

Resource based models of mutualism.

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1 **Abstract**

2 Mutualist interactions are thought to be ubiquitous, spanning all levels of biological
3 organisation, and involving most species on Earth. However, in contrast to population
4 interactions such as competition and predation, a comprehensive and succinct theoretical
5 explanation of mutualism has proved elusive. We use a new modelling framework that
6 represents obligation, mutualist benefits and mutualist costs in an extended consumer-
7 resource approach to develop simple, consistent models of mutualism. We show how
8 populations may stably transition between facultative and obligate mutualism and
9 demonstrate that our solutions do not depend on saturating functions. We show facultative and
10 obligate mutualisms between autotrophs and heterotrophs.

12 **1: Introduction**

13 The increasing need to understand and manage natural and man-made ecosystems requires
14 that researchers and managers recognise that, despite the popular conception that ‘nature is
15 red in tooth and claw’, most populations on Earth are involved in mutualist interactions
16 (Bronstein 2015a). Many approaches are used to understand and manage ecosystems
17 (McDonald-Madden et al. (2016); Bode et al. (2017); Tulloch, et al. (2018); Baker et al. (2018))
18 but in this paper, we introduce in a simple form a modelling framework that naturally
19 transitions from the usual population interactions of competition and predation to the less
20 frequently modelled mutualist interactions (in both facultative and obligate forms). We use a
21 consumer-resource approach, but replace the usual mutualist population assumptions by
22 explicit modelling of a resource pool (that represents links to the environment) and recycling
23 of the limiting resource through this pool.

25 Mutualist interactions may be central to the diversity of ecosystems (Gross 2008) and
26 interactions such as pollination provide vital services to agriculture (Potts et al. 2010).
27 Mutualisms are considered to be ubiquitous in nature (Bronstein 2015b) but the development
28 of a theory to explain mutualisms has lagged behind other population interactions (Levin 2012,
29 Assaneo et al. 2013, Holland 2015). We focus on obligate mutualism in this manuscript as the
30 ‘canonical’ example of the difficulties of including mutualism in resource management models.
31 This is an extension of the framework described in Cropp and Norbury (2015b) that describes

population interactions from competition through mixotrophy to facultative mutualism in a Lotka-Volterra model.

Obligate mutualism is a beneficial interaction between populations where each population requires the presence of another to survive (Holland and DeAngelis 2010). Obligate mutualism can involve three distinct (or explicit) processes, those of obligation, benefits and costs. Models of obligate mutualism can then be classified into three groups based on the mutualism processes they emphasise (see Fig. 1).

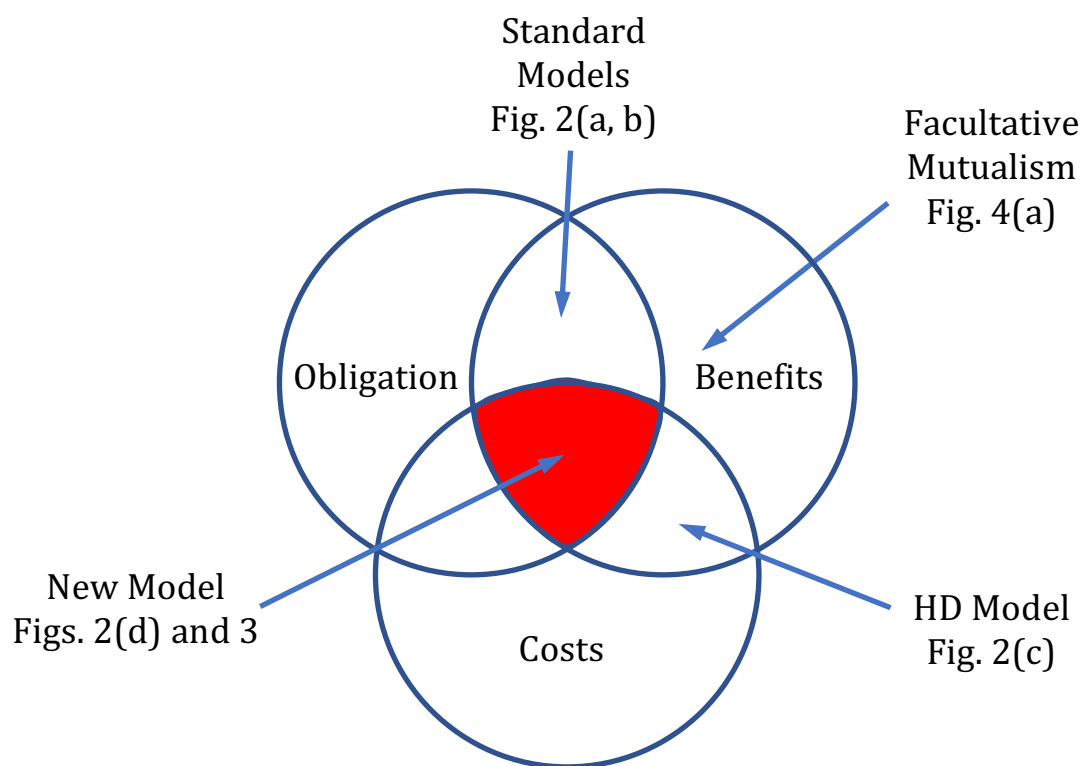


Fig. 1. Venn diagram of the three components of mutualist interaction. Most models have focussed on obligation and benefits, producing models with solutions described by Fig. 2(a, b). HD focussed on benefits and costs, and produced models with solutions described by Fig. 2(c). This manuscript focusses on models with all three components and produces solutions like Figs. 2(d) and 3.

Those models that emphasise the obligation of one population on another to be able to grow include the models of Dean (1983) and Graves et al. (2006), who modelled obligation through the growth term (i.e. pollination) and Gross (2008) who modelled obligation through the

mortality term (i.e. protection); those that emphasise the benefits obtained by the mutualist population include the models discussed by May (1976), Wright (1989) and Case (2000); and those that model significant mutualist costs when providing a mutualist benefit to a partner include Holland and DeAngelis (2001, 2009, 2010), and Holland (2015).

