



Stoichiometry in Producer–Grazer Systems: Linking Energy Flow with Element Cycling

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All organisms are composed of multiple chemical elements such as carbon, nitrogen and phosphorus. While *energy flow* and *element cycling* are two fundamental and unifying principles in ecosystem theory, population models usually ignore the latter. Such models implicitly assume chemical homogeneity of all trophic levels by concentrating on a single constituent, generally an equivalent of energy. In this paper, we examine ramifications of an explicit assumption that both producer and grazer are composed of two essential elements: carbon and phosphorus. Using stoichiometric principles, we construct a two-dimensional Lotka–Volterra type model that incorporates chemical heterogeneity of the first two trophic levels of a food chain. The analysis shows that indirect competition between two populations for phosphorus can shift predator–prey interactions from a (+, –) type to an unusual (–, –) class. This leads to complex dynamics with multiple positive equilibria, where bistability and deterministic extinction of the grazer are possible. We derive simple graphical tests for the local stability of all equilibria and show that system dynamics are confined to a bounded region. Numerical simulations supported by qualitative analysis reveal that Rosenzweig’s paradox of enrichment holds only in the part of the phase plane where the grazer is energy limited; a new phenomenon, the paradox of energy enrichment, arises in the other part, where the grazer is phosphorus limited. A bifurcation diagram shows that energy enrichment of producer–grazer systems differs radically from nutrient enrichment. Hence, expressing producer–grazer interactions in stoichiometrically realistic terms reveals qualitatively new dynamical behavior.

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1. INTRODUCTION

Energy flow through trophic levels is a fundamental and unifying principle in ecosystem science (Odum, 1968; Reiners, 1986; Hagen, 1992). It is based on two ideas. First, this approach separates an ecosystem into distinct trophic levels. The first level aggregates all biomass that transforms solar energy into a usable chemical form, i.e., primary producers (hereafter, producers). The next level comprises all organisms directly feeding on producers, i.e., herbivores or grazers. Carnivores, feeding on herbivores, are the third level, and so on. The other idea is that energy must dissipate as it flows through this vertical structure due to the second law of thermodynamics. Hence, as energy is transferred from one trophic level into the next, some part of it must be lost, forcing ecological transfer efficiency or production efficiency to be less than 100%.

Usually, population dynamics models assume a constant production efficiency, as in the classical Lotka–Volterra equations, which succinctly utilize the energy flow principle:

$$\frac{dx}{dt} = bx - f(x)y \quad (1a)$$

$$\frac{dy}{dt} = ef(x)y - dy. \quad (1b)$$

Here the system is divided into two trophic levels, prey and predator (x and y are their respective densities or biomasses in the same units) and the yield constant or the production efficiency (e), manifests the second law of thermodynamics ($0 \leq e < 1$). Since e is a constant and the functional response of the predator, $f(x)$, is a monotone non-decreasing function, it follows that higher prey density never lowers predator growth rate. In other words, energy enrichment of the first trophic level never decreases the flow of energy to the next level. In fact, all predator–prey relationships are considered as a (+, –) type, as indicated by the signs of the off-diagonal terms in the community matrix or Jacobian of system (1).

In the above discussion we used the terminology of energetics and never mentioned chemical elements. However, in reality, energy flow in a food web is intricately bound to chemical elements. Solar energy, once transformed by producers, flows through an ecosystem only as chemical energy in covalent bonding between various elements in organic compounds. Furthermore, organisms build themselves from a variety of essential nutrients such as carbon, nitrogen, phosphorous, sulfur, and calcium. Can the demand of organisms for multiple nutrients alter energy flow and predator–prey interactions in a way not accounted for by energetics considerations? Recent experiments involving zooplankton–phytoplankton interactions show that it can.

Urabe and Sterner (1996) grew algae (a producer) at different light intensities in batch cultures. The systems were open for light energy and carbon that entered

the system from air as CO₂. Phosphorus was limited while all other nutrients were present in abundance. As light input was increased, algal density increased through the entire range of light intensity. One would expect that the growth rate of zooplankton grazing on the algae would positively correlate with algal density. This indeed happened, but only from low to intermediate light levels. Further increases in light intensity resulted in yet higher algal density but lower animal growth rates. Why did high food density hurt the grazer growth rate? One cannot explain this paradoxical result in energy terms without making *ad hoc* assumptions. However, Urabe and Sterner gave a simple explanation involving the stoichiometry of two essential elements, carbon and phosphorus.

At higher light intensity, algae increased photosynthetic fixation of carbon. Since the quantity of phosphorus in the system was limited, this led to lower phosphorus to carbon ratio (P:C) in algal biomass. However, zooplankton physiology does not allow significant variation in body P:C ratio. This is a rather general property among consumer species. Thus, a growing grazer must maintain a specific chemical composition of its body (Andersen and Hessen, 1991; Sterner and Hessen, 1994). If the P:C in algal biomass becomes lower than the zooplankton's specific P:C ratio, then the grazer cannot utilize the excess energy (carbon) acquired from algae and simply excretes or egests it. In other words, under high light energy input, algae become *low quality food* for the grazer lowering the production efficiency in carbon terms [simultaneously, the grazer's assimilation of phosphorus increases; Elser and Urabe (1999)]. These and other results demonstrate that mass balance of multiple chemical elements can affect trophic dynamics (Elser *et al.*, 1998; Sterner *et al.*, 1998). However, current ecological theory fails to stress close connections between the cycling of chemical elements and the flow of energy in food webs. Possibly, the reason lies in the historical development of energy flow concepts and population dynamics theory.

Lotka (1925) pioneered thermodynamic applications in ecology in his book 'Elements of Mathematical Biology', the same book where he introduced and analysed predator–prey equations. In the chapter 'The Energy Transformers of Nature', Lotka wrote that the main variables in his general equations, 'aggregates of living organisms—are, in their physical relations, *energy transformers*'. As energy flows through the system, a fraction of it is lost because 'the second law of thermodynamics inexorably demands this payment of a tax to nature'. However, Lotka did not limit himself to applications of energetics principles to ecology and envisioned how additional physical-chemical laws might affect ecological dynamics. He stressed that living matter is not a homogeneous substance for energy transformation and storage, but instead is composed of multiple chemical elements: each energy transformer 'does not operate with a single working substance, but with a complex variety of such substances, a fact which has certain important consequences'. Therefore, Lotka thoroughly analysed and compared the ratios of essential chemical elements in organisms and their abiotic environment, one of the first applications of its kind. Furthermore, he used a special term, 'stoichiometry', to

denote ‘that branch of the science which concerns itself with material transformations, with the relations between the masses of the components’.

Unfortunately, Lotka’s work in the area of stoichiometry did not gain much popularity among ecologists. Instead, it was Lindeman’s (1942) classic paper, ‘The trophic-dynamic aspect of ecology’, that brought new meaning to ecosystem science. Lindeman separated lake communities into distinct trophic levels: phytoplankton, zooplankton, plankton predators and swimming predators. Using field data, he quantified energy transfer efficiencies between trophic levels. Like Lotka, Lindeman saw intricate connections between energy and nutrients and used the same arrows to denote both energy and nutrient flows on his famous diagram. Lindeman even discussed how the ratio of two essential elements, nitrogen to phosphorus (N : P), affects lake productivity. However, Lindeman’s work is primarily remembered in the context of energy flow in food chains. Subsequent events saw increasing separation of energy flow and biogeochemical cycling as distant phenomena to be studied separately.

In the next decade Howard Odum (1957, 1960), drawing parallels between ecological, physical and electrical systems, isolated energy from nutrients and created unambiguous pure energy flow diagrams. Concentrating on energy allowed him to avoid complications and confusion with recycling. Unlike nutrients, energy, once lost in respiration, cannot be recycled and therefore, flows through trophic levels unidirectionally. The convenience of such single common currency for an entire system became apparent to ecologists. Indeed, Howard’s brother, Eugene Odum (1959), made energy flow diagrams part of his influential ‘Theoretical Ecology’ book. It can be argued that from there, the energy flow concept, largely divorced from element cycling, has had a preeminent place in discussion of food web dynamics.

