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# Population Interactions in Ecology: A Rule-Based Approach to Modeling Ecosystems in a Mass-Conserving Framework\*

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**Abstract.** Mathematical biology/ecology teaching for undergraduates has generally relied on the Lotka–Volterra competition and predator–prey models to introduce students to population dynamics. Students are provided with an understanding of the application of dynamical system theory in simulating and understanding the behavior of the natural world, and they are provided with opportunities to practice phase plane analysis techniques such as determining the stability of equilibrium points and bifurcation analysis. This paper outlines a course in ecological modeling suitable for all students in the life sciences. The course is based on realistic ecological principles, such as using nutrient concentration to measure populations together with explicit resource availability to constrain population growth, and it considers simple Lotka–Volterra systems within this theoretical framework. An advantage of this approach is that the widely experimentally observed models of mixotrophy and mutualism can be naturally and simply introduced and analyzed. Continuous variation of models across a trophic level is now possible. Competitors can smoothly change to mutualist/mixotroph populations, which can further smoothly change to become predators, synthesizing in simple terms the relationships among trophic interactions within the Lotka–Volterra framework. Standard texts on mathematical ecology do not include mixotrophy, which is central to understanding trophic interactions.

**Key words.** dynamical systems, ecological modeling, mixotrophy

**AMS subject classifications.** 97M10, 92D25

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**I. Introduction.** The need to teach quantitative skills to modern life sciences undergraduate classes in context has long been recognized (for example, [14]) but remains a problem for many institutions and disciplines [16, 23]. Many physical science courses for undergraduate life scientists appear to be reworked discipline-based courses that have included “biological” examples that biologists do not find relevant [16]. In contrast, discipline-based mathematics education programs such as “The Math You Need, When You Need It (TMYN)” are argued to provide a more beneficial and targeted learning experience for nonmathematics undergraduates [23].

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The objective of this paper is to present a simple conceptual framework for teaching dynamical systems in marine ecology courses at the undergraduate level. This conceptual framework is based on examining dynamical systems of a particular form used to model many ecosystems. Although many science students will have had a basic introduction to graphical methods for studying dynamical systems, including solutions to linear, first-order, constant coefficient, homogeneous coupled systems and phase plane analysis (i.e., [15, 2, 11, 18]), it is appropriate to teach these techniques in parallel to this course.

We present students with a set of ecologically sensible criteria for interacting populations and map these criteria to mathematical rules that define a differential-equations-based model of a natural ecology. While it might be argued that simple physical systems are more accessible to all students of science and medicine, and that their solutions are informative in many disciplines, we suggest that the derivation of rules governing living systems, or ecologies, will be more intuitive and useful for students of life sciences. This is similar to an approach advocated for biology [16].

The form of ecological model considered here is based on physical principles such as independence of the per capita population growth rates from the population measuring scales and conservation of mass of the recycled nutrient that defines the ecology, as well as on ecological principles such as the explicit dependence of populations on finite resources. These principles are encapsulated by the rules of the conservative normal framework, which ensures that the systems have Kolmogorov form [3]. One of the objectives of this approach is to show how ecological principles produce dynamical systems with particular mathematical properties that both make for easier analysis allied to interesting results and provide constraints on parameter values to ensure ecological veracity. A final objective is to leave readers with the realization that ecological models can be derived logically, and that the usual, somewhat simple population dynamics models of competition, predation, and mutually supportive behavior may be linked both naturally in ecological terms using mixotrophy and, from a mathematical viewpoint, satisfyingly.

**2. A (Very) Brief History of Ecological Modeling.** First we note the work of a very few of the early contributors that laid the foundations of the modern field of ecosystem modeling.

**2.1. Malthus: The Principle of Population.** The Reverend Thomas Robert Malthus (1766–1834), a British cleric and economist, is known primarily for the influence of his work *An Essay on the Principle of Population* [13], in which he argued that populations grow geometrically while food supply grows only arithmetically. This essay is famous for inspiring Charles Darwin to consider the struggle for existence that all populations must therefore endure, and how the survival of the fittest might affect the attributes of a population. The key message in Malthus’s essay for ecosystem modeling is that the growth of any population is limited by the availability of its resources.

**2.2. Verhulst and Pearl: Carrying Capacity.** The Belgian mathematician Pierre Francois Verhulst (1804–1849) published the equation

$$(2.1) \quad \frac{dX}{dt} = rX \left( 1 - \frac{X}{K} \right),$$

where  $X(t)$  represents the number of individuals in a population at time  $t$ ,  $r$  represents the intrinsic growth rate of the population, and  $K$  represents the “carrying capacity,” or the maximum number of individuals that the environment can support [21]. Equation (2.1) came to be called the logistic equation.

This equation was rediscovered by Raymond Pearl, an American biologist (1879–1940), who published it in a study of the population of the United States [19]. The authors proposed on page 287 that

the hypothesis here advanced as to the law of population growth, even when fitted by a rough and inadequate method, so closely describes the known facts regarding the past history of that growth, as to make it potentially profitable to continue the mathematical development and refinement of this hypothesis further.

Pearl and Reed also cited Malthus in their argument that resources must inevitably place limits on population growth, and hence that simple curves of statistical best fit were of little value in predicting population sizes, even over short time periods. The logistic equation proposed by Verhulst is occasionally called the Verhulst–Pearl (or Pearl–Verhulst, with about an equal number of hits on Google) equation in recognition of its “joint” discovery.

**2.3. Lotka and Volterra: Predator-Prey Systems.** Alfred Lotka (1880–1949), an American mathematician, chemist, and statistician, and Vito Volterra (1860–1940), an Italian mathematician and physicist, independently, but almost simultaneously, published what are now known as the Lotka–Volterra equations for predator-prey systems [12, 22]. Perhaps not surprisingly, Verhulst’s earlier work was noted as being a motivation for both publications.

Volterra is said to have become interested in ecological modeling through his daughter and son-in-law, who were both marine biologists. They had data on Mediterranean fisheries, which indicated that a dramatic increase in the abundance of large predators (principally sharks) had occurred during World War I. They reasoned that this may have been due to the decline of fishing activity in the Mediterranean during the war and sought Volterra’s help to understand their data [11].

Lotka sought to apply the rigor of the physical sciences to biology, and published several works along these lines. His 1925 book *Elements of Physical Biology* (reissued in 1956 as *Elements of Mathematical Biology*) synthesized much of his work on biological systems and introduced the Lotka–Volterra equations we know today, which may be written as

$$(2.2) \quad \begin{aligned} \frac{dx}{dt} &= ax - by, \\ \frac{dy}{dt} &= cxy - dy, \end{aligned}$$

where  $x$  is the prey population and  $y$  the predator population. Here,  $a$  is the intrinsic prey growth rate,  $b$  the rate of predation of the predator on the prey,  $c$  the rate at which the predator population increases as a result of its predation on its prey, and  $d$  is the predator mortality rate. The Lotka–Volterra model makes a number of key assumptions:

- The prey population is not limited by the availability of food.
- The food supply of the predator population is determined solely by the size of the prey population.
- The rate of change of population is proportional to its size.
- The predators can eat an unlimited amount of food.

The Lotka–Volterra equations have the unfortunate property that their solution is a period cycle that is determined by its initial state and repeats unchanged forever. Lotka and Volterra later introduced similar simple models of two competing populations.

**2.4. Kolmogorov: Dynamics of Lotka–Volterra Systems.** An outstanding Russian mathematician, Andrey Kolmogorov (1903–1987) was interested in (among other things) the biological and mathematical conditions that would ensure that one predator—one prey models (such as the Lotka–Volterra equations) had ecologically reasonable solutions, either a stable equilibrium point or a stable limit cycle. The third option for these models is an unstable limit cycle, which he considered ecologically unreasonable because it allows populations to become infinitely large. Kolmogorov considered general predator-prey systems of the form

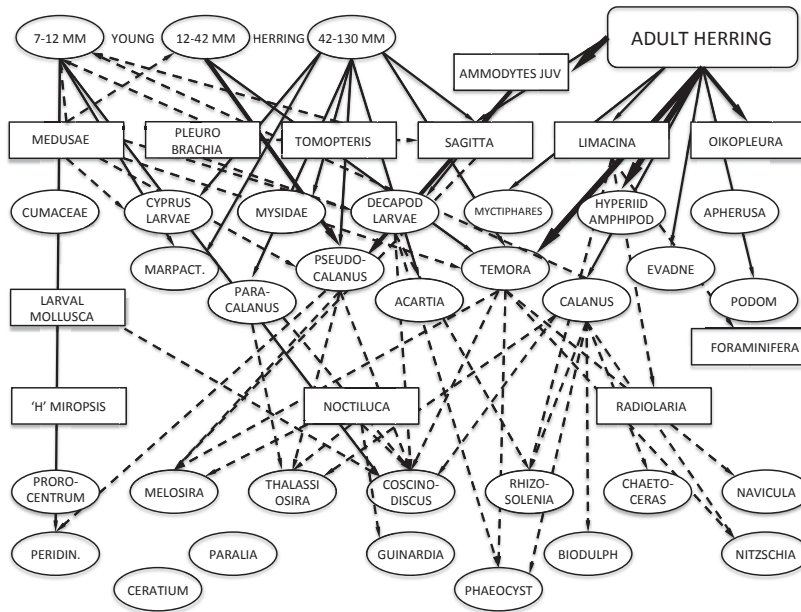
$$(2.3) \quad \begin{aligned} \frac{dH}{dt} &= F(H, P)H, \\ \frac{dP}{dt} &= G(H, P)P, \end{aligned}$$

where he stipulated that what we will call the life functions,  $F(H, P)$  and  $G(H, P)$ , are continuous and have first derivatives for  $H \geq 0$  and  $P \geq 0$ . Such systems are often known as “Kolmogorov systems” (K-systems). We note that Kolmogorov’s nine conditions (on the functional forms of  $F$  and  $G$ ) include an inconsistency between two of the conditions. This ambiguity, and the complexity of implementing Kolmogorov’s nine conditions [10] for just a two-population model, may be why this approach has not been much used or extended to more realistic systems by theoretical ecologists seeking to use mathematical models to understand the dynamics of real ecosystems. Carrying capacity has instead become the prevalent tool used in ecosystem models to constrain their populations from becoming infinite. However, the use of linear and quadratic terms only on the right-hand side (rhs) of (2.3) (known as Lotka–Volterra modeling) has the great advantage of analytical simplicity and will be used in the (later) examples.

**2.5. Gause: Competitive Exclusion.** Based on experimental work with mixed cultures of yeast and the protozoa *Paramecium*, Georgii Frantsevich Gause (1910–1986), a Russian biologist, published his *Principle of Competitive Exclusion* in 1932 [7]. This stated that no two species with similar ecological niches could coexist in a state of equilibrium, and the less efficient species would go locally extinct. Although still considered by some to be a fundamental principle of ecology, in the real world, many species are often found to coexist in natural ecologies [9].

**2.6. Hutchinson: The Paradox of the Plankton.** The English-American limnologist George Evelyn Hutchinson (1903–1991) proposed the *Paradox of the Plankton* [9] as many natural water bodies on Earth, including rivers, lakes, and oceans, contain many species of phytoplankton coexisting in relatively homogeneous environments on just a few resources such as light and nutrients, in contradiction of Gause’s Law. Many scenarios have been proposed to resolve the paradox [4], but no general resolution has been universally accepted, perhaps because plankton coexistence happens in such varied environments.

**2.7. Elton: Food Webs.** The English zoologist and animal ecologist Charles Sutherland Elton (1900–1991) pioneered the concepts of food webs and food chains in his book *Animal Ecology* [5]. Elton also introduced the concepts of functional groups of organisms, trophic levels, the trophic pyramid, ecological niches, and invasive species. Figure 2.1 shows a plankton and fish food web for the North Sea given on page 58 of Elton’s book [5]. The words in boxes in the figure describe the populations that are identified and (possibly) measured. The lines and arrows between boxes show the



**Fig. 2.1** Redrawing of Hardy’s figure of the North Sea plankton community (with phytoplankton shown at the base), which is predated on by herring. These are shown along the top row in their juvenile and adult stages. The middle rows show various zooplankton populations, while the arrows show “who eats whom” (after Elton [5]).

movement of resources (chemicals, organic matter, and populations that are food for other populations) between these populations. Modern computational models simplify these “real” food webs by considering grouped populations and focus on particular aspects of the food web such as the movement of carbon-based material.