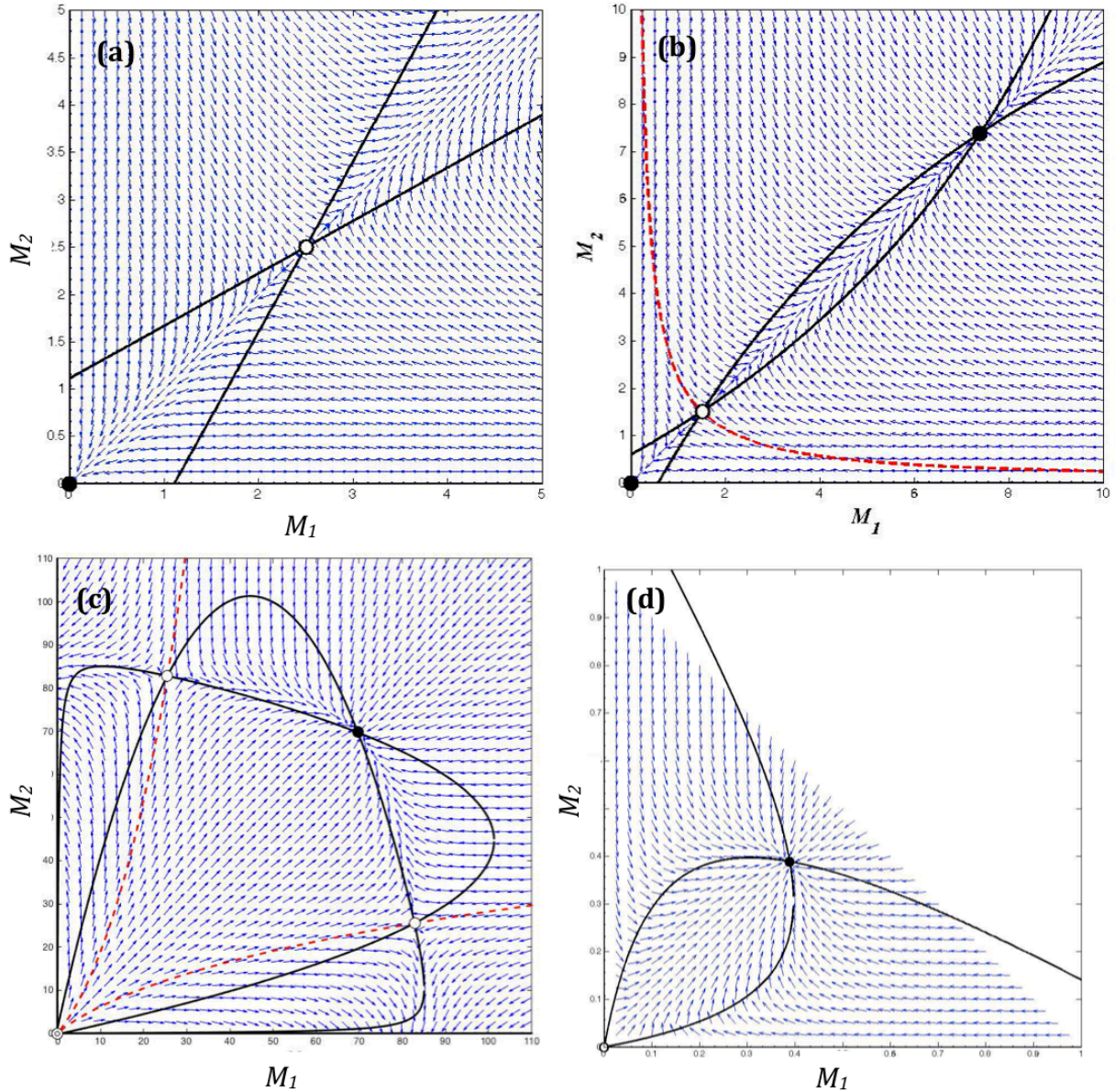


Fig. 2. (a) The vector field common to Lotka-Volterra models of obligate mutualism - one of the standard models. (b) The vector field common to many nonlinear models of obligate mutualism - one of the standard models. (c) The vector field for the consumer-resource obligate mutualism model of Holland and DeAngelis (2010). (d) Typical vector fields of models of obligate mutualism from the extended consumer resource

approach of this paper. The blue arrows show the vector fields, the solid black lines are the zero isoclines, and the dashed red lines are separatrices (that trajectories cannot cross). Filled circles show stable equilibrium points and open circles show unstable equilibrium points.

The phase plane of Fig. 2(a) is the classic Lotka-Volterra model “fail” diagram (see for example, Pastor 2008, Holland 2015), and is described by equation (1). The vector field of Fig. 2(b) is common to many models of obligate mutualism, that often use saturating functional forms, including those discussed by May (1976), Dean (1983), Wright (1989), Bazykin (1998), Case (2000), Kot (2001), Graves et al. (2006), Kang et al. (2011), and Johnson and Amarasekare (2013). These systems are described by equations of the form Bazykin (1998):

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

or Graves et al. (2006):

$$\begin{aligned}\frac{dx}{dt} &= x f_x = x \left[\left(r_{10} + (r_{11} - r_{10})(1 - e^{-k_1 y}) \right) - a_1 x \right] \\ \frac{dy}{dt} &= y f_y = y \left[\left(r_{20} + (r_{21} - r_{20})(1 - e^{-k_2 x}) \right) - a_2 y \right]\end{aligned}\quad (2)$$

We call these the standard models, of which only the saturating form is considered to have any degree of veracity. The only model of obligate mutualism that we are aware of that appears to have a substantially different phase plane to Fig. 2(a, b) is the consumer-resource model of Holland and DeAngelis (2010), shown in Fig. 2(c), which we refer to as HD. This model is described by equations of the form:

$$\begin{aligned}\frac{dM_1}{dt} &= M_1 f_{M_1} = M_1 \left[r_1 + c_1 \left(\frac{\alpha_{12} M_2}{h_2 + M_2} \right) - q_1 \left(\frac{\beta_1 M_2}{e_1 + M_1} \right) - d_1 M_1 \right] \\ \frac{dM_2}{dt} &= M_2 f_{M_2} = M_2 \left[r_2 + c_2 \left(\frac{\alpha_{21} M_1}{h_1 + M_1} \right) - q_2 \left(\frac{\beta_2 M_1}{e_2 + M_2} \right) - d_2 M_2 \right]\end{aligned}\quad (3)$$

This model explicitly includes significant costs (the terms beginning with $-q_1$ and $-q_2$) associated with providing mutualist benefits (Holland et al. 2002, Holland and DeAngelis 2010, Holland 2015), and it is these costs that wrap the smooth isoclines of the standard model into a “Turk’s head knot” of interlacing curves and represents a significant change to the standard model.

1
2 The models we propose in this paper produce vector fields like Fig. 2(d), which may be
3 considered intermediate to the standard model and HD. The models can also produce vector
4 fields superficially similar to the “fail” diagram in Fig. 2(a), but which are in fact valid solutions.
5 See Thompson et al. (2006) for examples of obligate mutualism in nature, and Holland and
6 DeAngelis (2010) for a description of over 20 ecological examples of both bidirectional and
7 unidirectional mutualism that this model applies to, and Holland et al. (2002), Holland et al.
8 (2005), and Holland and DeAngelis (2009) for further background to the costs and benefits
9 arising from mutualism studies of cactus and cactus moth pollination.

10
11 Mutualist interactions are distinct from other population interactions in that they have no
12 natural equivalent of local mass balance. Predator-prey interactions are constrained by the
13 axiom that a predator cannot gain more mass than its prey loses, while the acquisition of
14 resources by one population reduces the quantum of resources available to any competitor by
15 the same amount. Mutualist interactions involve the acquisition of benefits that are facilitated,
16 but not necessarily directly provided, by their mutualist benefactor. This results in the
17 population doing better than it would otherwise, which is reflected in consumer-resource
18 models by it acquiring a larger share of the resource pool than it otherwise would. Mutualism
19 is commonly represented in simple Lotka-Volterra models by each population having a positive
20 interaction coefficient with the other. However, as Murray (2001) notes, this simple Lotka-
21 Volterra approach does not produce useful results, suggesting that the representation of
22 obligate mutualism may require a more sophisticated conceptual framework. In particular, we
23 argue that mutualism can be sensibly represented in models that explicitly and rigorously
24 constrain the growth of every population by a finite limiting resource within the ecosystem -
25 this resource may be a recycling limiting nutrient or another population. This concept forms
26 the basis of the Conservative Normal (CN) approach that we use below to consider obligate
27 mutualism. Refer to the Appendix for a brief summary of this mass-conserving consumer-
28 resource framework as it applies to obligate mutualism and to Cropp and Norbury (2015b) for
29 a detailed explanation of the framework.

30
31 The Conservative Normal (CN) approach (Cropp and Norbury 2015b) provides a unifying
32 framework for studying the dynamics of interacting populations using only Lotka-Volterra (LV)
33 interaction terms for competition, mixotrophy, facultative mutualism and predation. We extend

this analysis to model facultative and obligate mutualism interactions by using a nonlinear term to represent obligation in the vein of Dean (1983) and Graves et al. (2006). This perforce requires the loss of some of the simplicity of the Lotka-Volterra approach, but we retain the notation and the essence of the LVCN (Lotka-Volterra Conservative Normal) approach to model the benefits and costs that arise from mutualist interactions. Explicit mass conservation is a core construct of CN theory: the ecosystem always has a constant, finite amount of a key (i.e. limiting) nutrient distributed among the interacting populations and the nutrient pool. Every population, together with its interactions, is explicitly measured (at any time) in terms of this common currency of conserved nutrient. Thus, benefits and costs can be properly and explicitly measured and compared.

Obligation is a catalytic process that does not usually involve direct transfers of mass between populations. However, conservation of total mass means the requirement that a catalytic population must be present in order for an obligate population to grow reduces the quantum of resource available to the obligate population. Hence, we modify our definition of a resource to include catalytic processes when considering constraints imposed on obligate populations by finite resources, thus giving an extension of the conservative framework to non-normal systems. Details are provided in the Appendix. In what follows we describe simple generic models of obligate mutualism that have stable and robust coexisting populations whose interactions have sensible ecological interpretations. We also demonstrate the smooth, stable transition from facultative to obligate mutualism that is possible in this extended CN framework.

2: Obligate Mutualism between Autotrophs

We use the following generic equations (4) to consider the simplest version of obligate mutualism between two autotroph populations x_1 and x_2 , where x_1 and x_2 represent the fraction of the total nutrient that is bound into each population. These equations arise from Lotka-Volterra equations for mutualism that have been cast in the CN framework and have an additional term included to represent obligation:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1 = x_1 \left(r_1 \left(\frac{x_2}{x_2 + \varepsilon_2} \right) N - a_{11}x_1 + a_{12}x_2 \right) \\ \frac{dx_2}{dt} &= x_2 f_2 = x_2 \left(r_2 \left(\frac{x_1}{x_1 + \varepsilon_1} \right) N + a_{21}x_1 - a_{22}x_2 \right) \end{aligned} \quad (4)$$

where scaling and constancy of overall mass (see CN Rules 0 and 2 in the Appendix) mean that the available autotroph resource (inorganic nutrient) $N = 1 - x_1 - x_2$. We leave N (the fraction of recycling nutrient in the nutrient pool) in these equations to simplify the analysis and interpretation. (Note in these heuristic autotroph models we assume instantaneous remineralisation of organic nutrient and hence do not explicitly model a detritus pool.) Here, r_1 and r_2 are the maximum net rates of inorganic uptake by each autotroph; ε_1 and ε_2 define both the transition from facultative ($\varepsilon_1 = 0 = \varepsilon_2$) to, and the level of, obligate mutualism (ε_1 and ε_2 positive); a_{11} and a_{22} are the natural mortality rates, a_{12} and a_{21} are mutualism interaction terms. Although obligate mutualism may be represented by any positive values of ε_1 and ε_2 , these parameters indicate the size of the population required to sustain the obligate mutualist (i.e. small values indicate only a small population is necessary, larger values indicate larger populations are necessary). Values of ε_1 and/or ε_2 greater than 1, while mathematically valid, suggest that half of the obligate mutualists maximum possible growth rate could only be achieved with the support of populations larger than could ever exist.