Has this development of energy flow principles influenced population dynamics theory? Consider that 70 years of development of the Lotka–Volterra equations has enhanced them with age, size and spatial heterogeneity. However, for the originator of this equations, Lotka, another kind of heterogeneity, ‘chemical heterogeneity’, was more important. It is ironic that this direction has not received much attention until very recently.

Recent advances in stoichiometric theory have revived Lotka’s work. Extending general approaches of resource ratio competition theory (Tilman, 1982), Sterner (1990), Hessen and Andersen (1992), Elser *et al.* (1998) and DeMott (1998) have investigated stoichiometric effects on algae–zooplankton interactions. Andersen (1997) explicitly used stoichiometric constraints in modeling the dynamics of pelagic systems; in particular, the assimilation efficiency of zooplankton in his model depends on nutrient content of phytoplankton. Kooijman’s (2000) dynamic energy and mass budgets theory encompasses energy and nutrient fluxes on cellular, organismal and population levels. We refer readers to Elser and Urabe (1999) for a review of recent progress in stoichiometric nutrient recycling theory and potential new directions proposed by these authors.

The simple two-dimensional Lotka–Volterra model (1) captures the essence of the energy flow principle, yet all vestiges of stoichiometric reality are absent. In this paper we build stoichiometric principles into Lotka–Volterra equations with a minimum of added complexity. As in the above described experiments, we are primarily interested in effects of light energy enrichment of producer–grazer systems. However, analytical and numerical analyses of the resulting model (Sections 3 and 4) provide more insight into system dynamics. For example, bifurcation analysis reveals qualitative differences in the effects of energy and nutrient enrichment on trophic dynamics.

2. MODEL CONSTRUCTION

In our qualitative model we concentrate on the first two trophic levels of a food chain, where the prey is a primary producer and the predator is a grazer. Since we will be drawing parallels with the above described experiments we can think of the producer as phytoplankton (algae) and the grazer as zooplankton (for example, *Daphnia*), both placed in a clear flask in a constantly stirred culture. Our simple ecosystem is open for light energy and carbon, which freely enters the system from the atmosphere for fixation by the producer. We will express our assumptions about other nutrients later in this section.

We start the model construction with the Rosenzweig–MacArthur variation of Lotka–Volterra equations as applied to our spatially homogeneous system:

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{K} \right) - f(x)y \quad (2a)$$

$$\frac{dy}{dt} = ef(x)y - dy, \quad (2b)$$

where

x is the density of producer (in milligrams of carbon per liter, mg C l^{-1}),

y is the density of grazer (mg C l^{-1}).

b is the intrinsic growth rate of producer (day^{-1}),

d is the specific loss rate of grazer that includes metabolic losses (respiration) and death (day^{-1}).

$f(x)$ is the grazer's ingestion rate, which we take here as a Holling type II functional response. In other words, $f(x)$ is a bounded smooth function that satisfies the following assumptions:

$$f(0) = 0, \quad f'(x) > 0, \quad f'(0) < \infty \quad \text{and} \quad f''(x) < 0 \quad \text{for } x \geq 0. \quad (3)$$

The choice of Holling type II function is largely for convenience. For most of the analysis that follows, one can choose Holling type I and III functional responses as well, though they may occasionally make analytical derivations more tedious.

The parameters e and K require special consideration and will undergo significant changes before we arrive at our terminal model (6). In model (2):

(a) e is a *constant* production efficiency (yield constant). This is the conversion rate of ingested food into grazer biomass. The basic model (2) is purely energetic in the sense that producer and grazer densities are given in energy equivalents. Such an approach makes the producer always of the same quality for the grazer and leaves no natural and internal mechanism to introduce food quality. In reality, the process of food assimilation is an extremely complex process that depends strongly on the quality of ingested food, which in turn depends on nutrient availability. Reducing such a complicated conversion to a single constant e is a weakness in many predator–prey models.

(b) K is the producer's *constant* carrying capacity that depends on some external factors bounding its density. The only controlled external factor for our system is light intensity. Suppose that we fix light intensity at a certain value and let the producer grow without the grazer and with ample nutrients. Then producer density will increase until self-shading ultimately stabilizes it at some value, K . While K is independent of any internal factors it positively correlates with light intensity as higher light input (that is, below photoinhibition level) allows the producer to reach higher density. What if some nutrient becomes limiting and a grazer is present in the system? Can such internal factors affect carrying capacity? In the more general context of population dynamics, is it a sound modeling practice to tie the upper bound of population density to a single constant?

Incorporation of stoichiometric reality into the model naturally resolves these problems. So let us proceed to this step, with our assumptions below.

Any form of life on the Earth builds itself out of various essential elements such as carbon, nitrogen, phosphorus, calcium, sulfur and potassium. We will track only two essential substances, carbon and phosphorus. We assume that all other nutrients are abundant in the system and that their content in producer biomass does not limit grazer growth. Since the bulk of dry weight of most organisms is carbon, we express biomass of the populations in carbon terms. There is nothing particular with the choice of phosphorus; any essential nutrient can be considered instead. We chose phosphorus because it is frequently a limiting nutrient in freshwater systems (Schindler, 1977; Elser *et al.*, 1990) and was limiting to both algae and grazers in the experiments of Urabe and Sterner (1996), and Sterner *et al.* (1998). What is important is that we introduce a second ‘working substance’.

ASSUMPTION 1. *The total mass of phosphorus in the entire system is fixed, i.e., the system is closed for phosphorus with a total of P (mg P l^{-1}).*

The following important stoichiometric principles lead to the next assumption. Every organism requires at least a certain, species-specific, fraction of phosphorus

in their biomass. We say ‘at least’, because in producers P : C can vary significantly within a species. For example, the green alga *Scenedesmus acutus* can have cellular P : C ratios (by mass) that range from 1.6×10^{-3} to 13×10^{-3} . In animals, P : C varies much less within a species. For example, *Daphnia*’s somatic elemental composition appears to be homeostatically regulated within narrow bounds (P : C around 31×10^{-3} by mass), even when food P : C diverges strongly (Sterner and Hessen, 1994).

ASSUMPTION 2. *Phosphorus to carbon ratio (P : C) in the producer varies, but it never falls below a minimum q (mg P/mg C); the grazer maintains a constant P : C, θ (mg P/mg C).*

ASSUMPTION 3. *All phosphorus in the system is divided into two pools: phosphorus in the grazer and phosphorus in the producer.*

Following Andersen (1997), we assume immediate recycling of phosphorus from excreted and dead matter and its immediate utilization by the producer. Hence, there is no free, inorganic phosphorus pool. We will address the validity of this assumption in the discussion section. Here, we only mention that in most freshwater systems the concentration of free phosphate in water is often very low or below detection because algae quickly absorb almost all available phosphorus.

Let us see how these three assumptions affect model (2). Light intensity limits producer density to K (mg C l⁻¹). However, even in the absence of such an external limitation, the combination of Assumptions 1 and 2 imposes another limit on the producer, P/q (mg C l⁻¹). Moreover, the grazer sequesters some phosphorus from the total pool of P ; to be exact, the grazer contains θy mg P l⁻¹ of phosphorus, thus further reducing the upper limit for producer density to $(P - \theta y)/q$ (mg C l⁻¹). Hence, the carrying capacity of the producer is defined by external (light energy) or internal (nutrient, the grazer) factors, which we express as the following minimum function:

$$\min\left(K, \frac{P - \theta y}{q}\right). \quad (4)$$

Next, we show how stoichiometry brings ‘food quality’ into the model and affects production efficiency of the grazer.

