

Lotka re-loaded: Modeling trophic interactions under stoichiometric constraints

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ABSTRACT

Nearly a century ago A.J. Lotka provided fundamental formulations for population modeling; less appreciated are his explorations of the underlying material (elemental) basis of life and its implications for ecology and evolution. This paper describes recent developments in ecological and biological stoichiometry that unify these aspects of Lotka's work. Stoichiometrically explicit versions of the Lotka–Volterra equations capture key missing aspects of food web interactions, such as the effects of food quality and nutrient recycling feedbacks, and encompass a richer, and potentially more realistic, set of dynamics than non-stoichiometric models. These stoichiometric models are now being further extended to include the recently discovered effects of excess dietary nutrient content on consumer performance. The multi-dimensional capacity of stoichiometric models is likely to be of particular value given the pressing need to anticipate the ecological effects of globally dynamic perturbations of multiple chemical elements (e.g. C, N, and P) due to human actions.

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1. Introduction

“For the drama of life is like a puppet show in which stage, scenery, actors and all are made of the same stuff. The players, indeed, ‘have their exits and their entrances,’ but the exit is by way of translation into the substance of the stage; and each entrance is a transformation scene. So stage and players are bound together in the close partnership of an intimate comedy; and if we would catch the spirit of the piece, our attention must not all be absorbed in the characters alone, but must be extended also to the scene, of which they are born, or on which they play their part, and with which, in a little while, they merge again.” – A.J. Lotka. *Elements of Physical Biology* (1925)

Perhaps all theoretical ecologists can readily elaborate on the foundational contributions of A.J. Lotka, and his contemporary V. Volterra, to theoretical population biology. Lotka and Volterra's work captured dynamical predator–prey systems in a pair of first-order, non-linear differential equations (Lotka, 1910), the eponymous “Lotka–Volterra equations” (LVE, hereafter) that have formed the core of much ecological modeling in the ensuing decades (Wangersky, 1978). These equations treat populations along a single currency axis, in terms of population numbers, biomass, or other metrics of abundance. Thus, it is fascinating to note that Lotka was deeply aware of the multi-currency nature of

living systems (see quote above) and devotes five chapters in *Elements of Physical Biology* to the “stage of the life drama,” including discussion of the water and element cycles along with attention to principles of stoichiometry and to the elemental composition of living biomass. (Another five chapters even dealt with the evolution of consciousness and its ultimate impacts on biosphere evolution.) Nevertheless, Lotka did not attempt to formally join these disparate parts of his thinking, never connecting population equations to the material composition of biota and the availability of chemical elements in the environment. Subsequently, theoretical biology followed an historical arc that led population dynamics and ecosystem biogeochemistry to become conceptually and operationally disjunct (Elser, 2006).

After a century, this divide is now beginning to break down. In this paper we attempt to describe empirical and theoretical developments that have built a bridge between theoretical population biology and ecosystem ecology in the form of the theory of “ecological stoichiometry” (summarized in Sterner and Elser, 2002) and its more recent morph, “biological stoichiometry” (Elser et al., 2000b). These developments provide a means to integrate population dynamics with the dynamics of key nutrient elements, such as carbon (C), nitrogen (N), and phosphorus (P), whose absolute and relative abundances are undergoing rapid change under human influence (Falkowski et al., 2000). Furthermore, stoichiometric reasoning has led to development of key ideas that connect important ecophysiological traits to underlying biochemical mechanisms, thus facilitating the integration of ecosystem perspectives with evolutionary frameworks (Elser, 2006; Elser and Hamilton 2007). In this paper we seek to summarize some of these developments

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and highlight some emerging areas that require more attention for theoreticians and modelers.

2. Conceptual background of ecological and biological stoichiometry

The challenge of developing a mechanistic and predictive theory of biological systems taken up by Lotka is daunting. However, there has been important progress in integrating population and biogeochemical perspectives in recent years via the development of the theory of ecological stoichiometry (Sternner and Elser, 2002), the study of the balance of energy and multiple chemical resources (usually elements) in ecological interactions. Ecological stoichiometry has been quite fruitfully deployed in analysis of competition for multiple resources (Tilman, 1982; Smith, 1983; Grover, 1997) and of plant–herbivore interactions in food webs (Sternner and Hessen, 1994; Elser and Urabe, 1999). In resource ratio competition theory (Grover, 1997), the outcome of a competitive interaction (i.e. coexistence of the two species vs. exclusion of one or the other) is seen to be the consequence of the relative abilities of the taxa to acquire key resources, especially at low levels, juxtaposed against the relative supply rates of those resources in the environment. Coexistence occurs when, for example, species A can reduce the level of resource 1 (say, phosphorus) to levels limiting to species B but simultaneously the availability of resource 2 (say, nitrogen) has been reduced by species B to levels limiting to species A. However, in environments presenting high supply ratios of N relative to P, species A can dominate (or even exclude B) but when the environment presents N and P in low proportion, species B wins. In ecological arenas, resource ratio theory has met with considerable success in explaining species distributions and relative abundance of species in communities, especially for microbes, cyanobacteria, algae, and vascular plants (Kilham, 1986; Tilman, 1988; Smith, 1992; Smith et al., 1995; Grover, 1997, 2000; Interlandi and Kilham, 2001).

Given this success in the study of competition among microbes, autotrophic algae, and plants for inorganic resources, ecologists have begun during the past decade to extend the reasoning of resource ratio theory up the food web, in particular to trophic interactions at the plant–herbivore interface. Here, consumers such as herbivores are seen to be complex chemical mixtures made of multiple constituents (C, N, P, etc.) that must be assembled in relatively fixed proportions from a food base, plants, that can diverge wildly in chemical composition due to the effects of nutrient limitation and the physiological ability of plant cells to vary their elemental composition. Thus, in many food webs herbivores consume plant biomass with C:nutrient ratios greatly exceeding that of their bodies (Elser et al., 2000a), resulting in reduced growth rates due to nutrient-limitation (Sternner and Hessen, 1994; Sternner and Schulz, 1998) and altered rates of excretion and recycling feedbacks to the ecosystem (Elser and Urabe, 1999). Stoichiometric food quality and nutrient recycling feedbacks have strong dynamical consequences that have been documented in a variety of lab and field settings (Urabe and Sternner, 1996a; Sternner et al., 1998; Urabe et al., 2002a,b) and that have begun to be explored in mathematical models (see below). Finally, stoichiometric reasoning is now moving beyond ecological study, as investigators are now trying to establish the evolutionary forces that drive, and constrain, variation in the relative resource requirements of different species and in establishing their cellular, genetic, and biochemical determinants at the proximate level. In doing so, it may be considered instead to be a theory of “biological stoichiometry” (Andersen et al., 2004; Elser et al., 2000b; Sternner and Elser, 2002; Elser and Hamilton, 2007). For example, Elser and colleagues (Elser et al., 1996, 2000b) have proposed the “Growth Rate Hypothesis” (GRH) to explain variation among organisms in biomass C:P and N:P ratios. Their argument reasons that rapid growth rate requires increased allocation to

P-rich ribosomal RNA to meet the protein synthesis demands of rapid growth. Thus, fast-growing organisms tend to have biomass with low C:P and N:P ratios, raising their requirements for P from their environment or diet and making them poor competitors for this potentially key resource. Considerable data supporting the GRH have begun to accumulate in diverse biota from microbes to zooplankton to insects to vascular plants (Main et al., 1997; Gorokhova et al., 2002; Vrede et al., 2002; Elser et al., 2003, 2007; Niklas et al., 2005; Reich et al., 2010; Loladze and Elser, 2011).

