

ORIGINAL CONTRIBUTION

Obligate Mutualism in an Extended Consumer-Resource Framework

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The development of a theory to underpin the obligate mutualist interactions that appear to be ubiquitous in nature has not proceeded at the same pace as the development of theory to support competition and predation. A constraint may be that obligate mutualism appears unable to be presented in the simple linear models that have so successfully served as heuristics for the other interactions. A number of simple nonlinear models have been used to propose explanations of obligate mutualism, but these solutions are often predicated on careful choices of functional forms. We present a theory of obligate mutualism in an explicit mass-conserving framework using simple models that are robust to choices of functional forms.

INTRODUCTION

Mutualist interactions, in which each species benefits from the presence of its partner mutualist species, have long been recognized as one of the most ubiquitous population interactions in nature [1-4]. In a major review of mutualism, Boucher [3] claimed that roughly half of all population interactions amongst green (*i.e.* photosynthesizing) species are co-operative, catalytic or in some way mutualist in that each population benefits from the presence of the other. Combined with the claim that over 99 percent of the biomass of planet Earth is green, Boucher argued that nature is not only “red in tooth and claw” but also has many mutually beneficial population inter-

actions. In a recent update, Bronstein [5] confirms that this view remains current, suggesting that virtually every species on Earth is involved in mutualist interactions.

However, the paucity of the theoretical basis for mutualism is reflected by ecological texts that devote many pages to the theory underpinning predator-prey and competitive interactions, but often just provide examples of mutualism in nature without attempting a theoretical explanation [6-8]. Ecological texts generally include the standard Lotka-Volterra models of competition and predation, but avoid or cursorily, discuss the standard Lotka-Volterra models of mutualism. This is perhaps because as Murray [9, p99] says:

“this area has not been as widely studied as the

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†Abbreviations: CN, Conservative Normal; LV, Lotka-Volterra; LVCN, Lotka-Volterra Conservative Normal; B98, Bazykin, 1998 [17]; GPP06, Graves, Peckham, 2006 [18]; HD10, Holland and DeAngelis 2010 [11]; KCMF11, Kang, Clark, 2011 [19]; CN0, Obligate mutualism model with only obligation present; CN1, Obligate mutualism model with obligation and mutual benefits present; CN2, Obligate mutualism model with only obligation, mutual benefits and mutual costs present; CN0n, Obligate mutualism model with only obligation present; CN1n, Obligate mutualism model with obligation and mutual benefits present; CN2n, Obligate mutualism model with only obligation, mutual benefits and mutual costs present.

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others even though its importance is comparable to that of predator-prey and competition interactions. This is in part due to the fact that simple models in the Lotka-Volterra vein give silly results."

It is perhaps the lack of simple models of mutualism in the vein of the Lotka-Volterra models that have so well explained competition and predation that has led to mutualism being given only tacit recognition in theoretical ecology as the third cornerstone of population interactions that field ecology suggests it must be.

While the theory underpinning facultative mutualism, in which the mutualists can each survive in the absence of the other, has seen some progress for example, [10], obligate mutualism, in which the mutualists cannot survive in the absence of the other, the theory underpinning has languished. Obligate mutualism has arguably been the bane of theoretical ecologists for many years, with perhaps the recent work of Holland and DeAngelis [11] being one of the few advances since the heuristic model of May [12]. Indeed, several of the recent models we will consider here have qualitatively the same characteristics as May's early model.

Mutualist interactions are distinct from other population interactions in that they have no natural equivalent of local mass balance. Predator-prey interactions are constrained by the axiom that the predator cannot gain more mass than its prey loses, while competitive interactions for resources involve explicit losses that are represented by a reduction in the availability of resources to a population due to their acquisition by a competitor. However, mutualist interactions involve the acquisition of benefits that are facilitated by their mutualist benefactor and result in the population doing better than it would otherwise. It is tempting to consider that these interactions may be represented in simple Lotka-Volterra models by making each population have a positive interaction with the other. However, as Murray [9] notes, this simple approach does not make sense, suggesting that the representation of obligate mutualism may require a more sophisticated conceptual framework.

Holland and DeAngelis [11] addressed this issue by developing a mutualism model in a consumer-resource framework, showing that saturating (Holling Type II / Michaelis-Menten) population interactions that explicitly represented mutualist benefits as a loss from the benefactor provided an improved model of obligate mutualism. However, this model did not constrain the quantity of the resource in the system. We suggest that all ecosystems have finite resources, and this places a fundamental constraint on the quantum of mutualist benefit that is available to the cooperating populations. The concept of limiting the amount of mutualist interaction has been criticized as an arbitrary means of introducing a stable equilibrium into an otherwise unstable system [13]. However, here we

present a theoretical framework that has conservation at its core and that has proved useful to answer a number of fundamental questions in ecology [14].

The concept of finite resources lies at the very heart of the Conservative Normal (CN⁺) framework [14,15] and this provides an appropriate context in which to consider obligate mutualism. The CN theory provides a unifying framework for studying the dynamics of interacting populations, and many population interactions may be explained in an explicitly mass-conserving consumer resource framework that uses only Lotka-Volterra interaction terms. Competition, mixotrophy, facultative mutualism and predation have all been successfully modeled with this simple approach [16]. Cropp and Norbury [14] showed that considering facultative mutualism in an explicit consumer-resource framework generated a natural definition of the distinction between weak and strong facultative mutualism. However, they concluded that it was not possible to represent obligate mutualism sensibly in a two-population LVCN model, and that it required either three or more populations in an LVCN model or nonlinear population interactions. In this work we use the latter to build simple heuristic models of obligate mutualism.

A number of models proposing explanations of obligate mutualism using nonlinear functions to represent population interactions have been published recently (for example, Bazykin [17], Graves, Peckham [18], Holland and DeAngelis [11], Kang, Clark [19]). We use these models, hereafter B98, GPP06, HD10 and KCMF11 respectively, as benchmarks for models of obligate mutualism that we will develop in the CN framework. Each of the B98, GPP06, HD10 and KCMF11 models adopts a different conceptual approach to obligate mutualism. Bazykin [17] considers a heuristic model based on a notional mutualist benefit and takes a dynamical systems approach; Graves, Peckham [18] consider a heuristic model that focuses on the influence of obligation and implements a bifurcation analysis; Holland and DeAngelis [11] utilize a consumer-resource conceptual framework that explicitly represents benefits and costs of mutualism; while Kang, Clark [19] apply Holland and DeAngelis' conceptual framework to a specific example of ant-fungus mutualism.

In the next section, we consider these four models of obligate mutualism, that have different conceptual bases and use different forms of nonlinear population interactions to represent obligate mutualism, in some detail. We summarize the properties of each model by their zero isoclines, equilibrium points and vector fields (Figure 1) and discuss the deficiencies of the ecological assumptions and interpretations for each model. We then describe the essential requirements of a successful model of obligate mutualism, leading to our suite of new models phrased within the CN framework, summarized in Figure 3. The

CN framework is described in detail elsewhere [14,15], but we include a brief description of the key attributes in Section 4. We conclude with a discussion of the ecological implications of these new models; the explicit representation of obligation, together with the benefits and costs of the interactions measured in a common, and finite, currency that give a new model with sensible outcomes.

MODELS OF OBLIGATE MUTUALISM

Many authors have identified the difficulty of representing obligate mutualism in linear systems analogous to those that have traditionally provided the basis for competition and predation theory [for example, 1,2,7,20,21] and have more recently been extended to interactions such as mixotrophy [14] that may be represented in the CN framework. It appears that it is not possible to represent obligate mutualism in linear CN systems, in which we include systems with planar zero isosurfaces such as the Lotka-Volterra CN (LVCN) models discussed in Cropp and Norbury [14].

We will propose simple models of obligate mutualism in the CN framework, but in order to establish a basis for comparison of our solutions against contemporary models that utilize other theoretical frameworks, we first examine the key attributes of the B98, GPP06, HD10, and KCMF11 models. The essence of these four models is summarized in the vector fields presented in Figure 1, and a brief outline of each model follows.