In this simple, heuristic model, in which mutualist benefits and costs have the same functional form, a_{12} and a_{21} represent the nets of the mutualism interactions (i.e. benefits minus costs). However, as noted by Holland and DeAngelis (2010), the costs and benefits of mutualism may have different functional forms and we consider the implications of this case in our nonlinear version of the model (see equation (10)) where these differences may be explicitly modelled in the manner of Holland and DeAngelis.

Note that qualitatively identical, and quantitatively almost identical, results to those presented below for the model (4) can be obtained with parameter sets identical to those used below if

the obligate function $\frac{x_i}{x_i + \varepsilon_i}$, $i = 1, 2$ in (4) is replaced with a simple linear term x_i . In contrast to the standard model (Bazykin 1998) and HD, which are sensitive to the form of the mutualism

terms, we only require that they increase in the mutualist variable. We have used the Michaelis-Menten/Holling Type II form solely in order to use (4) as a continuum model to smoothly transition from facultative to obligate mutualism. The population interactions for facultative mutualism in LVCN systems (defined by $\varepsilon_1 = 0 = \varepsilon_2$ in (4)) were considered in detail in Cropp and Norbury (2015a). We recall that there is no natural local mass balance for all the terms in LVCN models and we need to check a consistency condition (5) (see Appendix for details) to ensure that the model does not allow negative nutrient masses to occur (i.e. here it prevents $x_1 + x_2$ from exceeding one):

$$\left. \frac{dN}{dt} \right|_{N=0} = -x_1(a_{12}x_2 - a_{11}x_1) - x_2(a_{21}x_1 - a_{22}x_2) > 0, \quad \text{for } x_1 + x_2 = 1. \quad (5)$$

This provides a condition on the parameter values that constrains the level of net mutualist benefit that either population may acquire. This keeps all solutions of the models in the ecospace $E = \{0 < x_1, x_2 < 1 \text{ with } x_1 + x_2 < 1\}$. In words, this condition (2) says that when the nutrient pool ($N = 0$) is empty the net mutualist flows out of the pool $(a_{12} + a_{21})x_1x_2$ must be less than or equal to the flows into the pool from mortality $(a_{11}x_1^2 + a_{22}x_2^2)$.

In the following sections we build up our simple model by introducing the models CNO (obligation), CNOB (obligation and benefit), and CNOBC (obligation, benefit and cost). Finally, we consider a nonlinear saturating function version of these models.

2.1: Obligation: the CNO model

We consider the CNO model as the simplest conceptual model that reasonably represents obligate mutualism in a consumer-resource framework. The CNO model includes only the fact that each population requires the other to be present in order to grow. This is analogous to the Dean (1983) and Graves et al. (2006) models except that we do not make their assumption 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 CNO model is given by (4) with the parameter set:

$$r = \begin{bmatrix} 1 \\ 1 \end{bmatrix}, \quad A = \begin{bmatrix} 0.4 & 0 \\ 0 & 0.4 \end{bmatrix}, \quad \varepsilon = \begin{bmatrix} 0.5 \\ 0.5 \end{bmatrix}, \quad (6)$$

where r_1 , r_2 , a_{11} and a_{22} are values selected to ensure easily interpretable vector fields, isoclines and equilibrium points (Fig. 3(a)). Note that the mass consistency condition (5) is satisfied for all positive parameter values of r_1 , r_2 , a_{11} and a_{22} for this model. The CNO model predicts that obligate autotroph populations always coexist, having an unstable equilibrium point at the origin $\{0,0\}$ and a stable coexistence equilibrium point $\{x_1^*, x_2^*\}$ in the interior of E .

Reducing the mortality parameters a_{11} and a_{22} moves the coexistence point towards the lid until when $a_{11} = 0 = a_{22}$ the point exists on the lid. Increasing a_{11} and a_{22} moves the coexistence point towards the origin until it leaves the ecospace through a transcritical bifurcation with the equilibrium point at the origin. Note that in all these models choosing non-symmetric parameter values does not change the essential details of Fig. 2, as we demonstrate with the parameters in Fig. 3(e, f).

2.2: Obligation and mutualist benefit: the CNOB model

The CNOB model adds explicit mutualist benefits to the obligate interactions, that is, (4) with the parameter set:

$$r = \begin{bmatrix} 1 \\ 1 \end{bmatrix}, \quad A = \begin{bmatrix} 0.4 & 0.2 \\ 0.2 & 0.4 \end{bmatrix}, \quad \varepsilon = \begin{bmatrix} 0.5 \\ 0.5 \end{bmatrix}, \quad (7)$$

where again the non-zero parameters are given quite generic values to draw informative vector fields, isoclines and equilibrium points in Fig. 3(c). The mass consistency condition (2) places an upper bound on the amount of mutualist benefit that may be obtained by each population:

$$a_{12} + a_{21} < \min_{x_1 + x_2 = 1} \left(\frac{a_{11}x_1^2 + a_{22}x_2^2}{x_1x_2} \right). \quad (8)$$

Evaluating the bracketed term at $x_1 = x_2$ provides the useful rubric that the maximum mutualist benefit is constrained to be less than the recycled nutrient ($a_{12} + a_{21} < a_{11} + a_{22}$). 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 does not mean that the model has lost ecological validity, but reveals that the potential exists for it to lose validity if parameter values that do not satisfy (8) are used. Note the bifurcation behaviour of this model is similar to the CNO model.

1

2 **2.3: Obligation, mutualist benefits and costs: the CNOBC model**

3 We represent the costs of providing mutualist benefits in the CNOBC model by reducing the net
 4 mutualist benefit, that is, we parameterise (4) with the values:

$$5 \quad r = \begin{bmatrix} 1 \\ 1.5 \end{bmatrix}, \quad A = \begin{bmatrix} 0.4 & 0.15 \\ 0.25 & 0.2 \end{bmatrix}, \quad \varepsilon = \begin{bmatrix} 0.5 \\ 1.0 \end{bmatrix}, \quad (9)$$

6 to draw the vector fields, isoclines and equilibrium points in Fig. 3(e). The cost of providing
 7 mutualist benefits to the other population in this simplest case is equivalent to reducing the
 8 benefit received from the other population. We have introduced an asymmetry between x_1 and
 9 x_2 in this case, to demonstrate that the essence of the interactions does not depend on taking
 10 the same values for each population's parameters.

