of supply ratio to an alga's stoichiometry (**Figure 2a**). [The *H* metric of Sterner & Elser (2002) characterizes this flexibility as the inverse of a linear regression fit through a log-log plot of supply ratio versus tissue stoichiometry; numbers close to 1, like that for *Scenedesmus*, indicate complete flexibility. The autotroph "is what it has available to eat"]. Producers in other situations are probably less plastic (dramatically so in ponds; **Figure 2b**) for a variety of reasons [e.g., high losses from sinking, physiological
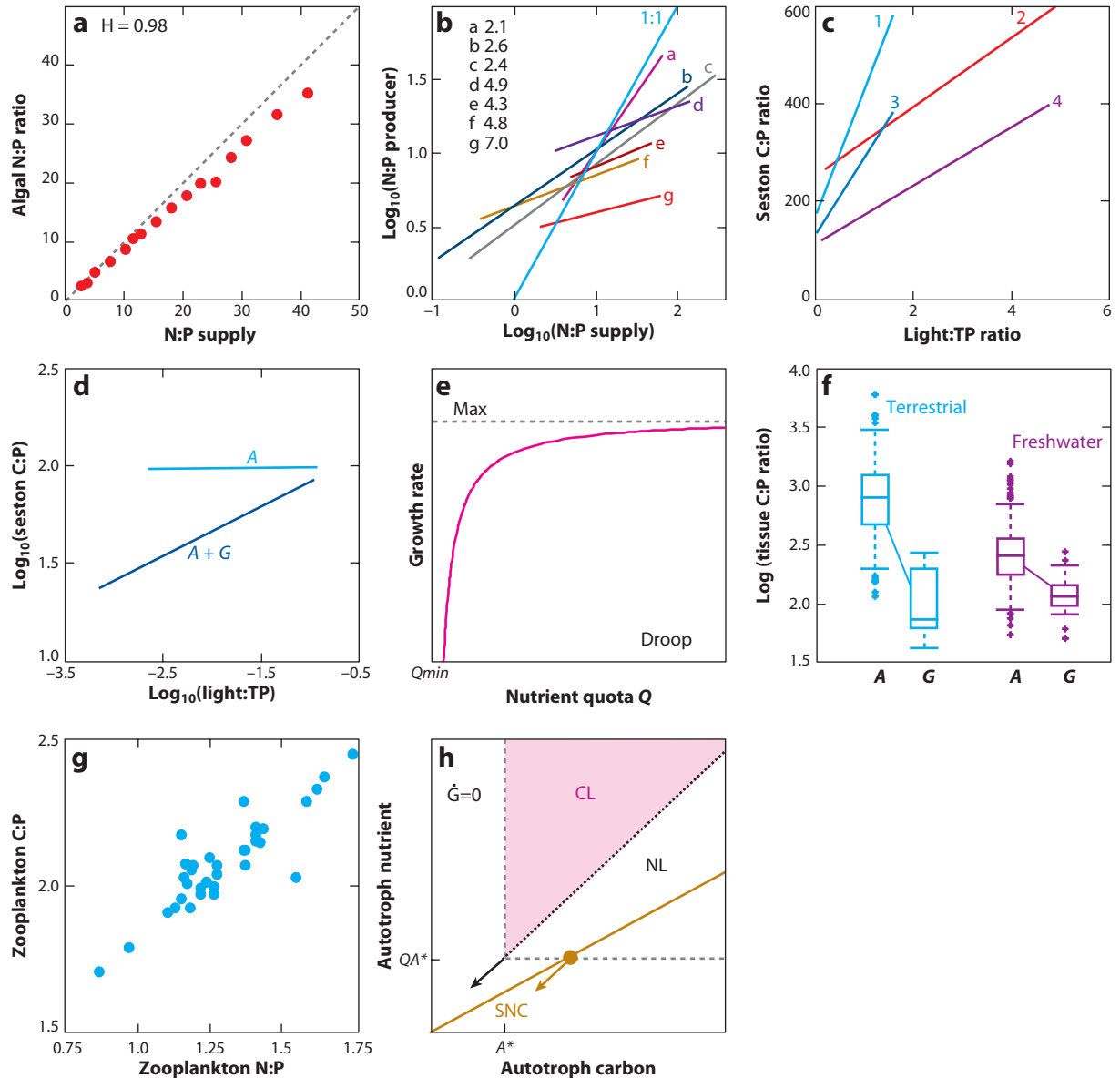
limits to nutrient storage, and physiological adaptation (Hall et al. 2005; Klausmeier et al. 2004b, 2007)]. Thus, physiological and environmental constraints reign in stoichiometric flexibility somewhat.

Second, large variation in light:nutrient supply drives variation in autotroph carbon:phosphorus content [the light:nutrient hypothesis (Hall et al. 2007a, Sterner et al. 1997)]. Light supply varies with depth, incident supply, and background turbidity [e.g., from dissolved organic carbon or sediments (Diehl 2002; Diehl et al. 2002, 2005; Hall et al. 2007a)]. Systems with high light relative to nutrients tend to produce higher carbon:phosphorus ratios in autotrophs (**Figure 2c**). This correlation emerges in lake (Hessen 2006, Sterner et al. 1997) and pond surveys (Cáceres et al. 2008, Hall et al. 2007a), lab experiments (Hessen et al. 2002, Urabe and Sterner 1996), and mesocosms (Diehl et al. 2002, 2005). However, in nature it likely involves interplay between external light-nutrient supply and grazing (Hall et al. 2007a, Hillebrand et al. 2008; **Figure 2d**).

2.1.2. Grazers tend to be more stoichiometrically homeostatic than autotrophs. Flexibility of producer stoichiometry matters for several reasons. Certainly, the growth rate of autotrophs increases with nutrient:carbon content, often represented via the variable stores (Droop) model (**Figure 2e**; Ågren 2004, 2008; Droop 1974; Grover 1997). Perhaps more importantly here, this flexibility creates tension in autotroph-grazer systems because grazers typically have much higher nutrient content (Andersen & Hessen 1991; **Figure 2f**). Large variation in phosphorus content among grazer species (**Figure 2g**) correlates with phosphorus-rich RNA, which then drives growth rate (Elser et al. 1996, Gillooly et al. 2005, Vrede et al. 2004); it can also reflect variation in bone content (Sterner & George 2000, Vanni et al. 2002). Furthermore, within species, grazers maintain relatively homeostatic tissue stoichiometry. Stoichiometric mismatches between nearly homeostatic, high-phosphorus grazers and plastic autotrophs mean that autotrophs often provide poor–quality food (Frost et al. 2006, Stelzer and Lamberti 2002, Sterner et al. 1993).

Poor food quality, in turn, means that grazers can become nutrient limited rather than carbon limited (Sterner & Elser 2002, White 1993). This opens up the stoichiometric resource niche of the grazer. To illustrate (**Figure 2g**), Hall (2004) modified an autotroph-grazer model to include nutrient limitation of grazers and nutrient recycling; assuming that carbon and phosphorus are essential resources, one can draw elbow-shaped nullclines for the grazer in a manner resembling those for autotrophs in the resource ratio model (Grover 1997, Tilman 1982); synthesizing units offer much smoother transitions between limitation by multiple elements (Diehl 2007, Kooijman 2000, Muller et al. 2001). The two legs of the grazer's nullclines are set by the minimal nutrient (QA^*, a function of grazer stoichiometry, but also other physiological traits) and carbon (A^*) requirements of the grazer; their intersection indicates a colimitation point [the threshold elemental ratio (Sterner & Elser 2002)]. In principle, these niche axes could be expanded to incorporate other elements (e.g., nitrogen, selenium) and fatty acids that can also limit growth (Becker & Boersma 2005, Boersma & Stelzer 2000).

The second niche parallel to the resource ratio model involves impact vectors, that is, the slope at which grazers impact carbon versus nutrients in their resources [via grazing (feeding rate) and nutrient recycling (particularly grazer stoichiometry), respectively]. The third parallel involves making an analogy to a supply point via a system nutrition constraint (SNC). Mathematically, the SNC comes from the autotroph's nullcline; its slope represents the autotroph's nutrient:carbon ratio, and its intersection with the grazer's nullcline determines whether the grazer is nutrient or carbon limited. Biologically, the SNC represents net feedbacks between resource supply, primary production, grazing, stoichiometric mismatches between autotroph and grazer, and nutrient

cycling (Hall 2004; **Figure 2g**). These latter two components are particularly important. Stoichiometric mismatches between plastic autotrophs and more homeostatic grazers substantially influence subsequent nutrient recycling following herbivory. Because grazers preferentially retain nutrients limiting their growth and recycle those supplied in excess, grazers can impact the amounts and ratio at which nutrients are recycled (Elser & Urabe 1999, Sterner 1990, Vanni 2002). Furthermore, grazers must rid themselves of excess carbon consumed when nutrient limited [via respiration, defecation, and excretion of dissolved organic carbon (Hessen et al. 2004)]; this excess carbon can fuel microbial growth.