The B98 Model

Bazykin [17] describes a simple mutualism model that represents mutualist interactions between two populations x_1 and x_2 with Holling Type II functional forms and includes quadratic mortality. B98 was led to this model by first demonstrating that simple models using Holling Type I functional forms for mutualist interactions or Holling Type II functional forms with linear mortality alone produced unrealistic results. In both cases model solutions either collapsed to the origin (extinction of both populations), or both populations became infinitely large. Bazykin then added intra-population competition (equivalent to quadratic mortality) to derive the B98 model:

$$\begin{aligned}\dot{x}_1 &= x_1 f_{x_1} = x_1 \left(-c_1 + \frac{P_1 x_2}{1 + D_1 x_2} - e_1 x_1 \right) \\ \dot{x}_2 &= x_2 f_{x_2} = x_2 \left(-c_2 + \frac{P_2 x_1}{1 + D_2 x_1} - e_2 x_2 \right)\end{aligned}\quad (1)$$

We give an example of Bazykin's solutions (Figure 1a) using a parameter set used by Bazykin:

$$\begin{aligned}c_1 &= 1 & P_1 &= 1.8 & D_1 &= 0.1 & e_1 &= 0.9 \\ c_2 &= 1 & P_2 &= 1.8 & D_2 &= 0.1 & e_2 &= 0.9\end{aligned}\quad (2)$$

Bazykin noted that when the functions describing the mutualist interactions did not saturate (*i.e.* $D_1 = 0 = D_2$) or when the model did not include quadratic mortality (*i.e.* $e_1 = 0 = e_2$) the zero isoclines were straight lines parallel to the axes and intersected in an (unstable) saddle point that sent solutions to the origin or infinity:

$$\begin{aligned}c_1 &= c_2, \quad D_1 = D_2, \quad e_1 = e_2, \quad P_1 = P_2, \quad x_1 = x_2, \\ \Rightarrow -c + \frac{Px}{1 + Dx} - ex &= 0, \\ D = 0 = e &\Rightarrow x_0 = \frac{c}{P} = 0.55\end{aligned}\quad (3)$$

As D_1, D_2 and e_1, e_2 are simultaneously increased from zero, the stable point at infinity approaches the unstable point near the origin until at $e_1 \approx 1.0515 \approx e_2$ for $D_1 = 0.1 = D_2$, or $D_1 \approx 0.1545 \approx D_2$ for $e_1 = 0.9 = e_2$, the stable and unstable points collide and disappear in a blue sky bifurcation. This represents quite catastrophic behavior, as an observer of an obligate mutualism interaction in a natural system would see the populations stably coexisting and then suddenly disappearing in response to a subtle change in their environment.

The internal equilibrium points are in fact sensitive to all parameters and respond to variations with one of two behaviors. Increasing e_1, e_2, D_1, D_2 or reducing c_1, c_2, P_1, P_2 , causes the two interior points to come closer together until they merge and disappear in a blue sky bifurcation leaving the stable origin as the only critical point of the system. The reverse variations drive the interior critical points apart, pushing the unstable point and the separatrices closer to the stable origin, and the stable coexistence critical point out to infinity.

Note that the B98 model includes a separatrix associated with the unstable equilibrium point that separates the stable coexistence obligate mutualist equilibrium point from the stable equilibrium point at the origin. This scenario occurs for all parameter values for which the coexistence equilibrium point exists in the positive quadrant. This means that small populations of obligate mutualists cannot survive, a property that might be considered an example of a strong Allee effect [22].

The GPP06 Model

Graves, Peckham, and Pastor [18] propose a mutualism model to rectify an inconsistency in the model of

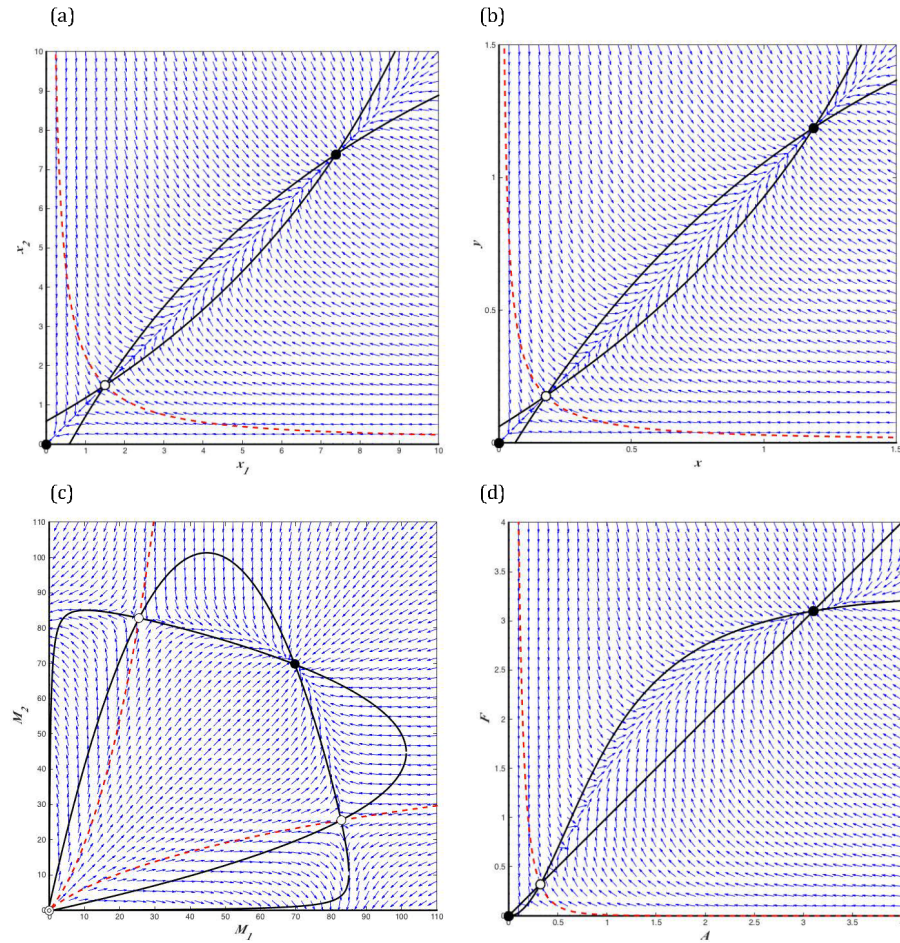


Figure 1. Vector field for: (a) the B98 model (1) for the parameter set (2); (b) the GPP06 model (4) for the parameter set (5); (c) the HD10 model (6) for the parameter set (7); and (d) the KCMF11 model (8) for the parameter set (9). The solid black lines show zero isoclines, dashed red lines show separatrices, open circles indicate unstable critical points and closed circles indicate stable critical points.

Dean [13], which contains singularities in the zero isoclines. The GPP06 model of obligate mutualism between two populations x and y is based on five key assumptions:

- Each species grows according to the logistic model;
- Each species affects the other's per capita growth rate, but not its self-limitation;
- An increase in either species cannot harm the other species;
- Each species has a maximum per capita growth rate; and
- The marginal rate of change of the per capita growth rate of each species due to an increase in the other species is proportional to the difference between the maximum growth rate and the current growth rate.