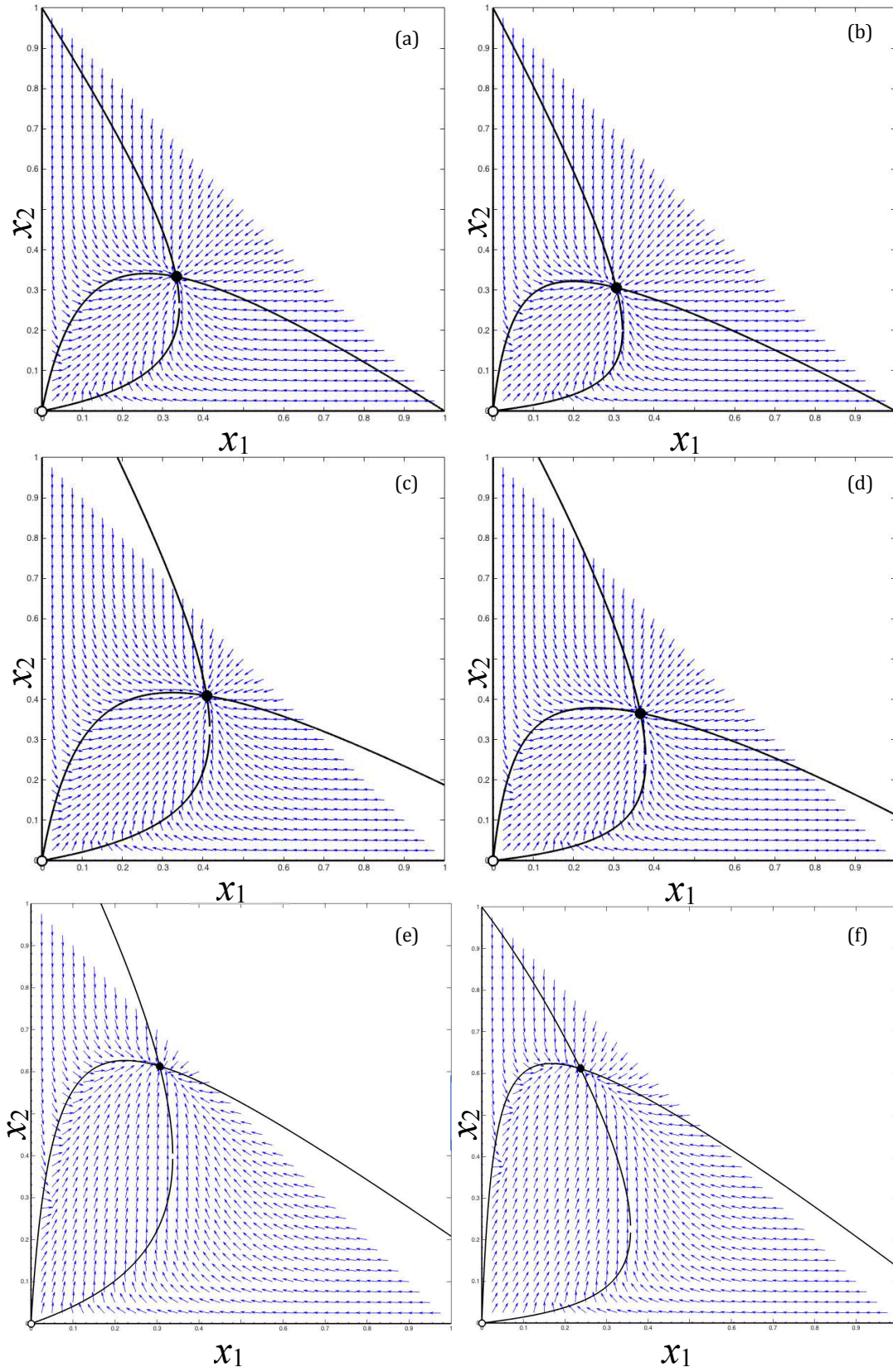


Fig. 3. Vector fields and isoclines for the autotroph obligate mutualism cases in the mutualist populations $x_1, x_2 \geq 0$ where $0 \leq x_1 + x_2 \leq 1$: (a) the CNO model; (b) the CNOn

model; (c) the CNOB model; (d) the CNOBn model; (e) the CNOBC model and (f) the CNOBCn model. Here, models (a) and (b) have obligation only, models (c) and (d) have obligation and benefit, while models (e) and (f) have obligation, benefits and costs. The n in the model name denotes the nonlinear (saturating) model version.

2.4: Nonlinearity: does it matter?

Nonlinearity may be included in the CNO, CNOB and CNOBC models in several ways. We focus 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 also consider a saturating (Michaelis-Menten) function for nutrient uptake to have every process saturating. We use the following equations to draw the phase plane sketches in the right-hand column of Fig. 3:

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 f_1 = x_1 \left(\mu_1 \left(\frac{x_2}{x_2 + \varepsilon_2} \right) \left(\frac{N}{N + \kappa_1} \right) + \omega_1 \left(\frac{x_2}{x_2 + \zeta_2} \right) - \chi_1 \left(\frac{x_2}{x_1 + \xi_1} \right) - \sigma_1 x_1 \right) \\ \frac{dx_2}{dt} &= x_2 f_2 = x_2 \left(\mu_2 \left(\frac{x_1}{x_1 + \varepsilon_1} \right) \left(\frac{N}{N + \kappa_2} \right) + \omega_2 \left(\frac{x_1}{x_1 + \zeta_1} \right) - \chi_2 \left(\frac{x_1}{x_2 + \xi_2} \right) - \sigma_2 x_2 \right)\end{aligned}\quad (10)$$

The parameter values used to draw these figures are:

- for the CNO model (Fig. 3(b)):

$$\begin{aligned}\mu_1 &= 1, \quad \kappa_1 = 2, \quad \varepsilon_1 = 0.5, \quad \sigma_1 = 0.4, \quad \omega_1 = 0, \quad \zeta_1 = 0, \quad \chi_1 = 0, \quad \xi_1 = 0, \\ \mu_2 &= 1, \quad \kappa_2 = 2, \quad \varepsilon_2 = 0.5, \quad \sigma_2 = 0.4, \quad \omega_2 = 0, \quad \zeta_2 = 0, \quad \chi_2 = 0, \quad \xi_2 = 0,\end{aligned}\quad (8)$$

- for the CNOBn model (Fig. 3(d)):

$$\begin{aligned}\mu_1 &= 1, \quad \kappa_1 = 2, \quad \varepsilon_1 = 0.5, \quad \sigma_1 = 0.4, \quad \omega_1 = 0.2, \quad \zeta_1 = 1, \quad \chi_1 = 0, \quad \xi_1 = 0, \\ \mu_2 &= 1, \quad \kappa_2 = 2, \quad \varepsilon_2 = 0.5, \quad \sigma_2 = 0.4, \quad \omega_2 = 0.2, \quad \zeta_2 = 1, \quad \chi_2 = 0, \quad \xi_2 = 0,\end{aligned}\quad (9)$$

- and for the CNOBC model (Fig. 3(f)):

$$\begin{aligned}\mu_1 &= 1, \quad \kappa_1 = 2, \quad \varepsilon_1 = 0.5, \quad \sigma_1 = 0.4, \quad \omega_1 = 0.2, \quad \zeta_1 = 1, \quad \chi_1 = 0.05, \quad \xi_1 = 0.1, \\ \mu_2 &= 1.5, \quad \kappa_2 = 2, \quad \varepsilon_2 = 1, \quad \sigma_2 = 0.2, \quad \omega_2 = 0.25, \quad \zeta_2 = 1, \quad \chi_2 = 0, \quad \xi_2 = 0.1.\end{aligned}\quad (10)$$

As the CNO model includes only obligation, it always satisfies our consistency condition. We check the consistency condition for the CNOBn model to determine the parameter constraints that limit the amount of mutualist benefit that the system can support. Note that the potential to violate the lid condition now exists if an excessively large value for the mutual benefits

received is specified. Finally, we check the consistency condition (2) for the CNOBCn model to determine the parameter constraints that limit the amount of mutualist benefit that the system can support for all $x_1 + x_2 = 1$ where $x_i > 0$:

$$\left. \begin{aligned} & (x_1 + \varepsilon_1)(x_2 + \varepsilon_2) [\omega_1(x_2 + \zeta_2) + \omega_2(x_1 + \zeta_1)] \\ & - (x_1 + \zeta_1)(x_2 + \zeta_2) [\chi_1(x_2 + \varepsilon_2) + \chi_2(x_1 + \varepsilon_1)] \end{aligned} \right\} < \frac{(x_1^2 \sigma_1 + x_2^2 \sigma_2)(x_1 + \zeta_1)(x_2 + \zeta_2)(x_1 + \varepsilon_1)(x_2 + \varepsilon_2)}{x_1 x_2}. \quad (12)$$

The CNOBn model has no mutualism benefits or costs ($\omega_1 = 0 = \omega_2$ and $\chi_1 = 0 = \chi_2$); the CNOBn model has no mutualism costs ($\chi_1 = 0 = \chi_2$) and the CNOBCn model has mutualist obligation, benefits and costs (i.e. all parameters are positive). We have introduced an asymmetry into the CNOBCn model to again make clear that, as for the linear form CNOBC, our results do not depend on symmetry or carefully contrived parameter values. Note that the mutualist benefit and cost terms in (10) have different functional forms (in contrast to the CNOBC model, but in keeping with the conjecture of Holland and DeAngelis (2010)). Panels b, d and f of Fig. 3 show that the phase plane (i.e. the ecospace E) features of the nonlinear models are very similar to those of the linear models for these parameter choices; it appears to make little difference when mutualist costs are assumed to have different functional forms to mutualist benefits in (7). For the nonlinear saturating function forms to make significant differences we need to choose more extreme parameter values.

3: Transitioning from facultative to obligate mutualism

Facultative mutualism is represented in (4) when $\varepsilon_1 = 0 = \varepsilon_2$. We use the generic model (4) to examine how a population can transition between facultative and obligate mutualism. We consider a simple transition from facultative to obligate interactions by parameterising (4) with the set:

$$r = \begin{bmatrix} 1 \\ 1 \end{bmatrix}, \quad A = \begin{bmatrix} 0.4 & 0.15 \\ 0.15 & 0.4 \end{bmatrix}, \quad \varepsilon = \begin{bmatrix} 0 \rightarrow 0.1 \\ 0 \rightarrow 0.1 \end{bmatrix}, \quad (13)$$

where again we choose values for the parameters to ensure clear vector fields, isoclines and equilibrium points in Fig. 4. Note that this model satisfies the mass consistency condition (5). Note also that Fig. 4 with Fig. 3(a, c, e) provides a smooth continuum linking facultative mutualism to our consideration of various forms of obligate mutualism.