By Assumption 2, the producer’s P : C varies. To express this variable quantity, we note that the producer’s phosphorus content is $P - \theta y$ mg P l⁻¹ (follows from Assumptions 1–3). Since we measure population densities in carbon terms and the producer’s density is x (mg C l⁻¹), it follows that the producer’s P : C is $(P - \theta y)/x$ (mg P/mg C).

While producer stoichiometry varies, by Assumption 2 the grazer must maintain a specific P : C, θ . Following Hessen and Andersen (1992), we say that the producer is optimal food for the grazer if its P : C is equal to or greater than θ . ‘Optimal’ here means that the grazer is able to maximally utilize the energy (carbon)

content of consumed food, ‘wasting’ any excess of phosphorus it ingests. Thus, we replace the constant production efficiency e in model (2) by the following parameter: \hat{e} is the maximal production efficiency, which is achieved if the grazer consumes food of optimal quality. Due to thermodynamic limitations, $\hat{e} < 1$.

If the producer’s $P : C < \theta$, then the grazer excretes or egests the excess of carbon in the ingested food in order to maintain its constant $P : C$. This reduces production efficiency in carbon terms. Hence, production efficiency is not a constant, but depends on both energetic and nutrient limitations. We express it as a minimum function:

$$\hat{e} \min\left(1, \frac{(P - \theta y)/x}{\theta}\right). \quad (5)$$

Finally, we incorporate the variable carrying capacity (4) and the variable production efficiency (5) into equations (2a) and (2b), resulting in:

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{\min(K, (P - \theta y)/q)}\right) - f(x)y, \quad (6a)$$

$$\frac{dy}{dt} = \hat{e} \min\left(1, \frac{(P - \theta y)/x}{\theta}\right) f(x)y - dy. \quad (6b)$$

As to the two minimum functions in this model: the main qualitative results presented in this paper are not affected by changing the minimum functions to their smoother analogs. Although the minimum function may require the analysis to be split into two cases, each of these cases is more clear and simple than their common smooth analog. In addition, note that

$$bx \left(1 - \frac{x}{\min(K, (P - \theta y)/q)}\right) = bx \min\left(1 - \frac{x}{K}, 1 - \frac{x}{(P - \theta y)/q}\right)$$

and

$$bx \left(1 - \frac{x}{(P - \theta y)/q}\right) = bx \left(1 - \frac{q}{(P - \theta y)/x}\right). \quad (7)$$

The left-hand side of (7) is a logistic equation, where $(P - \theta y)/q$ is the carrying capacity of the producer determined by phosphorus availability. The right-hand side shows that it can be viewed as Droop’s equation (Droop, 1974), where q is the minimal phosphorus content of the producer and $(P - \theta y)/x$ is its actual phosphorus content.

3. QUALITATIVE ANALYSIS

3.1. Boundedness and invariance. One of the unusual features of this model is that the carrying capacity of the producer depends on the density of the grazer. In

the absence of the grazer, the carrying capacity of the producer depends only on light and phosphorus availability, which we denote as

$$k = \min(K, P/q). \quad (8)$$

A technical note: the model is well defined as $x \rightarrow 0$. Conditions (3) assure that $f(x)/x$ has the following useful properties (see Appendix A):

$$\lim_{x \rightarrow 0} \frac{f(x)}{x} = f'(0) < \infty \quad \text{and} \quad \left(\frac{f(x)}{x} \right)' < 0 \quad \text{for } x > 0. \quad (9)$$

This means that $y'(t)$ is well defined as $x \rightarrow 0$, because $\min(1, (p - y)/x)f(x) = \min(f(x), (p - y)\frac{f(x)}{x})$.

An important consequence of Assumptions 1 and 2 is the boundedness of solutions. Indeed, if the total amount of phosphorus is bounded in the system and both populations require it, then their densities should be bounded as well (even if light input is abundant). Appendix B contains the proof of the following lemma.

LEMMA 1. *Solutions with initial conditions in the open rectangle $\{(x, y) : 0 < x < k, 0 < y < P/\theta\}$ remain there for all forward times.*

We can obtain even better bounds on solutions by considering the following. Total phosphorus in the system is P ; thus, the sum of phosphorus in the producer and the grazer cannot exceed P . Assumption 2 suggests that

$$qx + \theta y \leq P. \quad (10)$$

Thus, we expect that incorporation of stoichiometry into the model should confine its dynamics to $\{(x, y) : 0 < x < k, 0 < y, qx + \theta y \leq P\}$ which is a trapezoid if $K < P/q$ or a triangle if $K \geq P/q$. (see Fig. 1). The following theorem shows that this is indeed true.

THEOREM 2. *Solutions with initial conditions in the open trapezoid (or triangle if $K \geq P/q$)*

$$\Delta \equiv \{(x, y) : 0 < x < k, 0 < y, qx + \theta y < P\} \quad (11)$$

remain there for all forward times.

The proof of this theorem can be found in Appendix C, which takes advantage of the following simple scaling for facilitation of qualitative analysis. We eliminate the parameter θ , while our time scale (days) and all other parameters, except P and q , remain unchanged. Let

$$p := \frac{P}{\theta} \quad \text{and} \quad s := \frac{q}{\theta},$$

where

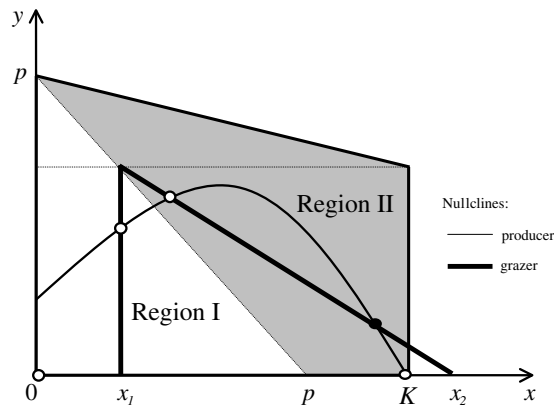


Figure 1. Stoichiometric properties confine dynamics to the trapezoid-shaped area, where the line, $qx + \theta y = P$ (note: $p = P/\theta$), divides the phase plane into two regions. In Region I, like in the classical Lotka–Volterra model, food quantity limits grazer growth. In Region II (the shaded area) food quality, i.e., the producer’s phosphorus content, constrains grazer growth. Competition for limiting nutrient between grazer and producer alters their interactions from $(+, -)$ in Region I to $(-, -)$ in Region II. This bends down the grazer nullcline in Region II. The shape of the grazer nullcline with two x -intercepts, x_1 and x_2 , creates a possibility for multiple positive steady states as shown on the figure. The horizontal line separates the phase plane in a different way: above this line, producer carrying capacity is limited by phosphorus; below, by light.

p is maximal grazer density allowed by total phosphorus in the system and $s = q/\theta$ is a dimensionless constant equal to the producer’s minimal P : C, q , divided by the constant grazer P : C, θ .

Then (4) and (5) become

$$\min\left(K, \frac{p - y}{s}\right) \quad \text{and} \quad \hat{e} \min\left(1, \frac{p - y}{x}\right).$$

Then system (6) becomes

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{\min(K, (p - y)/s)}\right) - f(x)y \tag{12a}$$

$$\frac{dy}{dt} = \hat{e} \min\left(1, \frac{p - y}{x}\right) f(x)y - dy. \tag{12b}$$

The theorem assures that all dynamics will be confined to a bounded region. We will use $\bar{\Delta}$ to denote the region Δ together with its boundary with the exception of a biologically insignificant point $(0, p)$ (at this point the grazer contains all phosphorus and thus the producer is absent from the system), i.e.,

$$\bar{\Delta} = (\partial\Delta \setminus (0, p)) \cup \Delta.$$

Note, that initial conditions outside of $\bar{\Delta}$ are meaningless, because they would mean that we start with higher phosphorus concentration in the system than the defined total concentration of P .