2.2. A Stoichiometrically Explicit Food Chain and the Paradoxes of Enrichment

Once these components become assembled into a model of autotroph-grazer interactions, new behaviors arise. They emerge from stoichiometric constraints imposed on carbon flow from autotrophs to grazers. Many of these results have been well presented elsewhere (Andersen 1997, Andersen et al. 2004, Hall 2004, Loladze et al. 2000, Muller et al. 2001), so here I largely describe one of most recent—and realistic—of the models (Diehl 2007). Diehl's model incorporates (*a*) flexible stoichiometry of autotrophs (and therefore variable conversion efficiency for grazers) as influenced by supply of light and nutrients, (*b*) smooth transitions, using synthesizing units, between nutrient and carbon limitation of a homeostatic grazer that recycles nutrients (Kooijman 2000, Muller et al. 2001), and (*c*) sinking of autotrophs from a water column to sediments where nutrient regeneration occurs.

With this biology, this stoichiometrically explicit food chain provides pointed updates to more standard predator-prey theory, particularly regarding response of predator-prey systems to enrichment (Andersen et al. 2004, Diehl 2007). To appreciate these advances, it is worth reviewing predictions stemming from the paradox of enrichment model. That model forecasts transitions from stable to oscillatory predator-prey dynamics with increasing resource supply. This prediction hinges on interplay between the density-dependent (logistic) growth of the autotroph and the saturating functional response of the grazer. These two key assumptions yield the familiar hump-shaped nullcline for autotrophs but a single, vertical nullcline for grazers (**Figure 3a**). Increases in carrying capacity push the hump-shaped autotroph nullcline up and to the right, eventually evoking large-amplitude oscillations (Murdoch et al. 2003). These oscillations can drive grazer density, through starvation-induced bottlenecks, close to zero but never quite there; stochasticity, however, could push grazers to extinction.

Similar oscillations are retained in stoichiometrically explicit variations on this model (Andersen et al. 2004, Diehl 2007), but mass balance can restrain oscillation size. However, new behaviors arise now because grazer nullclines become hump shaped owing to nutrient constraints on grazers. The transition from carbon to nutrient limitation of grazers bends the vertical grazer nullcline to the right, where it eventually intersects the autotroph axis at a point where terrible food quality prohibits grazer persistence (**Figure 3b**). These two hump-shaped curves can then intersect multiple times. With light enrichment (i.e., with decreasing depth), the Diehl (2007) model can predict familiar shifts from stable to oscillatory dynamics but then transition back to stable dynamics. This enhanced stability arises owing to constraints on growth of grazers imposed by their poor–quality resources (**Figure 3b**). With further light enrichment, multiple equilibria (alternative states) arise. An upper interior equilibrium, either stable (as illustrated) or unstable, becomes separated from a stable, grazer-extinction boundary equilibrium by an interior saddle. When the upper equilibrium is unstable, oscillations can persist or catastrophically drive the grazer deterministically extinct [first described by Andersen (1997); this seems rarer in the more realistic Diehl (2007) model]. When the upper interior equilibrium is stable instead, grazers can either persist or not, depending

on initial conditions. These multiple states, echoed experimentally (Sommer 1992, Urabe et al. 2002a), resemble an Allee effect and reveal underlying positive density dependency (facilitation) imposed by stoichiometric constraints. This facilitation effect stems from enhancement of resource quality by grazing (mortality and nutrient cycling). Although interesting, multiple equilibria probably arise much less often in nature than imagined by models because sinking losses in particular enhance algal quality enough to allow successful grazer invasion (Diehl 2007).

This stoichiometrically explicit model also reveals another paradox of light enrichment: Increased light supply to already nutrient-limited autotrophs can depress grazer biomass. This "too
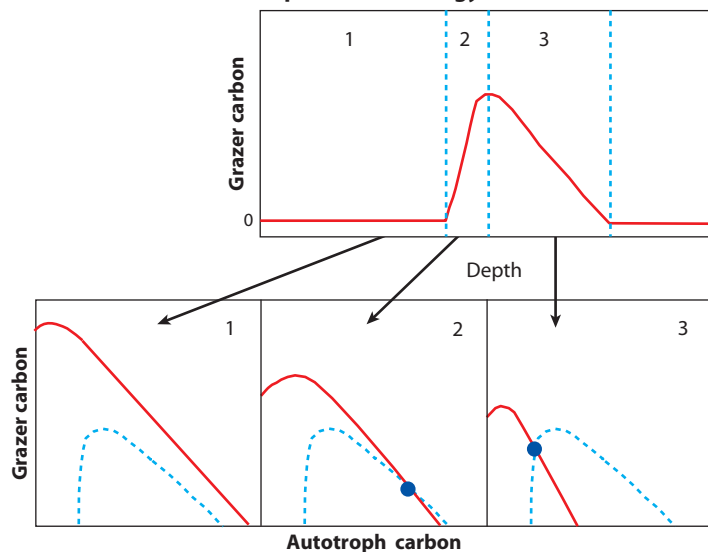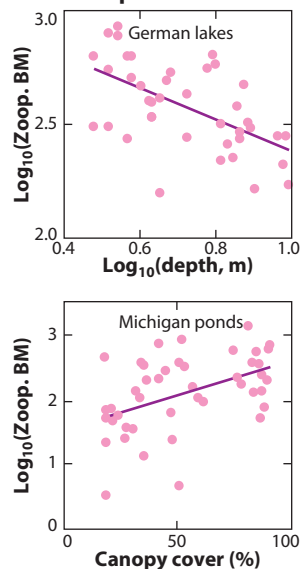

a Rosenzweig-McArthur model
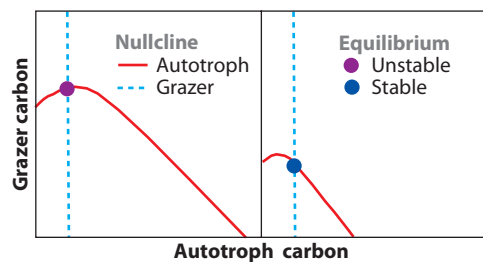
b Stoichiometric model: multiple attractors
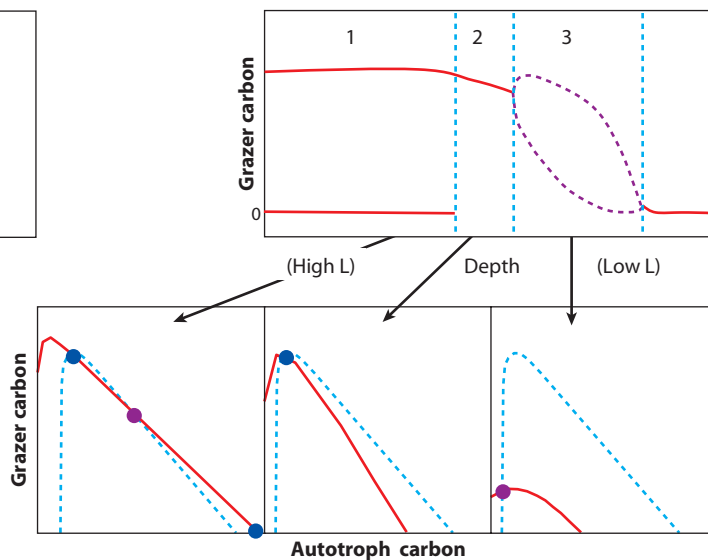
c Stoichiometric model: "paradox of energy enrichment"

d Example data

much of a good thing" result arises again because enrichment of this wrong resource exacerbates stoichiometric mismatches between autotrophs and grazers (Andersen et al. 2004, Diehl 2007, Loladze et al. 2000). The Diehl (2007) model predicts shifts in grazer biomass along a light supply gradient mediated by depth. In deeper systems, increasing light supply enhances grazer biomass (as one might imagine); however, in shallower systems, increasing light supply depresses grazer biomass (**Figure 3***c*). This counterintuitive result involves joint interplay between light as a driver of producer stoichiometry (and thus elemental imbalances), depth as a mortality term on autotrophs, and sediments as a delay in nutrient regeneration (Diehl 2007). Thus, this paradox of light enrichment most likely emerges in shallower systems, and the added realism may help explain some experimental results in planktonic systems (Sterner et al. 1998, Urabe et al. 2002a,b) and contrasting patterns between deeper lakes (Berger et al. 2006) and shallow ponds (Hall et al. 2007a). In this latter comparison, zooplankton grazer biomass increases with light in lakes but decreases with light in ponds (**Figure 3***d*).