**2.8. Bormann: Nutrient Budgets.** Developing understanding of ecosystems by measuring how they cycle nutrients through food webs, such as those described by Elton, is often attributed to the American ecologist F. Herbert Bormann (1922–2012) [1]. He insisted upon studying the dynamics of both biotic and abiotic nutrient compartments in order to understand an ecosystem.

**2.9. Holling: Interactions and Flows.** The arrows in Figure 2.1 represent the qualitative interactions between the populations that they link. Crawford S. (Buzz) Holling (1930–), a Canadian ecologist, showed that these interactions could be formally modeled using three functional types: linear (Type I), hyperbolic (Type II), and sigmoidal (Type III) [8]. These interactions between populations  $x$  and  $y$  are of the form

$$\begin{aligned}
 &axy \quad (\text{Holling Type I}), \\
 (2.4) \quad &\frac{axy}{x+b} \quad (\text{Holling Type II}), \\
 &\frac{ax^2y}{x^2+b} \quad (\text{Holling Type III}).
 \end{aligned}$$

The parameters in (2.4) are chosen to fit experimental data obtained in either the laboratory or the field. This quantifies the flows of nutrients along the arrows in Figure 2.1 and predicts how these flows will change as the populations change. Environmental changes cause the parameters  $a$  and  $b$  to change, and hence affect the nutrient flows, and eventually alter the behavior of the ecosystem. Holling Type I models are of Lotka–Volterra form and are used in the remainder of this paper.

**3. Resources: The Limits to Growth.** The complexity of obtaining analytical solutions to models with more than two populations has led to much ecological theory being derived from, and illustrated by, systems with two interacting populations. Introductory ecological theory usually considers single population models and simple models of interactions between both two competitors and a predator and its prey. The absurdity of unlimited growth is addressed early in these discussions, and a traditional solution is to introduce a parameter called a carrying capacity (section 3.1) to the lowest trophic level in a model [15, 18]. In section 3.2 we introduce the basis of a new approach, the explicit budgeting of a key nutrient that underpins the ecology of interest.

**3.1. The Ecological Meaning of Carrying Capacity.** In this section we outline the widespread use of carrying capacity to represent the limits imposed on population growth by the availability of finite resources. Many theoretical and applied models in ecology include a carrying capacity  $K$  for the lowest trophic level, the logistic equation (2.1) being the simplest example. Here, the equilibrium population size ( $X^*$ , where the population size does not change in time) occurs when  $X^* = K$ , so the carrying capacity represents the capacity for the environment to sustain the population indefinitely, and it always recovers the population to the value  $K$ .

The modern Lotka–Volterra competition model (as discussed by Pastor [18] and others) includes a carrying capacity for both populations:

$$(3.1) \quad \begin{aligned} \frac{dX_1}{dt} &= r_1 X_1 \left( 1 - \frac{(X_1 + a_{12}X_2)}{K_1} \right), \\ \frac{dX_2}{dt} &= r_2 X_2 \left( 1 - \frac{(X_2 + a_{21}X_1)}{K_2} \right), \end{aligned}$$

where  $r_1$  and  $r_2$  are the maximum per capita growth rates of  $X_1$  and  $X_2$ ,  $a_{12}$  represents the per capita effect of population  $X_2$  on population  $X_1$ , and  $a_{21}$  represents the per capita effect of  $X_1$  on  $X_2$ . This model assumes a different carrying capacity for each population ( $K_1$  for population  $X_1$  and  $K_2$  for population  $X_2$ ). Here, the  $X_1$  equilibrium population size occurs when  $X_1^* = K_1 - a_{12}X_2^*$ , and similarly the  $X_2$  equilibrium population size occurs when  $X_2^* = K_2 - a_{21}X_1^*$ . The carrying capacities might sensibly be interpreted to represent the capacity for the environment to sustain a population, say,  $X_1$ , indefinitely at  $X_1 = K_1$  if no other populations are present. The equilibrium population size  $X_1^*$  is reduced below the carrying capacity  $K_1$  if a competing population  $X_2$  is present, and vice versa.

The original Lotka–Volterra predator–prey model is well known to be structurally unstable, and hence is often modified by including a carrying capacity to constrain the prey’s growth:

$$(3.2) \quad \begin{aligned} \frac{dX_1}{dt} &= r_1 X_1 \left( 1 - \frac{X_1}{K} \right) - hX_1 X_2, \\ \frac{dX_2}{dt} &= \beta h X_1 X_2 - mX_2, \end{aligned}$$

where  $r$  represents the maximum per capita growth rate of  $X_1$ ,  $h$  represents the rate of predation of  $X_2$  on  $X_1$ ,  $\beta$  represents the fraction of  $X_1$  biomass that is converted to  $X_2$ , and  $m$  is the per capita mortality rate of  $X_2$ . Again,  $K$  may be considered the carrying capacity of the environment for  $X_1$  in the absence of  $X_2$ . Note that the equilibrium state of  $X_1$  is defined by  $m/\beta h$ , which is not related to  $K$ . We will see later that  $m/\beta h$  must be less than  $K$  if  $X_2$  is to survive in the system. This places a rather different interpretation on  $K$ , and its role in this system is not consistent with the previous interpretations.

**3.2. Carrying Capacity and Conservation of Nutrient Mass.** We now contrast the carrying capacity approach with an approach commonly used for biogeochemical modeling, that of conservation of mass of a limiting resource. In the latter approach, the finite capacity of the environment is represented in the model by a finite amount of (limiting) resource  $N$  that is conserved in the ecology under consideration. By a finite limiting resource we mean some resource (generally a nutrient or micronutrient which is essential for the growth of a population) that is available in some finite quantity, and which causes the growth of the population to cease when it has been used up. We use  $N$  to represent this nutrient in its available dissolved form in a given volume of the ocean, and refer to it when among the active (living) populations in the ecosystem being studied simply as the nutrient.

Liebig's Law of the Minimum (a principle developed in agricultural science by Carl Sprengel in 1828 and later popularized by Justus von Liebig) states that the nutrient in least supply constrains the growth of organisms, irrespective of the availability of other nutrients. This law is often invoked to justify the inclusion of only one limiting nutrient (usually nitrogen in the ocean) in ecosystem models. Contemporary complex plankton computer models may, however, resolve several (typically two or three) nutrients, such as carbon, phosphorous, calcium, and silicon, and micronutrients such as iron, that may limit the growth of various organisms at different times.

We consider the equivalence of simple Lotka–Volterra models, which use carrying capacity to reflect the constraints imposed on populations by finite resources, with equivalent models that include these constraints explicitly. It may be shown that Lotka–Volterra models with one and two trophic levels that use carrying capacity are equivalent to Lotka–Volterra models that explicitly include finite resources. Here we consider a nutrient mass-conserving Lotka–Volterra model with three trophic levels and leave the one- and two-trophic level cases as an exercise [3]. In the three-trophic level model an autotroph population  $x_1$  consumes a resource (inorganic nutrient  $N$ ), and a herbivore  $x_2$  consumes  $x_1$  and is in turn consumed by a carnivore  $x_3$ :

$$\begin{aligned}
 \dot{x}_1 &= \hat{r}N x_1 - \hat{c}_1 x_1 x_2 - d_1 x_1, \\
 \dot{x}_2 &= \hat{c}_1 x_1 x_2 - \hat{c}_2 x_2 x_3 - d_2 x_2, \\
 \dot{x}_3 &= \hat{c}_2 x_2 x_3 - d_3 x_3, \\
 \dot{N} &= d_1 x_1 + d_2 x_2 + d_3 x_3 - \hat{r}N x_1.
 \end{aligned}
 \tag{3.3}$$

Here  $x_1$ ,  $x_2$ ,  $x_3$ , and  $N$  are measured in the same currency, the mass or concentration of nutrient in that population or ecological compartment. Then  $x_1$  represents the mass of nutrient that is incorporated into the autotroph population, which feeds (at a per capita rate  $\hat{r}$  which, as always, will involve the available sunlight, etc.) directly on the inorganic (available) nutrient  $N$  dissolved in the seawater,  $x_2$  is a herbivore that feeds (at a per capita rate  $\hat{c}_1$ ) on the autotroph  $x_1$ , and  $x_3$  is a carnivore that



feeds on  $x_2$  at a per capita rate  $\hat{c}_2$ . The per capita mortality rates of the populations are given by  $d_1$ ,  $d_2$ , and  $d_3$ , respectively.

Conservation of mass means  $x_1 + x_2 + x_3 + N = N_T$ , where  $N_T$  is the total (constant) mass of nutrient that is cycling in the ecology, or equivalently  $dx_1/dt + dx_2/dt + dx_3/dt + dN/dt = 0$  together with  $N_T$ . Note that this property of the model implies the assumption of instantaneous remineralization of nutrient from dead organic form that is not available to the autotroph, to inorganic form  $N$  that is. This process is represented in the model in the  $d_1x_1$ ,  $d_2x_2$ , and  $d_3x_3$  terms.

Equation (3.3) may be rewritten using  $dx_1/dt + dx_2/dt + dx_3/dt + dN/dt = 0 \iff x_1 + x_2 + x_3 + N = N_T$  (with the usual meaning for  $N_T$ ) as

$$\begin{aligned} \dot{x}_1 &= \hat{r}(N_T - x_1 - x_2 - x_3)x_1 - \hat{c}_1x_1x_2 - d_1x_1, \\ \dot{x}_2 &= \hat{c}_1x_1x_2 - \hat{c}_2x_2x_3 - d_2x_2, \\ \dot{x}_3 &= \hat{c}_2x_2x_3 - d_3x_3. \end{aligned} \tag{3.4}$$

Equation (3.4) may be written as a Lotka–Volterra system with a carrying capacity  $K$ ,

$$\begin{aligned} \dot{x}_1 &= rx_1 \left(1 - \frac{x_1}{K}\right) - c_1x_1x_2 - \frac{r}{K}x_1x_3, \\ \dot{x}_2 &= c_1x_1x_2 - c_2x_2x_3 - d_2x_2, \\ \dot{x}_3 &= c_2x_2x_3 - d_3x_3, \end{aligned} \tag{3.5}$$

by defining new parameters  $K = N_T - d_1/\hat{r}$ ,  $r = \hat{r}K$ , and  $c_1 = \hat{r} + \hat{c}_1$ . This model is *not* equivalent to the usual three-trophic level Lotka–Volterra system with a carrying capacity [15, 11, 18],

$$\begin{aligned} \dot{x}_1 &= rx_1 \left(1 - \frac{x_1}{K}\right) - c_1x_1x_2, \\ \dot{x}_2 &= c_1x_1x_2 - c_2x_2x_3 - d_2x_2, \\ \dot{x}_3 &= c_2x_2x_3 - d_3x_3, \end{aligned} \tag{3.6}$$

because the usual form (3.6) does not include the interaction term  $\hat{r}x_1x_3 = (r/K)x_1x_3$ . This term in the mass conservation context represents the fact that the nutrient assimilated into the  $x_3$  population is not available to fuel  $x_1$ 's growth. We note that the use of a simple carrying capacity in three- (and higher) trophic level models is unrealistic because, although it constrains the population size of the lowest trophic level to ecologically reasonable limits, it can allow higher trophic levels to have unbounded growth [3]. This can occur because the nutrient is not explicitly budgeted in the system, even though the population gains and losses are measured in terms of that nutrient.

As we consider more complicated models with multiple populations, the view that  $K$  represents the “carrying capacity of the environment” becomes increasingly tenuous as the “environment” now includes other populations, and  $K$  should formally and consistently reflect this. More exotic models, such as those representing mutualism that require negative carrying capacities [18], do not meet this criterion. Rather than develop tenuous conceptual models to incorporate the influence of other populations on  $K$ , we present a theoretical framework that explicitly represents the finite resources that each population requires to survive and grow. We refer to this as the conservative normal framework because it conserves total nutrient mass in the system and

represents normal (or natural) populations that have smoothly increasing per capita rate dependencies on resources as the amount of resource increases.