Stoichiometric theory offers considerable promise for progress in mathematical biology and for application beyond the world of ecology. The core mechanisms that underpin ecological stoichiometry are easily formalized in mathematical terms, as in the Monod equation, the experimentally validated Droop equation characterizing how cell quota varies with growth rate (Droop, 1983), and functional and numerical forms for predation and nutrient recycling. Stoichiometric theory can perhaps be considered to be of “intermediate complexity,” capturing key eco-evolutionary trade-offs without adding an unmanageable number of new variables or assumptions. Because it builds on fundamental knowledge of living systems (biological chemistry, Darwinian evolution) and basic laws of nature (conservation of matter, the inability of living systems to create, transmute or destroy any chemical element, chemical stoichiometry), the theory of biological stoichiometry is fundamentally predictive with some of its core tenets being universally applicable to biological systems on all organizational, temporal, and spatial scales, and thus can be a guiding tool for experimentation and model formulation.

3. A simple mathematical framework for ecological stoichiometry in trophic interactions

The rapid advances in stoichiometric research just described have now allowed the embedding of stoichiometric concepts into the core equations from Lotka and Volterra’s pioneering work. Sternner and Elser (2002) have synthesized progress in the field. Sternner (1990) and Andersen (1997) were among the first to develop physio-ecological models featuring explicit stoichiometric constraints. Nisbet et al. (1991) considered situations in which nutrients stored in consumer biomass are temporarily unavailable for growth of producer species (algae, plant). Other lines of work in this area have been pursued, including studies by Grover (1997, 2003), Muller et al. (2001), Hall (2004), Diehl (2003), Ågren (2004), Kooijman (2005), Mulder and Bowden (2007), and Ballantyne et al. (2008). Key components of introducing stoichiometric constraints into the LVE are reviewed previously by Andersen et al. (2004). To illustrate the fundamental ways that merging stoichiometric and population perspectives enriches the theoretical possibilities captured in the LVE, we will detail, as an example, the underlying assumptions, mathematics, and outcomes of the approach of Loladze et al. (2000). However, it is important to note that the first steps in this direction were taken earlier by Andersen (1997) but considering only nutrient-limited producer growth and a slightly different approach to incorporating herbivore metabolic costs.

Loladze et al. (2000; also see Kuang et al., 2004) reframed the issues of ecological stoichiometry using an approach that builds on the LVE and its classical extensions by Rosenzweig–McArthur (1963):

$$x'(t) = bx \left(1 - \frac{x}{K}\right) - yf(x), \quad y'(t) = cf(x)y - dy.$$

In Rosenzweig–McArthur (RM), x is the total prey (producer) biomass (in units of mass), y is the total consumer biomass, K is the producer carrying capacity (due to external constraints, such as light limitation), b is the intrinsic growth rate of producer, c (<1) is the consumer biomass conversion constant, d is the consumer

death rate, including loss of biomass due to respiration, $f(x)$ is the consumer's functional response, which RM broadly assumes is a saturating concave down function (with a specific example being Holling type II ($f(x) = cx/(a + x)$)).

The Loladze et al. model ("LKE", hereafter) differs from RM in that it tracks two essential substances – carbon (~biomass) and a nutrient element, in this case phosphorus (P). A key implication of LKE is its application of the mass balance law to naturally include quality (i.e. nutrient content) as a determinant of consumer dynamics and thus encompass the potential for deterministic extinction of consumers when producer quality declines, even if the consumer's food is abundant. Its dynamics correspond well with a more mechanistically formulated model that contains more parameters (next section). The LKE model can be viewed as an example of a minimal stoichiometry model that can be extended to address questions in many ecological or evolutionary contexts without sacrificing mathematical tractability.

As with earlier models (e.g. Andersen, 1997), LKE makes the following assumptions (these are not entirely realistic, but they are not crucial for the outcomes; see Wang et al., 2008 and Stiefs et al., 2010):

- A1.** The system has a closed phosphorus cycle containing a given total mass, P, of phosphorus.
- A2.** The producer's biomass P:C ratio varies but never falls below a fixed minimum, q; the consumer maintains a constant P:C ratio, s, in its biomass.
- A3.** Phosphorus is either in the consumer or in the producer.

From A1 and A2, it follows that producer biomass in the system cannot exceed P/q . Since the consumer requires s grams of phosphorus for every gram of carbon, producer biomass is capped at $(P - sy)/q$. Hence, the effective carrying capacity of producer biomass is $\min(K, (P - sy)/q)$. Maximal transfer efficiency e is achieved if the consumer consumes food of optimal quality. If food quality (measured by $(P - sy)/x$) is less than s , then the transfer efficiency is proportionally reduced (by $[(P - sy)/x]/s$). LKE assumes (A3) that P in dead and excreted matter is immediately recycled and acquired by the producer species. This is reasonable in many cases in lakes and oceans (Andersen, 1997) but nevertheless relaxing the assumption does not change the major features of the model outcomes (Diehl, 2007). One obtains the LKE model by incorporating such stoichiometrically constrained carrying capacities and transfer efficiencies into the Rosenzweig–MacArthur equations:

$$x'(t) = bx \left(1 - \frac{x}{\min[K, (P - sy)/q]} \right) - f(x, y)$$

$$y'(t) = e \min \left\{ 1, \frac{(P - sy)}{(sx)} \right\} f(x)y - dy.$$

In this system of equations, because higher producer biomass can imply lower nutrient quality, traditional consumer–producer interactions (+, –) can change to (–, –) type when producer quality is low. This novel point is illustrated by numerical experiments analogous to laboratory experiments investigating stoichiometry of phytoplankton–zooplankton interactions (Urabe and Sterner, 1996b; Sterner et al., 1998; Hessen et al., 2002).