1
2 Comparison of Figs. 4(a) and 4(b) reveals the effect of each facultative mutualist population
3 becoming obligate on the other. Each facultative population in Fig. 4(a) has an unstable
4 boundary equilibrium point (the open circles on the axes) which becomes stable in the event of
5 the other population going extinct. When the populations become obligate (i.e. ε_1 and ε_2
6 become non-zero) these points immediately slide down their respective axes to the origin –
7 then we have Fig. 4(b) and the populations are obligate on each other. Although there is a
8 discontinuity in the boundary equilibrium points, this occurs exactly on the boundary of E
9 where a basic assumption of the CN framework, that the populations are sufficiently large that
10 we can ignore individuals, does not hold. However, the figure makes clear that although the
11 vector field precisely on the boundary does not smoothly vary from Fig. 4(a) to (b), the vector
12 field everywhere else in E , including near the boundary, transitions smoothly between the
13 facultative and obligate cases. The zero isoclines for the case $\varepsilon_1 = 0.001 = \varepsilon_2$ are almost identical
14 to the zero isoclines for the case $\varepsilon_1 = 0 = \varepsilon_2$, with the difference evidenced by a very strong
15 localised curvature being introduced very close to the boundary of E . Fig. 4 shows that as ε_1
16 and ε_2 increase the curvatures in the zero isoclines become less acute and transition smoothly
17 to the gentle curves of Fig. 3.
18

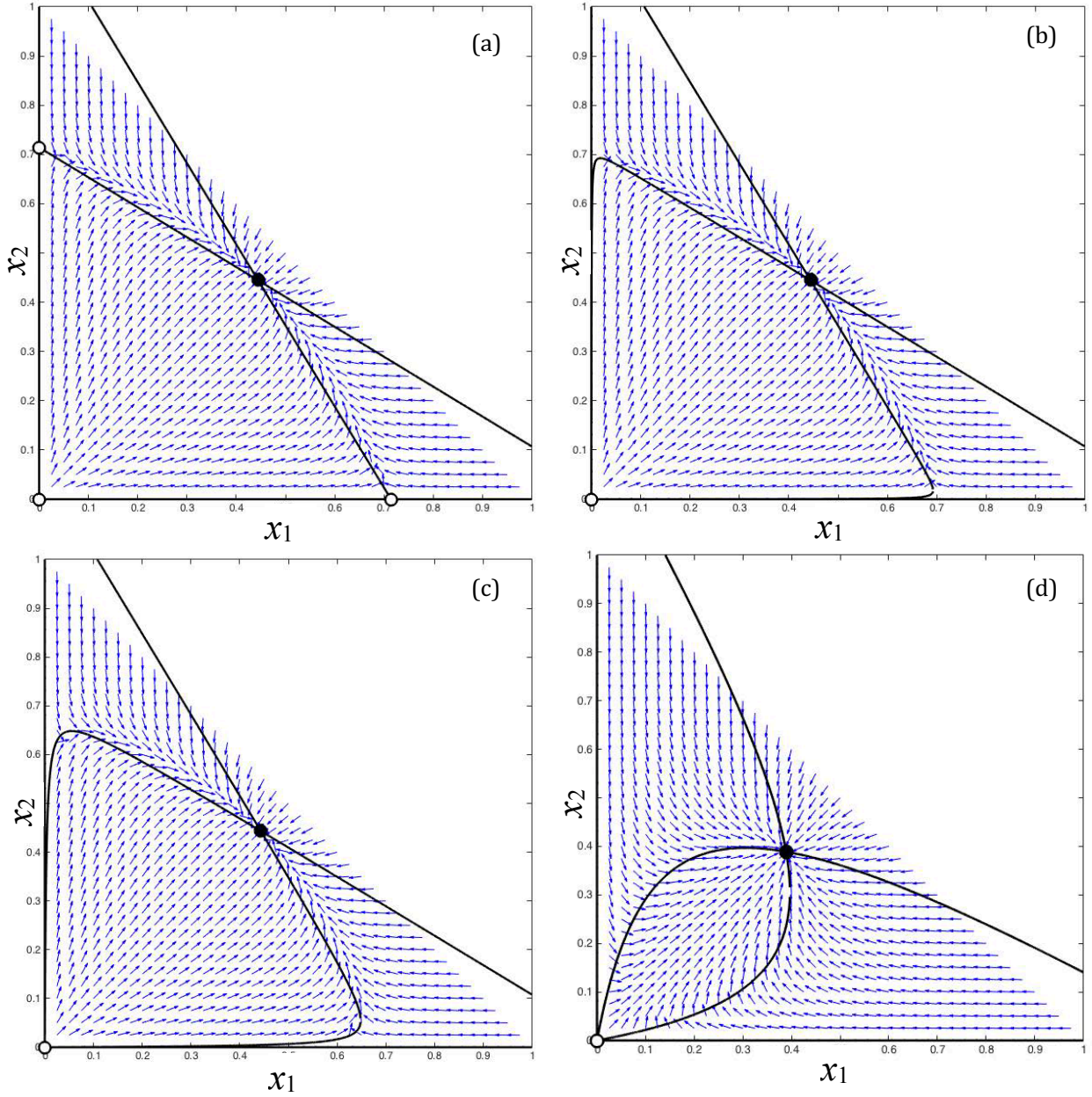


Fig. 4. Vector fields for the CNOBC model: (a) the facultative case with $\varepsilon_1 = 0 = \varepsilon_2$; and obligate cases (b) with $\varepsilon_1 = 0.001 = \varepsilon_2$; (c) with $\varepsilon_1 = 0.01 = \varepsilon_2$ and (d) with $\varepsilon_1 = 0.1 = \varepsilon_2$.

4: Obligate Mutualism between Heterotrophs

We now consider obligate mutualism between heterotrophs in the CN framework, also in the context of the three interactions discussed above: obligation, benefit and cost. For clarity, we consider just the net mutualism interactions, as there appears to be little heuristic value in including costs and benefits in different functional forms. We use the following generic

equations (14) to consider the simplest version of obligate mutualism between two heterotroph populations x_2 and x_3 that survive by consuming the same autotroph resource x_1 . Analogously to (4), these equations arise from Lotka-Volterra equations that have been cast in the CN framework and have an additional saturating term included to represent obligation:

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 f_1 = x_1 (r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3) \\ \frac{dx_2}{dt} &= x_2 f_2 = x_2 \left(-r_2 + a_{21} \left(\frac{x_3}{x_3 + \varepsilon_3} \right) x_1 - a_{22}x_2 + a_{23}x_3 \right) \\ \frac{dx_3}{dt} &= x_3 f_3 = x_3 \left(-r_3 + a_{31} \left(\frac{x_2}{x_2 + \varepsilon_2} \right) x_1 + a_{32}x_2 - a_{33}x_3 \right)\end{aligned}\quad (14)$$

Here the autotroph again has growth limited by the availability of inorganic nutrient, but in this case, the substitution $N = 1 - x_1 - x_2 - x_3$ has been made in equation (14). The first terms in the equations for x_2 and x_3 (r_2 and r_3) are density-independent mortality terms, the second terms are growth terms that include saturating obligation terms, the $a_{23}x_3$ and $a_{32}x_2$ terms are net mutualism terms (benefit – cost), and the $a_{22}x_2$ and $a_{33}x_3$ terms are density-dependent mortality terms.

The parameters are defined analogously to (4), and the values used to draw Figs 5 and 6 are:

$$r = \begin{bmatrix} 1 \\ 0.15 \\ 0.15 \end{bmatrix}, \quad A = \begin{bmatrix} 1.2 & 1.75 & 1.75 \\ 0.8 & 0.75 & 1 \\ 0.8 & 1 & 0.75 \end{bmatrix}, \quad \varepsilon = \begin{bmatrix} - \\ 0.01 \\ 0.01 \end{bmatrix}, \quad (15)$$

where $\varepsilon_2 = 0 = \varepsilon_3$ in Fig. 5. Note that qualitatively identical, and quantitatively similar, results to those presented below for the model (14) may be obtained with parameter sets similar to those used below if the obligate function $\frac{x_i}{x_i + \varepsilon_i}$, $i = 2, 3$ is replaced with a simple linear term

x_i . We have used the Michaelis-Menten/Holling Type II form again solely in order to use (14) as a continuum model to smoothly transition from facultative to obligate mutualism.

First we give an example of facultative mutualism between the two heterotrophs, where we set $\varepsilon_2 = 0 = \varepsilon_3$ in (14), to illustrate the similarity between obligate and facultative mutualism in higher trophic levels (Fig. 5).

