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STOICHIOMETRY, ECOLOGICAL

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Ecological stoichiometry is the study of the balance of energy and multiple chemical resources (elements) in ecological interactions. Recall that stoichiometry is a fundamental principle of chemistry dealing with the application of the laws of definite proportions and of the conservation of mass and energy in chemical reactions. Since all organisms are composed of multiple chemical elements such as carbon, nitrogen, and phosphorus brought together in nonarbitrary proportions, the same principles can be brought to bear in the study of fundamental aspects of ecology, including the role of nutrient limitations on growth and trophic interactions, as well as the cycling of chemical elements in ecosystems.

THE CONCEPT

Ecological stoichiometry considers how the balance of energy and elements at various scales affect and are affected by organisms and their interactions in ecosystems. Stoichiometric thinking has a long history in ecology, with fundamental early work contributed by Justus von Leibig (1803–1873), Alfred Lotka (1880–1949), and Alfred Redfield (1890–1983). Most work in ecological stoichiometry focuses on the interface between a consumer and its food resources. For herbivores consuming plants and algae, this interface is often characterized by dramatic differences in the elemental composition (stoichiometric imbalance) of each participant. Ecological stoichiometry primarily asks the following questions: (1) What causes these elemental imbalances in ecological communities? (2)

How does consumer physiology and life history respond to them? And (3) What are their consequences for ecological processes in ecosystems?

Elemental imbalances are defined by a mismatch between the elemental demands of a consumer and those provided by its resources. For example, carbon-to-phosphorus (C:P) ratios in the suspended organic matter in lakes (i.e., algae, bacteria, and detritus) can vary between 75 and 1,500, whereas C:P ratios of *Daphnia*, a crustacean zooplankter, remain nearly constant at 80:1. This excess of carbon can impose a direct element limitation (in this case by P) on the consumer, as it is unable to consume, extract, and retain enough of the limiting element to achieve maximal growth and reproduction.

A key concept in ecological stoichiometry is stoichiometric homeostasis, the degree to which organisms maintain a constant chemical composition in the face of variations in their environment, particularly in the chemical composition and availability of their food. As in the general biological notion of homeostasis (e.g., for body temperature in homeotherms), elemental homeostasis involves processes of regulation of elemental assimilation and retention that keep elemental composition within some biologically ordered range. Photoautotrophic organisms, such as vascular plants and especially algae, can exhibit a very wide range of physiological plasticity in elemental composition and thus are said to have relatively weak stoichiometric homeostasis. In contrast, other organisms—multicellular animals, for example—have a nearly strict homeostasis and thus can be thought of as having distinct chemical composition.

STOICHIOMETRY OF CONSUMER-DRIVEN NUTRIENT RECYCLING

The ecological interactions between grazers and their food producer encompass a rich set of dynamic relations poorly described by the classic gain/loss view of predators and prey. Herbivores from diverse habitats are known to affect their plant prey in complex ways. Reasons for these more complex dynamics include compensatory growth and nutrient recycling. For example, zooplankton grazers influence the chemical environment experienced by phytoplankton by way of rapid, coupled cycling of nutrients among phytoplankton, zooplankton, and the dissolved pools of these nutrients.

While energy flow and element cycling are two fundamental and unifying principles in ecosystem theory, many population models ignore the implications of element cycling and constraints on population growth. Such models implicitly assume chemical homogeneity of all

trophic levels by concentrating on a single constituent, generally an equivalent of energy or carbon. However, recent modeling efforts consistently show that depicting organisms as built of more than one thing (for example, C and an important nutrient, such as P or N) in stoichiometrically explicit models results in qualitatively different predictions about the resulting dynamics. Because elements are conserved, principles of mass conservation can be conveniently invoked to develop mathematical formulations of the dynamics of nutrient recycling. Indeed, aided by this law of mass conservation, Sterner in 1990 derived a simplistic but elegant mathematical formula describing the grazer recycled nutrient (grazer waste) as a simple function of the nutrient quality in the algal pool (food) in the case when grazers strictly maintain their nutrient ratio.