An exemplary set of nullclines from solution of the equations for a given parameter set is shown in Fig. 1 in a series in which light intensity (K) is increased. The phase plane is divided into two regions. In the white region, energy (carbon) availability limits consumer growth. In the gray region, food quality (phosphorus) limits consumer growth. Increasing energy input into the system may decrease producer quality and stabilize consumer–producer oscillations in the P-limited region. As K is increased (Fig. 1), the system exhibits a "paradox of energy enrichment": despite abundant food,

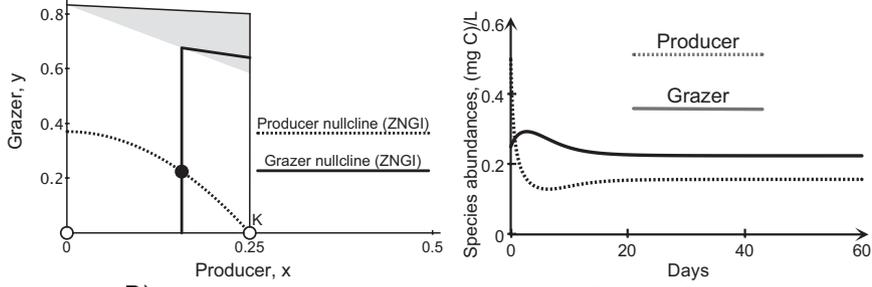
the consumer (depicted by red curve), faced with low food quality, is destined for deterministic extinction. Non-stoichiometric models cannot yield such predictions of the effects of deteriorating food quality. Intriguingly, this prediction of deteriorating food web performance and eventual consumer extinction due to increasing energy (light) inputs is supported by medium-scale artificial ecosystem experiments in Japan's "Aquatron" apparatus (Fig. 2; Urabe et al., 2002a) and its relevance to field situations has also been demonstrated (Urabe et al., 2002b; Diehl et al., 2005 but see Hall et al., 2007). Thus, we argue that the LKE model is a next-generation, "re-loaded", version of the LVE that effectively captures key mechanisms at the plant–herbivore interface and that makes qualitatively accurate predictions about trophic interactions regulated by the joint effects of light and nutrients.

While the analytical tractability of LVE and LKE are attractive features, one deficiency of these approaches is that they describe only a pairwise interaction and thus cannot contribute to better understanding patterns of species diversity in more complex systems. A small step to address this was taken by Loladze et al. (2004) who developed and analyzed a two-consumer version of the LKE model (LKE₂, hereafter):

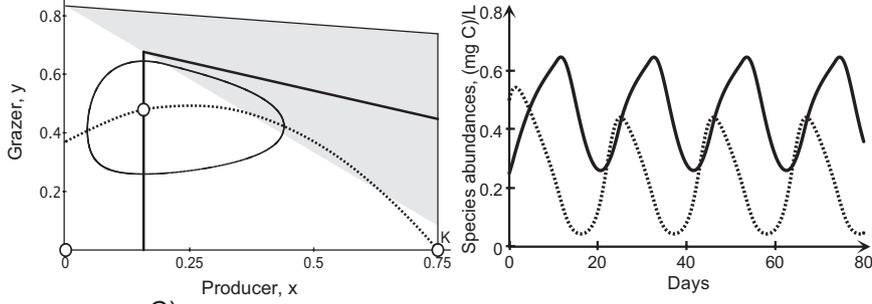
$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{\min\{K, (P - s_1y_1 - s_2y_2)/q\}} \right) - f_1(x)y_1 - f_2(x)y_2 \\ \frac{dy_1}{dt} &= e_1 \min \left\{ 1, \frac{(P - s_1y_1 - s_2y_2)/x}{s_1} \right\} f_1(x)y_1 - d_1y_1 \\ \frac{dy_2}{dt} &= e_2 \min \left\{ 1, \frac{(P - s_1y_1 - s_2y_2)/x}{s_2} \right\} f_2(x)y_2 - d_2y_2, \end{aligned}$$

where the notation is as in the LKE model but subscripts denote the two consumer species, which may differ in their elemental composition (s_i) and their functional responses (f_i). As with the original LKE, LKE₂ makes several unusual predictions about species interactions and dynamics that are driven by the important effects of food quality captured by prey stoichiometry. In particular, the model predicts that, in what might be considered a violation of the long-standing "Competitive Exclusion Principle" (CEP, Gause, 1934), there exist conditions (high light, low prey nutrient content) under which the two consumers can stably coexist (Fig. 3), despite the fact that there is only one prey item in the system. Furthermore, the two consumers can stably coexist while both being simultaneously limited by the phosphorus content in the prey. This is because, under conditions of poor food quality, the two consumers are not in a competitive (–, –) relationship with each other. Instead, they are in a facilitative (+, +) interaction, as grazing reduction of prey biomass and subsequent nutrient recycling serve to increase the per-capita nutrient supply to the prey, improving its quality for all. Intriguingly, empirical support for this prediction has been obtained: in the artificial ecosystem experiments discussed above (Urabe et al., 2002a), increased light intensity led to lower phytoplankton P content (lower P:C ratio) and impaired the proliferation of zooplankton; however, it also enhanced coexistence between the two *Daphnia* species present in the experiment. Under low light (good food quality), *Daphnia magna* was out-competed by *Daphnia pulex* but, under high light, *D. magna* maintained substantial co-dominance. Demographic data provided direct evidence of facilitation (data not shown): under low light, individual female fecundity showed normal negative density dependence (high population density was associated with low fecundity) while, under high light, female fecundity showed *inverse* density dependence, in which individual reproductive output was *positively* correlated with abundance. Given the promising nature of LKE₂ in accounting for these outcomes, more efforts are needed to develop multi-species food web models under stoichiometric constraints. In the following section we outline two other areas that would benefit

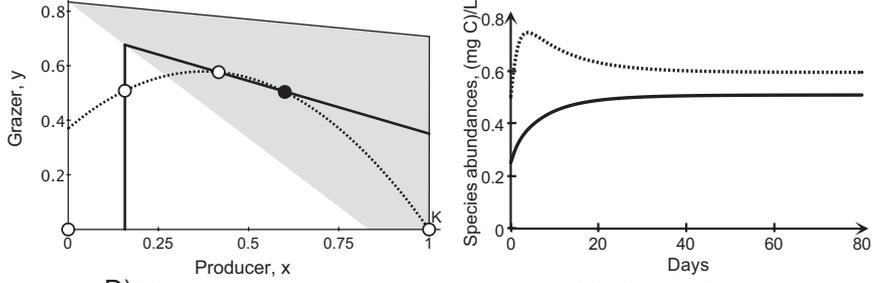
A) Low carrying capacity or light, $K=0.25$ mgC/L. High food quality



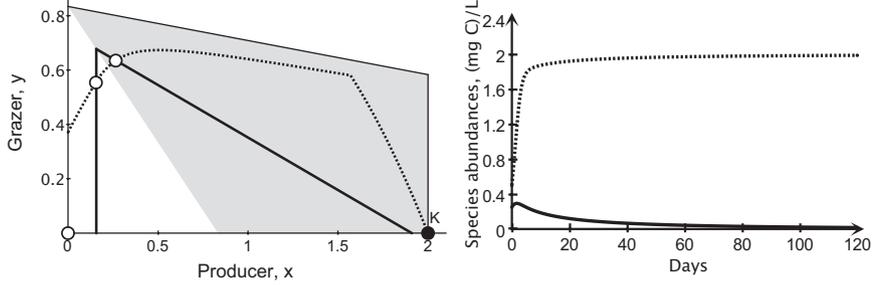
B) Medium carrying capacity or light, $K=0.75$ mgC/L. High food quality