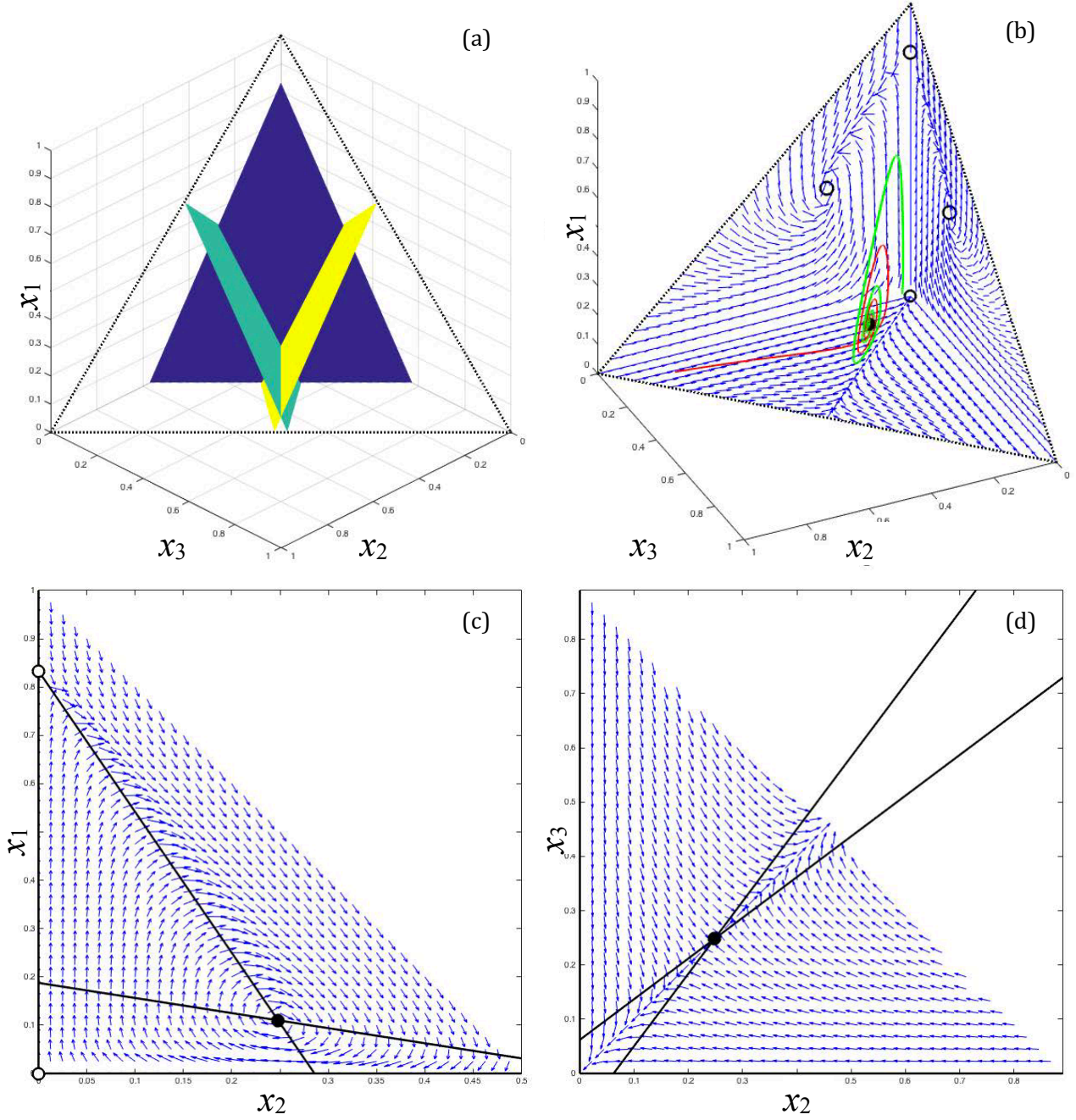


Fig. 5. Attributes of the facultative heterotroph mutualism model (14) (defined by $\varepsilon_2 = 0 = \varepsilon_3$) with parameter values (15) otherwise: (a) $f_i = 0$ isosurfaces for x_1 (blue), x_2 (yellow), and x_3 (green); (b) trajectories from different initial conditions with the unstable origin (open circle) and stable interior (filled circle) equilibrium points and scaled vector fields on the faces of E ; (c) the scaled vector field and zero isoclines for x_1 and x_2 on the vertical section through (b) along $x_2 = x_3$; and (d) the scaled vector field

**and zero isoclines for x_2 and x_3 on the horizontal section through the interior
equilibrium point where $x_1 = x_1^*$.**

Recall that the existence of the (unstable) equilibrium points on the faces $x_3 = 0$ and $x_2 = 0$ is precisely what defines the populations to be facultative. When $x_3 \equiv 0$, the boundary equilibrium point $(x_1^*, x_2^*, 0)$ is stable in the (x_1, x_2) reduced space, so that x_2 can survive when $x_3 = 0$ and vice versa. Alternately, the absence of these equilibrium points from E when ε_1 and ε_2 are nonzero defines the populations to be obligate and they cannot survive independently.

Fig. 5 shows the stable interior equilibrium point $\{x_1^*, x_2^*, x_3^*\}$ (filled circle in (b-d)) where the two facultative mutualist heterotroph populations coexist with their autotroph resource. Fig. 5(d) shows what appears to be a classic vector field for two obligate mutualists existing on unspecified resources (for example, Kot 2001, Pastor 2008) that suggests that the populations go extinct or to infinity. However, in Fig. 5(d) the stabilities of the equilibrium points are different to the classic case. The vector field in Fig. 5(d) appears incorrect when viewed in isolation, but the remainder of Fig. 5 (in particular the three-dimensional plot (b) with its stable internal equilibrium point and trajectories that spiral in to it) convinces us that considering the scaled vector field on the $\{x_2, x_3\}$ surface in isolation is misleading.

Next we simulate an example of obligate mutualism between heterotrophs, in which we reset ε_1 and ε_2 to the values in (15) in Fig. 6.

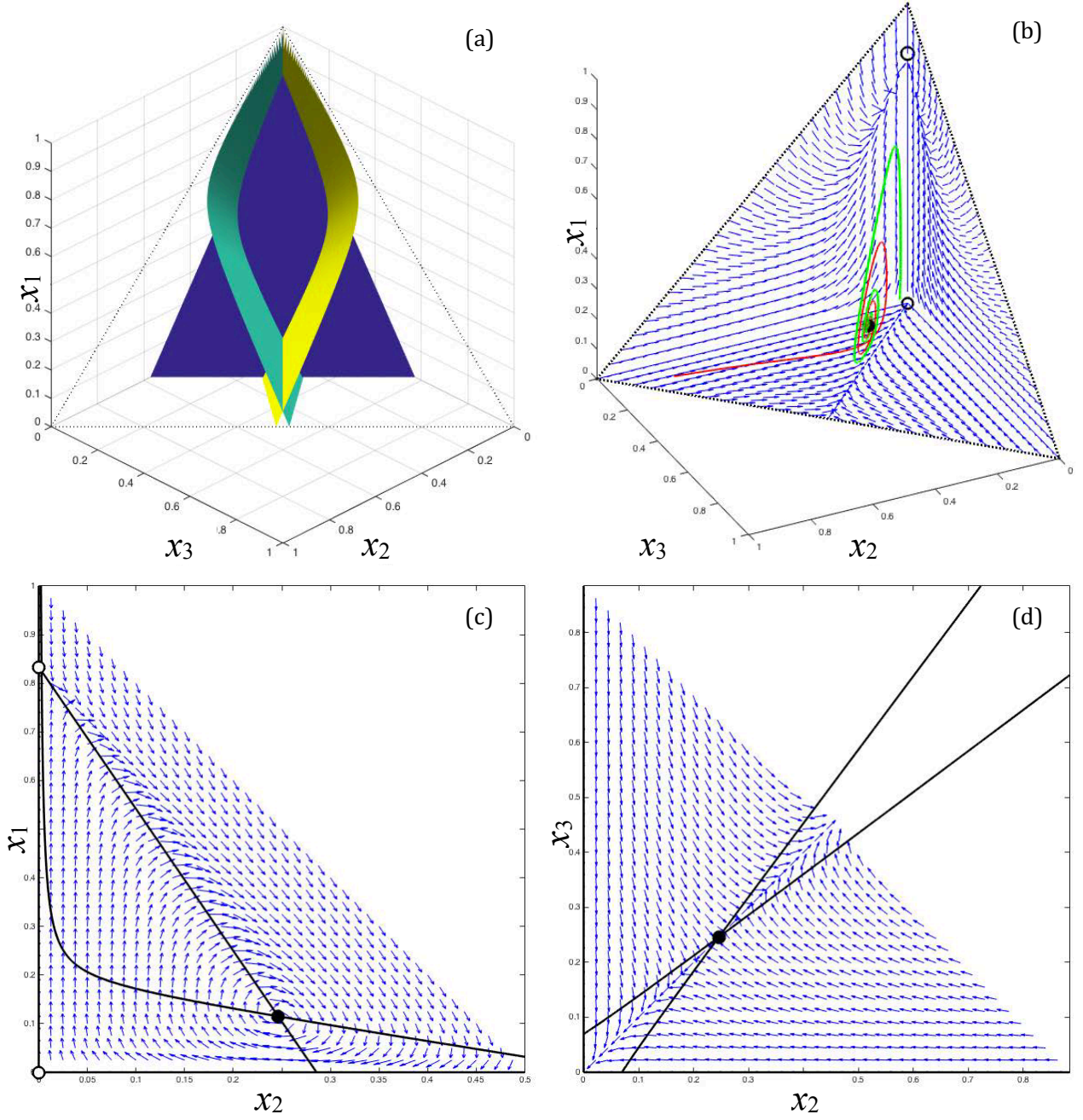


Fig. 6. Attributes of the obligate heterotroph mutualism model (equation (14) with parameter values (15)): (a) $f_i = 0$ isosurfaces for x_1 (blue), x_2 (yellow), and x_3 (green); (b) trajectories from different initial conditions with the unstable origin (open circle) and stable interior (filled circle) equilibrium points and scaled vector fields on the faces of E ; (c) the scaled vector field and zero isoclines for x_1 and x_2 on the vertical section through (b) along $x_2 = x_3$; and (d) the scaled vector field and zero isoclines for