Although the suite of extant, stoichiometrically explicit models offers new insights into predator-prey dynamics, a few additional components could yield even more powerful theory. For example, these models could relax the homeostasis assumption for consumers (DeMott et al. 1998, Grover 2003, 2004; Mulder & Bowden 2007), a change that might become especially pertinent if stoichiometric plasticity increases with warming temperatures (Woods et al. 2003). Additionally, more details concerning feeding biology should be added, for example, interactions of stoichiometric food quality and quantity with fatty acid content of autotrophs, gut processing time, toxins, and ingestion rates (Mitra & Flynn 2005). Third, enhanced representation of the stage structure of grazers seems important because juveniles may be moderately (e.g., cladocerans) or substantially (e.g., copepods) enriched with phosphorus (Sterner & Schultz 1998). High phosphorus demands of fast-growing juveniles create stoichiometry-induced bottlenecks in population growth that may then feed back on stage-structured interactions between juveniles, adults, and their prey (McCauley et al. 2008; Nelson et al. 2005, 2007). Thus, much remains to be explored in the realm of stoichiometrically explicit food chain dynamics.

2.3. Grazers, Recycling, and Autotroph Coexistence in the Pentagon Model

Ecological stoichiometry provides a way to unite two major niche models: the diamond web and the resource ratio. The diamond web model, which mixes competition between two species for

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Figure 3

Implications of stoichiometric mismatches for producer-grazer interactions in a food chain. (*a*) The classic paradox of enrichment model offers the pertinent foil. The intersection of hump-shaped producer (*red lines*) and vertical grazer (*blue lines*) nullclines indicates the location of the interior equilibrium. This equilibrium can be unstable (oscillatory) at high nutrient supplies of the producer but stable at lower carrying capacities. (*b, c*) Dynamics of stoichiometrically explicit analogs of this classic model produce a larger range of results (Diehl 2007). These cases stem from a change in the grazer nullcline, which increases almost vertically when the grazer is predominately carbon limited but becomes hump shaped as nutrients (poor food quality) limit grazers. Primary production depends on both nutrient and light supply (here noted by variation in depth of a water column), and the producer's nutrient:carbon content can vary. (*b*) Stoichiometric food chains can show multiple attractors. At low light supply (case 3), producers are rich in nutrient content, and the system oscillates (*purple dashed lines* on the depth-grazer carbon bifurcation plot indicate minimum and maximum values of these oscillations). As light supply increases (depth decreases), nutrients begin to limit grazers, and the system stabilizes (solid line in the bifurcation plot). At very high light supply, alternative stable states emerge; either the grazer persists with low densities of more nutrient-rich producers, or high densities of nutrient-poor producers cause extinction of the grazer. These two cases arise as the two nullclines cross twice. (*c*). The other paradox of light enrichment: Increasing light supply (shallower depth) first elevates grazer biomass, then (paradoxically) decreases grazer biomass until poor food quality catalyzes grazer extinction. (*d*) Contrasting patterns of light environment and zooplankton biomass in German lakes (*top*) and Michigan ponds (*bottom*).

a single resource with apparent competition, shows how consumers can promote coexistence (or induce alternative stable states) of competing autotrophs and shift species composition of their prey, depending on trait correlation structures among species and the environment [e.g., resource supply (Grover 1995, 1997; Holt et al. 1994; Leibold 1996)]. Coexistence in the diamond web minimally requires that superior competitors (i.e., lower resource requirement, R^*) are more vulnerable to predation.

The resource ratio model (**Figure 1c**) provides another mechanism for coexistence, alternative stable states, and shifts in species composition among competitors for two resources (Grover 1997, Tilman 1982). That model provides a convenient graphical foundation for the synthetic pentagon model (**Figure 1d**). If we assume that two inorganic (e.g., nitrogen, R_N^* and phosphorus, R_P^*) resources are essential (sensu Tilman 1982) but only one limits autotroph production at a time (Leibig's law of the minimum), then one can draw elbow-shaped nullclines in R_N-R_P space denoting zero net growth as governed by the autotroph's minimal requirements for nitrogen ($R_{N,j}^*$) and phosphorus ($R_{P,j}^*$) (**Figure 4a**). To this niche component, we add impact (consumption) vectors, which denote the ratio at which autotrophs consume resources. Here, shallower consumption vectors correspond to an autotroph with higher nitrogen:phosphorus consumption, demands, and content (**Figure 4a**). Finally, environmental resource supply, as noted by the supply point, determines whether the autotroph is limited by nitrogen (gray area), by phosphorus (white area), or both (**Figure 4a**). Coexistence of two autotrophs using these resources, then, requires a trade-off between minimal resource requirements (species 2 competes better for phosphorus; **Figure 4a**). Coexistence also demands that each species consumes relatively more of the resource that most limits it (**Figure 4b**), ensuring that intraspecific competition exceeds interspecific competition. Finally, the ratio of resource supply must be intermediate for coexistence. At more extreme supply points, species only compete for one resource, and the species with the lower requirement for that resource prevails.

The constraints imposed on this niche-based mechanism of coexistence by stoichiometrically explicit grazing arise in two ways (Andersen 1997, Daufresne & Loreau 2001, Grover 2002). First, mortality imposed by grazing elevates the autotroph's minimal nutrient requirements (Grover 1997, 2002); graphically, this involves shifting the nullcline up and over (from 1 to 1_G as illustrated **Figure 4c** via nullcline translation). Second, grazers change the relative and absolute amount of

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Figure 4

Competition among producers for multiple resources (nitrogen and phosphorus) with and without grazing (after Grover 2002). (*a*) To review, consumption of two essential resources yields an elbow-shaped nullcline for the autotroph, as determined by its minimal resource requirements (R_P^* and R_N^*). Supply points (*S*) above this curve support the autotroph, but the identity of the limiting resource (phosphorus, PL, or nitrogen, NL) depends on the location of the supply point relative to the slope of the impact (consumption) vector ($\bar{C}$). That slope depends on nitrogen (Q_N) relative to phosphorus content (Q_P); here, shallower slopes correspond to higher nitrogen:phosphorus content. (*b*) Outcomes of resource competition between two producers hinges on the intersection of each producer's (1 or 2) nullclines, orientation of their consumption vectors, and location of the supply point. Either producer 1 wins (*pink zone*), the species coexist (*purple zone*), or producer 2 wins (*white zone* above the nullclines). (*c*, *d*) For a single producer (1), presence of grazers (*G*) causes two major changes (as compared with panel *a*). First, the nullcline shifts up (from 1 to 1_G); then the supply point changes, owing to sequestering of nutrient and recycling by the grazer. Especially owing to this change in supply point, grazers can shift the identity of the limiting nutrient, as seen in panel *c*. In panel *d*, the producer remains phosphorus limited. Grazing may not (*e*) or may (*f*) disrupt opportunities for coexistence of the producers. The intersections of the new nullclines shift up, which can change the coexistence region of supply points (from *pink* to *purple regions*). The shift in supply point can push the system from a coexistence region to one where one producer is eliminated.