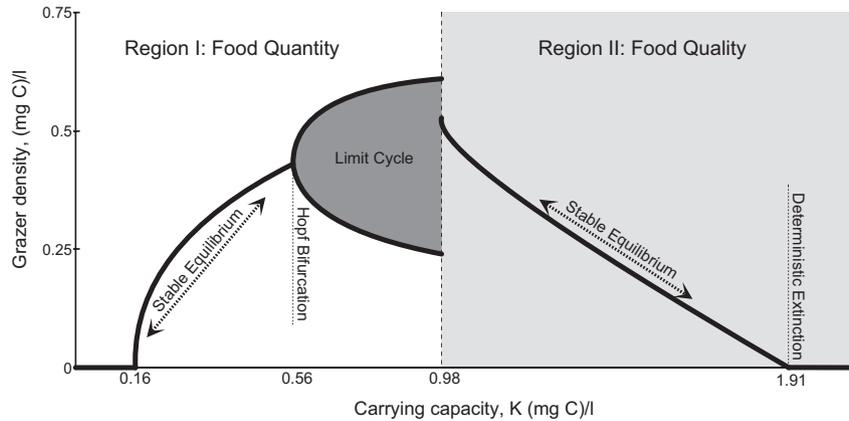
C) High carrying capacity or light, $K=1.0$ mgC/L. Low food quality



D) Very high carrying capacity or light, $K=2.0$ mgC/L. Very low food quality



E) Bifurcation diagram of the grazer's dynamics plotted against K



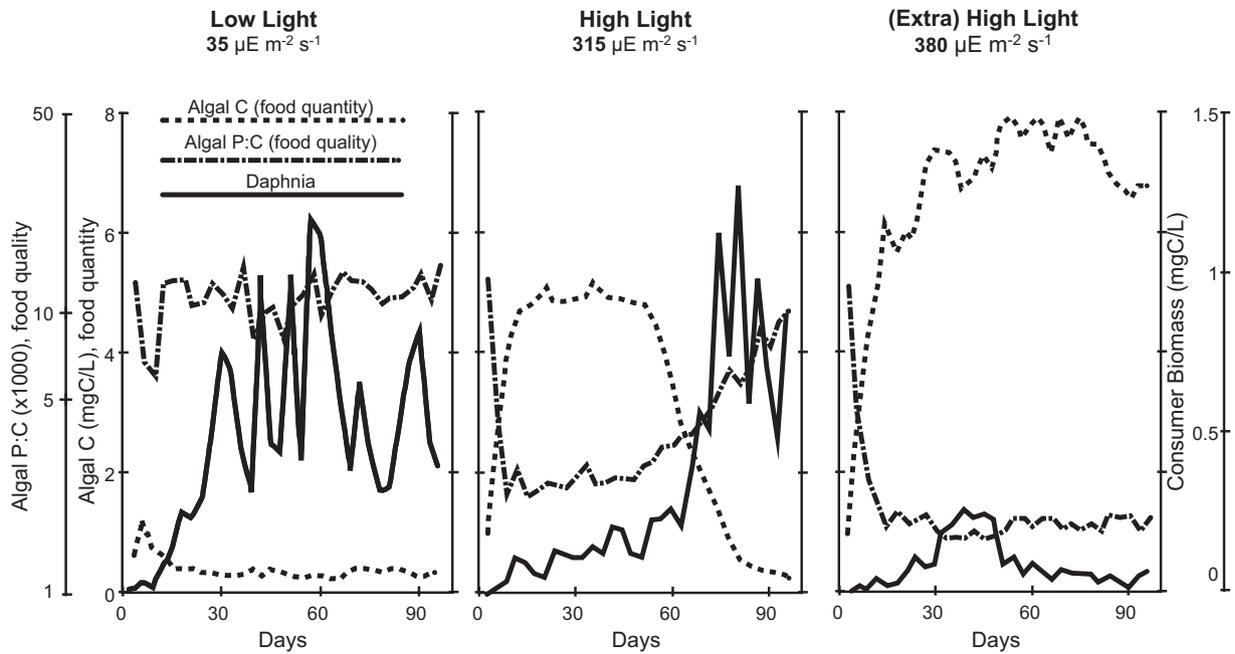


Fig. 2. Dynamics of an artificial ecosystem experiment testing the effects of light intensity on algae/*Daphnia* dynamics (Urabe et al., 2002a). As predicted by LKE, increasing light intensity leads to decreased food quality, impaired zooplankton production, and (at the highest light intensity), grazer extinction.

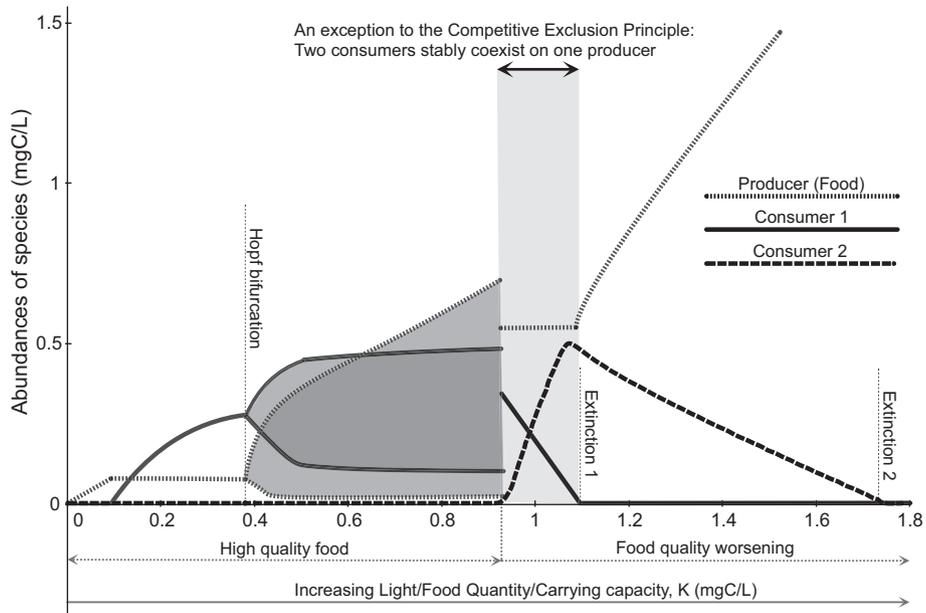


Fig. 3. Bifurcation diagram (based on K , ~light intensity) for LKE_2 . At low values of K , only the producer is in the system. As K increases, sufficient production is able to support Consumer 1 in the system. As K increases further, the producer and consumer 1 enter stable limit cycles, as in the original LKE model. However, with further increases in K , consumer 2 is able to enter the system and, across the range of K values indicated, stably coexists with consumer 1. At higher values of K , consumer 1 is eliminated (its parameter settings give it a higher P requirement) and, at the highest values of K , complete consumer extinction is predicted (as in the original LKE). Based on Loladze et al. (2004).