The following example provides a slightly simpler derivation of Sterner's nutrient recycling formula. Let P_N and P_P be the phytoplankton nitrogen (N) and phosphorus (P) pools, respectively, a_N and a_P be the grazers' accumulation efficiencies of N and P, respectively, Z_N and Z_P be the zooplankton N and P pools, respectively, R_{2N} and R_{2P} be the recycling rate of N and P to the dissolved pool feeding the phytoplankton, respectively, and g be the grazing rate. Moreover, let $b (=Z_N/Z_P)$ be the N:P ratio in the zooplankton pool, $s (=R_{2N}/R_{2P})$ be the N:P ratio in the waste recycled to the dissolved pool feeding the phytoplankton, and $f (=P_N/P_P)$ be the ratio of N to P in zooplankton food. It is easy to see that $R_{2N} = g P_N(1 - a_N)$ and $R_{2P} = g P_P(1 - a_P)$. Therefore,

$$s = R_{2N}/R_{2P} = f(1 - a_N)/(1 - a_P). \quad (1)$$

The assumption of grazers maintaining their tissue N:P ratio at a constant value is equivalent to saying that $b = Z_N/Z_P = a_N P_N/a_P P_P$, which implies $b = f a_N/a_P$.

Let L be the maximum possible accumulation efficiency of either N or P (the symbol L is used in honor of Justus Liebig). For both nutrients, the same maximum is used for convenience. When $f > b$, substitute L for a_P and replace a_N by bL/f in Eq. 1 to obtain

$$s = f(1 - bL/f)/(1 - L), \quad (2)$$

which is linear with respect to f . When $f < b$, substitute L for a_N and replace a_P by Lfb in Eq. 1 to obtain

$$s = f(1 - L)/(1 - Lfb), \quad (3)$$

which is nonlinear with respect to f . While greatly simplified, the model just described provides a formal means to

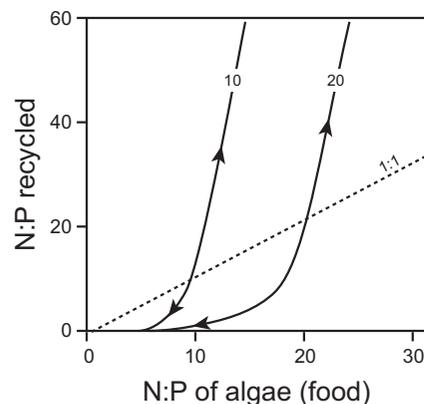


FIGURE 1 The effect of food N:P and consumer N:P on the N:P ratio of consumer-driven nutrient recycling according to Sterner's 1990 model. The predicted N:P ratio of two consumers are shown, assuming a maximum assimilation efficiency of limiting element of 0.90. The figure shows predicted recycling by a consumer such as *Daphnia* (N:P ~ 10), and the other illustrates predicted recycling by a copepod-like consumer (N:P ~ 20). Note that for a given food N:P ratio, the two consumers are predicted to recycle at potentially very different N:P ratios.

characterize the phenomenon of differential nutrient recycling by consumers, a process that can alter ecosystem-level nutrient availability and shift the nutrient regime experienced by the consumer's prey (e.g., algae). These effects have been well documented in various laboratory and field studies. Figure 1 shows the predicted recycling by a consumer such as *Daphnia* (N:P ~ 10) and the predicted recycling by a copepod-like consumer (N:P ~ 20) as predicted by the Sterner model (Eq. 2 and 3). Note that for a given food N:P ratio, the two consumers are predicted to recycle at potentially very different N:P ratios.