resources supplied to the producers because they can sequester nutrients in their biomass (at a certain phosphorus:nitrogen ratio) but also recycle nutrients, likely at ratios that are skewed from their original supply (Elser & Urabe 1999, Grover 2002, Sterner 1990). Two methods for graphically representing these effects have been developed. Here we illustrate how grazers can essentially change the supply point [from S to S_G, following Grover (2002)]. Below, we use the perhaps less intuitive but analytically powerful net production vectors. Grazers with high phosphorus:nitrogen (e.g., *Daphnia*) could shift their prey from nitrogen to phosphorus limitation (**Figure 4c**; Sterner et al. 1992) or exacerbate phosphorus limitation (**Figure 4d**; Rothhaupt 1997). Grazing, then, may continue to permit coexistence of autotrophs (**Figure 4e**) or may disrupt it by shifting the supply
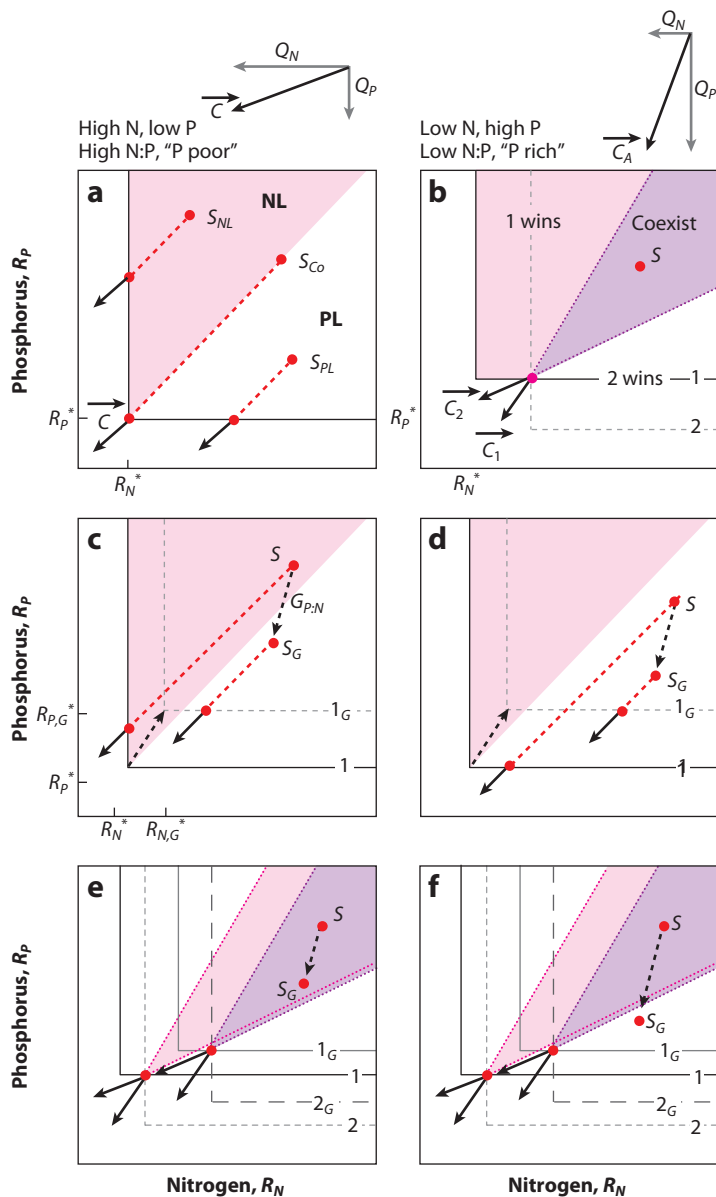
point (**Figure 4*f***). Thus, by incorporating stoichiometric constraints, grazers can destroy opportunities for coexistence (Andersen 1997, Grover 2002)—but perhaps also facilitate coexistence of species that could not persist together otherwise. These results seem relevant to aquatic systems, where nitrogen and phosphorus supply and grazing strongly shape phytoplankton communities (Cottingham et al. 1998, Elser et al. 2000b, Smith 1983). More generally, the pentagon shows how constraints imposed by stoichiometry offer mechanisms determining the balance between maintenance and degradation of diversity (Grover 2002).

2.4. Resource Ratio Theory for Grazers and New Roles for Inedible Autotrophs

Explicit stoichiometric representation of autotrophs opens the resource niche of grazers and can permit their coexistence. In essence, stoichiometry permits creation of a resource ratio theory for grazers (**Figure 4*e***), complete with predictions of coexistence, alternative stable states, and shifts in species composition along resource supply gradients. Here, I follow my linear treatment of this module, but more sophisticated models show increased opportunities for coexistence stably or via chaotic fluctuations (Deng & Loladze, 2007, Loladze et al. 2004). This module builds on the premises summarized in Section 2.1. Differences between carbon:phosphorus content among grazers permits creation of different nullclines for grazers in autotroph carbon (A)-nutrient (QA) space (**Figures 2*b*, 7*a,b***). These nullclines can cross in A-QA space assuming a trade-off in minimal requirements for those resources [i.e., one species is the superior nutrient competitor (species 1) while the other is the superior carbon competitor (species 2 in **Figure 5*a,b***). Intersecting nullclines create the possibility for coexistence, but coexistence also demands that each grazer has higher impact on the resource most limiting to its own growth (**Figure 5*a*** versus **5*b***). Again, the autotroph nullcline provides an analogy to a supply point (the SNC). If this SNC crosses the intersection of the two grazers' nullclines (at intermediate nutrient supply), coexistence or alternative stable states is possible (**Figure 5*a***). Furthermore, the model anticipates shifts of grazer composition along gradients of resources supplied to autotrophs. At low nutrient supply, autotroph quality is poor, and the superior nutrient competitor prevails; at high nutrient supply, plant quality increases, allowing the superior carbon competitor to displace the inferior nutrient competitor. In the intervening

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Figure 5

Outcomes of competition among producers for two resources packaged within a single producer, a variation with an inedible plant, some supporting data, and outcomes of an intraguild predation model. (*a, b*) Two grazers ($j = 1, 2$) with a trade-off in minimal requirements for carbon (A_j^*) and sequestered nutrient (QA_j^*) ensure that nullclines cross. Assuming that nutrient:carbon content of producers permits it [as determined by the slope of the system nutritional constraint, (SNC)], the two grazers can either coexist (*a*) or show alternative stable states (*b*). (*c*) Ultimately, light and nutrient supply, via their effects with grazing on plant stoichiometry, determine whether neither grazer can persist (*white region 0*), the superior nutrient competitor wins (G_1, *light blue, region 1*), the two grazers coexist (*blue region 2*), or the superior nutrient competitor wins (G_2, *dark blue region 3*). (Modified from Hall 2004.) (*d*) The nutrient-rich grazer *Daphnia* often (but not always) dominated high-nutrient mesocosms that produced sufficient sequestered nutrient; thus, *Daphnia* acted as the superior nutrient competitor but inferior nutrient competitor (Hall et al. 2004). (*e*) Addition of a neutrally inedible producer (A_I) changes the outcome of competition. The possibilities expand to the following: (1) G_1 excludes the other G_2 and A_I; (2) the two grazers coexist without A_I; (3) G_2 excludes other grazer and A_I; (4) G_2 and A_I exclude the other grazer; (5) G_2 and A_I exclude G_1. (*f*) The theoretical results involving A_I involve its indirect impact on stoichiometry of the edible autotroph. Such a relationship was seen in a mesocosm experiment (Hall et al. 2006). (*g*) Autotroph stoichiometry may promote coexistence in an omnivorous system (Diehl 2003). Poor resource quality (i.e., low nutrient quota, Q, framed in terms of nutrient:carbon ratios) of an autotroph resource, A, could promote coexistence (gray areas) of grazers (G, intraguild prey) with omnivores (O). Along a nutrient supply gradient, a window of coexistence at intermediately low Q allows coexistence, but with increasing nutrients, autotrophs become too nutrient rich for grazers to persist. (*h*) On the other hand, once high light lowers the nutrient content of autotrophs to a sufficient degree, the grazer and omnivore can coexist over a broad range of increased light.

window of coexistence, the superior nutrient competitor is carbon limited, whereas the superior carbon competitor is nutrient limited.