We next formalize the criteria that ensure that all populations have consistent and realistic ecological properties. This is irrespective of the number of interacting populations and the number of trophic levels, but we do restrict the form and complexity of the interactions to Holling Type I (see section 2.9). We note that the rules have been extended to include nonlinear life functions such as Holling Type II and III in Cropp and Norbury [3].

**4. The Conservative Normal Framework.** In this chapter we describe the rules, with their ecological interpretation, that set out a theoretical framework for constructing realistic ecological models within the Lotka–Volterra setup.

The conservative normal (CN) framework captures sufficient fundamental ecological properties of living marine systems with mathematical rules that computer models, whose simulations reproduce basic experimental results, may be constructed. These rules formalize basic ecological concepts, principally that all organisms have to consume resources to survive, that the availability of more resources improves the population's per capita growth rate, and that these resources are finite. We identify a system by defining a boundary to separate it from the rest of the ecological world. This may be a physical boundary such as the shore of a pond or the wall of a mesocosm, or a conceptual boundary such as considering the dynamics in a representative cubic meter of ocean. We then consider the ecological constraints that control the dynamics of populations living in the closed system and encapsulate these basic principles in formal mathematical rules. CN systems are population/ecological dynamical systems that comply with the following five CN rules.

LVCN systems are Lotka–Volterra systems (that is, systems with linear equations (4.1) for the per capita life functions) that are modified to explicitly include a limiting nutrient and that comply with the CN rules (see sections 4.1–4.5) for ecological verisimilitude. A general  $n$ -population Lotka–Volterra system has the form

$$(4.1) \quad \dot{x}_i = x_i f_i(x_1, x_2, \dots, x_n) = x_i \left( r_i - \sum_{j=1}^n a_{ij} x_j \right), \quad i = 1, 2, \dots, n,$$

where the constants  $r_i$ ,  $a_{ij}$  describe how the populations grow and interact and determine the actual forms of the life functions  $f_i$ . The  $r_i$  parameters describe the net (growth minus losses) interaction rates of the populations  $x_i$  with inorganic nutrient  $N$ . If  $x_i$  is an autotroph,  $r_i$  is positive, indicating that autotrophs utilize inorganic nutrient to grow and loss processes are relatively small, whereas if  $x_i$  is a heterotroph, which cannot utilize inorganic nutrient to grow,  $r_i$  is negative, indicating that only loss terms connect heterotrophs to inorganic nutrient. The  $a_{ij}$  parameters describe the rates of interactions between the population  $x_i$  and the population  $x_j$ . These parameters may take any sign, or be zero, depending on the nature of the interaction between the populations. For example, if  $x_j$  was a predator on  $x_i$ ,  $a_{ji}$  would be negative, indicating a transfer of mass from  $x_i$  to  $x_j$ , and  $a_{ij}$  would be positive, indicating that  $x_i$  lost mass to  $x_j$ . We shall return to this topic in greater detail in section 9.1, where we will consider the parameter profiles for various trophic strategies.

Lotka–Volterra models are often used as conceptual models when  $n$  is small, and for large simulation studies when  $n > 100$  [20], to understand the implications of basic processes such as species competition on population extinctions.

We shall, in common with almost all introductory ecological theory, consider the two-population LVCN system

$$(4.2) \quad \begin{aligned} \dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2), \\ \dot{x}_2 &= x_2(r_2 - a_{21}x_1 - a_{22}x_2). \end{aligned}$$

Every system of the form (4.2) has four equilibrium points in the  $x_1, x_2$  plane:

$$(4.3) \quad \begin{aligned} C_0 &: \{x_1^* = 0, x_2^* = 0\} \quad (\text{origin equilibrium point}), \\ C_1 &: \left\{x_1^* = \frac{r_1}{a_{11}}, x_2^* = 0\right\} \quad (\text{boundary equilibrium point}), \\ C_2 &: \left\{x_1^* = 0, x_2^* = \frac{r_2}{a_{22}}\right\} \quad (\text{boundary equilibrium point}), \\ C_3 &: \left\{x_1^* = \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}, x_2^* = \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}}\right\} \quad (\text{coexistence equilibrium point}). \end{aligned}$$

**4.1. CN Rule 0: How We Measure the System.** We assume each interacting population is sufficiently large in number (millions, billions, ...) that we can ignore the typical individual and instead define a measure of the population mass in the isolated physical volume that the ecosystem occupies. Plankton ecosystems are exemplars of these assumptions, and considerable ecological theory has been developed from the study of such systems. We measure each population by the amount of a key limiting nutrient that it contains—in marine systems this is typically nitrogen. At time zero ( $t = 0$ ) we measure the amount of the limiting nutrient in each living population  $\hat{x}_i$  present in the ecosystem, together with the amount of inorganic (dead) nutrient  $\hat{N}$  available to those  $n$  interacting populations:

$$(4.4) \quad \hat{x}_1 + \hat{x}_2 + \cdots + \hat{x}_n + \hat{N} = \hat{N}_T.$$

We then scale the measurements  $\hat{x}_i, \hat{N}$  by the total measure of nutrient  $\hat{N}_T$  that is cycling in the system, so that our populations are measured as fractions of the total nutrient in the system:

$$(4.5) \quad x_1(0) + x_2(0) + \cdots + x_n(0) + N(0) = 1,$$

with  $0 < x_i(0), N(0) < 1$ . Each living population is now measured in terms of the fraction (of the total amount of cycling nutrient) that is bound into the living tissues of the individuals of that population. The amount of inorganic nutrient  $N$  in the seawater is also expressed as a fraction of the total cycling nutrient, which has been scaled to be one. A key limiting nutrient is one in which each population in the ecology can be suitably measured; further, when the available inorganic nutrient is exhausted ( $N = 0$ ), all the other necessary nutrients for population life are still available. The explicit use of nutrient in the model ecology means that the costs and benefits of population interactions can be appropriately measured in this common currency.

**4.2. CN Rule 1: How Living Populations Change.** We make the assumption that there is no migration into or out of the model domain, that is, no individuals or inorganic nutrient cross the boundary that defines the model. Since the per capita population growth rates must be independent of the way in which we measure the living populations, we assume that the life functions  $\hat{f}_i$  defined in (4.6) are functions

only of  $x_i$  and  $N$ . The per capita population growth rate of any population  $x_i$  (positive) then satisfies

$$(4.6) \quad \frac{1}{x_i} \frac{dx_i}{dt} = \hat{f}_i(x_1, x_2, \dots, x_n; N).$$

Time is usually measured in days in marine plankton modeling and henceforth we follow this convention. The life functions  $\hat{f}_i$  describe how each population grows (or dies) dependent on interactions with the other populations in the system and with inorganic nutrient. Autotrophs and nonautotrophs have slightly different life functions:

$$(4.7) \quad \frac{1}{x_i} \frac{dx_i}{dt} = \hat{f}_i(x_1, x_2, \dots, x_n; N) = \begin{cases} r_i N - \sum_{j=1}^n \hat{a}_{ij} x_j & \text{for autotrophs,} \\ r_i - \sum_{j=1}^n a_{ij} x_j & \text{for nonautotrophs.} \end{cases}$$

The life functions will implicitly include parameters that quantify the rates of these interactions, so that, for instance, sunlight intensity, seawater acidity, etc., are implicitly included in the  $\hat{f}_i$ . Note that the form (4.6) ensures that the living population measures  $x_i(t)$  can never become negative, a fundamental property that all ecosystem models must share.

**4.3. CN Rule 2: Conservation of Nutrient Mass.** Consistent with the assumption that there is no population migration into or out of the model domain, we formally require that the mass of nutrient in the model domain remains constant for all time, that is, there is no loss or gain of the cycling nutrient (in either organic or inorganic form) into or from outside the model domain. The living population fractions  $x_i(t)$  and the inorganic nutrient fraction  $N(t)$  then always satisfy a conservation of total nutrient mass constraint for all time  $t > 0$ ,

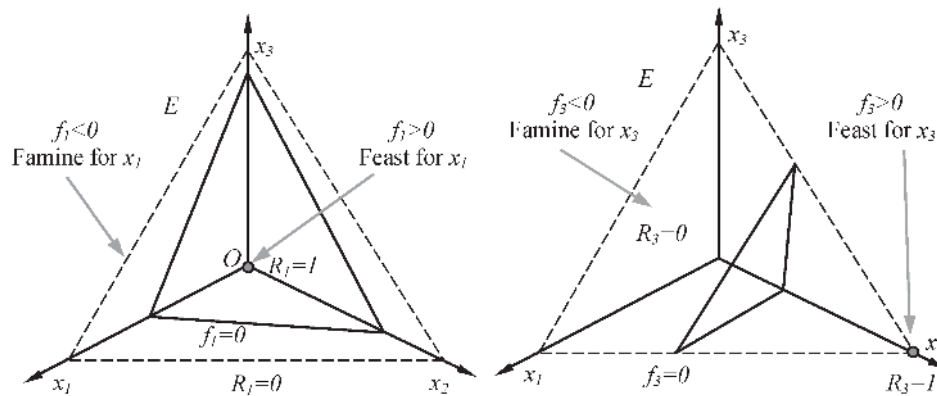
$$(4.8) \quad x_1(t) + x_2(t) + \dots + x_n(t) + N(t) = 1.$$

This fundamental constraint allows us to eliminate  $N(t)$  from the living population equations  $\hat{f}_i(x_1, \dots, x_n : 1 - \sum x_i) \equiv f_i(x_1, \dots, x_n)$ , so that (4.7) may be written, for all populations  $x_i(t) > 0$ , as

$$(4.9) \quad \frac{1}{x_i} \frac{dx_i}{dt} = f_i(x_1, x_2, \dots, x_n) = r_i - \sum_{j=1}^n a_{ij} x_j,$$

where for autotrophs  $a_{ij} = r_i + \hat{a}_{ij}$ . This also eliminates the need for a separate equation to describe the changes in inorganic nutrient, since once all the living populations are known from (4.9) we can infer the amount of  $N(t)$  at any time from (4.8).

**4.4. CN Rule 3: The Lid and the Ecospace.** The world's resources are finite, and this is particularly relevant to marine plankton models, where it is well known that phytoplankton regularly use up the entire available inorganic nutrient in the ocean mixed layer during their summer bloom—their population growth then ceases as a result. We must ensure that our ecosystem models have realistic behavior when the inorganic nutrient runs out. CN Rule 3 stipulates a lid, defined by  $\{x_1 + x_2 + \dots + x_n = 1\}$ , on the model's state space  $x_i > 0$  for all  $i$ , which ensures that the inorganic nutrient measure  $N(t)$  in the model cannot become negative. The lid completes the closure of the state space in which reasonable model solutions exist, and hence defines the ecospace  $E$  (see Figure 4.1).



**Fig. 4.1** The ecospace ( $E$ ), resources ( $R_i$ ), and zero isosurfaces ( $f_i = 0$ ) for an autotroph, where  $x_1$  feeds on inorganic nutrient (left panel), and for a nonautotroph, where  $x_3$  feeds on  $x_2$  (right panel). The dashed line shows the lid, part of the boundary of  $E$ , where  $N = 0$ . For the autotroph  $x_1$ , the origin is the feast and the lid is the famine; for the nonautotroph  $x_3$ , the feast is at the point  $x_2 = 1$  and the famine is on the face  $x_2 = 0$ .

We differentiate (4.8) to obtain an equation describing how  $N$  changes in accordance with CN Rule 2:

$$(4.10) \quad \frac{dN}{dt} = -\frac{dx_1}{dt} - \frac{dx_2}{dt} - \dots - \frac{dx_n}{dt} = -\sum_{i=1}^n x_i f_i(x_1, \dots, x_n) = -\sum_{i=1}^n x_i \left( r_i - \sum_{j=1}^n a_{ij} x_j \right).$$

Next, we need to check for sensible behavior on the lid  $\{x_1 + x_2 + \dots + x_n = 1\}$  (i.e., where  $N = 0$ ), since although  $N$  disappears from equations (4.9) we must never have  $N(t) < 0$  in (4.8), and this requires  $\sum x_i \leq 1$ . This implies a lid condition that whenever  $N = 0$  we have  $dN/dt = -\sum x_i f_i > 0$ , which amounts to a consistency condition on equations (4.9) to ensure that  $N(t) > 0$  when it is defined by (4.8).