Fig. 1. An exemplary set of nullclines from the Loladze, Kuang, and Elser (LKE) model (Loladze et al., 2000) as light intensity (K) is increased. Stoichiometric constraints limit dynamics to a trapezoid-shaped area, where a line divides the phase plane into two regions: the white-shaded region where (as in LVE) food quantity limits grazer growth and the gray-shaded region where food quality, i.e. producer P content, is poor. Competition for limiting P between grazer and producer alters the nature of their interactions from (+, -) in the C-limited region to (-, -) in the P-limited region, bending the grazer nullcline down. The shape of the grazer nullcline creates the possibility for multiple positive steady states, as shown. (A) At low light, there is a locally stable equilibrium equivalent to the Rosenzweig–McArthur version of LVE. (B) As light intensity increases, a stable limit cycle appears. (C) With further increase in K , the system is stabilized around an attractor in which the consumer is P-limited. (D) At the highest light intensity, the formerly neutrally stable intersection of the producer nullcline with the X-axis is stabilized. This locally stable attractor implies deterministic extinction of the consumer. (E) Bifurcation diagram summarizing the consequences of changes in K for the dynamic system. From Loladze et al. (2000).

from attention from modelers and theoreticians as well as from more contributions from empirical scientists in contributing necessary data for parameterization and testing.

4. Two new frontiers for stoichiometric food web modeling

There are many arenas where new modeling and theoretical investigations are needed to examine the consequences of stoichiometric mechanisms for predicted dynamics. Here we highlight two, one that would move beyond one simplification of existing frameworks like LKE and one that might use LKE frameworks to address newly discovered aspects of stoichiometric food quality on consumers.

4.1. Dietary mixing

While capturing an increased degree of realism by tracking more than one important currency, existing stoichiometric models such as LKE currently depict the primary producer (prey) as a single biomass pool that can vary in its abundance and its C:nutrient ratio but in which all biomass has uniform quality. This increases model tractability. However, because we do not know the degree to which consumer growth is sensitive to the packaging of potentially limiting nutrient among high C:nutrient prey items and low C:nutrient prey items nor do we fully understand how consumers respond behaviorally to nutritionally divergent food, we do not know how much realism these models have sacrificed by treating the prey as a single entity. Indeed, it is hard to evaluate this issue at present because, to date, most laboratory studies investigating stoichiometric effects have used unialgal chemostat cultures raised under different conditions of nutrient limitation so that algal biomass in different treatments contrasts in C:nutrient ratio but all cells in the population are chemically uniform (but see Sterner and Schwalbach, 2001; Hood and Sterner, 2010). Field studies, extrapolating from this laboratory work, have compared the C:nutrient ratios of suspended seston in lakes to elemental ratios deemed unsuitable in these unialgal studies (e.g. Elser and Hassett, 1994). However, lake and ocean seston is composed of a wide array of particles, including many different taxa and a variety of particle sizes. This results in a food base for *Daphnia* and other consumers that likely includes a mixture of particles, some of which have low C:nutrient ratios (e.g. bacterial cells) while some have high C:nutrient ratios (large nutrient-limited algae, detritus). The situation is similar in terrestrial ecosystems where there is considerable inter-specific variation in plant elemental composition (Elser et al., 2010) as well as variation within species among, for example, different parts of the plant (Kerkhoff et al., 2006). This produces interesting theoretical questions about behavioral responses related to classic work on optimal foraging (Charnov, 1976) and, more recently, to important advances in understanding and modeling of quality-dependent foraging decisions via nutritional geometry (Raubenheimer and Simpson, 1993; Simpson et al., 2004). New stoichiometric food web models are needed that capture these important aspects and determine their significance for theoretical outcomes; Vasseur and Fox (Vasseur, 2011) provide a step in this direction. Furthermore, more laboratory work is needed to evaluate whether or not the packaging of nutrient elements among different prey items has physiological impacts on the consumer, beyond its impact on foraging decisions.

4.2. The “stoichiometric knife edge”

The LKE model, and indeed all stoichiometrically explicit models to date, have considered the effects of “stoichiometric imbalance” (e.g. differences in the elemental composition between food and consumer) entirely on the basis of “not enough nutrients” (e.g.

P:C ratio of the food is lower than that in the consumer). This is natural, as nearly the entire empirical literature in ecological stoichiometry has also emphasized the effects of nutrient deficiency. However, recent empirical results strongly indicate that there are important consequences of consuming nutrient-rich food. Plath and Boersma (2001) raised *Daphnia magna* on algae with C:P ratios ranging from ~650 (low P) to ~30 (high P) and discovered, to their surprise, that animal growth rate was maximal at C:P ~180 and declined strongly for the most P-rich food. Investigating the mechanism for this response, they observed that the animals' feeding rates declined with increasing food P content. This led them to propose that *Daphnia* may be following a simple decision rule such as “eat until you get enough P, then stop.” In studies of a grazing snail feeding on P-limited stromatolite mats in México, Elser et al. (2005, 2006) also observed maximal growth and survivorship rates for snails feeding on mats with intermediate C:P ratios, leading them to propose a concept of a “stoichiometric knife edge.” Boersma and Elser (2006) drew these observations together with several other examples collected in the literature (including data for insects and fish) to argue that there are significant metabolic costs to maintaining stoichiometric homeostasis on P-rich diets and this may be a neglected mechanism operating in food webs. Similar reasoning should also apply to other nutrients beyond P. Indeed, this possibility is implicit in nutritional geometry (*sensu* Simpson and Raubenheimer (1993) and data are emerging that indicate that, contrary to widely accepted paradigms in plant–herbivore literature (e.g. White, 1993), increased plant nitrogen content is not necessarily a “good thing” and some herbivores are favored by suitably low plant nitrogen content, including economically important taxa such as locusts and grasshoppers (Joern and Behmer, 1997, 1998; Cease et al., 2012).

The emerging insight that high prey nutrient content can be detrimental to predators has not yet been introduced into models of predator–prey interactions. While this modification to LKE is not likely to have as substantial an impact on its predicted dynamics as the original addition of stoichiometric realism had for the LVE, the effects might be important and surprising. For example, poor quality of nutrient-rich prey might make nutrient-rich conditions uninhabitable, at least initially, for an herbivore if the primary producer prey sequester excess nutrient in their biomass. This might lead to interesting transient dynamics, as the herbivore may be unable to proliferate until the primary producers have grown sufficiently to dilute their internal nutrient stores to levels better tolerated by the herbivore. To our knowledge, these possibilities have not yet been examined in any model.

It will also be important in these new models to evaluate if the specific mechanism behind the “too much nutrient” effect matters for model outcomes. For example, is the effect behaviorally based (e.g. Plath and Boersma's decision rule discussed above) or is the negative effect of P a direct toxicity impinging on mortality? Or, does it reflect increased energetic costs of processing and excreting excess nutrient? Which of these mechanisms is operating will affect how the effect is modeled.

