OBLIGATE MUTUALISM IN A RESOURCE-BASED FRAMEWORK. *

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Abstract. Obligate mutualist interactions appear to be ubiquitous in nature but cannot be described by the simple models that have been so effective for developing the theory of other population interactions including competition, predation, mixotrophy and facultative mutualism. We present a teaching framework that extends the standard Lotka-Volterra analysis of these interactions to the more complicated obligate mutualism. This provides a useful addition to applications of dynamical systems theory for mathematics students and an advanced course in population dynamics for ecology students.

The theoretical framework used in this work is based on explicitly accounted resources, and per capita rates of change for populations that are negative when they have no resources and positive when they have maximal resources. We extend the Lotka-Volterra models by including terms that capture the “catalytic” effect of obligation, reflecting that while a population may be necessary for survival of another, the obligated population does not necessarily consume it. A key attribute of our consumer-resource approach is that the catalytic services provided by obligate mutualists are treated as pseudo-resources for the purposes of determining these rates of change. This framework allows all major ecosystem population interactions to be modelled within a single, simple consumer-resource framework, and reveals how populations can smoothly change their trophic status through a continuum of stable coexistence states.

Key words. obligate mutualism; facultative mutualism; conservation of limiting nutrient; finite resource; conservative normal framework;

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1. Introduction. Mutualist interactions, in which a population benefits from the presence of another population, have long been recognised as one of the most ubiquitous population interactions in nature [2, 3, 18, 21, 24]. In the first major review of mutualism Boucher [2] claimed that roughly half of all population interactions amongst green (i.e. photosynthesising) species are co-operative, catalytic or in some way mutualist in that each population benefits from the presence of the other. In particular, Boucher argued in 1985 that nature is not just “red in tooth and claw” but also has many mutually beneficial population interactions. This view has strengthened over the past 30 years, and mutualist interactions are now viewed as universal, involving virtually every species on Earth, as Bronstein described in the second major review of mutualism in 2015 [3]. However, the lack of simple models of obligate mutualism similar to the Lotka-Volterra models that have so well explained competition and predation has led to mutualism being given less recognition in theoretical ecology as the third cornerstone of population interactions that field ecology suggests it must be [13].

Mutualist interactions between populations are often classified into four common types: pollination, seed dispersal, protection and nutrition [3]. The pollination mutualism is well known, of great commercial and environmental significance, and may be facultative or obligate. The other mutualisms, although less well known, are no less widespread [3, 13, 17, 18]. Shimizu et al. [26] suggest that obligate pollination resulting from co-evolution of morphological traits between plants and pollinators may be

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even more common than historically thought.

We discuss three examples of obligate mutualism; food web diagrams for two of these are shown in Fig. 1. First we discuss obligate mutualism between plants in §3, then we look at a simple model of a plant and its pollinator in §4; finally we consider obligate mutualism between heterotrophs in §5, which requires at least three populations (dimensions). These examples introduce obligate mutualism into predator-prey and competition interactions, so that populations do better by acquiring a larger share of the resource than they otherwise would, but remain dependent on the presence of their obligate partner.

**Fig. 1.** Food web diagrams for: (a) a plant $x_1$ that is obligate upon its pollinator $x_2$ for reproduction; (b) two heterotrophs $x_2$ and $x_3$ that feed on a mutual autotroph prey $x_1$ and are obligate upon each other. The solid black lines show transfers of mass due to direct interactions such as photosynthesis ($N \rightarrow x_1$), harvesting of nectar ($x_1 \rightarrow x_2$ in (a)) or grazing ($x_1 \rightarrow x_2$ and $x_1 \rightarrow x_3$ in (b)), or respiration and mortality (flows back to $N$). The dashed black arrows show transfers of mass due to indirect interactions such as mutualist benefits. The circles indicate that the flow of mass shown by the solid or dashed black lines is facilitated by a mutualist interaction provided by the population linked to the circle by the solid or dashed dual line grey arrow [27]. For example, the flow of mass from $N$ to $x_1$ in (a) is facilitated by a pollinator $x_2$ that transfers gametes and allows the $x_1$ population to reproduce and grow. This signifies that while $x_2$ facilitates $x_1$’s reproduction and subsequent population growth, it does not contribute mass directly to the $x_1$ population. The indirect flows of mass associated with the dashed lines reflect the acquisition of an increased share of total resources resulting from an increase in population fitness due to a mutualist interaction. In (b) the dashed line between $N$ and $x_2$ shows a mutualist interaction facilitated by $x_3$. The transfer of mass may be to $x_2$, showing that the benefit of the mutualism to $x_2$ exceeds the cost, or mass may flow from $x_2$ to $N$ if the cost exceeds the benefit [13]. A similar interaction is possible for $x_3$ but is not shown to improve the clarity of the figure. The direct flow of mass between $x_2$ and $x_3$ may represent a facultative mutualism interaction or a predation interaction - in either case, as a direct flow of mass it is subject to local mass balance, and the net flow is unidirectional.