We can now define an ecospace  $E$  for solutions to the dynamical system (4.9) to be the unit simplex:

$$(4.11) \quad E \equiv \{0 < x_i, 0 < x_1 + x_2, \dots, x_n < 1\}.$$

The lid condition guarantees that solutions  $\{x_1(t), x_2(t), \dots, x_n(t)\}$  of equations (4.9) which start in  $E$  do not leave  $E$  through the lid.

We check that the nutrient equation  $\dot{N} = -\sum_{i=1}^n x_i (r_i - \sum_{j=1}^n a_{ij} x_j)$  is positive everywhere on the lid  $\{x_1 + x_2 + \dots + x_n = 1\}$ . This condition is not necessarily satisfied for all parameter values for LVCN systems and must be checked for each system considered. However, the lid condition does provide one generic condition on the parameters:  $\dot{N} > 0$  holds at each vertex of the lid  $x_j = 1$  with  $x_i = 0$  for  $i \neq j$ , where the vertices are given by  $j = 1, \dots, n$ , which implies

$$(4.12) \quad a_{jj} > r_j \text{ for each } j.$$

The lid condition therefore places on every population, irrespective of its trophic interactions or level, the constraint that the dependence of the per capita self-regulating effect on its increasing population size exceeds its maximum per capita growth rate.

Whenever a population has a net positive linear growth term  $r_i x_i$ , its quadratic mortality term  $-a_{ii} x_i^2$  must have  $a_{ii} > r_i > 0$ .

**4.5. CN Rule 4: Resources and Normal Ecosystems.** All living populations  $x_j$  require food to survive and grow. This food might be inorganic nutrient in the cases of autotrophs, or prey (i.e., other living organisms) in the cases of nonautotrophs. These resources  $R_j$  (for population  $j$ ) are finite and limit the growth of population  $x_j$  when they become depleted; hence resources should be explicitly represented in ecosystem models, otherwise a population could have unlimited growth. We define two basic criteria with which a living population (measured by  $x_j$ ) must comply:

- when its resources are maximal ( $R_j = 1$ ), the population  $x_j$  must be able to grow; and
- when there is no resource available ( $R_j = 0$ ), the population  $x_j$  must die.

This means that each life function must satisfy the natural resource constraints

$$(4.13) \quad f_j|_{R_j=1} > 0 > f_j|_{R_j=0},$$

where  $R_j$  is the resource that  $x_j$  requires for survival. Note: for nonautotroph populations  $x_j$  that feed on another population  $x_i$ ,  $R_j = x_i$  where  $i < j$ ; conventionally, the populations are numbered from the lowest trophic level to the highest. In the case of autotrophs, which feed on inorganic nutrient  $N$ , their resource is  $R_j = x_0 = N$ . This resource is a maximum at the origin of  $E$  (where all living populations are zero and hence the conservation of mass constraint means that inorganic nutrient must be maximum) and a minimum on the lid of  $E$ , which is defined by  $N = 0$ .

The food web description of the ecology implies that each population  $x_j$  has a resource  $R_j$  (which may be one or more of  $N, x_1, x_2, \dots, x_{j-1}$ ). This means that, for each  $x_j$ , we can divide the boundary of  $E$  into regions of “famine” where  $R_j = 0$  and regions of “feast” where  $R_j = 1$ . These resource constraints mean that the vertex of  $E$  where  $x_j = 1$  is always part of the famine boundary, since then all  $x_i = 0$  (for  $i < j$ ) using (4.8).

The conditions (4.13) mean that each population must have just one zero isosurface (defined by  $f_j = 0$ ) that divides the ecospace into two parts: a part in which the population can grow and a part in which the population declines (see Figure 4.1). Equilibrium points, where all populations remain constant, occur where these zero isosurfaces intersect. Note that each population also has a second zero isosurface (defined by  $x_j = 0$ ) which is part the boundary of  $E$ ; that is, a coordinate boundary of the ecospace (edge, face, etc.) is also a zero isosurface for the appropriate population. Boundary equilibrium points are defined by at least one of the  $x_j = 0$ . LVCN systems have the property that all zero isosurfaces (or isoclines)  $f_j = r_j - a_{j1}x_1 - \dots - a_{jn}x_n = 0$  are (hyper)planes that cut  $E$  into the part adjoining the  $x_j$  resource maximum, where  $f_j > 0$ , and the remaining part where  $f_j < 0$ . Note that a property of linear functions is that the life functions always monotonically increase along straight lines from the famine to the feast boundaries of  $E$ . Note further that the CN rules have additional criteria to deal with nonlinear systems that are not discussed here, but are available in Cropp and Norbury [3].

**4.6. CN Rules and Trophic Status.** CN Rule 4 does not provide generic parameter constraints (as CN Rule 3 does) because each population is usually evaluated from a different vertex or face of  $E$ . We must therefore derive different constraints for each population. Here, we shall apply the rules to an autotroph population as an example, and we consider the properties of other populations (mixotrophs, predators, etc.) in the later sections.

Autotrophs utilize inorganic nutrient  $N$  as their food source. This is implicitly represented in LVCN systems. The conservation of mass criterion  $N = 1 - x_1 - x_2 - \dots - x_n$  indicates that  $N$  is a maximum at the origin of  $E$ , where  $x_j = 0 \forall j$ , and is zero on the lid of  $E$ , where  $x_1 + x_2 + \dots + x_n = 1$ . The sign conditions (4.13) place constraints on the sign of the  $f_j$  at these extremes (see Figure 4.1). The maximum resource condition for an autotroph  $x_j$  feeding on inorganic nutrient  $N$  is evaluated at the origin of  $E$  and stipulates

$$(4.14) \quad f_j|_{R_j=N=1} > 0 \Rightarrow r_j > 0.$$

The zero resource condition may be evaluated at each of the lid vertices and stipulates that

$$(4.15) \quad f_j|_{R_j=N=0} < 0 \Rightarrow r_j < a_{ji}, \quad i = 1, 2, \dots, n,$$

which (as a bonus) ensures that autotrophs will always satisfy the lid condition following (4.10).

Summarizing (4.14) and (4.15) reveals that an autotroph population  $x_j$  will always be subject to the parameter constraints

$$(4.16) \quad 0 < r_j < a_{ji}, \quad i = 1, 2, \dots, n.$$

#### 4.7. A Single Autotroph LVCN Model.

The one-population LVCN system

$$(4.17) \quad \dot{x} = x(r - ax)$$

is the simplest possible LVCN model. Application of the CN rules to (4.17) provides the parameter constraint (a simplified version of (4.16))

$$(4.18) \quad 0 < r < a.$$

We again check the lid condition (as we did in finding (4.12)), whence it is easily seen that

$$(4.19) \quad \dot{N} = -x(r - ax) > 0 \quad \text{when} \quad x = 1,$$

that is,  $\dot{N}$  is always positive on  $N = 0$  for the parameter constraints (4.18). The lid condition is always satisfied for autotroph-only LVCN systems that satisfy the resource sign inequalities of CN Rule 4.

Equilibrium points are calculated by putting the rhs of (4.17) to zero. Boundary equilibrium points are defined to be where at least one  $x_j = 0$ ; here, the only boundary equilibrium point is the origin  $x^* = 0$ . The interior equilibrium point is where  $f_j = 0$ ; here, the interior equilibrium point is  $x^* = r/a$ . In what follows, when considering ecologies with more than one population, these points are known as autotroph points, because an autotroph population can survive at this size if the other populations are zero.

To calculate the stability of an equilibrium point we have to linearize the rhs of (4.17) at the equilibrium point, find the exponential solutions, and define the eigenvalues to be the exponents of the solutions. Stability occurs when the real parts of all the exponents are negative. Otherwise, the point is unstable. Here, the linearized rhs at the origin gives the stability equation  $\dot{y} = ry$ , with solution  $y = ce^{rt}$ . Since the eigenvalue  $\lambda = r > 0$ , the origin is unstable. Similarly, the stability equation at  $x^* = r/a$  is  $\dot{y} = -ry$ , with solution  $y = ce^{-rt}$ . Here, the eigenvalue  $\lambda = -r < 0$ , so the point  $x^* = r/a$  is stable.

The parameter constraint (4.18) means that for all one-population LVCN systems:

- The origin equilibrium point, henceforth labeled  $C_0$ , is an unstable node with the eigenvalue  $\lambda_{C_0} = r > 0$ . This indicates that an autotroph is always able to grow in a world composed only of inorganic nutrient (a feast).
- The autotroph-only equilibrium point, henceforth labeled  $C_1$ , always exists in the ecospace  $E$  as  $0 < x^* = r/a < 1$ . This point has one attracting eigenvalue  $\lambda_{C_1} = -r < 0$  and is stable.

The vector fields on the unit interval of the  $x$  axis point toward the autotroph point  $C_1$ . Note that this property still holds for the autotroph axes in a more general  $n$ -population system, where the multiple autotroph points are now  $r_j/a_{jj}$ .

**5. Predator-Prey LVCN Systems.** Our first example of introductory ecological theory (which also appears in nearly all mathematical biology and ecology texts) is that of predator-prey systems of the form (4.2). Recall that under the CN framework, systems of the form (4.2) are always derived from systems of the form (4.7), and we must remain mindful of the  $\hat{a}_{ij}$  parameters. In LVCN systems the lowest trophic level must always be an autotroph, so here, and by convention,  $x_1$  is the prey and  $x_2$  is the predator. Note that  $a_{21}$  is conventionally negative, so that  $-a_{21}x_1x_2$  represents the gain of material that the predator receives, and that which the prey loses is  $\hat{a}_{12}x_1x_2$ . Since we measure each population in the standard currency of nutrient, and the predator gains from the prey only by consuming it and converting it with some less-than-perfect efficiency into predator biomass, then  $-a_{21}x_1x_2 \leq \hat{a}_{12}x_1x_2$ . Hence, we may include the additional parameter constraint  $0 < -a_{21} \leq \hat{a}_{12}$ . If  $-a_{21} > \hat{a}_{12}$ , then the predator gains additional nutrient, which is a form of mutualism with  $x_1$  behaving as a catalyst—see section 9.