STOICHIOMETRY OF FOOD QUALITY AND POPULATION DYNAMICS

Early pioneering work by Andersen introduced stoichiometric principles to population dynamic models, beginning with an explicit assumption that both producer and grazer are composed of two essential elements: carbon and phosphorus. More recently, using stoichiometric principles, Loladze, Kuang, and Elser (2000) constructed a two-dimensional Lotka–Volterra model that incorporates chemical heterogeneity of the first two trophic levels of a food chain. In contrast to nonstoichiometric versions of Lotka–Volterra, the analysis shows that indirect competition between two populations for phosphorus can temporarily shift predator–prey interactions from a conventional gain/loss (+/–) interaction to loss/loss (–/–) relation. This leads to complex dynamics with multiple positive equilibria, where bistability and deterministic

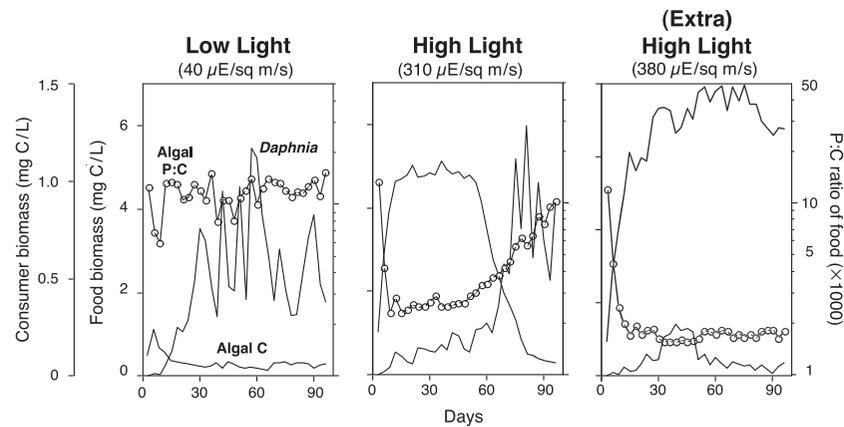


FIGURE 2 The stoichiometric effects of both light and nutrients on the dynamics of herbivorous zooplankter *Daphnia* and its algal prey *Scenedesmus* (modified from Urabe et al., 2002).

extinction of the grazer are possible. Stoichiometric constraints also naturally confine the predator–prey system dynamics to a naturally bounded region. Qualitative analysis reveals that Rosenzweig’s paradox of enrichment holds only in situations where the grazer is energy limited; a new phenomenon—the paradox of energy enrichment—may arise in the situations where the grazer is nutrient limited. The paradox of energy enrichment refers to the phenomenon in which intense energy (light) enrichment substantially elevates producer density but, despite such an abundant food supply, the grazer decreases its growth rate and drives itself to deterministic extinction. This surprising model prediction is confirmed by laboratory experimentation (see Fig. 2).

Specifically, the model of Loladze et al. selects phosphorus as the limiting nutrient and makes the following principal assumptions:

- (A1) The system has a closed phosphorus cycle containing a mass P of phosphorus.
- (A2) The producer’s P:C ratio varies but never falls below a fixed minimum, q ; the consumer maintains a constant P:C ratio, s .
- (A3) All phosphorus in the system is divided into two pools: phosphorus in the consumer and phosphorus 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, resource 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

eats food of optimal quality (i.e., that matches its own stoichiometric composition): if producer P:C is lower than that of the consumer (measured by $(P - sy)/x$ is less than s), then the transfer efficiency is reduced (by A3)) to $e[(P - sy)/xs]$. In both cases, transfer efficiency equals $e \min(1, (P - sy)/xs)$. One obtains the following model by incorporating such stoichiometrically constrained carrying capacities and transfer efficiencies into the Rosenzweig–McArthur equations:

$$\begin{aligned} x'(t) &= bx(1 - x/\min(K, (P - sy)/q)) - f(x)y, \\ y'(t) &= e \min(1, (P - sy)/(sx))f(x)y - dy. \end{aligned}$$

In this system of equations, because higher resource biomass can imply lower nutrient quality, traditional consumer–resource interactions (+, –) can change to the (–, –) type. The phase plane (Fig. 3) is divided into two regions. In region I, energy (carbon) availability regulates consumer growth. In region II, food quality (phosphorus) controls consumer growth. Increasing energy input into the system may decrease resource quality and stabilize consumer–resource oscillations in region II. If K is increased to an extreme, the system exhibits a “paradox of energy enrichment”: despite abundant food, the consumer, faced with low food quality, is destined for deterministic extinction.