These assumptions led Graves *et al.* to the model:

$$\begin{aligned} \frac{dx}{dt} &= x f_x = x \left[\left(r_{10} + (r_{11} - r_{10})(1 - e^{-k_1 y}) \right) - a_1 x \right] \\ \frac{dy}{dt} &= y f_y = y \left[\left(r_{20} + (r_{21} - r_{20})(1 - e^{-k_2 x}) \right) - a_2 y \right] \end{aligned} \quad (4)$$

where r_{11} and r_{21} are the maximum, and r_{10} and r_{20} are the unaided, growth rates for x and y respectively. k_1 and k_2 are the constants of proportionality of the fifth assumption, while a_1 and a_2 are the coefficients of self-limitation (second assumption). The first assumption requires that $a_1 > 0$ and $a_2 > 0$, the third assumption requires that $r_{10} \leq r_{11}$ and $r_{20} \leq r_{21}$, and the fifth assumption requires that $k_1 > 0$ and $k_2 > 0$. Graves *et al.* observed that the existence of the populations requires that $r_{11} > 0$ and $r_{21} > 0$. Obligate-obligate mutualism is defined in the GPP06 model by $r_{10} < 0$ and $r_{20} < 0$ with $r_{11} + r_{10} > 0$ and $r_{21} + r_{20} > 0$. They show

that coexistence of obligate mutualists is possible (Figure 1b) for a relatively small parameter range near:

$$\begin{aligned} r_{10} = -0.1 \quad r_{11} = 2 \quad k_1 = 0.8 \quad a_1 = 1 \\ r_{20} = -0.1 \quad r_{21} = 2 \quad k_2 = 0.8 \quad a_2 = 1 \end{aligned} \quad (5)$$

Graves *et al.* conclude on the basis of their model analysis that obligate-obligate mutualism might be rare, in apparent contrast with the common view that mutualism is the most important and ubiquitous interaction in nature [2, p. 225].

Note that the GPP06 model has the same arrangement of isoclines and equilibrium points as the B98 model and hence has the same property that small populations of obligate mutualists cannot survive. The model also has qualitatively the same response to variations in parameter values. Increasing a_1, a_2 or reducing $r_{10}, r_{20}, r_{11}, r_{21}, k_1, k_2$ causes the two interior points to come closer together until they merge and disappear in a blue sky bifurcation leaving the stable origin as the only critical point of the system. The reverse variations drive the interior critical points apart, pushing the unstable point and the separatrices closer to the stable origin, and the stable coexistence critical point out to infinity.

The HD10 Model

Holland and DeAngelis [11] consider the following mutualism model that they claim represents obligate-obligate mutualism between two populations M_1 and M_2 in a consumer-resource framework when $r_1 = 0 = r_2$:

$$\begin{aligned} \frac{dM_1}{dt} &= M_1 f_{M_1} = M_1 \left[r_1 + c_1 \left(\frac{\alpha_{12} M_2}{h_2 + M_2} \right) - q_1 \left(\frac{\beta_1 M_2}{e_1 + M_1} \right) - d_1 M_1 \right] \\ \frac{dM_2}{dt} &= M_2 f_{M_2} = M_2 \left[r_2 + c_2 \left(\frac{\alpha_{21} M_1}{h_1 + M_1} \right) - q_2 \left(\frac{\beta_2 M_1}{e_2 + M_2} \right) - d_2 M_2 \right] \end{aligned} \quad (6)$$

Here r_1 and r_2 are the intrinsic growth rates of the populations in the absence of the other population, while d_1 and d_2 describe the density-dependent self-limitations on growth. α_{12} and α_{21} are the saturation levels of the mutualist benefits and h_1 and h_2 are the half-saturation densities for these benefits. Similarly, β_1 and β_2 are described as the saturation levels of the mutualist costs and e_1 and e_2 are the half-saturation densities for these costs. Finally, c_1, c_2, q_1 and q_2 are “conversion rates” that translate the mutualist benefits and costs into “numerical responses” [11].

Holland and DeAngelis [11] make some general assumptions in developing this model:

- Mutualism has both positive and negative effects on a population, associated with the consumption and supply of resources;

- Populations have density-dependent self-limitation; and
- Populations have an intrinsic growth rate in the absence of mutualists that is independent of available resources.

In developing their specific example, Holland and DeAngelis further assume that the positive effect received by a mutualist is a saturating function of the benefactor, and the negative effect on a benefactor is a saturating function of itself. Holland and DeAngelis use Holling Type II functions for both cases in their example. They demonstrate (Figure 1c) that this model has stable obligate-obligate mutualist coexistence using the parameter set:

$$\begin{aligned} r_1 = 0 \quad \alpha_{21} = 0.9 \quad \beta_1 = 0.2 \quad q_1 = 1 \quad c_1 = 1 \quad d_1 = 0.01 \quad e_1 = 0.3 \quad h_1 = 0.3 \\ r_2 = 0 \quad \alpha_{12} = 0.9 \quad \beta_2 = 0.2 \quad q_2 = 1 \quad c_2 = 1 \quad d_2 = 0.01 \quad e_2 = 0.3 \quad h_2 = 0.3 \end{aligned} \quad (7)$$

HD10 represents an advance in that its arrangement of zero isoclines and its vector field are fundamentally different to previous models of obligate mutualism. Significantly, the HD10 model does not have a separatrix that separates the coexistence obligate mutualist equilibrium point from the origin, hence this model has the property that obligate mutualist populations of any size can coexist (Figure 1c). However, it contains two other separatrices. These allow systems with similar sized populations of obligate mutualists to stably coexist, but ensures that systems where one population or the other dominates will always be unstable. The HD10 model appears relatively robust to changes in the nonlinearity of the mutualist interactions but is very sensitive to variations in the quadratic mortality rate: increases send the mutualist equilibrium population levels to zero, while reductions quickly send them to infinity as in the B98 model.

The solution provided by the HD10 model relies on two fundamental attributes of the model: quadratic mortality and a Holling Type II function to describe the cost of providing resources. If either of these key elements are removed (*i.e.* we use linear mortality or a Holling Type I cost function) the vector field shown in Figure 1c collapses and all model solutions go to infinity. Conversely, the nature of the benefit function is less important, in fact we can remove the dependence of the benefit function on the other population (*i.e.* we set $h_1 = 0 = h_2$) without substantially affecting the vector field of Figure 1c. The conversion rates have differing effects: if we set $c_1 = 0 = c_2$ and remove the mutualist benefit altogether, then the vector field of Figure 1c collapses and the origin becomes globally stable as all the terms in the rhs of (6) are zero or negative. However, removing the cost of providing a mutualist benefit altogether by setting $q_1 = 0 = q_2$ has a rather unexpected effect – the shapes of the zero isoclines

simplify and intersect in a single stable coexistence point. The sensitivity of the HD10 model to variations in functional forms and parameter values to some extent argues against it as a metaphor of mutualism.

The KCMF11 Model

Kang, Clark, Maklyama, and Fewell [19] consider the following mutualism model, based on the consumer-resource approach of Holland and DeAngelis [11], that represents a specific obligate-obligate mutualism between leaf-cutter ants (A) and the fungus (F) that they farm for food:

$$\begin{aligned}\frac{dA}{dt} &= Af_A = A(r_a F - d_a A) \\ \frac{dF}{dt} &= Ff_F = F\left(\frac{r_f A^2}{b + aA^2} - r_c A - d_f F\right)\end{aligned}\quad (8)$$

They demonstrate that this model reproduces observed population data of the leaf-cutter ant - fungus obligate-obligate mutualist coexistence using the parameter set:

$$\begin{aligned}r_a &= 0.1 & d_a &= 0.1 & a &= 0.2 & r_c &= 0.0045 \\ r_f &= 0.7 & d_f &= 0.2 & b &= 0.002\end{aligned}\quad (9)$$

We increased the value of b to $b = 0.2$ to draw the vector field in Figure 1d. This does not change the basic layout of the zero isoclines, critical points or vector field, but moves the unstable point near the origin further from the origin and allows the properties of the vector field near the origin to be more clearly seen.

Kang *et al.* [19] assume that the benefit the ants receive from the fungus (the availability of fungus to feed on) may be modelled by a Holling Type I function while the benefit the fungus receives from the ants (the provision of processed leaves for the fungus to grow on) may be modelled by a Holling Type III function. These assumptions generate asymmetric zero isoclines unlike any of the other models, but which have a qualitatively similar arrangement of critical points, separatrix and vector field as the B98 and GPP06 models (Figure 1). The vector field for the KCMF11 model is significantly different to that of the HD10 model despite their similar conceptual framework. This is clearly due to the functional forms assumed, but raises the question of to what extent does the lack of explicit budgeting of resources constrain the efficacy of this approach.