These theoretical results can provide insight into community structure along environmental gradients of resource supply and predation. For instance, in a mesocosm experiment, *Daphnia* dominated high-nutrient environments where the stoichiometric quality of autotrophs was higher (Hall et al. 2004; see also Urabe et al. 2002b). *Daphnia* often competes better for carbon (Gliwicz 1990) but has fairly high nutrient demands (Andersen & Hessen 1991, Hall et al. 2004). Therefore, *Daphnia* may have high requirements for nutrients sequestered in autotrophs (i.e., high QA^*). When low-nutrient systems do not provide this minimal requirement, other grazers should dominate (Hall et al. 2004; **Figure 5d**). Additionally, selective predation on superior carbon competitors such as *Daphnia* can elevate the prey's minimal resource requirements beyond
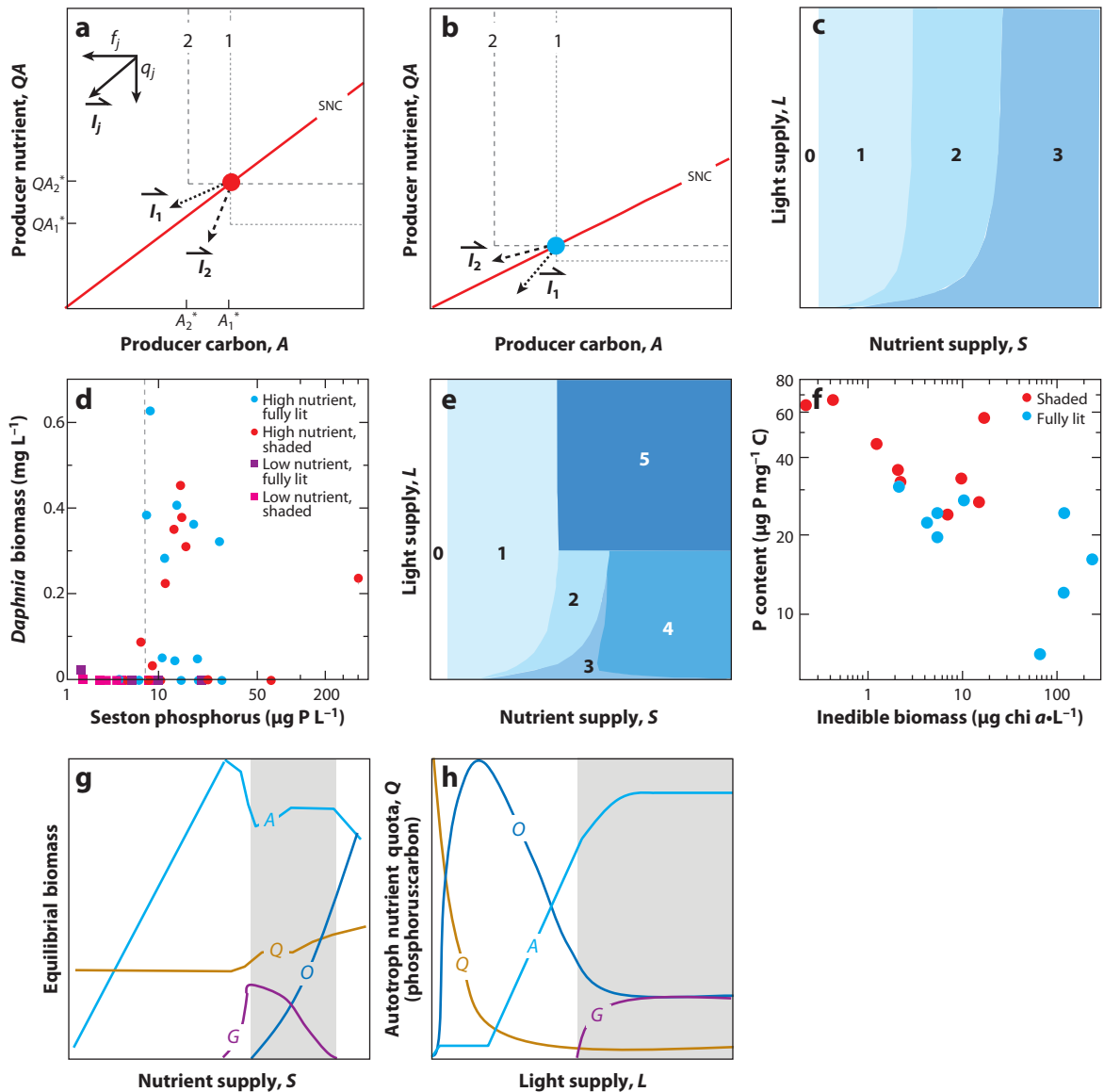
what the abiotic-biotic environment can support (Elser et al. 1998, Hall 2004, Hall et al. 2004). When combined, these stoichiometric and predation niche constraints offer a more predictive insight into incidence and abundance of (important) species such as *Daphnia*.

By expanding the stoichiometric niche of grazers, this resource-ratio-theory-for-grazers framework also reveals new pathways for autotroph-grazer interactions. Consider the extreme case of neutral inedibility (Hall et al. 2006, Grover 1995): Inedible autotrophs trade off competitive ability (i.e., higher R^*) and defense with edible autotrophs but do not otherwise interfere with grazing. However, because they compete with edible autotrophs for nutrients, these inedible autotrophs can influence the nutrient content of their competitors: Competition arises between grazer-edible autotroph systems and inedible autotrophs that can then influence community structure (Hall et al. 2006). For instance, at high light supply, the edible-autotroph-superior nutrient-competing grazer pair can exclude the superior carbon competitor and the inedible autotroph (because it can depress freely available nutrients to lower levels than required by the latter; region 1 in **Figure 5e**). As resource supply increases (still at high light), the inedible autotroph can invade but exclude the superior carbon competitor (region 5 in **Figure 5e**). Such cascade competition (Grover 1997) arises because the inedible autotroph governs nutrient content and nutrient sequestered in edible autotrophs (i.e., it strongly influences the SNC; **Figure 5f**), and keeps sequestered nutrient depressed below the minimal requirements of the second grazer. At lower light supply, coexisting grazers or the superior carbon competitor can depress freely available nutrients below levels required by the inedible autotroph (regions 2 and 3 in **Figure 5e**). That system outcompetes the inedible autotroph (Hall et al. 2006). Finally, the two autotroph–superior carbon competitor system can keep edible carbon depressed below the requirements of the superior nutrient competitor (region 4 in **Figure 5e**).

These results concerning producer heterogeneity matter for two interrelated reasons. First, they expand understanding of the role that producer heterogeneity plays in ecosystems (Grover 1995, 1997; Holt et al. 1994; Leibold 1996). Second, they highlight a challenging but important frontier for stoichiometric theory. Producers vary in other traits besides stoichiometric ones. For instance, they can resist or tolerate herbivory, and they compete with each other for nutrients and light (e.g., DeMott & Tessier 2002, Grover 1997, Passarge et al. 2006). Many of these traits influence plant-herbivore dynamics but also autotroph stoichiometry. Future theoretical and empirical efforts in eco-stoichiometry must incorporate the additional complications—but potentially important insights—that autotroph heterogeneity evokes. Such efforts might be steered using knowledge about correlation structures among the physiological traits involved (Litchman et al. 2007, Litchman & Klausmeier 2008). Without thoroughly embracing autotroph heterogeneity, however, eco-stoichiometry may not realize its full potential in community ecology.

2.5. Enhancement of Omnivory

Ecological stoichiometry can offer a solution to a puzzle in community ecology: What factors maintain omnivory? Omnivory (i.e., consumption of resources from more than one trophic level) seems common in natural systems (Polis et al. 1989), yet simple models of a very common type of omnivory (intraguild predation) predict that omnivores should often drive their competitor-prey extinct (Holt & Polis 1997). Intraguild predation models do allow three species' coexistence, provided that the omnivore is an inferior resource competitor (i.e., higher R^*). This trade-off ensures that the intermediate competitor-prey enjoys some advantages despite enhanced mortality from the omnivore. However, the region of parameter space that promotes three species' coexistence typically appears small and arises only at intermediate productivity. Thus, in theory, omnivory should not be particularly common.

To explore stoichiometry as an omnivory-promoting mechanism, Diehl (2003) modified a model of competition among grazers of a stoichiometrically plastic, dynamic resource (Loladze et al. 2004) by assuming that the omnivore was the inferior carbon competitor. Nonetheless, dynamic interaction between autotroph quality and quantity can facilitate coexistence, particularly when resource quality is low. Along a nutrient supply gradient, stoichiometric quality of resources (Q) increases; in the example given (**Figure 5f**, from Diehl 2003), the competitor-prey grazer (G) first enters the system with the poor-quality resource; with grazing, resource quality increases, eventually allowing the omnivore (O) to enter the system and then displace the grazer. However, with increasing light supply, autotroph quality drops sufficiently to allow both omnivores and grazers to coexist (**Figure 5f**). Poor resource quality facilitates coexistence by constraining increases in omnivore density and thus reducing extinction risk for the competitor-prey. This result matters because autotroph quality is often quite poor, particularly on land (Elser et al. 2000a, White 1993). Thus, stoichiometric constraints can facilitate coexistence generally and in omnivorous systems in particular (Denno & Fagan 2003).