Many authors have identified the difficulty of representing obligate mutualism in linear systems (for example, [13, 15, 22, 23, 24, 29]) as the dependency of one population on another can imply a need for curved (i.e. nonlinear) zero isoclines (see Fig. 2). A rule-based approach to teaching population interactions in ecology using dynamical systems theory was recently described by Cropp and Norbury [7]. This demonstrated how Lotka-Volterra (LV) models developed within the Conservative Normal (CN) framework could represent population interactions that smoothly varied from competition through mixotrophy and facultative mutualism to predation interactions while maintaining stable population coexistence equilibrium points. We now show that this
smooth continuum of population interactions can be extended to include obligate mutualism in simple heuristic models suitable for undergraduate teaching. Representing obligate mutualism in such models does, however, require specific terms that describe how one population is dependent on the presence of another population in order to grow, and hence requires more complex models than the simple LVCN models of [7].

Mutualist interactions involve the acquisition of benefits that are facilitated, but not directly provided, by their mutualist benefactor. Direct interactions, such as the transfer of mass from a prey to a predator, are constrained by the axiom that a predator cannot gain more mass than its prey loses. Mutualism is an indirect interaction similar to exploitation competition, in which the acquisition of resources by one population reduces the quantum of resources available to the populations in the ecosystem (including itself) by the same amount. In simple models this indirect benefit flows from the resource pool to the beneficiary, where the flow is a function of the population providing the mutualist benefit. The interaction is obligate when the beneficiary population cannot survive if its benefactor is absent.

The indirect nature of mutualist benefits requires natural constraints to prevent populations going to infinity in "an orgy of mutual benefaction", as noted by May [19]. Some treatments of mutualist interactions demonstrate that this issue may be obviated mathematically by introducing quadratic mortality terms to simple models (for example, Kot [15]). Instead, here we use models that explicitly constrain the growth of every population by including a finite resource, which may be either a recycling limiting nutrient or another population. These provide a key to ecologically realistic representations of obligate mutualism. The simple rules of the CN framework, that implement an explicit resource accounting, facilitate the understanding of obligate mutualist interactions while preventing unnatural outcomes.

This CN framework allows us to use a single simple Lotka-Volterra-like model of two interacting populations to represent a suite of population interactions ranging from competition through mixotrophy to predation, which is extended here to include facultative and obligate mutualism. We then show how this theory can be extended to higher dimensions. This framework can be used to teach ecology students with limited quantitative skills how to understand the theory of population interactions, and to teach mathematics students applications of dynamical systems theory in ecology and natural resource management.

We have elected to maintain a consistent basic equation structure through this manuscript that continues the notation from our previous paper [7], in which the signs in the equations are fixed, and the parameters may take any sign. It is important to note that the definitions of the parameters do not change, but the signs are determined by the trophic role. This facilitates a simple and consistent algebra throughout our analyses, intended to assist the mathematically weaker students to see past the mechanics of the algebra to its meaning. It also allows instructors to emphasise a subtle point, that while the basic form and algebra of the systems we consider remains to a large extent the same, our determinations of the trophic interactions that the models represent changes the signs of the parameters, the locations and orientations of isolines, the locations and stabilities of the equilibria, and the dynamical properties of the system. A disadvantage of this approach is that sometimes the relative parameter conditions that result are clumsy and counter-intuitive. Where this occurs we add brief explanations reminding readers of the interpretations. It is of course up to each instructor to choose whether they prefer a consistent framework in which the signs of the parameters reflect the trophic role of each population, or whether they write a new model for each interaction they examine.
2. Conservative Normal (CN) systems. The Conservative Normal (CN) approach \([5, 7]\) provides a unifying framework for studying the dynamics of interacting populations based on conservation of a finite total amount of a limiting nutrient that is cycled within a foodweb-based ecosystem (see Fig. 1 for the examples we consider later). Many fundamental population interactions can both be understood and taught with this approach. Further, this framework produces models with mathematical properties that provide useful techniques for the analysis of more complex models. Here, we extend the use of linear CN systems by including a nonlinear, or saturating, term to represent obligation in the vein of Dean \([9]\) and Graves et al. \([10]\). Otherwise we retain the notation and the essence of the linear approach to model the benefits and costs that arise from mutualist interactions.