All autotrophs in LVCN systems have the characteristics of autotrophs described in (4.16). Here we only have one autotroph, so  $0 < r_1 < a_{11}, a_{12}$ . The resource for the nonautotroph (grazer / predator) population  $x_2$  is the prey population  $x_1$  upon which it feeds. This resource  $R_2$  has a maximum at the point where  $x_1 = 1$  (feast) and a minimum on the edge of  $E$  where  $x_1 = 0$  (famine); see Figure 5.1. The maximum resource condition stipulates

$$(5.1) \quad f_2|_{R_2=x_1=1} > 0 \Rightarrow r_2 > a_{21},$$

while the zero resource condition evaluated on the zero resource edge at the origin of  $E$  reads

$$(5.2) \quad f_2|_{R_2=0} < 0 \Rightarrow r_2 < 0,$$

and evaluated at the other end of the zero resource edge where  $x_2 = 1$  reads

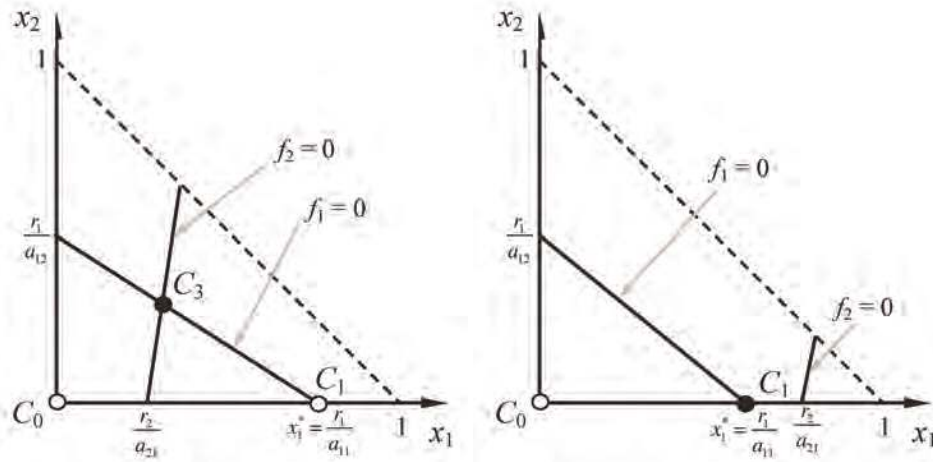
$$(5.3) \quad f_2|_{R_2=0} < 0 \Rightarrow r_2 < a_{22}.$$

A predator population  $x_2$  feeding on a single prey population  $x_1$  is subject to the parameter constraints (5.1)–(5.3):

$$(5.4) \quad a_{21} < r_2 < 0 \quad \text{and} \quad r_2 < a_{22}.$$

Because nonautotrophs  $x_j$  grow by consuming prey, the coefficient (in this example  $a_{ji}$ ) of their interaction with the prey population  $x_i$  must be negative, so that the interaction has a positive effect on the predator population. Note that the





**Fig. 5.1** The cases for a predator-prey system: coexistence (left) and extinction of  $x_2$  (right). In each case, the boundary equilibrium point  $C_0$  at the origin  $\{0,0\}$  is unstable and the prey point  $C_1$  at  $\{x_1^* = r_1/a_{11}, 0\}$  is unstable (left) or stable (right). The coexistence equilibrium point is stable whenever it exists in  $E$ . Stable equilibrium points are shown as black dots and unstable equilibrium points as white dots.

coefficient of the effect of the predator on the prey population remains positive, representing a negative effect of the predator on the prey. Many predator-prey models take  $r_2 < 0 = a_{22}$ .

The parameter constraints above have the following ecological interpretations:

- For the prey  $x_1$  (which must be an autotroph),  $0 < r_1 < a_{11}, a_{12}$  means that the maximum rates of intrapopulation competition and interpopulation predation (achieved when  $x_1 = 1, x_2 = 0$  and  $x_1 = 0, x_2 = 1$ , respectively) must exceed the maximum growth rate of the autotroph.
- For the predator  $x_2$ ,  $a_{21} < r_2 < 0$  means that the maximum rate of growth due to interpopulation predation must be more than the density-independent mortality rate.

We finally check the lid condition (equation (4.10)) using these parameter constraints. The lid condition

$$(5.5) \quad \dot{N} = -x_1(r_1 - a_{11}x_1 - a_{12}x_2) - x_2(r_2 - a_{21}x_1 - a_{22}x_2) > 0 \quad \text{when} \quad x_1 + x_2 = 1$$

holds for the restricted case  $r_1 \leq -r_2$  and  $a_{12} > -a_{21}$ . This case describes a predator with a sufficiently large linear mortality with respect to the linear growth rate of the prey. For the case  $a_{12} = -a_{21}$  (effectively an example of mutualism) with  $r_2$  and  $a_{22}$  very small the lid condition fails (a simple calculation shows that  $\dot{N} = -r_1^2/4a_{11}$  plus very small terms at its minimum value on the lid near where  $x_1 = r_1/2a_{11}$ ). This case describes a predator with very weak mortality terms (i.e., little constraint on its population growth), in which case conservation of nutrient fails.

For intermediate cases, a simple, pragmatic option is then to numerically evaluate (5.5). Otherwise, we substitute in the expression for  $x_2 = 1 - x_1$  and find its minimum for  $0 < x_1 < 1$ .

The parameter constraints mean that for all two-population LVCN predator-prey systems:

- The origin equilibrium point ( $C_0$ ) is a saddle with eigenvalues  $\lambda_{C_0-1} = r_1 > 0$  and  $\lambda_{C_0-2} = r_2 < 0$ . This indicates that an autotroph will always be able to grow along the  $x_1$  axis in a world composed only of inorganic nutrient.
- The prey (autotroph) boundary equilibrium point ( $C_1: 0 < x_1^* = r_1/a_{11} < 1$ ) has one attracting eigenvalue  $\lambda_{C_1-1} = -a_{11}x_1^* = -r_1 < 0$ . This indicates that the autotroph by itself always has an ecologically realistic equilibrium, and
  - The stability of  $C_1$  is determined by the sign of the predator’s life function evaluated at that point ( $\lambda_{C_1-2} = r_2 - a_{21}x_1^* = r_2 - a_{21}(r_1/a_{11})$ ). This indicates that if a predator (grazer) cannot grow on its prey (the autotroph), the prey alone will stably survive (as an exercise, verify that  $-a_{21}$  very small will lead to the eigenvalue  $\lambda_{C_1-2} \approx r_2 < 0$ ).
- The predator equilibrium point ( $C_2$ ) is not in the boundary of the ecospace  $E$  when  $a_{22} > 0 > r_2$  as  $x_2^* < 0$ , and when  $r_2 < a_{22} < 0$  as  $x_2^* > 1$ . This indicates that predators cannot exist without their prey.
- The existence of the coexistence equilibrium point ( $C_3$ ) in  $E$  depends solely on the intersection of the zero isoclines  $f_1, f_2 = 0$  in  $E$ . The condition  $0 < r_2/a_{21} < r_1/a_{11}$  ensures that the  $f_1 = 0$  and  $f_2 = 0$  isoclines intersect in  $E$  (see Figure 5.1 (left); it is left as an exercise to verify that the slopes of the isoclines, and their intersections with the  $x_1$  axis, are as shown). Otherwise,  $C_3$  cannot exist in  $E$  as  $r_2/a_{21} > r_1/a_{11}$  and  $r_2/a_{22} < 0$ —see Figure 5.1 (right) as an example of an inefficient predator where  $f_2 < 0$  at  $C_1$ . This predator can only grow at very high prey abundances.

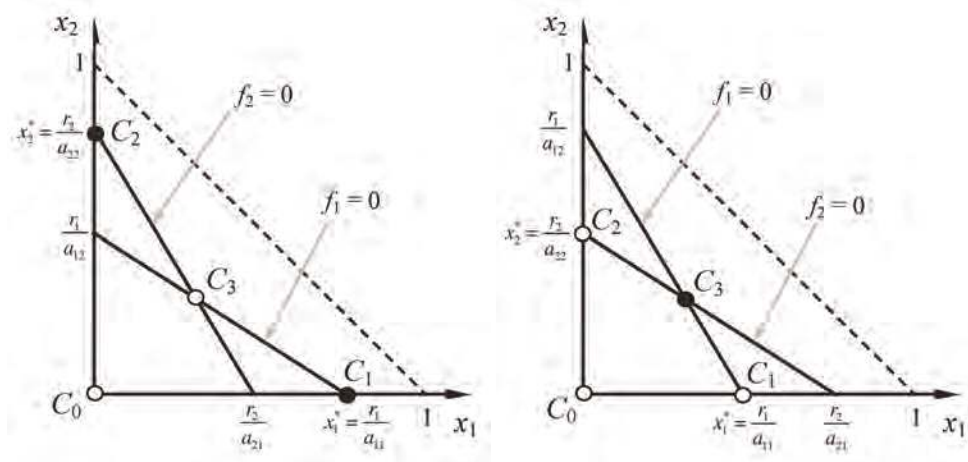
The sign of the predator’s competition eigenvalue at its prey autotroph point  $C_1$  therefore solely determines the major attributes of two-population predator-prey LVCN systems. Note that the condition  $\lambda_2 = r_2 - a_{21}x_1^* = r_2 - a_{21}(r_1/a_{11}) > 0$  is equivalent to  $r_2/a_{21} > r_1/a_{11}$ , which means that the system will have a stable predator-prey coexistence point  $C_3$  in  $E$  if the intercept  $\bar{x}_1$  of the predator zero isocline with  $x_2 = 0$ ,  $f_2 = r_2 - a_{21}\bar{x}_1 = 0$ , lies on the origin side of the prey boundary equilibrium point  $C_1$ . As an exercise consider the case  $r_2, a_{21}, a_{22} < 0$  and show that the above still applies.

Generally, we have the familiar result that when a predator is sufficiently weak, so that its life function  $f_2$  is negative at the prey autotroph point  $C_1$ , then the predator goes extinct.

**6. Competitor LVCN Systems.** Our second example is of a system of the form (4.1) that involves only competitors. In LVCN systems, the lowest trophic level must be an autotroph, so in the two-population competition LVCN system (4.2) or (4.7),  $x_1$  and  $x_2$  are competing autotrophs. Each autotroph has a detrimental effect on the other autotroph through indirect competition for nutrient; their parameter values are subject to the constraints in (4.16):

$$(6.1) \quad \begin{aligned} 0 < r_1 < a_{11}, a_{12}, \\ 0 < r_2 < a_{21}, a_{22}. \end{aligned}$$

We now check the lid condition (equation (5.5)) for the autotroph-only LVCN system using these parameter constraints. Since  $a_{11} > r_1$  and  $a_{12} > r_2$ ,  $a_{11}x_1 + a_{12}x_2 > r_1(x_1 + x_2) = r_1$  on  $x_1 + x_2 = 1$ . Then, in (5.5), each term is positive for the parameter constraints (6.1), and therefore the lid condition is always satisfied for these competitor systems.



**Fig. 6.1** The two cases where the coexistence point for  $x_1$  and  $x_2$  exists in  $E$  for a competitor LVCN system. In the left panel, the boundary equilibrium point  $C_0$  at the origin  $\{0, 0\}$  is unstable, the boundary autotroph equilibrium points  $C_1 = \{x_1^* = r_1/a_{11}, 0\}$  and  $C_2 = \{0, x_2^* = r_2/a_{22}\}$  are stable, and the coexistence equilibrium point  $C_3$  is unstable. In the right panel, the boundary equilibrium points at the origin  $C_0$ , at  $C_1$ , and at  $C_2$  are unstable, and the coexistence equilibrium point  $C_3$  is stable.

The competitor LVCN system has the equilibrium points described by equations (4.3), where here both boundary equilibrium points satisfy  $0 < x_i^* = r_i/a_{ii} < 1$ , and are autotroph points. The parameter constraints (6.1) mean that for all two-population LVCN competition systems (see Figure 6.1 for an illustration of the zero isoclines and equilibrium points) the following hold:

- The origin equilibrium point ( $C_0$ ) is an unstable node with eigenvalues  $\lambda_{C_0-1} = r_1 > 0$  and  $\lambda_{C_0-2} = r_2 > 0$ . This indicates that both autotrophs will always be able to grow in a world composed only of inorganic nutrient;
- The autotroph-only boundary equilibrium points ( $C_1$ :  $0 < x_1^* = r_1/a_{11} < 1$  and  $C_2$ :  $0 < x_2^* = r_2/a_{22} < 1$ ) each have one attracting eigenvalue ( $\lambda_{C_1-1} = -a_{11}x_1^* = -r_1 < 0$  and  $\lambda_{C_2-1} = -a_{22}x_2^* = -r_2 < 0$ ), so each autotroph population survives in the absence of the other.
- The existence of the equilibrium point  $C_3$  in  $E$  depends graphically on the intersection of the isoclines  $f_1 = 0$  and  $f_2 = 0$  inside  $E$ , and equivalently algebraically on the signs of the components of  $C_3$ ,  $a_{22}r_1 - a_{12}r_2$ ,  $a_{11}r_2 - a_{21}r_1$ , and  $a_{11}a_{22} - a_{12}a_{21}$ :
  - If intrapopulation competition exceeds interpopulation competition (i.e.,  $a_{11}a_{22} - a_{12}a_{21} > 0$ ), then  $C_3$  exists in  $E$  if  $a_{22}r_1 - a_{12}r_2$  and  $a_{11}r_2 - a_{21}r_1 > 0$ . The competition eigenvalue of each population is then positive at its competitor's boundary equilibrium point, that is,  $\lambda_{C_1-2} > 0$  and  $\lambda_{C_2-2} > 0$ , and  $C_3$  is stable.
  - If interpopulation competition exceeds intrapopulation competition (i.e.,  $a_{11}a_{22} - a_{12}a_{21} < 0$ ), then  $C_3$  exists in  $E$  if  $a_{22}r_1 - a_{12}r_2$  and  $a_{11}r_2 - a_{21}r_1 < 0$ . The competition eigenvalue of each population is now negative at its competitor's boundary equilibrium point, and  $C_3$  is unstable.
  - Otherwise,  $C_3$  does not exist in  $E$  and either  $C_2$  is stable and  $C_1$  is unstable or vice versa.