MUTUALISM: OBLIGATION, BENEFIT, AND COST

The B98, GPP06, HD10 and KCMF11 models of obligate mutualism take different approaches to representing this population interaction using different attributes of this interaction: obligation, benefit, and the cost of providing a benefit. We note that three of these models, B98, GPP06 and KCMF11, have vector fields that are not substantially different to those noted by May [12]. We also note that each population in all of the models has a population growth term that includes the other population. These obligation terms are differentiated from predation terms by a commensurate, similar loss term not appearing in the other population in each case. This distinction is somewhat blurred in the HD10 and KCMF11 models that include terms that represent the cost of providing a benefit to the other population.

B98 explicitly represents a nonlinear mutualist benefit while rendering the populations obligate by not having any other positive terms in the life function (that is, providing the populations with both linear and quadratic mortality terms). The distinction between an obligate mutualist interaction and a predation interaction is moot in this model, and the model does not differ from a model of bidirectional predation. These are common interactions in nature, where, for example, a prey might feed on the juvenile stages of its predator.

The GPP06 model in contrast represents obligation between populations explicitly but does not include a separate mutualism benefit. The zero isoclines, critical points, separatrices and vector field of the GPP06 model are qualitatively identical to those of the B98 model. The bifurcation behavior is also qualitatively the same, with increases in the magnitude of linear (c_1, c_2 in B98, r_{10}, r_{20} in GPP06) and quadratic (e_1, e_2 in B98, a_1, a_2 in GPP06) mortality rates generating identical behaviors.

The HD10 model takes a different approach and has very different zero isoclines, critical points, separatrices and vector field. It explicitly represents a mutualist benefit with a saturating term, and obligation by a lack of other avenues for growth, similarly to the B98 model. However, it uniquely includes terms representing the cost of providing a mutualist benefit to the other population. The inclusion of this term, combined with the quadratic mortality term, provides the HD10 model with its unusual zero isoclines that are the key to its representation of obligate mutualism. The nature of its zero isoclines provides it with a potentially much more complex bifurcation behavior than the B98 and GPP06 models. In this case, increasing the rate of quadratic mortality drives the coexistence critical point towards the origin, as it does in the B98 and GPP06 models, but instead of disappearing in a blue sky bifurcation in the interior of the ecospace it eventually disappears through a transcritical bifurcation with the origin.

Lastly, the KCMF11 model, although utilizing the same conceptual framework as HD10, has critical points, separatrices and a vector field more qualitatively like the B98 and GPP06 models than the HD10 model. However, the combination of a linear isocline and a nonlinear isocline to produce this vector field suggests that the choice of a Holling Type II function to represent benefit received by the fungus might eliminate the interior unstable critical point and the associated separatrix. The KCMF11 model is quite robust to variations from a Holling Type III to a Holling Type II interaction but, as with the B98, GPP06, and HD10 models, it is critically sensitive to changes from Holling Type II interactions to Holling Type I.

The B98 and GPP06 models, despite having very different conceptual bases and assumptions, have identical zero isoclines and vector fields. These vector fields are qualitatively similar to that of the KCMF11 model, an applied model derived from a conceptual consumer-resource approach. These vector fields have two similar properties: the first is that they contain a separatrix that divides the state space into two regions. There is a region near the origin where all populations always go extinct – small invading populations cannot survive in this system. The second similarity is that they each contain a blue sky bifurcation. These are not uncommon in ecological models and do not necessarily indicate a deficiency in the model. However, we suggest that in the case of a heuristic model, such as B98 or GPP06, the potential for a blue sky bifurcation in the middle of the state space is not a reasonable generic property.

The assumptions underpinning the HD10 model are substantially different to those of the B98 and GPP06 models, but form the basis of the assumptions underpinning the KCMF11 model. In particular, the B98 and GPP06 models assume that each population only has a positive benefit on the other, whereas the HD10 model includes a term that explicitly represents the cost to each population of providing a benefit to the other. The KCMF11 model in contrast models an asymmetric relationship where both populations receive a mutualist benefit, but only the fungus pays an explicit cost of providing the benefit. Assuming a cost of providing a mutualist benefit is not a common approach, but is critical to the HD10 model being able to represent obligate-obligate mutualism.

A further difference between the models is the representation of each population's intrinsic growth rate. The GPP06 model explicitly describes the obligate nature of each population on the other with a function that smoothly varies each population's growth rate from negative to positive depending on the population of its benefactor. It does this in a conceptual framework with no recognition of limiting resources, unlike the HD10 and KCMF11 models that utilize a consumer-resource approach. However, the representation of obligate-obligate mutualism

in the HD10 model renders the intrinsic growth of the populations unclear. The inclusion of both cost and benefit functions results in each population simultaneously functioning as a predator and a mutualist on its benefactor, as the benefit term may be partitioned into a predation component, equivalent to the cost of providing benefits of the benefactor, and a mutualism component that comprises the difference between the benefit acquired by the beneficiary and the cost incurred by the benefactor.

The diversity of approaches evident in the B98, GPP06, HD10, and KCMF11 models reflects that there is no consensus in theoretical ecology of the ingredients that comprise obligate mutualism. Traditionally, obligate mutualism models have included obligation and benefit as key concepts (although GPP06 relax "benefit" to "no harm"). The consumer-resource approach of HD10, that suggests that obligate mutualist interactions must include a cost of supplying a benefit to the other population, is a recent development.

We extend the consumer-resource concept by arguing that mutualist interactions must be, as are competition and predation, constrained by finite resources. Cropp and Norbury [14] showed that facultative mutualism could be represented in simple CN systems. We now consider obligate mutualism in the CN framework by considering the key interactions of obligation, benefit and cost while explicitly accounting for a constant, finite limiting nutrient.

CONSERVATIVE NORMAL (CN) SYSTEMS

The CN framework captures fundamental ecological properties of living systems with mathematical rules. These rules formalize basic ecological concepts, principally that all organisms have to consume resources to survive, and that these resources are finite. Conservation of the mass of a limiting nutrient is fundamental to ecosystems [23] and to the CN framework. Some may argue that such an assumption is unrealistic, and no real ecological system exactly conserves mass. Rather than debate the merits of this view, we draw analogy with the common assumption of linearity. Although it is similarly argued that no real ecological system has exactly linear processes, the simplifying assumption of linearity has led to substantial advances in theoretical ecology, as it has in other fields.

Detailed descriptions of the CN framework have been published elsewhere [14,15], so here we just present the essence of the framework. We preface this brief summary with the observation that obligate mutualism is not a "normal" interaction, where we use "normal" in the context of the CN framework. While the CN framework can be used to winnow out models that do not make ecological sense, there are exceptions to the rules that are ecologically realistic. We label systems with life functions

that do not increase monotonically along resource rays (*i.e.* that do not satisfy equation (17) below) as “exotic.” These systems are ecologically sensible, but may require the relaxation of certain rules, in particular equation (17) below. There are a number of such exotic systems: populations that co-operatively hunt, for which there is an “optimum” population size; omnivorous predators, that consume certain resources that they cannot survive on alone; and as we shall explain below, obligate mutualists.

We consider a general n population system of the form:

$$\dot{x}_i = x_i f_i(x_1, x_2, \dots, x_n), \quad i = 1, 2, \dots, n \quad (10)$$

The “life functions” f_i may include any form for the functions that represent the interactions between populations and include parameters that define the magnitude of the interactions.

CN Rule 0: Measuring the System

We assume each interacting population is sufficiently large in number 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. 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:

$$\hat{x}_1 + \hat{x}_2 + \dots + \hat{x}_n + \hat{N} = \hat{N}_T \quad (11)$$

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 these scaled measurements x_i are fractions of the total nutrient in the system:

$$x_1(0) + x_2(0) + \dots + x_n(0) + N(0) = 1 \quad (12)$$

with $0 < x_i(0)$, $N(0) < 1$. Each living population $x_i(t)$ 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 available inorganic nutrient $N(t)$ available to autotrophs from the implicit remineralization of organic material by microbes is also expressed as a fraction of the total cycling nutrient.