The CN framework captures the familiar and fundamental ecological properties of living systems with mathematical rules. These rules formalise basic ecological concepts, principally that all organisms have to consume resources to survive, that the more resources an organism has the better it thrives, and that these resources are finite. The resources and populations are measured in a common currency that is finite and is recycled in the foodweb without loss. A detailed description of the CN framework has been published previously \([7]\), so here we present the essence of the framework.

All CN systems measure populations \(x_i(t)\) at any time \(t\) in a currency of the key limiting resource (which is generally a nutrient, \(N\)), where the populations \(x_i\) have the basic per capita rate of change:

\[
\frac{dx_i}{dt} = \dot{x}_i = x_i f_i(x_1, x_2, ..., x_n), \quad \text{for } i = 1, 2, ..., n,
\]

for \(x_i(t) \geq 0\). The nonliving nutrient pool \(N\) is implicit in (1) as CN systems assume constancy of total mass of limiting nutrient cycling through the populations and the nutrient pool. Here, inputs and outputs of mass of limiting nutrient in any form, such as migration of populations or flows of inorganic nutrient, sum to zero, consistent with the accepted rubric that ecosystems recycle over 90% of their limiting nutrient \([30]\). Note this only applies to the limiting nutrient used as the currency of the system - the systems may be open to fluxes of all other nutrients and energy. This therefore makes no judgement on the stoichiometry of the systems we consider - fixed or varying stoichiometry relationships may be layered onto CN models depending on the objectives of the modelling exercise.

Constancy of the total amount of limiting nutrient provides the condition (after scaling) \(N = 1 - x_1 - x_2 - ... - x_n\) that may be used to recover the differential rate equation for the nonliving (abiotic) form \(N(t)\) of the resource. This means that all the differential equations explicitly in the model have the same Kolmogorov (per capita rate of change) form \((1)\), which simplifies the analysis of CN models. It also allows us to define an upper bound, or "lid", \(x_1 + x_2 + ... + x_n = 1\) (i.e. \(N = 0\)), on the model’s state space \(x_i > 0\) for all \(i\). The open ecospace \(E\) is then defined by:

\[
E \equiv \{x_i; 0 < x_i, x_1 + x_2 + ... + x_n < 1\}.
\]

Here, the property, that all the solutions of equations \((1)\) that start inside \(E\) remain inside \(E\), is ensured by the condition that \(\dot{N} > 0\) whenever \(N = 0\) on a
solution, as we discuss at equation (4). Examples of simple foodwebs with their limiting nutrient cycling between the populations and the nonliving resource pool are shown in Fig. 1. Note that the foodweb does not describe flows of other nutrients or energy. Further, note that the life functions $f_i$ include parameters and functions that describe the various ecological processes occurring in the foodweb.

The life function $f_i$ of population $x_i$ satisfies the natural resource constraints:

$$f_i |_{R_i = 1} > 0 > f_i |_{R_i = 0},$$

where $R_i$ is the $x_i$ population’s resource(s). Note that the resource $R_i$ may be other populations or material in the nutrient pool. This captures the standard ecological concepts that when a population has no resources it cannot grow, and if a population cannot grow when it has optimal resources available it is not viable. In ”normal” ecosystems (i.e. the Normal attribute of CN systems) each $f_i$ increases monotonically along straight lines (rays) in $E$ from every point of zero resource $R_i = 0$ to every point of maximum resource $R_i = 1$ (see Fig. 2). These resource growth properties are satisfied by the Holling Type I, II, and III functions [14] (and their generalisations) that are used by most theoretical ecologists and are found in most simulation codes. An example of non-normal growth is given in [7].