One modeling strategy to capture the Plath/Boersma decision rule is to introduce a fourth assumption:

A4. At most h units of P is ingested by each unit of grazer's biomass per unit time.

This assumption leads to a new expression for the grazer ingestion rate. The grazers ingest P at rate $f(x)Q$ but if $f(x)Q > h$, the P ingestion rate is capped at h .

$$u(x, y) = \begin{cases} f(x), & f(x)Q \leq h \\ \frac{h}{Q}, & f(x)Q > h \end{cases} = \left\{ f(x), \frac{h}{Q} \right\}$$

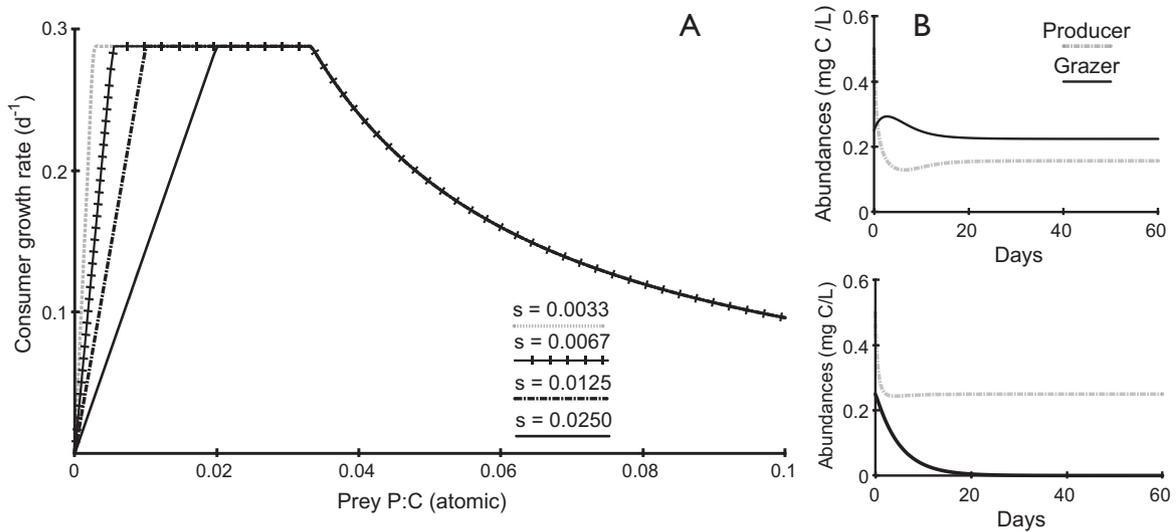


Fig. 4. Introduction of a “knife-edge” into a stoichiometric predator–prey model. (A) Predicted dependence of grazer growth rate on producer P content from the modified LKE model (see Section 4.2 for full explanation) for different values of consumer P:C ratio (*s*) Note that grazer growth rate is low both when food P content is low (e.g. producer P:C ratio is low), reflecting a dietary P limitation *and* when food P content is high (e.g. producer P:C ratio is high), reflecting a decision rule suggested by Plath and Boersma (2001) in which the grazer feeds to some maximum P intake rate but in doing so fails to meet its C requirements when food P:C ratio is very low. (B) Dynamics of the modified LKE model for high values of nutrient availability (high P) showing consumer extinction (bottom panel); the original LKE model has stable persistence of the consumer for this parameter combination (top panel). Note predicted extinction of the consumer in the modified LKE model under high nutrient availability.

The grazer’s production efficiency is also modified in the following way. Let *Q* be the P:C ratio of the producer and *s* the P:C ratio of the grazer. Similar to the LKE model, grazer growth rate may be limited by the available P; alternatively, if P is in excess, the growth rate may be limited by the amount of available C. *Q* is actually the P:C ratio of the producer before ingestion. A portion of this ingested C is required for metabolic costs such as respiration. *e* is the maximal conversion efficiency in terms of carbon so that *Q/e* is the P:C ratio of the post-ingested producer representing the amount of P and C available for growth. When *Q/e* ≤ *s*, there is not excess P and the grazer’s growth rate is determined by the P content of the producer. The grazer ingests *u(x,y)Q* units of P, and the grazer’s growth rate, *g(x,y)*, satisfies *g(x,y) = u(x,y)Q/s*. On the other hand, when *Q/e* > *s*, there is excess P. In this situation, the grazer’s growth is no longer limited by P but instead by the amount of available C. The grazer ingests *u(x,y)* units of C and *u(x,y)e* units of P are available for growth. The growth rate then satisfies *g(x,y) = u(x,y)e*. Overall, the growth expression is:

$$g(x, y) = \begin{cases} \frac{Q}{s} u(x, y), & \frac{Q}{e} \leq s \\ eu(x, y), & \frac{Q}{e} > s \end{cases} = \min \left\{ e, \frac{Q}{s} \right\} u(x, y)$$

Together, these expressions predict a hump-shaped growth rate response to food P:C ratio; examples of these for different values of *s* (consumer P:C ratio) are shown in Fig. 4. The overall result is the following modified version of LKE:

$$x' = bx \left(1 - \frac{x}{\min \{K, ((P - sy)/q)\}} \right) - \min \left\{ f(x), \frac{h}{Q} \right\} y$$

$$y' = \min \left\{ e, \frac{Q}{s} \right\} \min \left\{ f(x), \frac{h}{Q} \right\} y - dy$$

Analysis of LKE-type models with the stoichiometric knife edge are currently in progress. Some exemplary dynamics are shown in Fig. 4B. In general, the dynamics are similar to those for the original LKE model for most parameter domains except, as would be expected, for high values of overall nutrient availability (high value

of P), when extinction of the consumer is a notable outcome not present in the original LKE model (Fig. 4B bottom vs. top).

The preceding material explores one way of modeling the possibility that the inhibitory effect of high food nutrient content is imposed by a mechanism involving behavioral decision rules. Alternatively, the negative effect of high P:C ratio could come from an energy cost of P disposal that can be introduced via the respiration term in which eventually the respiration rate approaches the rate of C ingestion and assimilation. A direct toxicity (“poisoning”) due to excess nutrient might be captured by making the constant consumer mortality term, *d*, dependent on food P content. Models that encompass these hypothesized mechanisms are needed to establish the extent to which different mechanisms might alter predicted outcomes that follow from the “stoichiometric knife edge”.