CN Rule 1: Describing Changes in Living Populations

The CN framework requires that the per capita population growth rates are independent of the way in which we measure the living populations, and satisfy:

$$\frac{1}{x_i} \frac{dx_i}{dt} = \hat{f}_i(x_1, x_2, \dots, x_n; N) \quad (13)$$

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. Recall that the $\hat{f}_i$ implicitly include parameters that quantify the rates of environmental interactions.

CN Rule 2: Conservation of Nutrient Mass

We make the assumption that there is no population migration or nutrient flow in to or out of the model domain and require that the total mass of nutrient in the model domain remains constant for all time (*i.e.* $\hat{N}_T$ is constant). The living population fractions $x_i(t)$ and the inorganic nutrient fraction $N(t)$ then satisfy a conservation of total nutrient mass constraint for all time $t > 0$.

$$x_1(t) + x_2(t) + \dots + x_n(t) + N(t) = 1 \quad (14)$$

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 (13) may be written in the form (10), for $x_i(t) > 0$. The elimination of an explicit differential equation for inorganic nutrient means that all the equations in the model have the same (Kolmogorov) form (10), which simplifies the analysis of CN models.

Equation (14) allows us to define a lid $\{x_1 + x_2 + \dots + x_n = 1\}$ (*i.e.* $N = 0$), on the model's state space $x_i > 0$ for all i . The lid completes the closure of the state space in which reasonable model solutions exist, and defines the ecospace E :

$$E \equiv \{0 \leq x_i, 0 \leq x_1 + x_2 + \dots + x_n \leq 1\} \quad (15)$$

CN Rule 3: Normal Ecosystems

All living populations x_j require food to survive and grow. This food may be inorganic nutrient in the cases of autotrophs, or prey (*i.e.* other living organisms) in the cases of non-autotrophs. These resources R_j are finite and limit the growth of population x_j when they become depleted; hence resources should be explicitly represented for every population in ecosystem models, as otherwise a population could have unlimited growth [15]. We define two basic criteria that a living population (measured by x_j) must comply with:

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

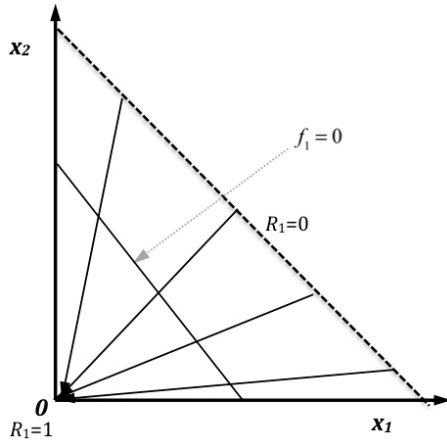


Figure 2. Schematic of the ecospace for a simple two population model showing the points of maximum and minimum resource for x_1 (an autotroph) and rays from several points of zero resource to the point of maximum resource.

famine), the population x_j must die.

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

$$f_j \Big|_{R_j=1} > 0 > f_j \Big|_{R_j=0} \quad (16)$$

Evaluation of this rule on the boundaries of the ecospace places constraints on allowable parameter values that we shall return to in our consideration of benefits obtained by populations via obligate mutualism.

The CN framework places further constraints on the life functions, that in a normal ecology the f_j change monotonically within E . As we follow a life function from any point of minimum resource to any point of maximum resource along a ray, the life function f_j must monotonically increase (Figure 2). The direction of the ray is given by the unit vector defined by the usual direction cosines (γ_k is the angle between this direction vector and the k th co-ordinate axis), $(\cos\gamma_1, \cos\gamma_2, \dots, \cos\gamma_n)$:

$$\cos\gamma_1 \frac{\partial f_j}{\partial x_1} + \cos\gamma_2 \frac{\partial f_j}{\partial x_2} + \dots + \cos\gamma_n \frac{\partial f_j}{\partial x_n} > 0 \quad (17)$$

This condition implements a simple rule – the more resource a population has, the faster it can grow. Combined with equation (16), it specifies properties of “normal” populations whose dynamics may be described by the usual Michaelis-Menten [24] and Holling [25] terms. “Normality” excludes organisms that have specific population sizes at which they do better, such as some yeasts which produce toxins that accumulate and reduce their

own growth at high population densities [26].

A Consistency Condition

The world’s resources are finite and we must ensure that our ecosystem model has realistic behavior when the key limiting inorganic nutrient runs out. We place a consistency condition on the lid that guarantees that solutions $\{x_1(t), x_2(t), \dots, x_n(t)\}$ of equations (10) which start in E do not leave E through the lid. This requires that $N(t)$ remains positive, and consequently that mass conservation is always physically sensible. Differentiating equation (14) and using (10) provides the lid consistency condition:

$$\frac{dN}{dt} = -\frac{dx_1}{dt} - \frac{dx_2}{dt} - \dots - \frac{dx_n}{dt} = -\sum_{i=1}^n x_i f_i > 0 \quad \text{when } N=0 \quad (18)$$

ensuring $N \geq 0$ for all time. Equation (18) is an important constraint that should be checked for all systems that include mutualist interactions. It provides generic conditions on the parameters that constrain the magnitude of mutualist benefits that can be obtained without violating the basic principle that mass cannot be created.

Implications of the CN Approach

The CN approach makes two key assumptions or approximations, that we can identify a limiting resource that may be used to measure all populations and resources in the system; and that this resource is conserved by the system. It is axiomatic that all living systems are limited by the availability of resources – this view dates back to Malthus [27] and was a key consideration of Darwin’s theory of evolution [28]. We identify the key limiting resource, which may be one of a number of limiting resources, to use as a currency to describe the system. This does not imply that all populations in the ecosystem are limited by the same resource. For example, plants are limited by the availability of inorganic nutrients (the limiting nutrient is commonly used as the model currency), but herbivores are limited by the availability of the plants. We measure the amounts of inorganic nutrients and plants in the same currency, but they are clearly different resources.

The CN framework makes the approximation that the quantity of limiting resource cycling in the system is conserved. While many resources, such as energy and non-limiting nutrients, may flow through ecosystems, most ecosystems are adapted to hold onto their limiting nutrients very tightly, and recycle over 90 percent [29]. The CN approximation that the limiting resource is conserved, *i.e.* that 100 percent is recycled in the system, is a very good first approximation to real systems.

We also note that the CN framework’s use of a single limiting resource to describe ecosystems does not

preclude the modelling of populations and systems with varying stoichiometry. We do not consider this issue in the heuristic examples below, but variable stoichiometries may be modelled with simple additions to the basic systems.

Obligate Mutualism as an Exotic CN System

The CN framework is a consumer – resource conceptualization predicated on explicit accounting of mass of limiting nutrient. It considers explicitly resource-limited growth with implicit nutrient recycling and constancy of total nutrient mass. Consequently, the basic CN framework does not represent population interactions, that we might term “services,” that do not involve flows of mass. To represent the provision of services to another population we need to relax certain CN rules and consider “exotic” CN systems.

The obligation of one population on another, that is where a second population provides a “catalytic” service such that the second population has to be present in order that the first population can grow, is not a normal CN system. CN Rule 3 requires that a population must be able to grow at any point in the ecospace where a resource is maximal, however, it is easily seen that while this rule is intuitive and appropriate for simple heuristic systems, for systems with many populations, in which a single population may have many resources, relaxation of this rule may be required. For example, an omnivore may consume many resources, some of which may fuel growth but are insufficient for the omnivore to survive on independently. In such cases, it would be reasonable that the CN Rule 3 be relaxed for that resource for that population.

Obligate mutualism requires a different relaxation of CN Rule 3. Consider the simplest example of obligate mutualism in which a population has a single resource and is obligated on the presence of a single other population to be able to grow. The maximal point of the single resource for the population lies at a vertex of E , where all other populations are zero, and the population supplying the service to the obligated population must be zero. We therefore place a caveat on CN Rule 3 for obligate systems and evaluate the maximum resource condition of $(16)f_j | R_{j=1} > 0$ assuming that the obligate population is non-zero. This is consistent with the axiom underpinning this rule, that if a population cannot grow when experiencing its most ideal conditions, it cannot exist in nature and there is little point in including it in a model.