The resource space, which occupies the same abstract space as the eco-space, is defined by the resource variables $\{x_0, x_1, x_2, \ldots, x_{n-1}\}$. Here $x_0 \equiv N = 1 - x_1 - \ldots - x_n$ is a ”hidden” or ”implicit” resource variable for autotrophs. Ensuring that the life functions have the correct signs on the boundaries of the resource/eco-space usually restricts the allowable parameter values.

Finally, CN systems include a consistency check that guarantees that the model cannot predict unrealistic outcomes such as negative mass of the limiting nutrient $N$. Kolmogorov form ensures that solutions of equations (1) which start in $E$ do not leave $E$ through the (hyperplane) boundaries $\{x_i = 0\}$ defined by the axes of the Cartesian coordinate system; however, Kolmogorov form does not prevent populations from going to infinity (with $N$ becoming negative) through the lid of the eco-space defined by $x_1 + x_2 + \ldots + x_n = 1$. The lid consistency condition:

$$\frac{dN}{dt} = - \frac{dx_1}{dt} - \frac{dx_2}{dt} - \ldots - \frac{dx_n}{dt} = - \Sigma x_i f_i > 0 \text{ when } N = 0,$$

ensures that $N > 0$ for all time by limiting the outflow from the nutrient reservoir to be less than the inflow when it is empty. We note here that the use of a ‘carrying capacity’, as an alternative to (4), in some cases allows an infinite reservoir of nutrient.

We demonstrate the importance of checking the lid consistency condition in §5.5 by means of an example.

2.1. LVCN Systems. We develop Lotka-Volterra Conservative Normal (LVCN) systems from the standard Lotka-Volterra equations, where each $f_i$ is a linear function:

$$\dot{x}_i = x_i f_i(x_1, x_2, \ldots, x_n) = x_i (r_i - \sum_{j=1}^{n} a_{ij} x_j) \text{ for } i = 1, 2, \ldots, n,$$

by introducing an explicit dependency on the availability of inorganic nutrient $N$ for growth into every equation that describes an autotroph (commonly a plant, $p$)
population. For each plant $p$ of the $m$ plants in the system we define $\hat{a}_{pj} = a_{pj} - r_p$, for $p = 1, 2, \ldots, m$ and $j = 1, 2, \ldots, n$, to be the net direct competitive interactions between the plant and the $n$ populations, and then find:

\begin{equation}
\hat{x}_p = x_p(r_pN - \sum_{j=1}^{n} \hat{a}_{pj}x_j) \quad \text{for } p = 1, 2, \ldots, m, \text{ and } 1 \leq m \leq n.
\end{equation}

This form of the model shows the growth dependence of the plants explicitly on $N$ in the nutrient pool, so that all the populations and their resources are shown explicitly. Note that $n$ differential equations have $n$ solutions $\{x_i(t)\}$ of (5) uniquely determined by their initial conditions $\{x_i(0)\}$ that belong to $E$. The condition (4) ensures that $\{x_i(t)\}$ remains in $E$ for all time.

2.2. Obligation in LVCN Systems. Obligate mutualist populations require the presence of another population in addition to their resource(s) in order to grow. The interaction is "catalytic" when there is no direct exchange of mass between these populations. Obligate mutualist systems are therefore not "normal" CN systems as defined above, and in [7]. The attributes of obligate mutualism require us to modify how we apply the inequalities (3) to these systems: we create pseudo-resources and apply the conditions to them when obligation is involved.

Consider an obligate mutualist population $x_i$ ($i \geq 1$) that consumes a single resource $R_i = x_h$ ($h \geq 0$) and is obligated on the presence of another population $x_j$ ($j \geq 1$ and $j \neq h, i$) to be able to grow. The maximal point of the single actual resource for the population lies at a vertex of $E$, where $x_h = 1$ and all other populations, including the population supplying the service to the obligated population, are zero. Note that the sign constraint (3) cannot be satisfied at such a vertex point in $E$ because the population cannot grow there as its obliging population $x_j$ is zero.