3.2. Nullclines. To simplify the analysis, we rewrite system (12) in the following form:

$$x' = xF(x, y) \quad (13a)$$

$$y' = yG(x, y), \quad (13b)$$

where

$$F(x, y) = b \left(1 - \frac{x}{\min(K, (p-y)/s)} \right) - \frac{f(x)}{x} y \quad (14a)$$

$$G(x, y) = \hat{e} \min \left(1, \frac{p-y}{x} \right) f(x) - d = \hat{e} \min \left(f(x), (p-y) \frac{f(x)}{x} \right) - d. \quad (14b)$$

Conditions (9) assure that system (13) is well defined and partial derivatives of F and G exist almost everywhere on $\bar{\Delta}$:

$$F_x = \frac{\partial F}{\partial x} = \frac{b}{\min(K, (p-y)/s)} - \left(\frac{f(x)}{x} \right)' y \quad (15)$$

$$F_y = \frac{\partial F}{\partial y} = \begin{cases} -\frac{f(x)}{x} < 0 & \text{if } y < p - sK \\ -(bsx)/(p-y)^2 - \frac{f(x)}{x} < 0 & \text{if } y > p - sK \end{cases} \quad (16)$$

$$G_x = \frac{\partial G}{\partial x} = \begin{cases} \hat{e} f'(x) > 0 & \text{if } y < p - x \\ \hat{e}(p-y) \left(\frac{f(x)}{x} \right)' < 0 & \text{if } y > p - x \end{cases} \quad (17)$$

$$G_y = \frac{\partial G}{\partial y} = \begin{cases} 0 & \text{if } y < p - x \\ -\hat{e} \frac{f(x)}{x} < 0 & \text{if } y > p - x. \end{cases} \quad (18)$$

A very important feature of the model is the change in the sign of G_x , which measures the effect of producer density on grazer net growth rate. Conventional ecological theory considers this effect as positive (or 0 in the case of the saturation of grazer response) and thus traditionally classifies grazer–producer and indeed all other predator–prey interactions as (+, −). However, in this model the line, $y = p - x$, divides the phase plane into two regions (see Fig. 1):

- (i) Region I, $y < p - x$, where only food quantity (energy or carbon) limits grazer growth, (+, −), and

- (ii) Region II, $y > p - x$, where food quality (phosphorus content) constrains grazer growth, $(-, -)$.

Hence, in Region I the grazer growth benefits from higher prey densities like in classical predator–prey theory. However, in Region II the grazer indirectly competes with its prey for phosphorus. Such competition shifts the grazer–producer relationship from a conventional $(+, -)$ in Region I to an unusual $(-, -)$ in Region II. This shift is responsible for the peculiar shape of the grazer nullcline, which in most predator–prey models is a non-decreasing line. Before we consider its shape in model (6), let us state our last assumption, without which the grazer will not have a chance to persist.

ASSUMPTION 4. *The maximal net growth rate of the grazer is positive.*

Mathematically, this is equivalent to the following inequality

$$\max_{\bar{\Delta}} G(x, y) > 0. \quad (19)$$

The grazer nullcline is determined by

$$G(x, y) = 0. \quad (20)$$

From continuity of $G(x, y)$, (19) and $G(0, 0) < 0$ it follows that (20) has a solution. Hence, the grazer nullcline exists in $\bar{\Delta}$ and its slope is given by

$$-G_x/G_y. \quad (21)$$

Using (17), (18) and (21) we find that in Region I, the grazer nullcline is a vertical segment (undefined slope) like in the Rosenzweig–MacArthur model, while in Region II it is declining. The declining grazer nullcline reflects the negative effect of diminishing food quality at higher producer density. Next, we show that the grazer nullcline has exactly two x -intercepts, which are solutions of

$$g(x) \equiv G(x, 0) = 0. \quad (22)$$

Since $g'(x) = G_x(x, 0)$, (17) yields that $g(x)$ is strictly increasing for $0 \leq x < p$ and strictly decreasing for $p \leq x$. Hence, $\max_{x \geq 0} g(x) = g(p)$. Observe that on $\bar{\Delta}$,

$$G(x, 0) \geq G(x, y). \quad (23)$$

Using (23) and (19), we find that

$$g(p) = \max_{x \geq 0} g(x) = \max_{x \geq 0} G(x, 0) \geq \max_{\bar{\Delta}} G(x, y) > 0. \quad (24)$$

Thus $g(x)$ is a continuous function that is strictly increasing on the interval $(0, p)$ while being negative on its left end ($g(0) < 0$) and positive on its right end ($g(p) > 0$). Thus, on this interval (22) has a unique solution, which we denote x_1 (see Fig. 1). The boundedness of $f(x)$ yields that $g(x) < 0$ for large enough x , and by similar arguments we find that (22) has a unique solution on (p, ∞) , which we denote x_2 . Thus, $0 < x_1 < p < x_2$. In other words, the grazer nullcline has one x -intercept in Region I and a second one in Region II. Andersen (1997), and Schwinning and Parson (1996) analysing their higher dimensional models obtained hump-shaped nullclines by projecting manifolds on a plane. Interestingly, Schwinning and Parson (1996) reported the change in the type of grass–legume interactions from $(+, -)$ to $(-, -)$ due to a shift in the relative importance of nitrogen limitation to a light limitation. Here, the triangle-shaped grazer nullcline reflects the negative role of worsening food quality on the grazer in Region II.

The producer nullcline is a solution of $F(x, y) = 0$. This yields a continuous curve with y -intercept at $(0, b/f'(0))$ and x -intercept at $(k, 0)$.

3.3. Equilibria on the boundary. To find equilibria we solve

$$xF(x, y) = 0 \quad (25a)$$

$$yG(x, y) = 0. \quad (25b)$$

The only boundary equilibria are $E_0 = (0, 0)$ and $E_1 = (k, 0)$.

To determine the local stability of these equilibria, we consider the Jacobian of system (13):

$$\begin{pmatrix} F(x, y) + xF_x(x, y) & xF_y(x, y) \\ yG_x(x, y) & G(x, y) + yG_y(x, y) \end{pmatrix}. \quad (26)$$

At the origin it takes the form

$$J(E_0) = \begin{pmatrix} b & 0 \\ 0 & -d \end{pmatrix}.$$

Since the determinant is negative, the eigenvalues have different signs. Thus, the origin is always unstable in the form of a saddle.

At E_1 the Jacobian is

$$J(E_1) = \begin{pmatrix} -b & F_y(k, 0) \\ 0 & G(k, 0) \end{pmatrix}.$$

If $G(k, 0)$ is positive, then the determinant is negative, yielding that E_1 is unstable. This means that the grazer can invade the system around this equilibrium point. Otherwise, E_1 is locally asymptotically stable. The following proposition provides a graphical criterion for the stability of E_1 .

PROPOSITION 3. *The steady state E_1 is a saddle if it lies between the two x -intercepts of the grazer nullcline, i.e., if $x_1 < k < x_2$. If $k \notin [x_1, x_2]$, then E_1 is locally asymptotically stable.*

Proof. Recall that $G(k, 0) = g(x)$ and $g(x_1) = g(x_2) = 0$. Hence, $g(k) > 0$ for $x_1 < k < x_2$, which means $G(k, 0) > 0$ holds, and hence E_1 is a saddle. If $k < x_1$ or $k > x_2$, then $g(k) < 0$, making E_1 locally asymptotically stable. \square

3.4. Internal equilibria. Next we derive a simple graphical test that will determine the local stability of any internal equilibrium of our system. Equilibria are the intersection points of the producer and the grazer nullclines. Note that the slope of the producer and grazer nullclines at (x, y) are defined by $-(F_x/F_y)$ and $-(G_x/G_y)$, respectively. The hump-shaped grazer nullcline creates a possibility for multiple positive equilibria as Fig. 1 shows. Suppose that (x^*, y^*) is one such equilibria, i.e., $F(x^*, y^*) = 0$ and $G(x^*, y^*) = 0$.