2.6. Three-Level Systems and Trophic Cascades

Explicit consideration of stoichiometry may yield new insights into tritrophic food chains and webs. For instance, it could enhance understanding of variation in trophic cascade strength among ecosystems. The trophic cascade offers one of those classic ideas in ecology that still remains theoretically contentious. Trophic cascades involve indirect effects of predators on autotrophs mediated through their direct effects on grazers but also nutrient cycling (Vanni et al. 2006). Controversy centers on pronounced variation in cascade strength seen among ecosystems, and several nonstoichiometric hypotheses might explain this broad-scale variation (Borer et al. 2005, Shurin et al. 2002, Shurin & Seabloom 2005). However, stoichiometric mismatches between autotrophs and grazers could also be involved. Terrestrial plants typically contain much more indigestible carbon, owing to structural and defensive compounds, than do aquatic producers, and therefore have higher carbon:phosphorus and carbon:nitrogen ratios than aquatic autotrophs (Borer et al. 2005, Cebrian 1999, Elser et al. 2000a). If herbivores grow less efficiently on this poorer resource, they should control autotroph biomass to a diminished degree; therefore, predators may induce smaller cascades (Borer et al. 2005, Hall et al. 2007b).

We approached this food quality hypothesis using a minimal and very linear tritrophic food chain. First, we assumed fixed autotroph stoichiometry, which allowed us to disentangle digestion resistance (i.e., reduced maximal conversion efficiency) from low nutrient:carbon content, a trait that influences of conversion efficiency but also how biomass and nutrient are allocated among trophic levels. Then we permitted flexible plant stoichiometry, but both variations yielded similar results (Hall et al. 2007b). First, variation in fixed nutrient stoichiometry and minimal nutrient quota (k_Q) likely cannot explain variation in cascade strength among ecosystems because the biomass-allocation effects cancel out or overwhelm the influence of conversion efficiency effects of stoichiometry. However, producer stoichiometry can correlate with cascade strength (i.e., higher nutrient content yields stronger cascades) when variation in digestion resistance varies systematically among ecosystems (**Figure 6a**). These results prompt us to pay careful attention to the interplay between plant defenses, species composition, and stoichiometry—and to think rigorously about causality.

This stoichiometry-compositional interface seems particularly germane for another recent, tritrophic result. In an aquatic mesocosm experiment manipulating both nutrient and light supply, trophic transfer efficiency from autotrophs to predators (i.e., the proportion of primary production moving through grazers to predators) reached its peak in low-light, high-nutrient environments

but was lowest in high-light, low-nutrient environments (Dickman et al. 2008; **Figure 6b**). Not surprisingly, this increase in transfer efficiency correlated with increased phosphorus:carbon content of phytoplankton. That said, a correlated response of phytoplankton community structure arose along the light-nutrient gradient: Phytoplankton in low-light, high-nutrient environments were smaller, more edible, and likely higher in fatty acid content (see also DeMott & Tessier 2002). Thus, trophic transfer efficiency here involved a correlated response of several major components of resource quality: stoichiometry, species composition, and perhaps fatty acid content of autotrophs.

Resource stoichiometry can also cascade up to influence top predators. Changes in autotroph stoichiometry can shape density, species composition, and nutrient content of grazers [i.e., prey quantity and quality for predators (Boersma et al. 2008, Fagan & Denno 2004)]. If the low-nutrient content of grazers could limit predators, poor resource quality for herbivores could ultimately
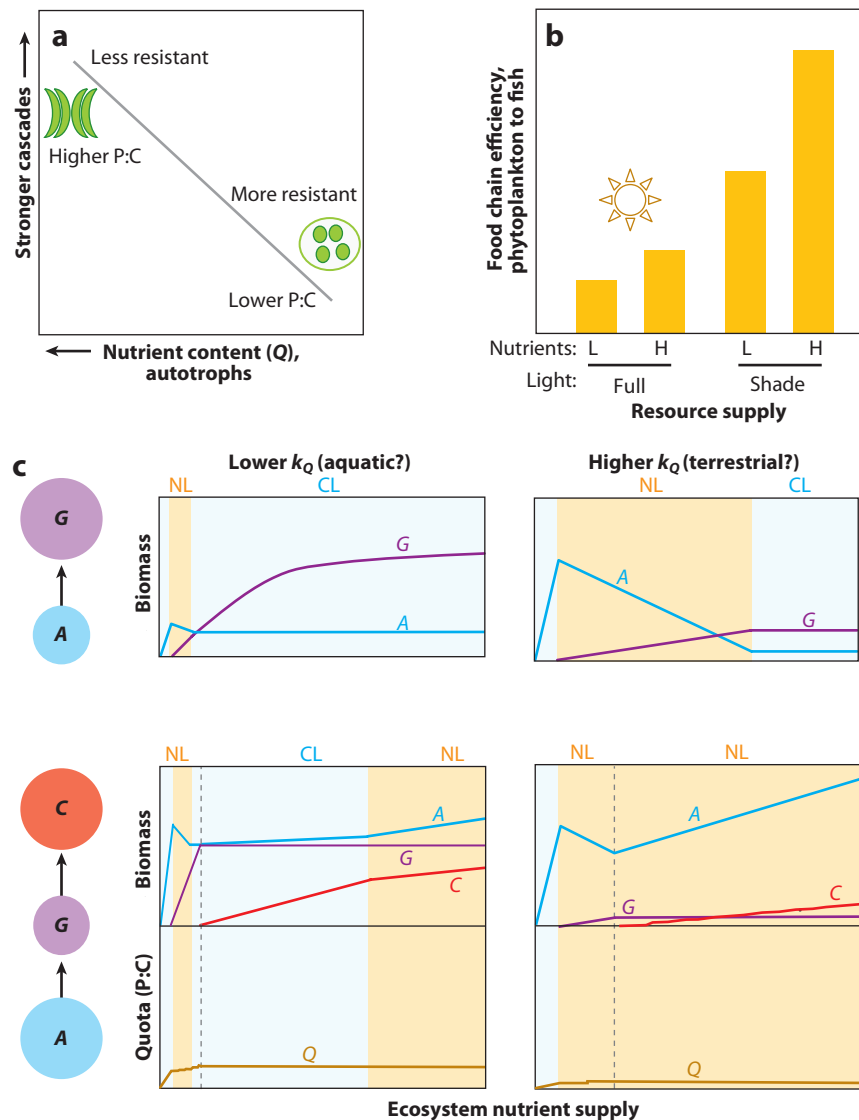
reduce predator control of grazers and mute cascades (Kagata & Ohgushi 2006). This possibility was ignored in our own tritrophic model (Hall et al. 2007b), but to be fair, the carbon-limited predator assumption often holds [e.g., most fishes (Schindler & Eby 1997)] but perhaps should be challenged because the stoichiometry of predators may vary interspecifically more than appreciated (Hendrixson et al. 2007, Vanni et al. 2002). Fast-growing, phosphorus-rich invertebrate predators could be particularly sensitive to the nutrient content of their prey (Boersma et al. 2008, Denno & Fagan 2003, Fagan et al. 2002). Perhaps food chain models, then, should incorporate the stoichiometric niche of predators (creating a resource ratio theory for predators): Could such next-generation models better predict shifts in predator abundance and composition in response to decreasing nutrient loadings (Jeppesen et al. 2005) and increased CO_2 concentrations (Urabe et al. 2003)? Both of these factors diminish the stoichiometric quality of the base of food chains.

Finally, even if predators do not become nutrient-limited, they can induce the nutrient limitation of grazers. With sufficient nutrient supply, predators can shift grazers from carbon to nutrient limitation or maintain the nutrient limitation of grazers at any resource level (Hall et al. 2007b; **Figure 6c**). These results emerged because the minimal nutrient requirement of grazers elevates with mortality rate. Imposition of nutrient limitation by predators might influence how biomass is allocated among trophic levels: Once grazers become nutrient-limited, the biomass of producers increases more steeply and that of predators increases less steeply with further enrichment (**Figure 6c**; Hall et al. 2007b). Additionally, by pushing grazers around in their stoichiometric niche, predators might expand opportunities for coexistence beyond that foreseen from uni-currency modules (Grover 1997, Holt et al. 1994, Leibold 1996). Thus, further development of stoichiometrically explicit, tritrophic models could prove fruitful for predictions of food chain efficiency and coexistence.