The conditions for coexistence of two populations in a competition LVCN system are more detailed than those for a two-population predator-prey system, but again are determined by the signs of the competition eigenvalues at the boundary equilibrium points. We may synthesize these conditions for this simple system:

$$(6.2) \quad \left. \begin{aligned} a_{22}r_1 - a_{12}r_2 > 0 &\Rightarrow \frac{r_1}{r_2} > \frac{a_{12}}{a_{22}} \\ a_{11}r_2 - a_{21}r_1 > 0 &\Rightarrow \frac{a_{11}}{a_{21}} > \frac{r_1}{r_2} \end{aligned} \right\} \Rightarrow \frac{a_{12}}{a_{22}} < \frac{r_1}{r_2} < \frac{a_{11}}{a_{21}} \Rightarrow a_{11}a_{22} > a_{12}a_{21}.$$

This classic result says that systems in which intrapopulation competition is stronger than interpopulation competition will have stable coexisting populations. Similarly, systems with

$$(6.3) \quad a_{11}a_{22} < a_{12}a_{21}$$

will have unstable coexistence points, and the result of competition will depend on the initial conditions. Note that for systems with more than one autotroph, competitor populations have to be fitter in order to survive: that is, the population  $x_i$  must have its life function positive at its competitor autotroph points in order to persist and coexist.

Finally, the intermediate cases

$$(6.4) \quad \frac{r_1}{r_2} > \frac{a_{11}}{a_{21}}, \frac{a_{12}}{a_{22}} \quad \text{and} \quad \frac{r_1}{r_2} < \frac{a_{11}}{a_{21}}, \frac{a_{12}}{a_{22}}$$

have clear outcomes, where  $x_1$  dominates the system and  $x_2$  goes extinct in the first case and the reverse in the latter case. This situation, where the  $f_1 = 0$  and  $f_2 = 0$  isoclines do not intersect in  $E$ , is intermediate to the cases shown in Figure 6.1. In all the above examples the algebraic inequalities can be related to the isocline geometry, and this is left as an exercise. In the above two sections we have introduced familiar population types and their interactions from our new point of view that includes exact conservation of the recycling nutrient. In the next two sections we introduce new population interactions that are not analyzed in the usual introductory ecological texts.

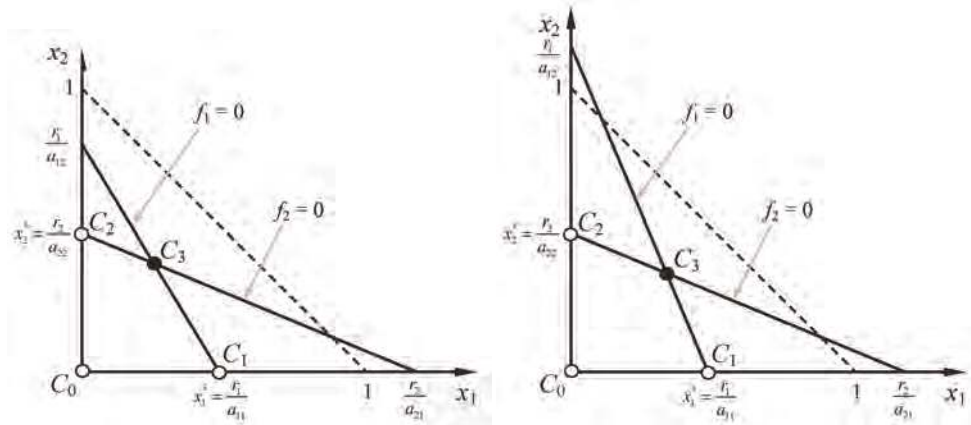
**7. Mixotroph LVCN Systems.** We now consider our first new LVCN system of two competing autotrophs in which one of the autotrophs ( $x_2$ ) also consumes the other autotroph ( $x_1$ ). Such behavior, where an organism grows both by photosynthesising and by feeding on other phytoplankton, is called mixotrophy. Recent research has suggested that mixotrophy is common in marine protists [6] and hence it is an interesting case for two-population LVCN systems, being intermediate between a pure competition system and a pure predation system.

A mixotroph  $x_2$  in an LVCN system utilizes inorganic nutrient  $N$  as a food source via photosynthesis and also grazes upon a second organism  $x_1$ . The maximum resource for the mixotroph is located on the  $x_1$  axis ( $0 \leq x_1 \leq 1$ ) and the point of zero resource is  $\{0, 1\}$  (see Figure 7.1). The maximum resource condition for the mixotroph  $x_2$  evaluated at the origin of  $E$  (where it feeds exclusively on inorganic nutrient  $N$ ) reads

$$(7.1) \quad f_2|_{R_2=N=1} > 0 \Rightarrow r_2 > 0,$$

while evaluation at  $x_1 = 1, x_2 = 0$  (where  $x_2$  feeds exclusively on  $x_1$ ) gives

$$(7.2) \quad f_2|_{R_2=x_1=1} > 0 \Rightarrow r_2 > a_{21}.$$



**Fig. 7.1** The cases for a mixotroph system: coexistence with an autotroph (left) and coexistence with another mixotroph (right). In each case, the boundary equilibrium point at the origin  $C_0: \{0, 0\}$ , the autotroph/mixotroph point  $C_1: \{x_1^* = r_1/a_{11}, 0\}$ , and the mixotroph point  $C_2: \{0, x_2^* = r_2/a_{22}\}$  are always unstable. In either the autotroph-mixotroph case or the mixotroph-mixotroph case the coexistence point  $C_3$  may exist outside  $E$ . If it exists inside  $E$ , the coexistence equilibrium point is stable.

The zero resource condition for a mixotroph  $x_2$  is evaluated at  $x_1 = 0$ ,  $x_2 = 1$  and provides the condition

$$(7.3) \quad f_2|_{R_2=0} < 0 \Rightarrow r_2 < a_{22}.$$

Summarizing (7.1)–(7.3) reveals that a mixotroph population ( $x_2$ , feeding on nutrient and a prey  $x_1$ ) is subject to the parameter constraints

$$(7.4) \quad 0 < r_2 < a_{22}, \quad a_{21} < r_2.$$

Here, we restrict our definition of a mixotroph to when  $a_{21} \geq 0$  and define a mixotroph with the property that  $a_{21} < 0$  to be a mutualist. We discuss mutualist populations in section 8.

Applying the general parameter constraints imposed by the CN rules for autotrophs (4.16) and mixotrophs (7.4) to an autotroph-mixotroph LVCN system provides the following parameter constraints:

$$(7.5) \quad \begin{aligned} 0 < r_1 < a_{11}, a_{12}, \\ 0 \leq a_{21} < r_2 < a_{22}. \end{aligned}$$

We now check the lid condition (equation (5.5)) using these parameter constraints. The first (autotroph) term of the lid condition is, as before, always positive for the parameter constraints (7.5). The second (mixotroph) term is zero when  $x_2 = 0$  and positive when  $x_2 = 1$ , but may be negative inbetween. It is convenient to numerically evaluate (5.5) for an individual parameter set to determine the sign of  $\dot{N}$  everywhere on  $x_1 + x_2 = 1$  (alternatively, a minimization example in elementary calculus). If  $\dot{N}$  is positive everywhere on  $x_1 + x_2 = 1$ , then the parameter set gives a valid LVCN mixotrophy system.

The mixotroph LVCN system has the equilibrium points described by equations (4.3), where the boundary equilibrium points are now an autotroph point and

a mixotroph point. The parameter constraints (7.5) mean that for all autotroph-mixotroph LVCN systems:

- The origin equilibrium point ( $C_0$ ) is an unstable node with eigenvalues  $\lambda_{C_0-1} = r_1 > 0$  and  $\lambda_{C_0-2} = r_2 > 0$ . This indicates that both the autotroph and the mixotroph will always be able to grow in a world composed only of inorganic nutrient.
- The autotroph boundary equilibrium point ( $C_1$ :  $0 < x_1^* = r_1/a_{11} < 1$ ) has one attracting eigenvalue ( $\lambda_{C_1-1} = -a_{11}x_1^* = -r_1 < 0$ ), so the autotroph population could survive in the absence of the mixotroph. Note that the parameter constraints (7.5) ensure that  $C_1$  is always unstable as the mixotroph competition eigenvalue at  $C_1$  ( $\lambda_{C_1-2} = r_2 - a_{21}x_1^*$ ) is always positive.
- The mixotroph boundary equilibrium point ( $C_2$ :  $0 < x_2^* = r_2/a_{22} < 1$ ) has one attracting eigenvalue ( $\lambda_{C_2-2} = -a_{22}x_2^* = -r_2 < 0$ ), so the mixotroph population could survive in the absence of the autotroph. The stability of this point depends on the sign of the competition eigenvalue of the autotroph ( $\lambda_{C_2-1} = r_1 - a_{12}x_2^*$ ) at this point.
- The existence of the coexistence equilibrium point ( $C_3$ ) in  $E$  depends on the signs of  $a_{22}r_1 - a_{12}r_2$ ,  $a_{11}r_2 - a_{21}r_1$ , and  $a_{11}a_{22} - a_{12}a_{21}$ . Observe from Figure 7.1 (left panel) that if  $r_1/a_{12} < r_2/a_{22}$ , the  $f_1 = 0$  and  $f_2 = 0$  isoclines will not intersect in  $E$ . If they do intersect, then  $\lambda_{C_3-1} = r_1 - a_{12}x_2^* > 0$  and  $C_3$  exists in  $E$  and is stable irrespective of the sign of  $a_{21}$ .

The case when both populations are mixotrophs provides the following parameter constraints:

$$(7.6) \quad \begin{aligned} 0 &\leq a_{12} < r_1 < a_{11}, \\ 0 &\leq a_{21} < r_2 < a_{22}. \end{aligned}$$

Again, it is convenient to numerically evaluate (5.5) as for an individual parameter set to determine the sign of  $\dot{N}$  everywhere on  $x_1 + x_2 = 1$ , again requiring positivity. It is left as an exercise for the reader to determine the properties of the critical points as above. The arrangement of the isoclines in Figure 7.1 (right panel) gives a clue to these properties.

**8. Mutualist LVCN Systems.** We now consider our second new population interaction, an LVCN system of the form (4.2) for an autotroph  $x_1$  and a mutualist  $x_2$  (i.e., a mixotroph with  $a_{21} < 0$ ), that is, the mutualist prefers consuming the autotroph to consuming nutrient. Such behavior is analogous to certain definitions of mutualism in the literature [18], but is often not treated in depth “in part due to the fact that simple models in the Lotka–Volterra vein give silly results” [17, p. 99]. We shall show that this is not the case for LVCN systems. As a mutualist,  $x_2$  grows more strongly when there is more  $x_1$  present in the ecosystem; i.e.,  $x_2$  benefits from  $x_1$ ’s presence, and the relevant interaction coefficient  $a_{21}$  changes sign compared to the previous two cases.

The autotroph  $x_1$  and mutualist  $x_2$ , respectively, satisfy (4.16) and (7.4) with

$$(8.1) \quad \begin{aligned} 0 &< r_1 < a_{11}, a_{12}, \\ a_{21} &< 0 < r_2 < a_{22}. \end{aligned}$$

We again numerically check the lid condition (equation (5.5)), now using parameter constraints (8.1). If  $\dot{N}$  is positive everywhere on  $x_1 + x_2 = 1$ , then the parameter set gives a valid LVCN mutualist system.