MODELS OF OBLIGATE MUTUALISM

We consider obligate mutualism in the CN framework in the context of the three interactions discussed above: obligation, benefit, and cost. A significant advantage of the CN framework is that explicit mass con-

servation is a core construct of the theory: the ecology always has a limit on the key resource. This differentiates it from the B98 and GPP06 models that do not consider resources or the constraints on growth that they impose, and the conceptual consumer-resource basis of the HD10 and KCMF11 models, that consider resources but do not explicitly account for resource budgets. A further conceptual advantage of the CN framework is that each population, together with its interactions, can be explicitly measured (at any time) in terms of this common currency of key limiting resource. Thus, benefits and costs can be properly and explicitly measured and compared. In what follows $u_i = u_i(t)$ denotes the time-varying population values and u_i^* denotes the equilibrium population value.

Obligation: the CN0 Model

We introduce the CN0 model as the simplest conceptual model that reasonably represents obligate mutualism in a rigorous consumer-resource framework. We commence with the CN0 model that includes only the fact that each population requires the other to be present in order to grow. This is analogous to the GPP06 model; however, we do not assume that the marginal rate of change of the per capita growth rate of each species due to an increase in the other species is proportional to the difference between the maximum growth rate and the current growth rate. This CN0 model is:

$$\begin{aligned} \frac{du_1}{dt} &= u_1 f_{u_1} = u_1 (\mu_1 u_2 N - \sigma_1 u_1) \\ \frac{du_2}{dt} &= u_2 f_{u_2} = u_2 (\mu_2 u_1 N - \sigma_2 u_2) \end{aligned} \quad (19)$$

where, by differentiating the conservation of mass condition ($u_1 + u_2 + N = 1$, implicit in all CN models) we obtain an equation that describes the dynamics of the implicit inorganic nutrient:

$$\frac{dN}{dt} = -\frac{du_1}{dt} - \frac{du_2}{dt} \quad (20)$$

We use (20) to check that the lid consistency condition $\dot{N} |_{N=0} > 0$ holds and that the model makes physical sense. This also constrains all solutions to the models to an ecospace $E = \{0 \leq u_1, u_2 \leq 1\}$. We use the arbitrary parameter set

$$\begin{aligned} \mu_1 &= 1, & \sigma_1 &= 0.2, \\ \mu_2 &= 1, & \sigma_2 &= 0.2, \end{aligned} \quad (21)$$

to draw the vector fields, isoclines, and critical points (Figure 2a). Note that the lid condition $\dot{N} |_{N=0} > 0$ that ensures that the model cannot have unphysical behavior such as predicting negative masses of inorganic nutrient, is satisfied for all positive parameter values for this mod-

el. This model predicts that obligate populations always coexist.

Reducing the quadratic mortality parameters σ_1 and σ_2 moves the coexistence point towards the lid until when $\sigma_1 = 0 = \sigma_2$ the point exists on the lid (in this case at $u_1^* = \frac{1}{2} = u_2^*$). Increasing σ_1 and σ_2 moves the coexistence point towards the origin until at $\sigma_1 \approx 1 \approx \sigma_2$ it leaves the ecospace through a transcritical bifurcation with the equilibrium point at the origin.

Including Mutualist Benefit: the CN1 Model

We derive the CN1 model by adding explicit mutualist benefits to the obligate interaction:

$$\begin{aligned} \frac{du_1}{dt} &= u_1 f_{u_1} = u_1 (\mu_1 u_2 N + \omega_1 u_2 - \sigma_1 u_1) \\ \frac{du_2}{dt} &= u_2 f_{u_2} = u_2 (\mu_2 u_1 N + \omega_2 u_1 - \sigma_2 u_2) \end{aligned} \quad (22)$$

We use the arbitrary parameter set

$$\begin{aligned} \mu_1 &= 1, \quad \sigma_1 = 0.2, \quad \omega_1 = 0.1, \\ \mu_2 &= 1, \quad \sigma_2 = 0.2, \quad \omega_2 = 0.1, \end{aligned} \quad (23)$$

to draw the vector fields, isoclines, and critical points (Figure 2c). The lid consistency condition places an upper bound on the amount of mutualist benefit that may be obtained by each population:

$$\omega_1 + \omega_2 < \frac{\sigma_1 u_1^2 + \sigma_2 u_2^2}{u_1 u_2} \quad (24)$$

This expression is undefined at the extremities of the lid, where mutualist coexistence ceases, but evaluating it at $u_1 = u_2$ provides the useful rubric that the maximum mutualist benefit is constrained to be less than the recycled nutrient ($\omega_1 + \omega_2 < \sigma_1 + \sigma_2$). We note that adding explicit mutualist benefits to the simplest model extends the intersections of the zero isoclines with the axes outside the ecospace. This is of itself not an indicator that the model has lost ecological validity, but indicates that the potential exists for it to lose validity if parameter values are used that do not satisfy the lid condition.

Including Mutualist Costs: the CN2 Model

We derive the CN2 model by adding explicit mutualist costs in their simplest form to the simplest form of obligate interaction with mutualist benefits:

$$\begin{aligned} \frac{du_1}{dt} &= u_1 f_{u_1} = u_1 (\mu_1 u_2 N + \omega_1 u_2 - \chi_1 u_2 - \sigma_1 u_1) \\ &= u_1 (\mu_1 u_2 N + (\omega_1 - \chi_1) u_2 - \sigma_1 u_1) \\ \frac{du_2}{dt} &= u_2 f_{u_2} = u_2 (\mu_2 u_1 N + \omega_2 u_1 - \chi_2 u_1 - \sigma_2 u_2) \\ &= u_2 (\mu_2 u_1 N + (\omega_2 - \chi_2) u_1 - \sigma_2 u_2) \end{aligned} \quad (25)$$

We use the arbitrary parameter set

$$\begin{aligned} \mu_1 &= 1, \quad \sigma_1 = 0.2, \quad \omega_1 = 0.1, \quad \chi_1 = 0.05, \\ \mu_2 &= 1, \quad \sigma_2 = 0.2, \quad \omega_2 = 0.1, \quad \chi_2 = 0.05, \end{aligned} \quad (26)$$

to draw the vector fields, isoclines, and critical points (Figure 2e). The cost of providing mutualist benefits to the other population in the simplest case is equivalent to reducing the benefit received from the other population. This in turn modifies the lid consistency condition and increases the upper bound on the amount of mutualist benefit that may be obtained by each population:

$$\omega_1 + \omega_2 < \frac{\sigma_1 u_1^2 + \sigma_2 u_2^2}{u_1 u_2} + \chi_1 + \chi_2 \quad (27)$$

The effect of adding a cost of providing a mutualist benefit is evident in Figure 3e by the zero isoclines reverting to look more like the CN0 model and the movement of the coexistence point towards the origin. This is consistent with a reduction in the net mutualist benefit received by each population.

NONLINEARITY: DOES IT MATTER?

We indicate briefly in this section that more realistic models of obligate mutualism can be readily found by replacing the Lotka-Volterra terms with Michaelis-Menten terms (equivalently Holling Type II terms for Holling Type I). The right-hand column of Figure 3 shows that the phase plane (ecospace) features are similar, as are the ecological interpretations. Nonlinearity may be included in the CN0, CN1 and CN2 models in several ways. The number of options that might be considered to investigate this topic fully is exhausting (but will be investigated in subsequent work), so we just consider common nonlinear options, focusing on the fundamental difference between linear (*i.e.* Holling Type I, Lotka-Volterra, etc.) and saturating (*i.e.* Holling Type II, Michaelis-Menten, etc.) functional forms. We assume a saturating (Michaelis-Menten) function for nutrient uptake in all cases to ensure every process is nonlinear.