x_2 and x_3 on the horizontal section through the interior equilibrium point where

$$x_1 = x_1^*.$$

Fig. 6 shows the stable interior equilibrium point $\{x_1^*, x_2^*, x_3^*\}$ (filled circle in (b-d)) where the two obligate mutualist heterotroph populations coexist with their autotroph resource. The obligate nature of the interaction between x_2 and x_3 is revealed by the absence of equilibrium points on the (x_1, x_2) and (x_1, x_3) planes (cf. Fig. 6(b)). Again, Fig. 6(d) shows what appears to be a classic vector field for two obligate mutualists, which is usually interpreted to indicate that obligate mutualists cannot coexist. However, the other panels in Fig. 6 convince us that considering the scaled vector field on the $\{x_2, x_3\}$ surface in isolation is misleading, and the two obligate mutualist populations can coexist.

Unscaled vector fields (not shown) reveal that the vectors in Figs. 5(c) and 6(c) pointing inwards on the lid of E in the plane through which the sections in Figs. 5(d) and 6(d) are taken have a much larger magnitude than the vectors pointing out of E between the zero isoclines in Figs. 5(d) and 6(d). The sum of these vectors is a vector pointing into E , hence the lid consistency condition is not violated and the solutions do not go to infinity. We show the scaled vector fields (as do most authors) to reveal the dynamics of the system, as the lengths of the unscaled vectors vary by several orders of magnitude. In this example, the magnitudes of the vectors between the isoclines in Figs. 5(d) and 6(d) are so small the unscaled vectors are rendered as dots.

Comparison of Figs 5 and 6 suggests that a smooth transition between facultative and obligate mutualism is also possible in higher trophic level interactions. The transition again includes a discontinuity on the boundary of E where the two predator-prey equilibrium points $\{x_1^*, x_2^*, 0\}$ and $\{x_1^*, 0, x_3^*\}$ (the open circles on the (x_1, x_2) and (x_1, x_3) planes in Fig. 5(b)) move through the $\{x_1^*, 0, 0\}$ equilibrium point and subsequently leave E immediately ε_2 and ε_3 become nonzero. This is evident when comparing the $f_i = 0$ isosurfaces for x_2 and x_3 in Figs 5(a, c) and 6(a, c). However, the discontinuity again occurs exactly on the boundary where the model assumptions

do not hold, and the vector field just inside the boundary (and in the rest of E), where the model assumptions do hold, transitions smoothly between the facultative and obligate cases.

5: Discussion

Competition, predation and mutualism are considered the tripod of population interactions upon which ecological analysis of communities rests (Holland and DeAngelis 2010). 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 in the 1920s, 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 (Cropp and Norbury 2012, 2015b). Our results suggest that this could be considered a direct result of not including an explicit resource accounting.

The consideration of a conservative system (in which all populations have explicit finite resources) allows obligate mutualism to be included in a single synthesising theoretical framework. This framework includes all population interactions from competition between autotrophs, through various forms of mixotrophy and facultative mutualism, to obligate mutualism between heterotrophs. This framework identifies smooth transitions between what were previously perceived to be distinct, unrelated population interactions, and allows adaptation, represented by continuous single-parameter variations, to take populations smoothly from one interaction extreme to any other, all the time maintaining stable coexistence.

Cropp and Norbury (2015a) show that it is possible to model facultative mutualism using Lotka-Volterra models if the models are developed in the CN framework (i.e. LVCN models), which explicitly represent the constraints of finite resources on the populations. In these simple LVCN models, facultative mutualist autotrophs look like mixotrophs (organisms, commonly plankton, that both photosynthesise and predate on other organisms). This is because benefits acquired 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

1 indistinguishable from photosynthesis. While Cropp and Norbury (2015a) show that LVCN
2 models can represent competition, predation, mixotrophy and facultative mutualism
3 seamlessly in simple models with two populations, it appears that obligate mutualism cannot
4 be represented in such LVCN models. Attempts to arrange planar isoclines of LVCN models with
5 more than two populations suggest that obligate mutualism requires curved zero isoclines, as
6 suggested by Holland and DeAngelis (2010), although Fig. 5 reveals that this curvature need
7 not necessarily be in the plane of the mutualists. However, obligate mutualism can be
8 represented in LVCN models by including an additional Lotka-Volterra interaction representing
9 obligation. This is intuitive in mutualist interactions such as pollination, where the plant
10 population cannot grow if a pollinator does not provide its services. Cropp and Norbury (2018)
11 shows how a single model in the CN framework can reconcile the classical obligate mutualism
12 models of, for example, May (1976) and Bazykin (1998), with the solution of Holland and
13 DeAngelis (2010). Further, they set out the conditions for the existence of an Allee effect (Allee
14 and Bowen, 1932), which is fundamental to the classical solution, but may or may not exist in
15 the solutions of Holland and DeAngelis (2010) or Cropp and Norbury (2018).

16
17 A conceptual consumer-resource framework may not be sufficient to model all the major
18 population interactions. When models are written explicitly in a common currency of a finite,
19 conserved limiting resource, then all populations in the model must depend on an explicit, finite
20 resource (which in the case of a heterotroph is another population in the model). The models
21 of obligate mutualism between autotrophs presented here have distinctive vector fields
22 intermediate between the standard models and HD. These vector fields are consistent across
23 all autotroph models that include obligation, irrespective of whether they also assume benefits
24 and costs, or whether the interactions are represented by linear or nonlinear processes. While
25 CN models of obligate mutualist autotrophs have fundamentally different isoclines to the
26 standard nonlinear and HD models of obligate mutualism, those of obligate mutualist
27 heterotrophs have zero isoclines and vector fields on sections in the mutualism plane that are
28 strikingly similar to the classical Lotka-Volterra examples. However, the presence of an explicit
29 resource population, together with a finite total amount of resource, means that these vector
30 fields have very different stability properties.

31
32 Obligate mutualism is shown to be continuously and stably connected to facultative mutualist
33 systems for both autotrophs and heterotrophs. Our approach provides models of obligate

mutualism that are relatively simple in computer simulation, mathematical analysis and ecological interpretation. While we have focused here on simple generic models for their heuristic value, CN models also provide a bridge between theoretical and applied models. Even complex CN models are amenable to a little mathematical analysis (in particular, to predict extinctions and invasions) and may indicate appropriate ways to measure real systems in terms of a common currency, the limiting nutrient. These models are useful for undergraduate teaching, for comparison with experimental outcomes and data, and for the general theoretical understanding of mutualism.

The framework arises from the imposition of an “ecological axiom”: that all population interactions must be explicitly quantified and accounted for in a common currency of which there is a finite total amount. This applies to all ecosystem models, but crucially to those that seek to represent mutualism. The CN framework is built on just such a finite resource accounting, and it allows construction of simple models that provide sensible representations of both facultative and obligate mutualist interactions, with their benefits, costs and obligations explicitly represented. This synthesises the three pillars of ecology, that is, competition, predation and mutualism, to provide a more complete modelling framework in applied ecology for building better simulation models for the management of living natural resources.

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7: Appendices

Conservative Normal (CN) systems

The CN framework captures fundamental ecological properties of food web based living systems with mathematical rules. These rules formalise basic ecological concepts, principally that all organisms have to consume resources to survive, and that these resources are finite. The constancy of the total mass of a limiting nutrient is fundamental to modelling ecosystems (Sterner et al. 2011) and to the CN framework. Rather than debate the merits of this view, although it is recognized that ecosystems generally recycle over 90% of their limiting nutrient (Vitousek and Matson 2012), we draw analogy with the common assumption of linearity. Although it may be argued that no real ecological system has exactly linear processes, the simplifying assumption of linearity in some ecosystem models has led to substantial advances in theoretical ecology, as it has in other fields.