2.7. Stoichiometric Constraints in Autotroph-Decomposer Interactions

Eco-stoichiometry provides a powerful lens for examining the interface of autotroph-decomposer and autotroph-decomposer-grazer interactions (Cherif & Loreau 2009, Moe et al. 2005;

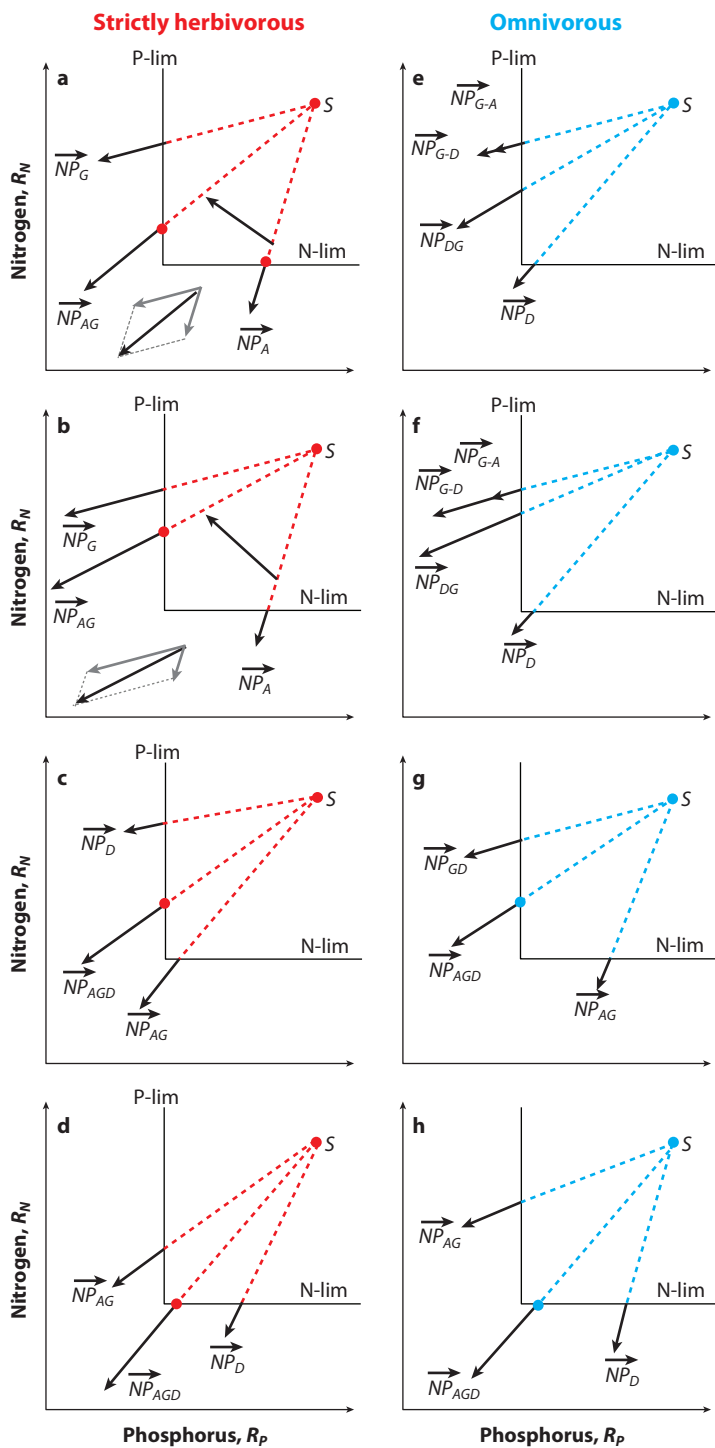←——

Figure 6

Stoichiometrically explicit, three–trophic-level systems. (*a*) Trophic cascades are often stronger in aquatic systems than in terrestrial ones. This pattern might correlate with magnitude of stoichiometric imbalances between autotrophs and herbivores, which can be even more pronounced on land. Two pathways that could drive low-nutrient content of terrestrial autotrophs include high resistance to digestion and low minimal nutrient quota (k_Q). A tritrophic model suggests that links between autotroph stoichiometry and strength of trophic cascades can arise due to the digestion resistance pathway (Hall et al. 2007b). (*b*) A recent aquatic mesocosm experiment (Dickman et al. 2008) suggests that food chain efficiency (i.e., proportion of energy moving from autotrophs to consumers of grazers) changes along gradients of light and nutrient supply. More specifically, efficiency was highest in shaded but high-nutrient systems. (*c*) A simple food chain model suggests that top consumers (*C*) can enhance less-efficient nutrient limitation (NL) and reduce more efficient carbon limitation (CL) of grazers (*G*). Along a nutrient supply gradient, we see the typical shifts from nutrient-limited grazers to carbon-limited grazers in two-level systems. However, in three-level systems, consumers elevate minimal nutrient requirements of grazers; as a result, grazers eventually (higher k_Q case, more likely perhaps in aquatic systems) shift to nutrient limitation with sufficient enrichment. Once consumers elicit the nutrient limitation of grazers, autotroph biomass (*A*) increases more quickly, whereas consumer biomass (*C*) increases less quickly with enrichment (grazer biomass remains constant). Consumers could always maintain the nutrient limitation of grazers' enrichment too (lower k_Q, terrestrial). Once consumers enter the system (pass the *gray dashed vertical lines*), plant nutrient quota (*Q*, phosphorus:carbon) becomes fixed. Thus, consumers play a strong role in influencing plant stoichiometry (Hall et al. 2007b)

Figure 1i,j,k). These types of interactions center on the stoichiometric consequences of non-grazed primary production that enters detrital food webs (Cebrian 1999). Nutrients released from that detritus via decomposition can considerably impact resource supply and therefore the nutrient limitation of autotrophs (Danger et al. 2007, Daufresne et al. 2006, Cherif & Loreau 2009; **Figure 1i,k**). This result should not seem too surprising, because microbial decomposers do not merely mineralize nutrients; they may compete fiercely for nutrients and can have high and relatively homeostatic nutrient content relative to plants and detritus (Makino et al. 2003). Decomposers can also strongly influence ratios at which nutrients are lost from systems [with implications for plant competition and dynamics (Daufresne et al. 2006; **Figure 1k**)]. Thus, stoichiometry can govern the flow of energy and nutrients between autotrophs, decomposers, and detritus. From a food web perspective, the plot thickens because grazers can fuel the growth of microbes when they excrete excess carbon, particularly when they are nutrient-limited (Darchambeau et al. 2003), but grazers can also ingest decomposers (**Figure 1i**). Through these subsidies, decomposers might elevate nutrient cycling from grazers (Cherif & Loreau 2009; **Figure 1i**). Thus, a stoichiometrically explicit focus on autotrophs, grazers, and decomposers should produce new insights into community structure and ecosystem functioning.

As a step forward, Cherif & Loureau's (2009) model produces an elegant graphical exploration of these factors for nutrient limitation of autotrophs. It builds on the now-familiar resource ratio model, complete with elbow-shaped nullclines for an autotroph (**Figure 3a**). However, it summarizes joint effects of consumption and recycling from all players of the autotroph-grazer-decomposer food web using net production vectors (NP_j) rather than change in supply points (**Figure 7**). These enhanced impact vectors correspond to the ratio at which the entire food web or its components consume resources. The beauty of this approach (see also Daufresne & Loreau 2001, Daufresne et al. 2006) hinges on the graphical simplicity of vector addition. For instance,