5. Conclusions and prospects

The Lotka–Volterra equations have a rightful place of honor in the history of ecological modeling. The approach of ecological stoichiometry (Sterner and Elser, 2002), as well as conceptually similar frameworks such as nutritional geometry (Simpson and Raubenheimer, 1993) and dynamic energy budgets (Kooijman, 2005), move beyond this core and allow key aspects of functioning ecosystems, such as the dynamic nature of nutrient-dependent food quality and feedbacks via nutrient recycling, to be captured in ways that are absent from the LVE despite Lotka’s deep awareness of the elemental nature of life and the key role of biogeochemical cycles in sustaining life. Furthermore, understanding of the biochemical and genetic bases of some of the key underlying drivers of organismal stoichiometric variation may help in advancing new generations of ecological models that encompass rapid evolutionary dynamics (Hairston et al., 2005; Schoener, 2011; Matthews et al., 2011) and that capitalize on emerging insights from metagenomics and functional genomics (Jeyasingh and Weider, 2007). Furthermore, as human activities globally alter the biogeochemical cycles of key elements of life – C, N, and P – understanding how such changes can impact food webs gains a particular relevance. We believe that re-loading LVE

with stoichiometric realities provides a fruitful and quantitatively feasible framework to improve our understanding in this area. It is easy to imagine that Lotka would have enjoyed these current endeavors and, to recognize his contributions in taking these first steps forward, we close with another quote from *Elements of Physical Biology*:

“... all honor to the minds that discerned through the mists of dawn the bold features of the landscape to be revealed in the sunlight of later day.”

References

- Ågren, G.I., 2004. The C:N:P stoichiometry of autotrophs – theory and observations. *Ecology Letters* 7, 185–191.
- Andersen, T., 1997. *Pelagic Nutrient Cycles: Herbivores as Sources and Sinks*. Springer-Verlag, Berlin/Heidelberg/New York, 190 pp.
- Andersen, T., Elser, J.J., Hessen, D.O., 2004. Stoichiometry and population dynamics. *Ecology Letters* 7, 884–900.
- Ballantyne, F., Menge, D.N.L., Ostling, A., Hosseini, P., 2008. Nutrient recycling affects autotroph and ecosystem stoichiometry. *American Naturalist* 171, 511–523.
- Boersma, M., Elser, J.J., 2006. Too much of a good thing: on balanced diets and maximal growth. *Ecology* 87, 1325–1330.
- Cease, A.J., Elser, J.J., Ford, C.F., Hao, S., Kang, L., Harrison, J.F., 2012. Livestock overgrazing promotes locust outbreaks by lowering plant nitrogen content. *Science* 335, 467–469.
- Charnov, E.L., 1976. Optimal foraging, marginal value theorem. *Theoretical Population Biology* 9, 129–136.
- Diehl, S., 2003. The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. *Ecology* 84, 2557–2567.
- Diehl, S., 2007. Paradoxes of enrichment: Effects of increased light versus nutrient supply on pelagic producer–grazer systems. *American Naturalist* 169, E173–E191.
- Diehl, S., Berger, S., Wöhrl, R., 2005. Flexible nutrient stoichiometry mediates environmental influences on phytoplankton and its resources. *Ecology* 86, 2931–2945.
- Droop, M.R., 1983. 25 years of algal growth kinetics: a personal view. *Botanica Marina* 26, 99–112.
- Elser, J.J., 2006. Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. *The American Naturalist* 168, S25–S35.
- Elser, J.J., Dobberfuhl, D., MacKay, N.A., Schampel, J.H., 1996. Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. *BioScience* 46, 674–684.
- Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., Watts, T., Hobbie, S., Fagan, W., Schade, J., Hood, J., Sterner, R.W., 2003. Growth rate – stoichiometry couplings in diverse biota. *Ecology Letters* 6, 936–943.
- Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H., Sterner, R.W., 2000a. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408, 578–580.
- Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Enquist, B.J., 2010. Biological stoichiometry of plant production: metabolism, scaling, and ecosystem response to global change. *New Phytologist* 186, 593–608.
- Elser, J.J., Hamilton, A.L., 2007. Stoichiometry and the new biology: the future is now. *PLoS Biology* 5, e181, doi:10.1371/journal.pbio.0050181.
- Elser, J.J., Hassett, R.P., 1994. A stoichiometric analysis of the zooplankton–phytoplankton interaction in marine and freshwater ecosystems. *Nature* 370, 211–213.
- Elser, J.J., Schampel, J.H., Kyle, M., Watts, J., Carson, E.W., Dowling, T.A., Tang, C., Roopnarine, P.D., 2005. Response of grazing snails to phosphorus enrichment of modern stromatolitic microbial communities. *Freshwater Biology* 50, 1826–1835.
- Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M., Weider, L.J., 2000b. Biological stoichiometry from genes to ecosystems. *Ecology Letters* 3, 540–550.
- Elser, J.J., Urabe, J., 1999. The stoichiometry of consumer-driven nutrient cycling: theory, observations, and consequences. *Ecology* 80, 735–751.
- Elser, J.J., Watts, J., Schampel, J.H., Farmer, J.D., 2006. Early food webs on a trophic knife-edge? Experimental data from a modern microbialite-based ecosystem. *Ecology Letters* 9, 295–303.
- Falkowski, P., Scholes, R.J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Hogberg, P., Linder, S., Mackenzie, F.T., Moore, B., Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V., Steffen, W., 2000. The global carbon cycle: a test of our knowledge of Earth as a system. *Science* 290, 291–296.
- Gause, G.F., 1934. *The Struggle for Existence*. Hafner, New York.
- Gorokhova, E., Dowling, T.A., Weider, L.J., Crease, T., Elser, J.J., 2002. Functional and ecological significance of rDNA IGS variation in a clonal organism under divergent selection for production rate. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269, 2373–2379.
- Grover, J., 2003. The impact of variable stoichiometry on predator–prey interactions: a multinutrient approach. *American Naturalist* 162, 29–43.
- Grover, J.P., 1997. *Resource Competition*. Chapman & Hall, London, 342 p.
- Grover, J.P., 2000. Resource competition and community structure in aquatic microorganisms: experimental studies of algae and bacteria along a gradient of organic carbon to inorganic phosphorus supply. *Journal of Plankton Research* 22, 1591–1610.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., Fox, J.A., 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* 8, 1114–1127.
- Hall, S.R., 2004. Stoichiometrically-explicit competition between grazers: species replacement, coexistence, and priority effects along resource supply gradients. *American Naturalist* 164, 157–172.
- Hall, S.R., Leibold, M.A., Lytle, D.A., Smith, V.H., 2007. Grazers, producer stoichiometry, and the light: nutrient hypothesis revisited. *Ecology* 88, 1142–1152.
- Hessen, D.O., Faerovig, P.J., Andersen, T., 2002. Light, nutrients, and P:C ratios in algae: Grazer performance related to food quality and quantity. *Ecology* 83, 1886–1898.
- Hood, J.M., Sterner, R.W., 2010. Diet mixing: Do animals integrate growth or resources across temporal heterogeneity? *The American Naturalist* 176, 651–663.
- Interlandi, S.J., Kilham, S.S., 2001. Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology* 82, 1270–1282.
- Jeyasingh, P.D., Weider, L.J., 2007. Fundamental links between genes and elements: evolutionary relevance of ecological stoichiometry. *Molecular Ecology* 16, 4649–4661.
- Joern, A., Behmer, S.T., 1997. Importance of dietary nitrogen and carbohydrates to survival, growth, and reproduction in adults of the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia* 112, 201–208.
- Joern, A., Behmer, S.T., 1998. Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. *Ecological Entomology* 23, 174–184.
- Kerkhoff, A.J., Fagan, W.F., Elser, J.J., Enquist, B.J., 2006. Phylogenetic and functional variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist* 168, E103–E122.
- Kilham, S.S., 1986. Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 351–360.
- Kooijman, S.A.L.M., 2005. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Cambridge, UK.
- Kuang, Y., Huisman, J., Elser, J.J., 2004. Stoichiometric plant–herbivore models and their interpretation. *Math. Biosci. Engin.* 1, 215–222.
- Loladze, I., Elser, J.J., 2011. The origins of the Redfield nitrogen-to-phosphorus ratio are in a homeostatic protein-to-RNA ratio. *Ecology Letters* 14, 244–250.
- Loladze, I., Kuang, Y., Elser, J.J., 2000. Stoichiometry in producer–grazer systems: linking energy flow with element cycling. *Bulletin of Mathematical Biology* 62, 1137–1162.
- Loladze, I., Kuang, Y., Elser, J.J., Fagan, W.F., 2004. Competition and stoichiometry: coexistence of two predators on one prey. *Journal of Theoretical Biology* 65, 1–15.
- Lotka, A.J., 1910. Contribution to the theory of periodic reactions. *Journal of Physical Chemistry* 14, 271–274.
- Lotka, A.J., 1925. *Elements of Physical Biology*. Williams and Wilkins, Baltimore.
- Main, T., Dobberfuhl, D.R., Elser, J.J., 1997. N:P stoichiometry and ontogeny in crustacean zooplankton: a test of the growth rate hypothesis. *Limnology and Oceanography* 42, 1474–1478.
- Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., Sullam, K.E., Bird, K.C., Thomas, M.K., Hanley, T.C., Turner, C.B., 2011. Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters* 14, 690–701.
- Mulder, K., Bowden, W.B., 2007. Organismal stoichiometry and the adaptive advantage of variable nutrient use and production efficiency in *Daphnia*. *Ecological Modelling* 202, 427–440.
- Muller, E.B., Nisbet, R.M., Kooijman, S., Elser, J.J., McCauley, E., 2001. Stoichiometric food quality and herbivore dynamics. *Ecology Letters* 4, 519–529.
- Niklas, K.J., Owens, T., Reich, P.B., Cobb, E.D., 2005. Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecology Letters* 8, 636–642.
- Nisbet, R.M., McCauley, E., Deroos, A.M., Murdoch, W.W., Gurney, W.S.C., 1991. Population dynamics and element recycling in an aquatic plant herbivore system. *Theoretical Population Biology* 40, 125–147.
- Plath, K., Boersma, M., 2001. Mineral limitation of zooplankton: stoichiometric constraints and optimal foraging. *Ecology* 82, 1260–1269.
- Raubenheimer, D., Simpson, S.J., 1993. The geometry of compensatory feeding in the locust. *Animal Behaviour* 45, 953–964.
- Reich, P.B., Oleksyn, J., Wright, I.J., Niklas, K.J., Hedin, L., Elser, J.J., 2010. Evidence of a general 2/3-power leaf nitrogen to phosphorus scaling among major plant groups and biomes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 277, 877–883.
- Rosenzweig, M.L., MacArthur, R.H., 1963. Graphical representation and stability conditions of predator–prey interactions. *American Naturalist* 97, 209.
- Schoener, T.W., 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331, 426–429.
- Simpson, S.J., Raubenheimer, D., 1993. A multilevel analysis of feeding behavior – the geometry of nutritional decisions. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 342, 381–402.
- Simpson, S.J., Sibly, R.M., Lee, K.P., Behmer, S.T., Raubenheimer, D., 2004. Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* 68, 1299–1311.