The Jacobian (26) at (x^*, y^*) takes the following form:

$$J(x^*, y^*) = \begin{pmatrix} x^*F_x(x^*, y^*) & x^*F_y(x^*, y^*) \\ y^*G_x(x^*, y^*) & y^*G_y(x^*, y^*) \end{pmatrix}.$$

Its determinant and trace are

$$\text{Det}(J(x^*, y^*)) = x^*y^*(F_xG_y - F_yG_x) \tag{27}$$

$$\text{Tr}(J(x^*, y^*)) = x^*F_x + y^*G_y. \tag{28}$$

We split the analysis into two cases depending on whether the equilibrium (x^*, y^*) is in Region I or II:

- (i) Suppose, (x^*, y^*) lies in Region I ($y^* < p - x^*$). Then (16)–(18) yield that at (x^*, y^*) , $F_y < 0$, $G_x > 0$, $G_y = 0$. Therefore, the sign of (27) is positive, while

$$\text{sign}(\text{Tr}(J(x^*, y^*))) = \text{sign}(F_x) = \text{sign}\left(-\frac{F_x}{F_y}\right).$$

Since the fraction $-(F_x/F_y)$ is the slope of the producer nullcline it follows that (x^*, y^*) is locally asymptotically stable if the producer nullcline is declining at (x^*, y^*) . If it is increasing at (x^*, y^*) , then the equilibrium is a repeller.

- (ii) Suppose, $y^* > p - x^*$. Then (16)–(18) yield that at (x^*, y^*) , $F_y < 0$, $G_x < 0$, $G_y < 0$. An elementary derivation shows that

$$\begin{aligned} \text{sign}(\text{Det}(J)) &= \text{sign}(F_xG_y - F_yG_x) = \text{sign}\left(\frac{F_xG_y - F_yG_x}{F_yG_y}\right) \\ &= \text{sign}\left(-\frac{G_x}{G_y} - \left(-\frac{F_x}{F_y}\right)\right). \end{aligned}$$

Hence, if the slope of the producer nullcline at (x^*, y^*) is greater than the grazer's, then the determinant (27) is negative, yielding (x^*, y^*) as a saddle. If the grazer nullcline has larger slope, then the determinant is positive which makes the eigenvalues of the same sign as the trace (28). Recalling that G_x and G_y are negative, we find that

$$0 > -\frac{G_x}{G_y} > -\frac{F_x}{F_y}. \quad (29)$$

Condition (29) together with $F_y < 0$ yields that $F_x < 0$. Therefore, the trace (28) is negative, so (x^*, y^*) is locally asymptotically stable if the grazer nullcline has larger slope than the producer's.

We summarize the conditions for the stability of all possible equilibria (with the exception of non-generic cases, such as touching nullclines or 0 eigenvalues; which are biologically insignificant) in the following theorem. The acronym LAS stands for locally asymptotically stable.

THEOREM 4. Boundary equilibria: *The origin is a saddle. The only other equilibrium on the boundary is $E_1 = (k, 0)$. It is a saddle if it lies between the two x -intercepts of the grazer nullcline, i.e., if $x_1 < k < x_2$. If it lies outside of $[x_1, x_2]$, then E_1 is LAS.*

Internal equilibria: *In Region I the internal equilibrium is LAS if the producer nullcline at it is decreasing; if the producer nullcline at it is increasing, then the equilibrium is a repeller. In Region II any internal equilibrium is LAS if the producer nullcline at it declines steeper than the grazer's; otherwise, the equilibrium is a saddle.*

4. NUMERICAL EXPERIMENTS

In this section we provide results of numerical experiments that are in some sense analogous to previously considered laboratory experiments investigating stoichiometric aspects of phytoplankton–zooplankton interactions (Urabe and Sterner, 1996; Sterner *et al.*, 1998). We choose the functional response as a Monod type function, i.e.,

$$f(x) = \frac{cx}{a + x}. \quad (30)$$

The parameter values are listed in the Table 1, where we used Andersen (1997), and Urabe and Sterner (1996) for guidance in setting parameters at biologically realistic values. We used XPP software developed by Bard Ermentrout (<http://www.pitt.edu/~phase>) for the numerical runs and as an aid in obtaining all figures.

Table 1. Model parameters.

Parameter		Value	Units
P	Total phosphorus	0.025	mg P l ⁻¹
\hat{e}	Maximal production efficiency in carbon terms	0.8	
b	Maximal growth rate of the producer	1.2	day ⁻¹
d	Grazer loss rate (includes respiration)	0.25	day ⁻¹
θ	Grazer constant P/C	0.03	(mg P)/(mg C)
q	Producer minimal P/C	0.0038	(mg P)/(mg C)
c	Maximum ingestion rate of the grazer	0.81	day ⁻¹
a	Half-saturation of grazer ingestion response	0.25	mg C l ⁻¹
K	Producer carrying capacity limited by light	0.25–2.0	mg C l ⁻¹

The last parameter, K , indirectly reflects light intensity or energy input into the system. For example, $K = 0.5 \text{ mg C l}^{-1}$ means that with ample nutrients and without predation, the producer density will tend to 0.5 mg C l^{-1} . We will increase K from 0.25 to 2.0 mg C l^{-1} in four numerical runs (see Figs 2 and 3). We start with the same initial conditions $x = 0.5 \text{ mg C l}^{-1}$, $y = 0.25 \text{ mg C l}^{-1}$ for all four runs. All values below are in mg C l^{-1} and rounded to thousandths.

- (i) $K = 0.25$; population densities stabilize around a stable equilibrium with $x = 0.16$, $y = 0.22$ [Fig. 2(a)].
- (ii) $K = 0.75$; population densities do not tend to certain values any more. Instead, they oscillate around an unstable equilibrium with $x = 0.16$, $y = 0.48$ [Fig. 2(b)].
- (iii) $K = 1.0$; oscillations disappear and a stable equilibrium emerges with $x = 0.59$, $y = 0.51$ [Fig. 2(c)].
- (iv) $K = 2.0$; producer density approaches $x = 2$; however, the grazer, despite ample food supply, is heading toward deterministic extinction, $y = 0$ [Fig. 2(d)].

The phase planes corresponding to these numerical runs together with the two theorems give us a better idea of underlying dynamics and allow us to rigorously determine the stability of all equilibria. When $K = 0.25$, the producer nullcline is decreasing at the equilibrium making it stable by Theorem 4 [Fig. 3(a)]. When $K = 0.75$, the producer nullcline is increasing at the equilibrium making it unstable; however, a stable limit cycle surrounds the equilibrium and attracts the trajectory [Fig. 3(b)]. When $K = 1$, the producer nullcline twice intersects the grazer nullcline in Region II. By Theorem 4 the lower equilibrium (0.59, 0.51) is stable, because the producer nullcline at it declines steeper than the grazer's [Fig. 3(c)]. When $K = 2$, the boundary equilibrium $E_1 = (2, 0)$ lands on the right of both x -intercepts of the grazer nullcline, and therefore is stable [Fig. 3(d)].