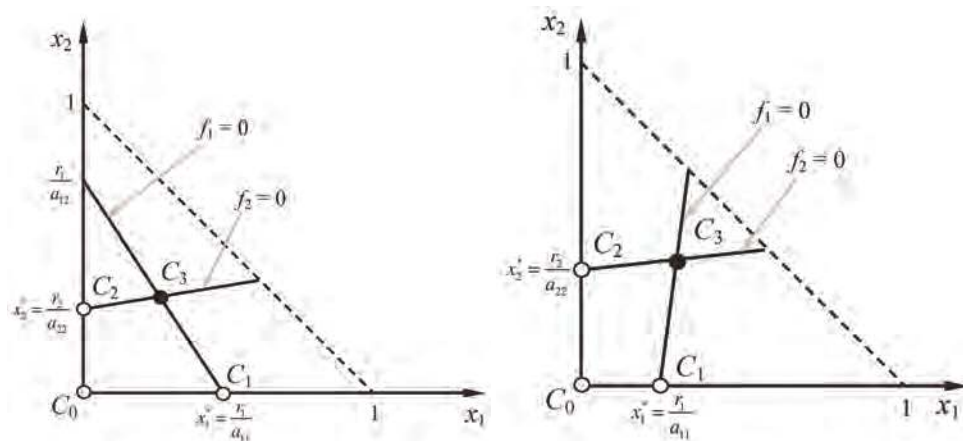
The autotroph-mutualist LVCN system has the equilibrium points described by equations (4.3), where the boundary equilibrium points are now an autotroph point and a mutualist point. The parameter constraints (8.1) mean that for these systems:

- The origin equilibrium point ( $C_0$ ) is an unstable node with eigenvalues  $\lambda_{C_0-1} = r_1 > 0$  and  $\lambda_{C_0-2} = r_2 > 0$ . This indicates that both the autotroph and the mutualist are always able to grow in a world composed only of inorganic nutrient.
- The boundary equilibrium points ( $C_1: 0 < x_1^* = r_1/a_{11}, 1$  and  $C_2: 0 < x_2^* = r_2/a_{22}, 1$ ) have one attracting eigenvalue each ( $\lambda_{C_1-1} = -a_{11}x_1^* = -r_1 < 0$  and  $\lambda_{C_2-2} = -a_{22}x_2^* = -r_2 < 0$ ), so each population could survive in the absence of the other. The parameter constraints ensure that the competition eigenvalue of the mutualist population ( $\lambda_{C_1-2} = r_2 - a_{21}x_1^*$ ) at each boundary point is always positive and the mutualist population can always invade.
- When the boundary points are unstable, the coexistence equilibrium point ( $C_3$ ) is always stable. The only further consideration is whether the point exists in  $E$ . The condition for existence in  $E$  is that  $x_1^* + x_2^* \leq 1$ , that is,  $a_{22}r_1 - a_{12}r_2 + a_{11}r_2 - a_{21}r_1 \leq a_{11}a_{22} - a_{12}a_{21}$ . It can be seen from Figure 8.1 that as the interaction terms  $a_{12}$  and  $a_{21}$  reduce, the interior equilibrium point  $C_3$  moves closer to the lid.

The case when both populations are mutualists provides the following parameter constraints:

$$(8.2) \quad \begin{aligned} a_{12} < 0 < r_1 < a_{11}, \\ a_{21} < 0 < r_2 < a_{22}. \end{aligned}$$

Similarly to the mixotroph case, it is convenient to numerically evaluate (5.5) for an individual parameter set to determine the sign of  $\dot{N}$  everywhere on  $x_1 + x_2 = 1$ , again requiring positivity. It is again left as an exercise for the reader to determine the properties of the critical points as above. The arrangement of the isoclines in



**Fig. 8.1** The cases for an autotroph-mutualist system (left) and a mutualist-mutualist system (right). In the left case, the boundary equilibrium points at  $C_0 = \{0, 0\}$ ,  $C_1 = \{x_1^* = r_1/a_{11}, 0\}$ , and  $C_2 = \{0, x_2^* = r_2/a_{22}\}$  are always unstable if  $r_1/a_{12} > r_2/a_{22}$ ; in the right case they are always unstable. The coexistence equilibrium point  $C_3$  is always stable but only has meaning when it exists in  $E$ . The lid condition places limits on useful parameter values.

Figure 8.1 (right panel) gives a clue to these properties. Valid LVCN systems of this form provide examples of facultative mutualism. When the lid condition fails we might interpret this as one population trying to benefit too enthusiastically from the presence of the other.

## 9. Ecological Implications of CN Rules.

**9.1. General Properties of Populations in LVCN Systems.** CN Rule 4 illuminates dramatic differences between competing autotroph, nonautotroph (predator), and mixotrophy/mutualist populations in LVCN systems. The comparative parameter constraints are as follows:

- For autotrophs,  $x_i$ :  $0 < r_i < a_{ij}$ ,  $j = 1, 2, \dots, n$ .
- For predators  $x_j$  feeding on prey  $x_i$  ( $i < j$ ):  $a_{ji} < r_j < 0 < a_{jk}$ ,  $k = 1, 2, \dots, n$ ,  $k \neq i$ .
- For a mutualist  $x_j$  feeding on nutrient and benefiting from the presence of another mutualist  $x_i$ :  $a_{ji} < 0 < r_j < a_{jk}$ ,  $k = 1, 2, \dots, n$ ,  $k \neq i$ .

A fundamental difference between the properties of autotrophs and predators is reflected in the  $r_j$ , which represent the net rates of density-independent processes in  $x_j$ . As predators can only grow by consuming a prey population, they do not have any density-independent per capita growth processes. Hence, for predators the  $r_j$  represent only the rates of density-independent per capita mortality, and  $r_j$  must be negative.

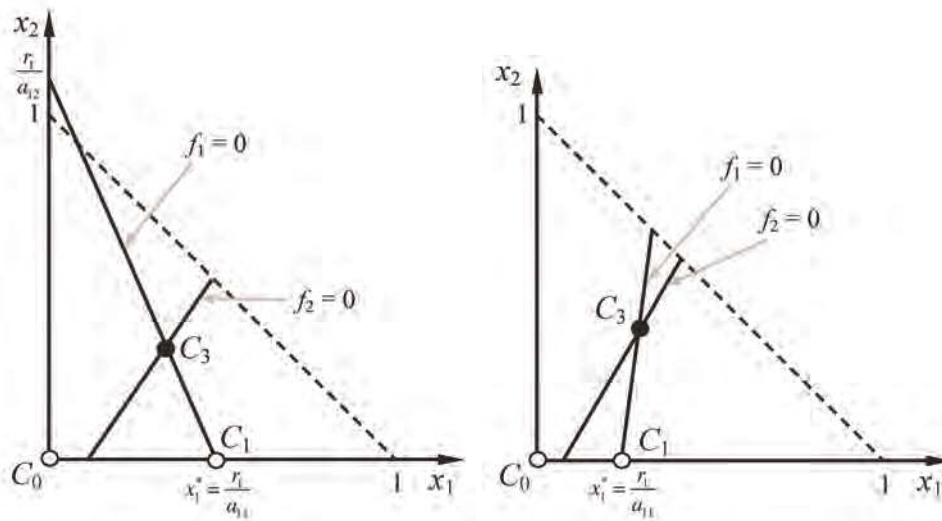
A further fundamental difference between autotrophs and predators is seen in the effect of other populations on the population of interest, say  $x_j$ . For autotrophs, all populations, including itself, have a negative effect on growth because they bind nutrient in organic form that is then not available to the other autotrophs. Similarly, all populations, apart from prey populations, have a negative effect on predators, but prey populations have a positive effect on their predator populations. When mixotrophs become mutualists, they also benefit from their new “prey” population(s).

**9.2. Adaptation of Mixotrophs in LVCN Systems.** The parameter constraints, and consequent isocline locations, for mixotrophs/mutualists reveal that their life strategy is intermediate between autotrophs and predators. Comparison of Figures 6.1, 7.1, and 8.1 reveals the adaptation of a population  $x_2$  from autotrophy through mixotrophy to mutualism by rotation of the  $f_2 = 0$  isocline anticlockwise. We commence the rotation by reducing  $a_{21}$  in Figure 6.1, which causes the  $x_1$  intercept  $r_2/a_{21}$  to move to the right. The autotroph adapts into a mixotroph when  $r_2/a_{21}$  exceeds 1 (see Figure 7.1, left panel). As the isocline continues rotating,  $a_{21}$  reduces through zero when the isocline becomes horizontal.

The major change that occurs for  $a_{21} < 0$  is that  $x_2$  now prefers to consume  $x_1$  rather than  $N$  (see Figure 8.1); we define  $x_2$  as a mutualist due to the similarity of these isoclines with those of the standard definition of a mutualist [18]. The change of sign of  $a_{21}$  signifies that the strength of grazing on  $x_1$  has increased to the point where  $x_2$  receives a direct net growth benefit from  $x_1$  rather than an indirect net benefit from a reduction of competition due a reduction in the  $x_1$  population size. The properties of the mutualist remain essentially unchanged for further decreases in  $a_{21}$  until  $x_1$  goes extinct, when the interior coexistence point  $C_3$  collides with the mutualist axis.

Decreasing  $a_{21}$  from large positive values through zero to large negative values fully describes the adaptation options available to  $x_2$  in a single trophic level in these systems. Similar options are available to  $x_1$ , as may be seen in Figures 6.1, 7.1, and





**Fig. 9.1** The cases for a mutualist, with  $a_{21} < 0$ , adapting to become a predator with a mixotroph prey (left) and with a mutualist prey (right). In each case, the boundary equilibrium points at the origin  $C_0 = \{0, 0\}$  and  $C_1 = \{x_1^* = r_1/a_{11}, 0\}$  are unstable. The coexistence equilibrium point  $C_3$  is always stable but only has meaning when it exists in  $E$ . The lid condition places limits on useful parameter values.

8.1. These options correspond to rotating the population isoclines; in the next section we consider translations.

**9.3. Adaptation of Mutualists in LVCN Systems.** Finally, we note that a certain continuous parameter variation leads to another interesting change of population behavior. Comparing Figures 5.1 (left panel) and 8.1 we see that a further transition is possible, that of mutualist, feeding on both  $N$  and  $x_1$ , to predator, feeding only on  $x_1$ . For fixed intermediate negative values of  $a_{21}$  (see Figure 8.1), reductions in  $r_2$  result in the translation of the zero isocline  $f_2 = 0$  in the  $-x_2$  direction.

Figure 9.1 shows the result of the mutualist  $x_2$  adapting (by making  $r_2 < 0$ ) to become a predator from a mixotroph-mutualist system (left panel) and from a mutualist-mutualist system (right panel). The outcome of a mutualist  $x_2$  adapting to become a predator from an autotroph-mutualist system is shown in Figure 5.1 (left panel).

When  $r_2$  decreases through zero, the isocline  $f_2 = 0$  passes through the origin; then  $x_2$  changes from a mutualist to a predator by ceasing to feed on  $N$ , and we have a predator-prey system (see Figure 5.1, left panel). This translation can occur irrespective of whether  $x_1$  is an autotroph, a mixotroph, or sometimes even a mutualist. This suggests a mechanism for the creation of new trophic levels.

**10. Extension to Higher Dimensions.** The CN framework is easily extended to higher-dimensional systems than the two populations we have used as examples above. Figure 4.1 provides an example of how the resource sign conditions may be applied to a three-population model. The CN rules remain the same, but the additional dimensions provide more options for trophic profiles and interactions and dynamics. Here, we provide a brief introductory analysis of a generic three-population LVCN system to demonstrate the application of the CN rules in higher dimensions.