Nonlinear Obligation: the CN0n Model

The CN0n model includes a saturating function for both the nutrient uptake and obligation:

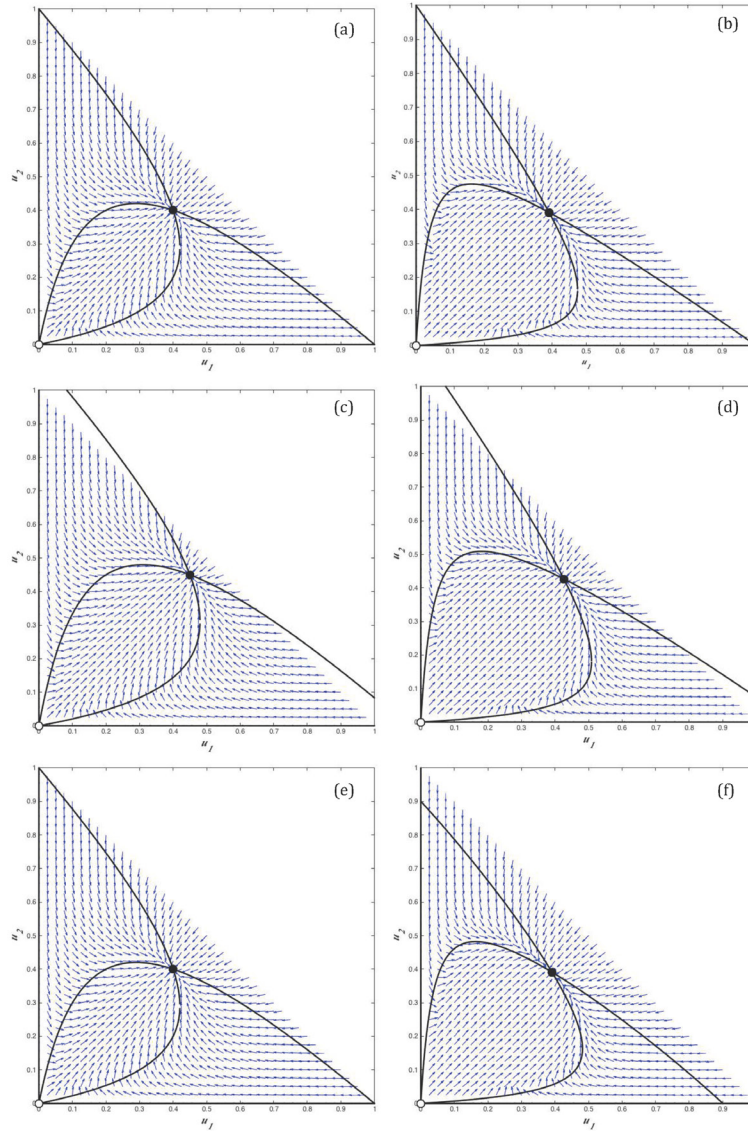


Figure 3. Vector field for: **(a)** the CN0 model (19) for the parameter set (21); **(b)** the CN0n model (28) for the parameter set (29); **(c)** the CN1 model (22) for the parameter set (23); **(d)** the CN1n model (30) for the parameter set (31); **(e)** the CN2 model (25) for the parameter set (26); and **(f)** the CN2n model (33) for the parameter set (34). The solid black lines show zero isoclines, dashed red lines show separatrices, open circles indicate unstable critical points and closed circles indicate stable critical points.

$$\begin{aligned} \frac{du_1}{dt} &= u_1 f_{u_1} = u_1 \left(\mu_1 \left(\frac{u_2}{u_2 + \xi_2} \right) \left(\frac{N}{N + \kappa_1} \right) - \sigma_1 u_1 \right) \\ \frac{du_2}{dt} &= u_2 f_{u_2} = u_2 \left(\mu_2 \left(\frac{u_1}{u_1 + \xi_1} \right) \left(\frac{N}{N + \kappa_2} \right) - \sigma_2 u_2 \right) \end{aligned} \quad (28)$$

where we use the arbitrary parameter set:

$$\begin{aligned} \mu_1 &= 1 & \kappa_1 &= 2 & \sigma_1 &= 0.2 & \xi_1 &= 0.1 \\ \mu_2 &= 1 & \kappa_2 &= 2 & \sigma_2 &= 0.2 & \xi_2 &= 0.1 \end{aligned} \quad (29)$$

Comparison of Figure 3a and 3b indicates that the nonlinear forms increase the curvature of the zero isoclines but make no qualitative difference to the vector field and very little quantitative difference. The CN0 model is quite robust to assumptions of the form that the interactions should take.

Nonlinear Obligation and Nonlinear Benefit: the CN1n Model:

The CN1n model includes saturating functions for nutrient uptake, obligation, and mutualist benefits:

$$\begin{aligned}\frac{du_1}{dt} &= u_1 f_{u_1} = u_1 \left(\mu_1 \left(\frac{u_2}{u_2 + \xi_2} \right) \left(\frac{N}{N + \kappa_1} \right) + \omega_1 \left(\frac{u_2}{u_2 + \zeta_2} \right) - \sigma_1 u_1 \right) \\ \frac{du_2}{dt} &= u_2 f_{u_2} = u_2 \left(\mu_2 \left(\frac{u_1}{u_1 + \xi_1} \right) \left(\frac{N}{N + \kappa_2} \right) + \omega_2 \left(\frac{u_1}{u_1 + \zeta_1} \right) - \sigma_2 u_2 \right)\end{aligned}\quad (30)$$

where we use the arbitrary parameter set:

$$\begin{aligned}\mu_1 &= 1 & \kappa_1 &= 2 & \sigma_1 &= 0.2 & \xi_1 &= 0.1 & \omega_1 &= 0.1 & \zeta_1 &= 1 \\ \mu_2 &= 1 & \kappa_2 &= 2 & \sigma_2 &= 0.2 & \xi_2 &= 0.1 & \omega_2 &= 0.1 & \zeta_2 &= 1\end{aligned}\quad (31)$$

We again check the lid condition for parameter constraints that limit the amount of mutualist benefit that the system can support:

$$\begin{aligned}\frac{dN}{dt} \Big|_{N=0} &= -u_1 \left(\omega_1 \left(\frac{u_2}{u_2 + \zeta_2} \right) - \sigma_1 u_1 \right) - u_2 \left(\omega_2 \left(\frac{u_1}{u_1 + \zeta_1} \right) - \sigma_2 u_2 \right) > 0 \\ \Rightarrow u_1 (u_1 + \zeta_1) + \omega_2 (u_2 + \zeta_2) &< \frac{u_1^2 \sigma_1 (u_2 + \zeta_2) + u_2^2 \sigma_2 (u_1 + \zeta_1)}{u_1 u_2}\end{aligned}\quad (32)$$

Again, we vary u_1 , with $u_2 = 1 - u_1 - u_2$ and $0 < u_1, u_2 < 1$, to find a useful parameter inequality from (32).

It is obvious from comparing Figure 3c and 3d that the inclusion of nonlinear forms of obligate and mutualist interactions has not fundamentally changed the vector field, isoclines, or critical points of the system. Note that the CN1n model reduces to the CN0n model when $\omega_1 = 0 = \omega_2$. The most substantive difference between the CN0n and CN1n models is, as for the CN0 and CN1 models, that the zero isoclines extend outside the ecospace for the CN1 and CN1n models, indicating that the potential now exists to violate the lid condition by specifying an excessively large value for the mutual benefits received.