The bifurcation diagram (see Fig. 4) provides further insight on how grazer density responds to light energy enrichment as K increases from 0 to 2.2. When

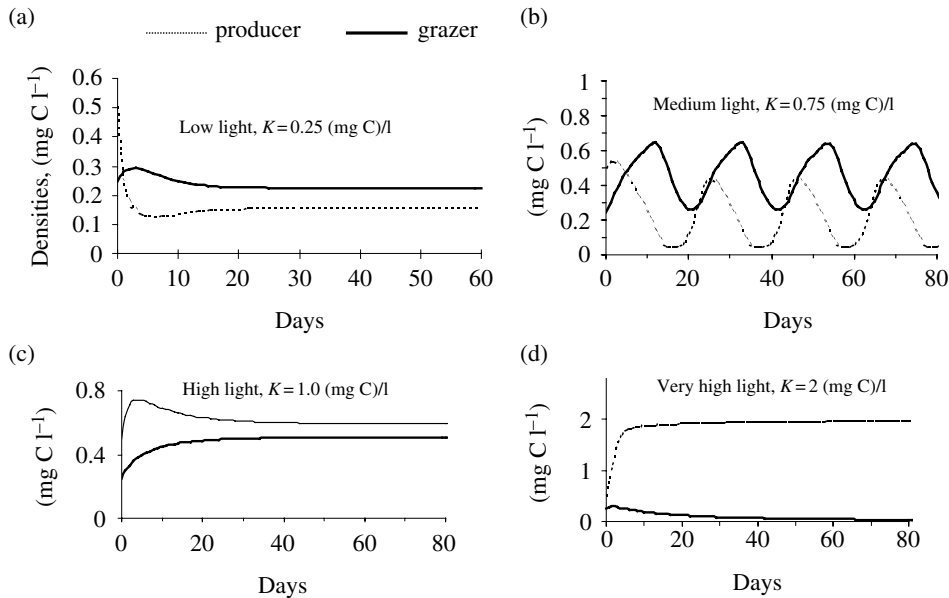


Figure 2. In all four runs, parameters are in biologically realistic range as in Table 1. The initial conditions are $x = 0.5 \text{ (mg C l}^{-1}\text{)}$, $y = 0.25 \text{ (mg C l}^{-1}\text{)}$. In (a) and (b) we observe Rosenzweig's paradox of enrichment: an increase in K destabilizes the equilibrium. However, a further increase in K leads to: (c) stabilization of the system [with a higher producer/grazer ratio than in (a)] and (d) deterministic extinction of the grazer.

$0 < K < 0.16$, the grazer does not survive due to starvation, since a boundary equilibrium $E_1 = (K, 0)$ is stable. As K gradually increases from 0.16 to 0.98 the system exhibits Rosenzweig's paradox of enrichment (Rosenzweig, 1971): the grazer density rises (while the producer density is fixed at 0.16) until $K = 0.56$ when the system undergoes a supercritical Hopf bifurcation and the equilibrium loses its stability to a limit cycle, the amplitude of which increases with K . Thus far the system dynamics were confined to Region I, where it behaves similarly to the Rosenzweig–MacArthur model. However, at $K = 0.98$ the dynamics sharply change: the limit cycle disappears in an infinite period bifurcation (or saddle-node bifurcation, depending on terminology), where a saddle and a stable equilibrium emerge in Region II. As K further increases the grazer density declines (while the producer density increases). Here higher producer abundance is associated with lower grazer biomass, as in the Sterner *et al.* (1998) experiments. When $K = 1.91$ exchange of stability takes place, where E_1 gains stability again and for any $K > 1.91$ the grazer does not survive.

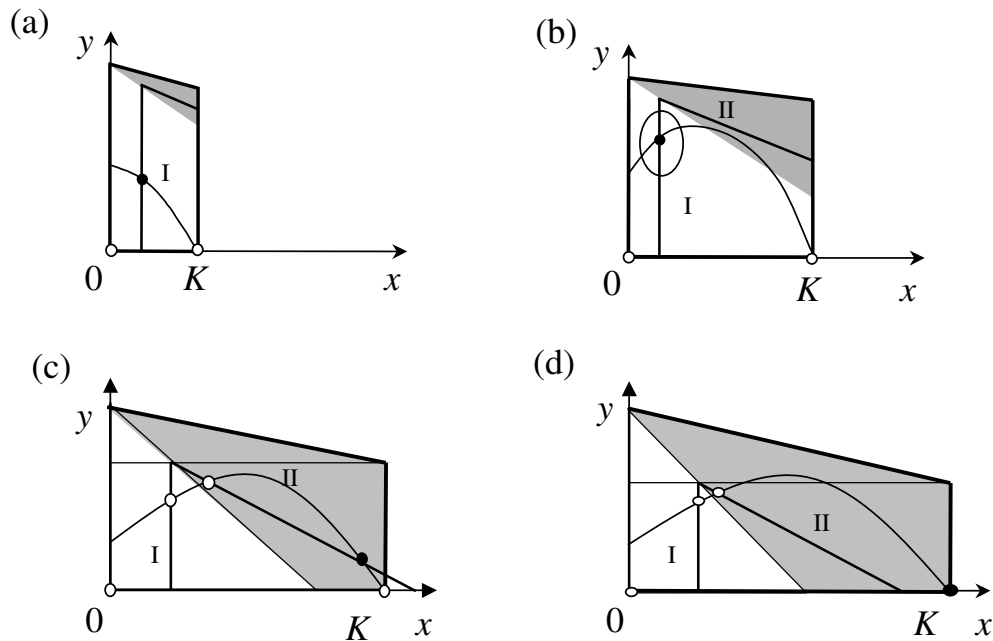


Figure 3. These four phase planes correspond to the four numerical runs in Fig. 2. The stability type of all equilibria easily follow from the second theorem. In (a) and (b) the dynamics is confined to Region I, where the model behaves similarly to the Rosenzweig–MacArthur model. In (c) and (d) the system dynamics enters Region II, where a stable equilibrium emerges. Note that, in (c) higher values of K would correspond to lower grazer density and higher producer abundance. This trend continues until the predator cannot survive in (d).

5. DISCUSSION

Many population dynamics models, like classical models (1a), (1b) and (2a), (2b), assume that organisms and their food are made of a single constituent that is the equivalent of energy. Such an assumption is supported by the concept of energy flow that views trophic levels as homogeneous substances for energy storage and transformation. This powerful simplification of reality is very convenient and has proven to be useful, however some of its drawbacks are not always realized. For example, this assumption yields that organisms should assimilate food with constant efficiency, because food made of a single substance cannot change its quality. Although our everyday experience suggests that even quality of our own food varies widely, constant production efficiencies have been a standard assumption in population dynamics theory. These constants are usually scaled away during analysis, which eliminates any clues on their effects on population dynamics. Nevertheless, several researchers [e.g., Edelman-Keshet and Rausher (1989), Koppel *et al.* (1996) and Huxel (1999)] considered plant–herbivore models with variable food quality. However, the reliance of these models on a single ‘working

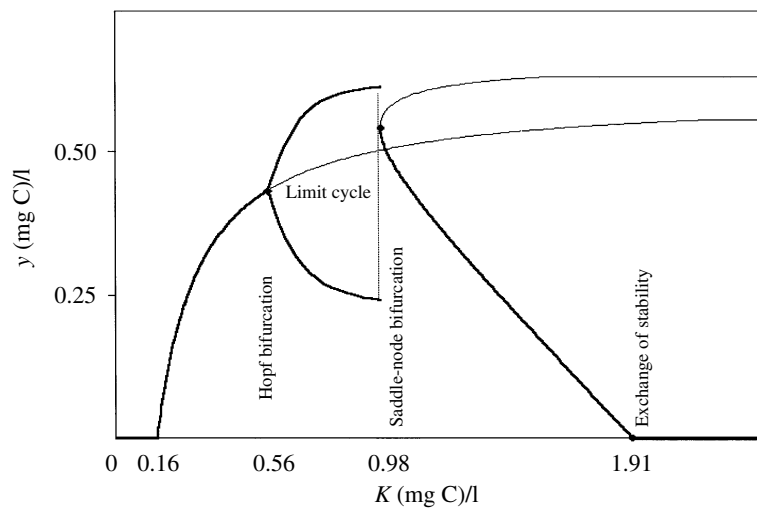


Figure 4. A bifurcation diagram of the grazer density plotted against K , where K indirectly reflects energy (light) input into the system. Bold and thin lines represent stable and unstable equilibria, respectively. All other parameters are as in Table 1, except K that varies from 0 to 2.4. For $K < 0.16$ the grazer cannot persist due to starvation and for $K > 1.91$ it cannot persist due to low food quality. As K varies from 0.16 to 0.56 the grazer density at stable equilibrium increases. However, at $K = 0.56$ the stable equilibrium loses its stability to a limit cycle, an amplitude of which increases with K ($0.56 < K < 0.98$). In other words, the system exhibits Rosenzweig's paradox of enrichment. This trend stops at $K = 0.98$, when the limit cycle through an infinite period bifurcation disappears and the grazer density tends to a newly emerged stable equilibrium. As K increases from 0.98 to 1.91, worsening food quality gradually lowers the grazer density at this equilibrium. The grazer is able to persist only for $0.16 < K < 0.91$.

substance' precluded the inclusion of actual mechanisms governing food quality.