- Smith, V.H., 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221, 669–671.
- Smith, V.H., 1992. Effects of nitrogen:phosphorus supply ratios on nitrogen fixation in agricultural and pastoral ecosystems. *Biogeochemistry* 18, 19–35.
- Smith, V.H., Bierman, V.J., Jones, B.L., Havens, K.E., 1995. Historical trends in the Lake Okeechobee ecosystem IV. Nitrogen:phosphorus ratios, cyanobacterial dominance, and nitrogen fixation potential. *Archiv fur Hydrobiologie Suppl.* 107, 71–88.
- Sterner, R.W., 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. *American Naturalist* 136, 209–229.
- Sterner, R.W., Clasen, J., Lampert, W., Weisse, T., 1998. Carbon:phosphorus stoichiometry and food chain production. *Ecology Letters* 1, 146–150.
- Sterner, R.W., Elser, J.J., 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Sterner, R.W., Hessen, D.O., 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics* 25, 1–29.
- Sterner, R.W., Schulz, K.L., 1998. Zooplankton nutrition: recent progress and a reality check. *Aquatic Ecology* 32, 261–279.
- Sterner, R.W., Schwalbach, M., 2001. Diel integration of food quality by *Daphnia*: luxury consumption by a freshwater planktonic herbivore. *Limnology and Oceanography* 46, 410–416.
- Stiefs, D., van Voorn, G.A.K., Kooi, B.W., Feudel, U., Gross, T., 2010. Food quality in producer-grazer models: a generalized analysis. *American Naturalist*, 176367–176380.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, New Jersey.
- Urabe, J., Elser, J.J., Kyle, M., Sekino, T., Kawabata, Z., 2002a. Herbivorous animals can mitigate unfavorable ratios of energy and material supplies by enhancing nutrient recycling. *Ecology Letters* 5, 177–185.
- Urabe, J., Kyle, M., Makino, W., Yoshida, T., Andersen, T., Elser, J.J., 2002b. Reduced light increases herbivore production due to stoichiometric effects of light:nutrient balance. *Ecology* 83, 619–627.
- Urabe, J., Sterner, R.W., 1996a. Regulation of herbivore growth by balance of light and nutrients. *Proceedings of the National Academy of Sciences of the United States of America* 93, 8465–8469.
- Urabe, J., Sterner, R.W., 1996b. Regulation of herbivore growth by the balance of light and nutrients. *Proceedings of the National Academy of Sciences of the United States of America* 93, 8465–8469.
- Vasseur, D.A., Fox, J.W., 2011. Character convergence under competition for nutritionally-essential resources: adaptive dynamics models. *American Naturalist* 178, 501–514.
- Vrede, T., Persson, J., Aronsen, G., 2002. The influence of food quality (P:C ratio) on RNA:DNA ratio and somatic growth rate of *Daphnia*. *Limnology and Oceanography* 47, 487–494.
- Wang, H., Dunning, K., Elser, J.J., Kuang, Y., 2008. *Daphnia* species invasion, competitive exclusion, and chaotic coexistence. *Discrete and Continuous Dynamical Systems, Series B* 12, 481–493.
- Wangersky, P.J., 1978. Lotka–Volterra population models. *Annual Review of Ecology and Systematics* 9, 189–218.
- White, T.C.R., 1993. *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer-Verlag, New York.