We now introduce a pseudo-resource (in which the obliging population functions analogously to a catalyst) so that for these extended CN systems (3) holds when the pseudo-resource $\hat{R}_i$ equals its maximum $\hat{R}_i = \hat{R}_i^{**} \leq 1$, or its minimum $\hat{R}_i = 0$. To characterise the population growth, we include the obliging population in the pseudo-resource on the line $x_h + x_j = 1$. We introduce a smoothly differentiable pseudo-resource function $\phi_i(x_h, x_j)$ with the properties that:

- $\phi_i(x_h, x_j) = 0$ when the resource $x_h = 0$,
- $\phi_i(x_h, x_j) = 0$ when the obliging population $x_j = 0$,
- $0 < \phi_i(x_h, x_j) \leq 1$ when $0 < x_h, x_j < 1$.

The pseudo-resource function maximum on the line $x_h + x_j = 1$ (for $x_h, x_j > 0$) then gives the maximum of the pseudo-resource $\hat{R}_i^{**}$ with $\max \phi_i(x_h, 1 - x_h) = \hat{R}_i^{**}$ at $x_h = x_h^{**} \in (0, 1)$.

The life function $f_i$ of the obligated population $x_i$ then has the properties dictated by (3) for the pseudo-resource, that $f_i|_{\hat{R}_i^{**} > 0}$ and $f_i|_{\hat{R}_i = 0 < 0}$. The simplest form of pseudo-resource function is the Holling Type I function $\phi_i(x_h, x_j) = x_h x_j$, and we use this in §3 to discuss interactions between obligate mutualist autotrophs.

Fig. 2(a) shows an example of an autotroph population $x_1$ that feeds on resource $R_1 = N = x_0$. It has a single maximum at the origin, and a line of zero resource on the lid $x_1 + x_2 = 1$. The life function $f_1$ increases monotonically along all rays from all points of zero resource to the point of maximum resource. Fig. 2(b) shows an example of an obligate mutualist autotroph population $x_1$ that feeds on resource $R_1 = N = x_0$ and is obligated on the presence of another population $x_2$ to be able to
grow. Its pseudo-resource $\hat{R}_1$ has a maximum $0 < \hat{R}_1^{**} \leq 1$ somewhere on the $x_2$ axis and has zero pseudo-resource everywhere on the $x_1$ axis and on the line $x_1 + x_2 = 1$. The zero isocline $f_1 = 0$ divides the line of pseudo-resource $(N + x_2 = 1$, the part of the $x_2$ axis $0 < x_2 < 1$) into regions where $x_2$ can grow (the middle) and regions where it can’t (the ends). The point of maximum pseudo-resource $\{0, x_2^{**}\}$ where $\hat{R}_1^{**} = \max(\hat{R}_1)$ is identified, and the resource rays are drawn to this point from the points of zero pseudo-resource (where $N = 0$ and/or $x_2 = 0$).

We see in Fig. 2 that all pseudo-resource rays drawn from points of zero pseudo-resource to the point of maximum pseudo-resource $\hat{R}_1^{**}$ comply with the CN requirement for normality, in that $f_1$ increases monotonically along every such ray. The obligate mutualist extensions of LVNCN systems considered here are then normal systems when catalyst populations are considered in the definition of pseudo-resources.

2.3. The Pseudo-resource Function. Many forms of pseudo-resource functions may be used in obligate mutualism models. One might use an alternative form of pseudo-resource function $\phi_i(x_h, x_j; \epsilon_j)$ with the additional property that $\hat{R}_i$ collapses to $R_i$ when $\epsilon_j = 0$ and there is no obligation of $x_i$ on $x_j$. Such functions bridge the models of obligate to facultative mutualism as $\epsilon_j \to 0$. We use the Holling Type II function $\phi_i(x_h, x_j; \epsilon_j) = x_h \frac{x_j}{x_j + \epsilon_j}$, where $\epsilon_j > 0$ is a half-saturation constant that measures the degree of the obligation of $x_i$ on $x_j$, in §4 and §5 to capture this property, although other functions may be used.