In this paper we acknowledge the fact that all organisms build themselves from multiple chemical elements in certain proportions. Our producer–herbivore system is open for light energy and carbon but closed for another essential nutrient, phosphorus. The grazer must acquire energy (carbon) but also a second necessary constituent, phosphorus. With two 'working substances' there is no need for any *ad hoc* assumptions about variability in production efficiency. Instead, the flexible chemical composition of the producer together with the constant stoichiometry of the grazer naturally introduce 'food quality' into the system, which in turn leads to varying production efficiency of the grazer. In reality, other nutrients (such as N or Ca) can also influence grazer–producer interactions (White, 1993). The following modification of model (6) accommodates n limiting nutrients without increasing

the dimension of the system:

$$x' = bx \left[1 - \frac{x}{\min(K, (N_1 - \theta_1 y)/q_1, \dots, (N_n - \theta_n y)/q_n)} \right] - f(x)y$$

$$y' = \hat{e} \min \left(1, \frac{(N_1 - \theta_1 y)/x}{\theta_1}, \dots, \frac{(N_n - \theta_n y)/x}{\theta_n} \right) f(x)y - dy,$$

where

- N_i is the total amount of the i th nutrient in the system,
- q_i is the producer's minimal i th nutrient content,
- θ_i is the grazer's constant (homeostatic) i th nutrient content and all other parameters are as in system (6).

The limitation of the above model as well as models (6a) and (6b) is the absence of a free nutrient pool and lack of delay in nutrient recycling as assumed in Assumption 3. In nutrient-limited pelagic systems the concentration of free phosphorus is very low or below detection. Such a low concentration should not be ignored if one wishes to model competition among multiple producers. Since we model only one producer species, we can assume that it simply absorbs all potentially available phosphorus. However for terrestrial systems, even with a single producer, soil compartments and delays in nutrient release are of major importance (Agren and Bosatta, 1996) and addition of a free nutrient pool appears to be necessary. Another limitation is that models (6a) and (6b) are homogeneous in all aspects except of chemical composition of organisms. However, such 'chemical heterogeneity' profoundly effects producer-grazer interactions.

- The demand of both populations for limiting phosphorus naturally bounds the densities of both populations, even when light energy input into the system is unlimited (see Fig. 1).
- The carrying capacity of the producer, instead of being a static and external factor, becomes a multivariable function that depends on energy (light) input, nutrient concentration and grazer density [see Eqns (4) and (5)].
- In the system where every organism competes with every other organism for the limiting nutrient, competition effects superimpose on predator-prey interactions. This divides the grazer-producer phase plane into two regions. In Region I energy (carbon) availability regulates grazer growth and grazer-producer interactions are the traditional (+, -) type. However, in Region II food quality (phosphorus content) controls grazer growth and changes grazer-producer relationships to a competitor type (-, -). This creates a possibility for multiple positive equilibria and deterministic extinction of the grazer (see Fig. 1).
- The system exhibits a paradox of *energy enrichment*. Intense energy (light) enrichment substantially elevates producer density, however, despite such an abundant food supply the grazer decreases its growth rate and drives itself to deterministic extinction [see Figs 2(d), 3(d) and 4].

From an energetics point of view the paradox of energy enrichment is a true paradox: higher energy (food) consumption should not decrease growth rate. However, it is easily solved by ‘food quality’ arguments, as higher producer densities correspond to its lower phosphorus content and thus, lower production efficiencies for the grazer. Hence, in estimating effects of enrichment on producer–grazer and longer food chains one should take into account both food quantity and food quality. For example, carbon dioxide enrichment may affect herbivores through changes in producer abundance but also in its stoichiometry. Since both light and nutrients can affect quality as well as quantity, a question arises: how does energy enrichment (that leads here to carbon enrichment of the producer) differ from nutrient enrichment? Motivated by this question we constructed a bifurcation diagram (Fig. 5), where different dynamical outcomes were presented on the K – P plane (K is associated with light intensity and P is total phosphorus in the system). We find a striking difference between light and phosphorus enrichment. Light energy enrichment (horizontal arrow) may destabilize as well as stabilize the system, but ultimately leads to the deterministic extinction of the grazer. In contrast, phosphorus enrichment (vertical arrow) can only destabilize the system; however, it does not lead to the extinction of the grazer. Rosenzweig’s paradox of enrichment (usually viewed as destabilization of predator–prey interactions through Hopf bifurcation) holds only in a limited light–phosphorus range. Yet, under wider definition as system destabilization or grazer’s extinction, the paradox of enrichment holds in a rather wide K – P range.

In Fig. 5 the various regions of stable attractors do not overlap, meaning that only one stable attractor exists for any particular (K , P) pair and other parameters are fixed as in Table 1. However, bistability may arise for certain sets of parameter values that deviate from the ones in Table 1 but are still in a biologically realistic range. For example, in Fig. 6, depending on initial conditions, the system can be attracted to a stable limit cycle or a stable equilibrium. This suggests that in such systems an externally caused shift in population density may significantly change system behavior and producer/grazer ratio.

The introduction of stoichiometric reality into population dynamics theory raises other questions. How will space, age, or size-structured models be affected by stoichiometric considerations? When a stoichiometric perspective is brought to bear on all interactions, how will the community matrix of an ecosystem change? Will competitive and mutualistic interactions always be a (–, –) or (+, +) type, respectively? Will the competitive exclusion principle still hold in a model that is chemically heterogeneous but homogeneous in all other aspects? The analysis of the model shows that stoichiometry may dampen potentially destructive oscillations by reducing energy flow to the grazer (see Fig. 2(b), 2(c) and Fig. 4). Here, a certain degree of weakening of predator–prey interactions contributes to the stability of the system. This supports the McCann (2000) statement that “weak interactions serve to limit energy flow in a potentially strong consumer–resource interactions and, therefore, to inhibit runaway consumption that destabilizes the dynamics of

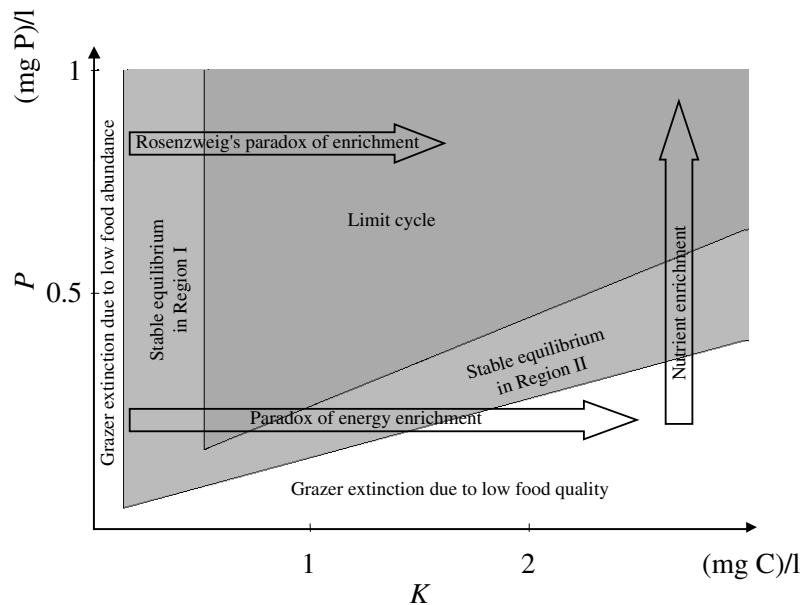


Figure 5. The regions of existence of all stable attractors are drawn on the K - P plane with all other parameters fixed as in Table 1. Energy enrichment of the system (the long horizontal arrow) leads the grazer through (steady state)/(cycle)/(steady state)/(deterministic extinction). It drastically differs from nutrient enrichment (the vertical arrow) that may destabilize the system; however, it does not lead to grazer extinction. Rosenzweig's paradox of enrichment holds in a limited range of light/nutrient parameters, where the system undergoes Hopf bifurcation. Note, that balanced light/nutrient enrichment, (e.g., along the shaded area of the stable equilibrium in Region II) may leave the system dynamics qualitatively unchanged. Hence, the effects of enrichment strongly depend on its type: energy, nutrient or combined energy/nutrient enrichment.

food webs". The question arises as to how stoichiometry contributes to the diversity and stability of an ecosystem.