Recent efforts have extended this approach to >1 consumer species to evaluate the impacts of stoichiometric constraints on species coexistence. The competitive exclusion principle (CEP) states that no equilibrium is possible if n species exploit fewer than n resources. This principle does not appear to hold in nature, where high biodiversity is commonly observed, even in seemingly homog-

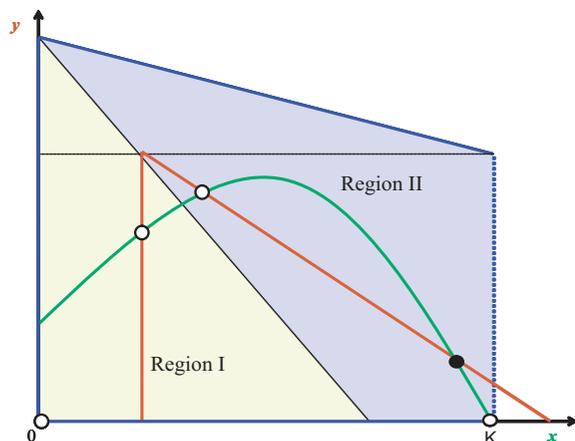


FIGURE 3 Stoichiometric properties divide the phase plane into two regions. In region I, as in the classic Lotka–Volterra model, food quantity limits predator growth. In region II, food quality (phosphorus content of the prey) constrains predator growth. Competition for limiting nutrient between predator and prey alters their interactions from (+, –) in region I to (–, –) in region II. This bends down the predator nullcline in the latter region. This nullcline shape with two x-intercepts creates a possibility for multiple positive steady states, as shown on the figure.

enous habitats. While various mechanisms such as spatial heterogeneity or chaotic fluctuations have been proposed to explain this coexistence, none of them entirely invalidates this principle. However, Loladze and colleagues in 2004 showed that stoichiometric constraints can facilitate the stable maintenance of biodiverse communities, as observed in the 2002 empirical work of Urabe and colleagues. Specifically, they showed a stable equilibrium is possible with two predators on a single prey. At this equilibrium, both predators can be limited by the nutrient content of the prey. This suggests that chemical heterogeneity within and among species provides effective mechanisms that can support species coexistence and that may be important in maintaining biodiversity.

DYNAMICAL OUTCOMES AND PREDICTIONS

Ecological stoichiometric theory is an advance in food web ecology because it incorporates both food-quantity and food-quality effects in a single framework and allows key feedbacks such as consumer-driven nutrient recycling to occur. The consequences of these appear to stabilize predator–prey systems while simultaneously producing rich dynamics with alternative domains of attraction and occasionally counterintuitive outcomes, such as coexistence of more than one predator species on a single-prey item and decreased herbivore performance in response to increased light availability experienced by the

autotrophs. These theoretical findings are consistently supported by recent laboratory and field studies considering stoichiometric effects on autotroph–herbivore systems, such as algae–*Daphnia* interactions. Specifically, empirical evidence for alternative stable states under stoichiometric constraints, negative effects of solar radiation on herbivores via stoichiometric food quality, and diversity-enhancing effects of poor food quality have been produced. Stoichiometric theory provides a promising framework for both quantitative and qualitative improvements in the predictive power of theoretical and computational population ecology, a top priority in light of the alarming multitude and degrees of anthropogenic and natural perturbations experienced by populations.