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Figure 7

Graphical depiction of the links between the resource limitation of primary productivity and food web architecture, where autotrophs (*A*) are eaten by herbivores (*H*) that do not eat carbon-limited decomposers (*d*, strictly herbivorous case, as may be more common in terrestrial systems, *a–d*) or may eat them (omnivorous case, *e–f*, perhaps more common in freshwater pelagic systems). The eight panels depict the now-familiar nullclines of the producer along axes of freely available nitrogen (R_N) and phosphorus (R_P) and supply points (*S*). The arrows correspond to net production vectors of the different pieces of the A-D-H food web. These vectors have shallow slopes at low nitrogen:phosphorus ratios and steeper slopes at higher nitrogen:phosphorus; their magnitude reflects equilibrial biomass of the component being examined. (*a*) Without decomposers, phosphorus-limited grazers (more shallow slope of net production vector NP_G) can make nitrogen-limited autotrophs (steep NP_A) become phosphorus-limited, (*b*) especially as the feeding rate of the herbivore increases (because the elevated feeding rate elongates NP_G). In both cases (*a*, *b*), the net production vector for the autotroph-herbivore system (NP_A) becomes the sum of the two component vectors (see small insets). (*c*) Decomposers with nitrogen:phosphorus ratios that are even smaller than the nitrogen:phosphorus ratio (shallower NP_D) of the combined autotroph-herbivore system exacerbate the phosphorus limitation of grazers, whereas (*d*) those with higher nitrogen:phosphorus ratios can pull a phosphorus-limited autotroph-herbivore system toward nitrogen limitation. (*e*) When omnivorous herbivores eat decomposers, the net production vector for the herbivore (NP_G) has two components: that fueled by consumption of autotrophs, NP_{G-A}, and that fueled by decomposers, NP_{G-D}. The net production vector of the food web involving decomposers, NP_{DG}, then involves both the roles of decomposers as recyclers but also a food source. (*f*) Higher consumption of decomposers by omnivores means that the net production vector becomes more similar to that of the herbivore; that is, NP_{DG} approaches NP_G. Nonetheless, decomposers can convert an otherwise nitrogen-limited autotroph in the A-H system into a phosphorus-limited one, or a nitrogen-limited autotroph in the A-H system into a phosphorus-limited plant. Modified from Cherif & Loreau 2009.

Strictly herbivorous — **Omnivorous**

a, b, c, d, e, f, g, h panels plotting Nitrogen, R_N (vertical axis) versus Phosphorus, R_P (horizontal axis), with P-lim and N-lim axes, source point S, and vectors $\overrightarrow{NP_G}$, $\overrightarrow{NP_{AG}}$, $\overrightarrow{NP_A}$, $\overrightarrow{NP_D}$, $\overrightarrow{NP_{DG}}$, $\overrightarrow{NP_{G-A}}$, $\overrightarrow{NP_{G-D}}$, $\overrightarrow{NP_{GD}}$, $\overrightarrow{NP_{AGD}}$.

autotrophs (A) alone might be nitrogen-limited at a given supply point (based on the autotroph's relatively high nitrogen:phosphorus content yielding a steeper $\mathbf{NP}_A$ vector), but grazers (G) with lower nitrogen:phosphorus content (and shallower $\mathbf{NP}_G$) pull the autotroph toward phosphorus limitation (**Figure 7a,b**; Daufresne & Loreau 2001). This effect is determined by addition of the two vectors whose slope reflects nitrogen:phosphorus content and whose magnitude mirrors the equilibrial biomass of that component.

Building on this approach, one can see how recycling, nutrient competition, and subsidies from grazers to low-nitrogen:phosphorus decomposers (D, e.g., bacteria, shallow $\mathbf{NP}_D$) can push a nitrogen-limited autotroph in an *A-G* system to phosphorus limitation in an *A-G-D* system (**Figure 7c**); conversely, a high-nitrogen:phosphorus decomposer (e.g., fungus, steep $\mathbf{NP}_D$) can induce nitrogen limitation from autotrophs that would otherwise be phosphorus limited when grazed. The same logic can be applied when grazers eat decomposers. Then the net production vector contribution from grazers ($\mathbf{NP}_G$) arises from the sum of consumption of autotrophs ($\mathbf{NP}_{G-A}$) and decomposers ($\mathbf{NP}_{G-D}$; **Figure 7e,f**). Decomposers subsidize grazers and therefore can accentuate the role of grazers in determining the limitation of autotrophs. Once these new feeding relationships are incorporated, it remains possible that decomposers shift the identity of limiting nutrients for autotrophs (**Figure 7g,h**).

This model structure then offers a template on which to add other biology pertinent to decomposers. For instance, because aggregate assemblages seem more stoichiometrically plastic than single species of bacteria (Danger et al. 2008, Makino et al. 2003, Makino & Cotner 2004), one could incorporate smooth changes in stoichiometry of decomposer assemblages (Danger et al. 2008, Schade et al. 2005). Competition between fungi (lower phosphorus) and bacteria (higher phosphorus) could be further explored (perhaps building on Cherif & Loreau 2007; **Figure 1j**). Stoichiometry should enhance insight into positive and negative feedback mechanisms inherent in plant-soil-fungal interactions that may maintain plant diversity (Bever 2003, Hoeksema & Schwartz 2003, Schwartz & Hoeksema 1998, Umbanhower & McCann 2005). Finally, stoichiometric match-mismatches can influence carbon sequestration versus respiration by microbes. Low-nutrient content of detritus typically means lower and slower decomposition and hence possibly net sequestration of carbon (Hessen et al. 2004). Thus, food web interactions in soil offer fertile ground for future developments in eco-stoichiometry and for enhanced understanding of global carbon cycling.

3. CONCLUSIONS

A stoichiometric approach to food webs reveals mechanisms that can enhance or degrade diversity and predict changes in community structure along environmental gradients. This enhanced predictive power matters because human activities manipulate many of those gradients. Stoichiometry, then, should enhance predictive insight into responses of communities and ecosystems to these activities. The stoichiometric approach hinges on a biogeochemical trait, stoichiometric body composition (e.g., carbon:nitrogen:phosphorus ratio). This trait plays roles in two aspects of a species' niche (Chase & Liebold 2003, Leibold 1995): It influences a species' requirements from the environment (e.g., high-phosphorus species might have high-phosphorus requirements, all else being equal) and a species' impact on its environment, particularly through nutrient cycling. This biogeochemical trait is just one component of a species' niche, however. Stoichiometric body composition needs integration with other traits that influence consumer-resource interactions (e.g., plant defenses). Full realization of the power—and limitations–of a stoichiometrically explicit approach to food webs ultimately demands this integration and close attention paid to factors that constrain stoichiometric imbalances in species interactions in the first place

(e.g., Diehl 2007; Hall et al. 2005; Klausmeier et al. 2004b, 2007). Such integration will provide challenges but should produce new discoveries.

The theory presented here shows how the stoichiometric niche can promote diversity. For instance, nutrient limitation of grazers (found after focusing on nutrient requirements) permitted coexistence in a resource ratio for grazers model (Hall 2004, Loladze et al. 2004) and stabilized intraguild predation (Diehl 2003). However, stoichiometric impacts of species can degrade diversity; for instance, grazers disrupted the coexistence of autotrophs through skewed nutrient cycling (Grover 2002), and inedible autotrophs prevented grazer coexistence (Hall et al. 2006). Such diversity destruction is likely only temporary, because migration and evolution of species with more complimentary niches could restore diversity. Thus, at the least, eco-stoichiometry provides vehicles to understand how changes in species composition reflect the interplay between food web architecture and stoichiometric constraints.

By embracing this interplay, a stoichiometric approach to food webs also provides new insights into more aggregate and ecosystem-level properties of communities. We saw how eco-stoichiometry could be used to understand changes in biomass accrual among species and trophic levels. For instance, the paradox of light enrichment depends on stoichiometric constraints in food chains and physical constraints (Diehl 2007, Loladze et al. 2000). Additionally, in a tritrophic model, inducement of the nutrient limitation of grazers by predators can change biomass accrual among trophic levels (Hall et al. 2007b). Also, food web architecture and stoichiometry jointly determine which resources limit primary production (Cherif and Loreau 2009, Daufresne et al. 2006, Daufresne and Loreau 2001). All of these results reveal how stoichiometric niches create causal links between food webs and the net results of anthropogenic changes in resource supplies to ecosystems.

The utility of this theory requires careful examination of when and why stoichiometry-influenced niches matter. When are stoichiometric niches important? When can other aspects of a species' niche (e.g., autotroph heterogeneity) dominate or swamp out stoichiometric constraints? Close evaluation of the correlations between stoichiometric composition and other traits might provide a starting point to tackle this issue. Additionally, more rigorous treatment of these modules could enhance predictive power. Linear models (like many reviewed here) offer starting points, but exciting biology such as positive density dependence fully manifests itself in nonlinear variations (Andersen et al. 2004), so new insights likely require more nonlinear treatments. Finally, new modules need exploration. A particularly pertinent one comes from disease ecology: Resource quality of hosts and active manipulation of relative resource supply in hosts—by hosts—can influence epidemiology (Frost et al. 2008, Smith 2007; **Figure 1*l***). Thus, further development of stoichiometric food web theory and continued focus on constraints imposed by mass balance will enhance understanding of disease and other species interactions.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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