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APPENDIX A: THE PROPERTIES OF THE FUNCTIONAL RESPONSE, $f(x)$

We have that $(f(x)/x)' = (xf'(x) - f(x))/x^2$. Let $l(x) \equiv xf'(x) - f(x)$. Then by (3), $l(0) = 0$ and $l'(x) = xf''(x) < 0$. Hence, $(f(x)/x)' < 0$ for $x > 0$. By definition of a limit and since $f(0) = 0$, it follows that $\lim_{x \rightarrow 0} (f(x)/x) = f'(0)$.

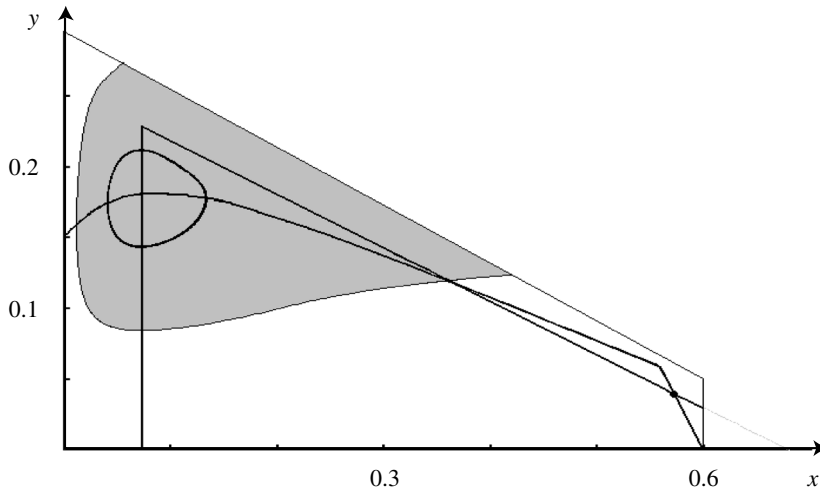


Figure 6. The regions of some stable attractors in Fig. 5 may overlap for certain sets of parameter values leading to bistability. For example, for $P = 0.003$, $e = 0.7$, $b = 1$, $d = 0.21$, $\theta = 0.01$, $q = 0.004$, $c = 0.8$, $a = 0.13$, $K = 0.6$, the stable limit cycle (whose basin of attraction is shaded) coexists with the stable equilibrium that attracts all solutions which start in the non-shaded region of the trapezoid.

APPENDIX B: THE PROOF OF THE LEMMA

Proof. Let us prove by contradiction, i.e., assume that there is time $t_1 > 0$, s.t. a trajectory with initial conditions in the open rectangle, $x(0) \in (0, k)$ and $y(0) \in (0, p)$, touches or crosses the boundary of the closed rectangle $[0, k] \times [0, p]$ for the first time. Since the boundary consists of four sides, four cases are possible. Corners are excluded in the first two cases.

Case 1. Assume $x(t_1) = 0$ (left border). Let $y_1 = \max_{t \in [0, t_1]} y(t) < p$ and $\bar{f} = f'(0)$. Then,

$$\begin{aligned} x' &= bx \left(1 - \frac{x}{\min(K, (p - y)/s)} \right) - f(x)y \\ &\geq bx \left(1 - \frac{x}{\min(K, (p - y_1)/s)} \right) - \bar{f}xy \\ &\geq \left(b \left(1 - \frac{k}{\min(K, (p - y_1)/s)} \right) - \bar{f}y_1 \right) x \equiv \alpha x, \end{aligned}$$

where α is a constant. Thus, $x(t) \geq x(0)e^{\alpha t}$, which implies that $x(t_1) \geq x(0)e^{\alpha t_1} > 0$. Therefore, no trajectory can touch the left-hand-side border of the rectangle.

Case 2. Assume $x(t_1) = k$ (right border). Then

$$x' \leq bx \left(1 - \frac{x}{\min(K, p/s)} \right) \leq bx \left(1 - \frac{x}{k} \right).$$

The standard comparison argument yields that $x(t) < k$ for all $t \in [0, t_1]$ and thus, no trajectory touches the right-hand-side border.

Case 3. Assume now $y(t_1) = 0$ (bottom border). Then, $y' = e \min(1, (p - y)/x) f(x)y - dy \geq -dy$. Hence, $y(t) \geq y(0)e^{-dt} > 0$. This excludes the possibility that a trajectory touches corners $(0, 0)$ and $(k, 0)$ as well.

Case 4. Assume $y(t_1) = p$ (top border). Then

$$y' \leq \hat{e} \frac{p - y}{x} f(x)y \leq \hat{e}(p - y)f'(0)y = \hat{e}f'(0)py \left(1 - \frac{y}{p}\right).$$

Using the standard comparison argument we find that $y(t) < p$ for all $t \in [0, t_1]$. This case takes care of the remaining two corners $(0, p)$ and (k, p) . \square

APPENDIX C: THE PROOF OF THE BOUNDEDNESS AND INVARIANCE THEOREM

Proof. Lemma 1 assures that trajectories will satisfy the first two inequalities in (11). Suppose that the last inequality in (11) is not true. Then let $t_1 > 0$ be the first time it is violated, i.e.,

$$sx(t_1) + y(t_1) = p. \quad (\text{C1})$$

Since for all $t \in [0, t_1)$, $sx(t) + y(t) < p$, it follows that

$$sx'(t_1) + y'(t_1) \geq 0. \quad (\text{C2})$$

From (C1) it follows that $x(t_1) = (p - y(t_1))/s$, which we substitute in (12(a)) to obtain bounds on $x'(t_1)$:

$$\begin{aligned} x'(t_1) &= bx(t_1) \left(1 - \frac{x(t_1)}{\min(K, (p - y(t_1))/s)}\right) - f(x(t_1))y(t_1) \\ &\leq bx(t_1) \left(1 - \frac{x(t_1)}{(p - y(t_1))/s}\right) - f(x(t_1))y(t_1) = -f(x(t_1))y(t_1). \end{aligned} \quad (\text{C3})$$

From (C1) it follows that $s = (p - y(t_1))/x(t_1)$, which we substitute in (12(b)) to obtain bounds on $y'(t_1)$:

$$\begin{aligned} y'(t_1) &= \hat{e} \min\{1, (p - y(t_1))/x(t_1)\} f(x(t_1))y(t_1) - dy(t_1) \\ &\leq \hat{e} \frac{p - y(t_1)}{x(t_1)} f(x(t_1))y(t_1) = \hat{e}sf(x(t_1))y(t_1). \end{aligned} \quad (\text{C4})$$

Using (C3), (C4) and the fact that $\hat{e} < 1$, we obtain the following:

$$\begin{aligned} sx'(t_1) + y'(t_1) &\leq -sf(x(t_1))y(t_1) + \hat{e}sf(x(t_1))y(t_1) \\ &= sf(x(t_1))y(t_1)(-1 + \hat{e}) < 0. \end{aligned}$$

This contradicts (C2) and completes the proof. \square

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