Detailed descriptions of the CN framework have been published elsewhere (Cropp and Norbury 2012, 2015a), 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 vast majority of published applied ecological models satisfy the CN framework, and the CN rules can be used to winnow out models that do not make ecological sense, there are ecologically realistic models that do not simply satisfy all the CN rules. We label these exceptions “exotic” systems as they are sensible,

but require modification of what constitutes a resource to include “catalysts”. There are a number of such exotic systems: populations where too much resource “poisons” the environment, populations that co-operatively hunt, for which there is an “optimum” population size; omnivorous predators that benefit from consuming certain resources that they cannot alone survive on; and as we shall explain below, obligate mutualists.

We consider a general n population system of the form:

$$\dot{x}_i = x_i f_i(x_1, x_2, \dots, x_n), \quad i = 1, 2, \dots, n. \quad (\text{A1})$$

The “life functions” f_i may include any form (such as Holling Type I, II, or III) 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 nonliving nutrient (i.e. dead organic matter such as detritus and dissolved organic matter, and re-mineralized inorganic nutrient) \hat{N} available to those n interacting populations:

$$\hat{x}_1 + \hat{x}_2 + \dots + \hat{x}_n + \hat{N} = \hat{N}_T. \quad (\text{A2})$$

We then scale the measurements \hat{x}_i , \hat{N} by the total measure of nutrient pool \hat{N}_T that is cycling in the system, so that the scaled measurements x_i , N are fractions of the total recycling nutrient in the system:

$$x_1(0) + x_2(0) + \dots + x_n(0) + N(0) = 1, \quad (\text{A3})$$

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 (in all forms) that is bound into the living tissues of the individuals of that population. The nonliving nutrient fraction $N(t)$ represents all other forms of nutrient, that is, all forms of inorganic nutrient and organic nutrient in various stages of re-mineralization. For convenience, we refer to this as just inorganic nutrient as we only make the distinction here between autotrophs and heterotrophs.

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:

$$\frac{1}{x_i} \frac{dx_i}{dt} = \hat{f}_i(x_1, x_2, \dots, x_n; N) . \quad (\text{A4})$$

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: Constancy of Total 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 recycling 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 nonliving nutrient fraction $N(t)$ then satisfy a constancy of total nutrient mass constraint for all time $t > 0$:

$$x_1(t) + x_2(t) + \dots + x_n(t) + N(t) = 1 . \quad (\text{A5})$$

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 (A4) may be written in the form (A1), for $x_i(t) > 0$. The elimination of an explicit differential equation for the nonliving nutrient $N(t)$ means that all the remaining differential equations in the model have the same (Kolmogorov) form (A1), which simplifies the analysis of CN models.

Equation (A5) 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 :

$$E \equiv \{0 < x_i, 0 < x_1 + x_2 + \dots + x_n < 1\} . \quad (\text{A6})$$

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 heterotrophs. These resources R_j are finite and limit the growth of population x_j when they become depleted. 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 famine), the population x_j must die.

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

$$f_j \Big|_{R_j=1} > 0 > f_j \Big|_{R_j=0} . \quad (\text{A7})$$

Evaluation of this rule on the boundaries of the ecospace may place constraints on allowable parameter values. The CN framework places further constraints on the life functions, that in a normal ecology the f_j change monotonically along resource rays within E . As we follow a life function from any point of minimum resource on the boundary of E to any point of maximum resource along such a ray, where the direction of the resource 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 ($\cos\gamma_1, \cos\gamma_2, \dots, \cos\gamma_n$)) the life function f_j must monotonically increase:

$$\cos\gamma_1 \frac{\partial f_j}{\partial x_1} + \cos\gamma_2 \frac{\partial f_j}{\partial x_2} + \dots + \cos\gamma_n \frac{\partial f_j}{\partial x_n} > 0 . \quad (\text{A8})$$

Obligate mutualist populations require the presence of another population in addition to their resource(s) in order to grow but the interaction is 'catalytic' in that there is (usually) no direct exchange of mass between the populations. Obligate mutualist systems are therefore not 'normal' CN systems, similarly to populations that have optimal population sizes (for example cooperative hunters) or omnivores that benefit from multiple resources but consume some resources that they cannot survive on independently. We address such 'exotic' obligate systems after completing the description of the CN framework with the Consistency Condition below.

A Consistency Condition

When resources are explicitly represented using local mass balance (as in a predator consuming prey) then we easily find CN systems, but if population benefits are more implicitly defined as in mutualism models, then we need to check that resource is available for such benefits. The mass consistency condition provides such a check. The consistency condition guarantees that a CN model cannot predict a negative mass, that is, that solutions $\{x_1(t), x_2(t), \dots, x_n(t)\}$ of equations (A1) which start in E do not leave E through the “lid” of the ecospace defined by $x_1 + x_2 + \dots + x_n = 1$. This ensures that $N(t)$ remains positive, and consequently that mass conservation is always physically sensible. Differentiating equation (A5) and using (A1) provides the lid consistency condition:

$$\frac{dN}{dt} = -\frac{dx_1}{dt} - \frac{dx_2}{dt} \dots - \frac{dx_n}{dt} = -\sum_{i=1}^n x_i f_i > 0 \quad \text{when } N = 0, \quad (\text{A9})$$

ensuring $N \geq 0$ for all time. Equation (A9) is an important constraint that should be checked for these systems that include mutualist interactions. It provides generic conditions on the parameters that constrain the magnitude of mutualist benefits that could be obtained without violating the basic principle that mass cannot be “borrowed” from outside the system.

Obligate Mutualism as an Exotic CN System

The CN framework summarised above is a consumer – resource conceptualisation predicated on explicit accounting of the mass of limiting nutrient. It explicitly accounts for transfers of mass between populations due to resource-limited growth (via inorganic nutrient uptake or predation) and losses due to mortality and predation and includes implicit recycling of limiting nutrient and constancy of total nutrient mass. The CN framework provides simple and intuitive conditions for many ecosystems but requires some modification or extension when applied to ‘exotic’ 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 process as it does not involve a direct explicit transfer of mass. CN Rule 3 requires that a population must be able to grow at any point in the ecospace where a resource is maximal, however, when applying this rule to systems that

1 include the provision of services, we need to treat the service as if it were a resource. This
2 treatment is consistent with the CN framework as it is a zero sum game – the presence of a
3 catalysing population in a closed ecosystem must reduce the quantum of resources available to
4 the other populations.

5
6 Consider the simplest example in which an obligate mutualist population x_i has a single
7 resource $R_i = x_h$ and is obligated on the presence of another population x_j (which may be an
8 inorganic resource x_0) to be able to grow. The maximal point of the single resource for the
9 population lies at a vertex of E , where $x_h = 1$ and all other populations, including the population
10 supplying the service to the obligated population, are zero. The sign constraint of equation (A7)
11 cannot be satisfied at such a point. However, if for the purposes of Rule 3 we treat the servicing
12 population as a resource instead of a catalyst, then $R_i = x_h + x_j$ and the point of maximum
13 resource R_i^* lies somewhere on the line of maximum “resource” $x_h + x_j = 1$. (Note the location
14 of R_i^* depends on the specific nature of the obligate interaction.) CN Rule 3 then stipulates that
15 $f_i \Big|_{R_i^*} > 0$ similarly to any population with multiple resources. This generalisation of what is
16 regarded as a resource captures the effect of the abundance of the obliging population on the
17 utilisation of resources by the obligate population, a key assumption of the Dean (1983) and
18 Graves et al. (2006) models.

20 **Obligate Mutualism in linear CN Systems**

21 It appears that it is not possible to represent obligate mutualism in linear CN systems, in which
22 we include systems with planar zero isosurfaces such as the Lotka-Volterra CN (LVCN) models
23 discussed in Cropp and Norbury (2015a). The difficulty in representing obligate mutualism in
24 linear CN systems arises from the requirement for obligation on another population. This
25 eliminates obligate autotroph populations, as autotroph populations in linear CN systems
26 always have a boundary equilibrium point at which they can exist in the absence of any other
27 population. Obligate populations in linear CN systems must then be heterotrophs - in the
28 simplest scenario these are herbivores that graze on autotrophs, as at least one autotroph must
29 always exist in any CN system. If we ignore the trivial case of obligation, that of a predator on

1 its prey, then on any face of the solution space of the system (the ecospace E) in order that a
2 heterotroph does not exist in the absence of its mutualist benefactor, the zero isoclines on that
3 face cannot intersect. In a heterotroph-autotroph interaction, this means that the autotroph-
4 only boundary equilibrium point is stable, as it must lie in the part of the solution space where
5 the heterotroph is not growing, that is, the heterotroph must go extinct. Thus it appears that it
6 is not possible to represent obligate-obligate mutualism by judiciously arranging planar zero
7 isosurfaces. Here we use a nonlinear population interaction to build simple heuristic models of
8 obligate mutualism.