APPLICATIONS AND EXTENSIONS OF THE THEORY

Ecological stoichiometry seeks to discover how the chemical content of organisms shapes their ecology. Ecological stoichiometry has been applied to studies of nutrient recycling, resource competition, animal growth, and nutrient limitation patterns in whole ecosystems. More recently, it has been extended to evolutionary domains in an attempt to understand the biochemical and evolutionary determinants of observed variations in organisms' C:N:P ratios. Stoichiometric frameworks are equally applicable to the phenomena at the suborganismal level, such as the study of within-host diseases, which include various cancers, as well as phenomena at the whole biosphere level, such as the effects of multiple alterations of biogeochemical cycles on in the biosphere.

SEE ALSO THE FOLLOWING ARTICLES

Allometry and Growth / Biogeochemistry and Nutrient Cycles / Ecosystem Ecology / Energy Budgets / Food Webs / NPZ Models

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STORAGE EFFECT

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Environmental conditions vary in space and time, and to the extent that this causes demographic rates to vary (e.g., fecundity, survival, germination), environmental variation affects long run growth. Variation can have both positive and negative effects on growth. It is well known, for example, that fluctuations in yearly recruitment depress the long run growth rate. However, variation can also provide opportunities that allow species to persist which would otherwise have been competitively excluded. Variation dependent coexistence mechanisms are often referred to generically as storage effects, after the best known example of these mechanisms, but there are more properly three ways in which variation can promote coexistence: storage effects, relative nonlinearity, and, for spatial or spatiotemporal variation, growth density covariance.

THE MUTUAL INVASIBILITY CRITERION FOR COEXISTENCE

Species are deemed able to coexist if each can invade a system dominated by the other. The idea is that if either species were reduced to low density, it could increase its population again instead of dwindling to extinction. Mathematically, we consider each species in turn as the low density species (the invader) and set the populations of the other species (the residents) to their stationary stable distributions i.e., we let the residents come to equilibrium in the absence of the invader. Then we calculate the long-run growth rate of the invader, assuming that the invader is of sufficiently low density that

it does not contribute to the competition felt by itself or the residents. If the long-run growth rate is positive for each species in the role of invader, then each species could recover from low density and we conclude that the species will coexist.

STORAGE EFFECT

Storage effects can occur for both spatial and temporal variation. Storage effects happen when the invader experiences low competition in favorable environments and has the ability to store that double benefit. For example, consider two plant species, one of which grows well in cool summers and the other of which grows well in hot summers. An invader of either species will experience low competition in the years it finds favorable, for the resident is its only source of competition and the resident is experiencing an unfavorable year. The high productivity experienced by the invader at these times may be stored in the form of dormant seeds or, in the case of perennials, in stems, bulbs, or tubers. Alternatively, the invader and resident may partition space instead of time: one may prefer shade while the other prefers full sun, for example, or the resident and invader may have different tolerances for soil pH or drainage. The resident and invader may also prefer the same times or locations but to different degrees. For example, both deciduous and evergreen trees are most productive in summer, but deciduous trees are highly productive in summer and not at all in winter, while evergreens are somewhat more productive in summer and somewhat less productive in winter.

RELATIVE NONLINEARITY

Relative nonlinearity can also occur for both spatial and temporal variation. If growth is a nonlinear function of competition (and it normally is), then competition fluctuations above and below average will not affect growth in the same way. More specifically, if growth is a concave up function of competition, as in Fig. 1A, then below average competition boosts growth more than above average competition reduces growth. In this case, the population benefits when competition varies from time to time or place to place. If, on the other hand, growth is a concave down function of competition, as in Fig. 1B, then the population is harmed by above average competition more than it is helped by below average competition. In this situation, variable competition reduces long run growth.

Of course, if both the resident and the invader respond to competition in precisely the same way, then their long-run growth rates will be increased or decreased