**10.1. A Three-Population LVCN System.** We consider the three-population LVCN system (see Figure 10.1)

$$(10.1) \quad \begin{aligned} \dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3), \\ \dot{x}_2 &= x_2(r_2 - a_{21}x_1 - a_{22}x_2 - a_{23}x_3), \\ \dot{x}_3 &= x_3(r_3 - a_{31}x_1 - a_{32}x_2 - a_{33}x_3). \end{aligned}$$

Every system of the form (10.1) has eight equilibrium points in the  $x_1, x_2, x_3$  space:

$$(10.2) \quad \begin{aligned} C_0 &: \{x_1^* = 0, x_2^* = 0, x_3^* = 0\} \quad (\text{origin equilibrium point}), \\ C_1 &: \left\{x_1^* = \frac{r_1}{a_{11}}, x_2^* = 0, x_3^* = 0\right\} \quad (\text{boundary equilibrium point}), \\ C_2 &: \left\{x_1^* = 0, x_2^* = \frac{r_2}{a_{22}}, x_3^* = 0\right\} \quad (\text{boundary equilibrium point}), \\ C_3 &: \left\{x_1^* = 0, x_2^* = 0, x_3^* = \frac{r_3}{a_{33}}\right\} \quad (\text{boundary equilibrium point}), \\ C_4 &: \left\{x_1^* = \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}, x_2^* = \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}}, x_3^* = 0\right\} \\ &\quad (\text{boundary equilibrium point}), \\ C_5 &: \left\{x_1^* = \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}, x_2^* = 0, x_3^* = \frac{a_{11}r_3 - a_{31}r_1}{a_{11}a_{33} - a_{13}a_{31}}\right\} \\ &\quad (\text{boundary equilibrium point}), \\ C_6 &: \left\{x_1^* = 0, x_2^* = \frac{a_{33}r_2 - a_{23}r_3}{a_{22}a_{33} - a_{23}a_{32}}, x_3^* = \frac{a_{22}r_3 - a_{32}r_2}{a_{22}a_{33} - a_{23}a_{32}}\right\} \\ &\quad (\text{boundary equilibrium point}), \\ C_7 &: \left\{x_1^* = \frac{|A_1^r|}{|A|}, x_2^* = \frac{|A_2^r|}{|A|}, x_3^* = \frac{|A_3^r|}{|A|}\right\} \quad (\text{coexistence equilibrium point}). \end{aligned}$$

Here, we introduce for  $C_7$  the notation for Cramer’s Rule method that may be used to calculate the locations of all critical points in LVCN systems. The notation  $|A_i^r|$  means the determinant of the matrix of interaction coefficients  $A$ , where the  $i$ th column of  $A$  has been replaced with the vector  $r$ .

**10.2. Parameter Constraints from the Resource Sign Conditions.** The extension of LVCN systems to three populations allows for more trophic interactions, including the possibility of omnivorous predators: we shall only consider a sample of these here. Application of the resource sign condition (4.13) to  $x_1$ , an autotroph, provides the parameter constraints

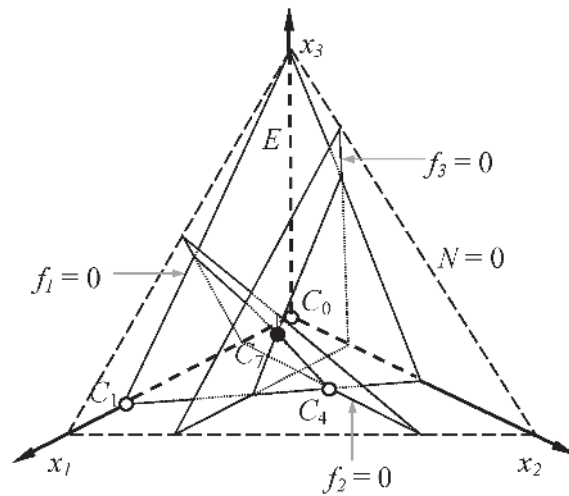
$$(10.3) \quad 0 < r_1 < a_{11}, a_{12}, a_{13}.$$

Alternatively,  $x_1$  might be a mixotroph feeding on  $x_2$ , in which case it would have the parameter constraints

$$(10.4) \quad 0 < a_{12} < r_1 < a_{11}, a_{13},$$

or a mixotroph feeding on  $x_3$ , with

$$(10.5) \quad 0 < a_{13} < r_1 < a_{11}, a_{12},$$



**Fig. 10.1** The generic case for an autotroph  $x_1$ , with a herbivore  $x_2$  feeding on  $x_1$  and a carnivore  $x_3$  feeding on  $x_2$ . The boundary equilibrium points  $C_0 : \{0, 0, 0\}$ ,  $C_1 = \{x_1^*, 0, 0\}$ , and  $C_4 = \{x_1^*, x_2^*, 0\}$  are unstable.

or perhaps even both  $x_2$  and  $x_3$ , with

$$(10.6) \quad 0 < a_{12}, a_{13} < r_1 < a_{11}.$$

Similarly, if  $x_2$  predated on  $x_1$  and was predated upon by  $x_3$ , it would have the parameter constraints

$$(10.7) \quad a_{21} < r_2 < 0 < a_{21}, a_{23}.$$

We note that many other trophic interactions, and hence parameter constraints, are possible in three-trophic level systems. The exhaustive exploration of these trophic interactions is left as an exercise.

**10.3. A Three-Trophic Level LVCN System.** We now consider the example of a three-trophic level LVCN system, where  $x_1$  is an autotroph,  $x_2$  is a mixotroph that both photosynthesizes and predaes on  $x_1$ , and  $x_3$  is a carnivore that predaes on  $x_2$ . These populations are identified by the parameter constraints that define their trophic interactions:

$$(10.8) \quad \begin{aligned} 0 < r_1 < a_{11}, a_{12}, a_{13}, \\ 0 < a_{21} < r_2 < a_{22}, a_{23}, \\ a_{32} < r_3 < 0 < a_{33}, r_3 < a_{31}. \end{aligned}$$

As we have defined  $x_3$  as a carnivore, which does not eat plants, we can set  $a_{31} = 0$  to reflect that there is no direct interaction (transfer of mass) between  $x_1$  and  $x_3$ . The lid condition in this case is given by

$$(10.9) \quad \begin{aligned} \dot{N} = & -x_1(r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3) - x_2(r_2 - a_{21}x_1 - a_{22}x_2 - a_{23}x_3) \\ & - x_3(r_3 - a_{31}x_1 - a_{32}x_2 - a_{33}x_3) > 0 \text{ when } x_1 + x_2 + x_3 = 1. \end{aligned}$$

The lid condition must be checked, as although the first term is always positive from (10.8), the second and third terms can have either sign depending on the parameter values. Analytically, we put  $x_3 = 1 - x_1 - x_2$  and find the minimum of  $\dot{N}$  for  $0 \leq x_1 + x_2 \leq 1$ , or we check this numerically.

This system has the equilibrium points described by equations (10.2), where the edge equilibrium points are an autotroph point, a mixotroph point, and a carnivore point. The parameter constraints (10.8) mean that for this system:

- The origin equilibrium point ( $C_0$ ) is an unstable saddle with eigenvalues  $\lambda_{C_0-1} = r_1 > 0$ ,  $\lambda_{C_0-2} = r_2 > 0$ , and  $\lambda_{C_0-3} = r_3 < 0$ . This indicates that both the autotroph and the mixotroph will always be able to grow in a world composed only of inorganic nutrient.
- The autotroph boundary equilibrium point ( $C_1$ :  $0 < x_1^* = r_1/a_{11} < 1$ ) has one attracting eigenvalue ( $\lambda_{C_1-1} = -a_{11}x_1^* = -r_1 < 0$ ), so the autotroph population could survive in the absence of the mixotroph. Note that the parameter constraints (10.8) ensure that  $C_1$  is always unstable as the mixotroph competition eigenvalue at  $C_1$  ( $\lambda_{C_1-2} = r_2 - a_{21}x_1^*$ ) is always positive.
- The mixotroph boundary equilibrium point ( $C_2$ :  $0 < x_2^* = r_2/a_{22} < 1$ ) has one attracting eigenvalue ( $\lambda_{C_2-2} = -a_{22}x_2^* = -r_2 < 0$ ), so the mixotroph population could survive in the absence of the autotroph. The stability of this point depends on the sign of the competition eigenvalues of the autotroph and carnivore ( $\lambda_{C_2-1} = r_1 - a_{12}x_2^*$  and  $\lambda_{C_2-3} = r_3 - a_{32}x_2^*$ , respectively) at this point.
- The predator boundary equilibrium point  $C_3$  does not exist in  $E$  as  $x_3^*$  is always negative at this point.
- The existence of the boundary equilibrium point ( $C_4$ ) in  $E$  depends on the signs of  $a_{22}r_1 - a_{12}r_2$ ,  $a_{11}r_2 - a_{21}r_1$ , and  $a_{11}a_{22} - a_{12}a_{21}$ . If  $r_1/a_{12} < r_2/a_{22}$ , the  $f_1 = 0$  and  $f_2 = 0$  isoclines will not intersect in  $E$ . If they do intersect, then  $\lambda_{C_4-1} = r_1 - a_{12}x_2^* > 0$  and  $C_4$  exists on the boundary of  $E$ . It will be unstable if  $\lambda_{C_4-3} = r_3 - a_{32}x_2^* > 0$  (as  $a_{31} = 0$ ).
- The boundary equilibrium point ( $C_5$ ) does not exist in  $E$  as  $x_3^*$  is always negative at this point.
- The existence of the boundary equilibrium point ( $C_6$ ) in  $E$  depends on the intersection of the zero isoclines  $f_2, f_3 = 0$  in  $E$ . The condition  $0 < r_3/a_{32} < r_2/a_{22}$  ensures that the  $f_2 = 0$  and  $f_3 = 0$  isoclines intersect and that  $C_6$  exists in  $E$ .

The parameter constraints that lead to the existence of  $C_7$  in  $E$  are not simply articulated. We do observe that many more trophic interactions and more complex dynamical behaviors (including chaos; see [11, p. 216] for an example) are possible in three-population LVCN systems than in two-population systems. The exploration of these scenarios and solutions could provide hours of interesting exercises.

**II. Discussion.** This article proposes a framework for teaching dynamical systems, using simple examples of ecological models to undergraduate students in marine science and ecology. More generally, this course provides an example of mathematical modeling in the life sciences. It establishes a mathematical basis for ecologically rigorous models of ecosystems based on fundamental concepts such as explicit, natural dependence of populations on the availability of finite resources, and conservation of mass of a nutrient that measures the resources that the populations depend on for their existence. This provides clear linkages between ecological and mathemat-

ical properties of ecosystem models that ensure the models have realistic ecological attributes and interesting mathematical behavior.

Our introduction of a new perspective on mixotrophic systems facilitates the understanding of an extended range of Lotka–Volterra models that is not only rationally complete with respect to continuous parameter variation, but also has intuitive ecological classification properties. Here, mutualistic ecological behavior occurs as a limiting behavior type, and this (facultative) mutualist behavior then further leads to the creation of predators and the definition of a new trophic level. All of these stable and continuously varying interactions may be characterized by rotation and translation of the population isoclines, which many students prefer to trying to understand basic concepts from algebra.

The CN properties are a simple set of rules that provide all the constraints necessary to ensure that the models have ecological properties that mathematically constrain the dynamics of the system to an ecologically realistic phase space, the ecospace  $E$ . We observe that CN systems all have Kolmogorov form and articulate the simple general properties of coexistence of populations and certain mathematical benefits that flow from this form.

We use simple examples of Lotka–Volterra type (LVCN systems) to demonstrate this approach to understanding these dynamical systems. LVCN systems have the great advantage that the partial derivatives associated with the Jacobian matrix of the system are all easily derived; in fact, the second derivatives are constants. This shifts the emphasis of the analysis for nonmathematical students from the algebraic challenges of calculating equilibrium points and their local stability using partial derivatives to the process of understanding the properties of the system. We also emphasize the benefits of considering the boundary equilibrium points of Kolmogorov systems rather than the usual focus on the interior equilibrium points.

Finally, we note that the linking of competition to mutualism across a single trophic level is achieved by means of the intermediate mixotrophic population interactions. These linkages are both smooth and stable with respect to appropriate parameter variations. There is then the further advantage that mutualist population interactions may be linked to predator behavior at a new trophic level, again in a smooth and stable manner. Therefore, not only do we see all the more familiar elements of population interaction in theoretical ecology, but we also have smooth and stable population adaptation through the new mixotroph populations, all of which are underpinned by a strict accounting for the recycling nutrient. In our experience of teaching such a course, we found that students reacted very positively to this mixture of rule-based ecological axioms, geometry of moving lines, and natural ecological interpretations of the results.

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