Nonlinear Obligation, Nonlinear Benefit and Nonlinear Costs: the CN2n Model

The CN2n model includes saturating functions for nutrient uptake, obligation and mutualist benefits and costs:

$$\begin{aligned}\frac{du_1}{dt} &= u_1 \tilde{f}_{u_1} = u_1 \left(\mu_1 \left(\frac{u_2}{u_2 + \xi_2} \right) \left(\frac{N}{N + \kappa_1} \right) + \omega_1 \left(\frac{u_2}{u_2 + \zeta_2} \right) - \chi_1 \left(\frac{u_2}{u_1 + \varepsilon_1} \right) - \sigma_1 u_1 \right) \\ \frac{du_2}{dt} &= u_2 \tilde{f}_{u_2} = u_2 \left(\mu_2 \left(\frac{u_1}{u_1 + \xi_1} \right) \left(\frac{N}{N + \kappa_2} \right) + \omega_2 \left(\frac{u_1}{u_1 + \zeta_1} \right) - \chi_2 \left(\frac{u_1}{u_2 + \varepsilon_2} \right) - \sigma_2 u_2 \right)\end{aligned}\quad (33)$$

here we use the arbitrary parameter set:

$$\begin{aligned}\mu_1 &= 1, & \kappa_1 &= 2, & \sigma_1 &= 0.2, & \xi_1 &= 0.1, & \omega_1 &= 0.1, & \zeta_1 &= 1, & \chi_1 &= 0.05, & \varepsilon_1 &= 1, \\ \mu_2 &= 1, & \kappa_2 &= 2, & \sigma_2 &= 0.2, & \xi_2 &= 0.1, & \omega_2 &= 0.1, & \zeta_2 &= 1, & \chi_2 &= 0.05, & \varepsilon_2 &= 1,\end{aligned}\quad (34)$$

We again check the lid condition for parameter constraints that limit the amount of mutualist benefit that the system can support:

$$\frac{dN}{dt} \Big|_{N=0} = -u_1 \left(\omega_1 \left(\frac{u_2}{u_2 + \zeta_2} \right) - \chi_1 \left(\frac{u_2}{u_1 + \varepsilon_1} \right) - \sigma_1 u_1 \right) - u_2 \left(\omega_2 \left(\frac{u_1}{u_1 + \zeta_1} \right) - \chi_2 \left(\frac{u_1}{u_2 + \varepsilon_2} \right) - \sigma_2 u_2 \right) > 0 \quad (35)$$

which gives:

$$\frac{(u_1 + \varepsilon_1)(u_2 + \varepsilon_2) \left[\omega_1 (u_2 + \zeta_2) + \omega_2 (u_1 + \zeta_1) \right]}{-(u_1 + \varepsilon_1)(u_2 + \varepsilon_2) \left[\chi_1 (u_2 + \varepsilon_2) + \chi_2 (u_1 + \varepsilon_1) \right]} < \frac{(u_1^2 \sigma_1 + u_2^2 \sigma_2)(u_1 + \varepsilon_1)(u_2 + \varepsilon_2)(u_1 + \varepsilon_1)(u_2 + \varepsilon_2)}{u_1 u_2} \quad (36)$$

Comparison of Figure 3e and 3f reveals that there is very little difference between the zero isoclines for the CN2 and CN2n models, and that the vector fields are only subtly quantitatively changed. As might be expected, the inclusion of costs of providing mutualist benefit gives an intermediate case between CN0/CN0n, where no benefits are provided, and CN1/CN1n where benefits are provided without cost.

DISCUSSION

Lotka-Volterra models with their assumption that interactions between populations can be represented by simple functions that produce linear or planar zero isoclines arguably initiated the field of theoretical ecology and have provided the basis for much of the theory we have today. They have been especially successful in establishing a solid theoretical basis for competition and predation interactions, but have failed to provide a similarly useful theory for mutualist interactions, and in particular have abjectly failed to represent obligate mutualism in any useful way. The standard Lotka-Volterra models of mutualism predict that only “strong” facultative mutualism interactions allowed stable coexistence of the populations [21].

Cropp and Norbury [14] showed that it was possible to model facultative mutualism using Lotka-Volterra models if the models were developed in the CN framework (*i.e.* LVCN models) that explicitly represented the constraints of finite resources on the populations. This work showed that the traditional distinction made between weak and strong mutualism in Lotka-Volterra models, that is useful for competition models, is inappropriate, and that a distinction that arises naturally in the CN framework is more useful. Cropp and Norbury showed that facultative mutualists looked like mixotrophs (organisms, commonly plankton, that both photosynthesize and predate on other organisms) in their heuristic LVCN models. This is because the benefits that they acquire via mutualist interactions are represented by transfers of mass from the inorganic nutrient pool directly to the population, and in heuristic LVCN models this process is indistinguishable

from photosynthesis. While Cropp and Norbury [14] showed that LVCN models could represent competition, predation, mixotrophy and facultative mutualism seamlessly in simple LVCN models with two populations, it appears that obligate mutualism cannot be represented in LVCN models. Attempts to arrange planar isoclines of LVCN models with more than two populations has suggested that obligate mutualism requires curved zero isoclines. In this respect, the LVCN models again appear to produce results consistent with traditional approaches, as many, if not all, published models of obligate mutualism have curved zero isoclines and several authors have noted, as Bazykin [17] did, that their solutions collapse if their zero isoclines are straightened.

The key observation for obligate mutualism that arises from Cropp and Norbury [14] is that mutualist interactions have no natural local mass balance – there is no obvious constraint on the magnitude of the benefit that one population can gain from another. Holland and DeAngelis [11] advocated the use of a consumer-resource framework and suggested that models of mutualism needed to include the cost of providing a mutualist benefit to another population in addition to including the benefit gained from it. We argue that a conceptual consumer-resource framework is not sufficient to model population interactions, that instead, models must be written in a common currency of a finite, conserved limiting resource. Models in the CN framework are able to explicitly represent the fundamental components of obligate mutualism: obligation, benefit and, if appropriate, cost. The explicit accounting of resources in this framework allows constraints on the magnitude of mutual benefit to be articulated, and consequently provides objective grounds to dismiss models that violate these constraints as nonsensical.

The requirement for a mutualist to be obligate on another population has presented a major stumbling block in the development of a theory of obligate mutualism. In some Lotka-Volterra models authors have contrived counter-intuitive scenarios such as negative intrinsic growth rates, or in logistic examples negative carrying capacities, to prevent populations from existing independently, and some of these ideas have carried across into more complex models. Indeed, the distinction between mutualist interaction and bilateral predation is solely conceptual in the models of Bazykin [17] and Holland and DeAngelis [11] while Kang, Clark [19] presents an unusual arrangement that could represent asymmetrical bilateral predation. The model of Graves, Peckham [18] explicitly represents obligation, but not separate mutualist benefits or costs, which results in a vector field qualitatively identical to those of May [12], Bazykin [17] and Graves, Peckham [18]. In contrast, the models of

have vector fields of a form not seen previously that are consistent across all models that include obligation, irrespective of whether they also assume benefits and costs, or whether the interactions are represented by linear or nonlinear processes.

All the CN models of obligate mutualism considered here, that include a variety of assumptions about the form of mutualism (specifically, the obligation, benefit and cost of mutualism expressed in the common currency of a finite resource), provide plausible models and solutions for obligate-obligate mutualism. These CN models, which include explicitly accounted consumer-resource relationships, have fundamentally different isoclines to the B98, GPP06 and HD10 models. Our models of obligate mutualism are straightforward to understand in ecological terms, and suggest appropriate ways to obtain and use data in terms of a common currency, the limiting nutrient. These new population models complete in the CN framework (when added to those in Cropp and Norbury [14]) the usual triad of competition, predation, and mutualism central to theoretical ecology [for example, 1,7,20,30].

CONCLUSION

Competition, predation, and mutualism are considered the tripod of population interactions that underpin the usual ecological analysis of communities. The familiar Lotka-Volterra models provide basic and wide-ranging understanding of the mechanisms of competition and predation, but various forms of parasitism, symbiosis and obligate mutualism/cooperation have defied a similar simple but general theoretical explanation. We argue that all of the obligations, gains, and losses, where appropriate, of mutualist interactions need to be explicitly quantified and accounted for (in a common currency) in all ecosystem models, but crucially in those that seek to represent obligate mutualism. The CN framework is built on just such a finite resource accounting and it allows construction of simple models that are both obligate and mutually beneficial. This completes the usual theoretical analyses of population interactions in community ecology within the CN framework. More significantly, it provides models of obligate mutualism that are straightforward both in ecological interpretation and in mathematical terms, while still remaining generic. These models are then useful for undergraduate teaching, for comparison with experimental outcomes and data, and for the general theoretical understanding of mutualism.

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