The simplest form of a pseudo-resource function is $\phi_i(x_h, x_j) = x_h x_j$. We need to find where $\hat{R}_i^{**}$ occurs in, or on the boundary of, $E$. To find the maximum possible value of $\phi_i$, we substitute $x_j = 1 - x_h$ as all other populations are zero on this boundary, and calculate the derivative of $\phi_i = x_h(1 - x_h)$, $d\phi_i/dx_h = 1 - 2x_h$, and note that the maximum of $\phi_i$ occurs at $x_h = 1/2$ (where the derivative vanishes). This gives $\hat{R}_i^{**} = 1/4$. Then for the $x_i$ population to be viable, $f_i > 0$ at $\hat{R}_i^{**}$, where
$x_h = 1/2 = x_j$ with all other populations $x_k = 0$, on the boundary of $E$. (We use this simplest function in our first example, §3 where we model two autotroph populations, both with obligated growth functions.)

Real ecosystems can be effectively modelled by the above functions with appropriate choices of parameters. We discuss in §3, 4, and 5 examples of mutualist interactions such as pollination that involve obligation in the populations’ ability to grow; similar results may be obtained for examples that involve protection mutualisms that reduce populations’ mortality rate (for an elegant example, see Gross [11]).

3. Obligate Mutualism between Autotrophs. There are many examples of obligate mutualisms between autotrophs, for example the modification of local environments by ‘nurse’ plants in order to facilitate the establishment of other plant species discussed by Bruno [4], and the defense mutualisms that Gross [11] suggests may underpin biodiversity. The former occurs between two autotroph populations that both consume inorganic nutrient $N$ (in different forms) to grow and provide each other with access to their metabolic byproducts, while the latter represents mechanisms by which each population reduces the mortality rate of the other.

Here we consider an extremely simple example of a bidirectional mutualism that represents the dependency of the autotrophs $x_1$ and $x_2$ upon each other to be able to grow:

\[
\begin{align*}
\dot{x}_1 &= x_1 f_1(x_1, x_2, N) = x_1 (r_1 x_2 N - m_1 - a_{11} x_1 - a_{12} x_2), \\
\dot{x}_2 &= x_2 f_2(x_1, x_2, N) = x_2 (r_2 x_1 N - m_2 - a_{21} x_1 - a_{22} x_2),
\end{align*}
\]

where again $N = 1 - x_1 - x_2$. We utilise the limiting resource as a currency to measure the size of the populations and other resources in the system - in many cases, the resource for one population will be another population. Because the limiting, recycled nutrient is available in a finite quantity, the take-up and sequestration of nutrient by one population may limit the resource available to another population.

Here, we consider the case where $x_1$ and $x_2$ are obligate upon each other to be able to access the inorganic nutrient $N$ and grow. Similar mutualist behaviour occurs when each plant species protects the other (reduces its mortality) against the environment in various manners such as plant robustness, chemical alteration of their environment, or herbivore defence, as described in [4, 11].

3.1. Parameter Sign Conditions for Obligate Mutualism. To ensure that $x_1$ and $x_2$ are viable obligate mutualists we identify the points $\{0, x_2^{**}\}$ and $\{x_2^{**}, 0\}$ where $\hat{R}_1^{**}$ and $\hat{R}_2^{**}$ respectively, the values of the maximum possible pseudo-resources, occur on the boundary of $E$.

For $x_1$ we use the simplest pseudo-resource function $\phi_1(x_2, N) = x_2 N$, and ensure that $f_1 > 0$ at $\{0, x_2^{**}\}$. To find the maximum of $\phi_1(N, x_2)$ on $N = 1 - x_2$, $0 \leq x_2 \leq 1$, we evaluate the derivative:

\[
\frac{d\phi_1}{dx_2} = \frac{d}{dx_2}[x_2(1-x_2)] = 1 - 2x_2.
\]

The maximum of the pseudo-resource function $\hat{R}_1^{**}$ is located at $x_2^{**} = 1/2$ (with $x_1^{**} = 0$), at which point the maximum pseudo-resource available to $x_1$ is $\hat{R}_1^{**} = 1/4$. Then, from (3) extended to pseudo-resources, for $x_1$ to be a viable population...
$f_1|_{R_1^*} > 0$. Evaluating $f_1|_{R_1^*}$ by substituting $\{x_1^*=0, x_2^*=1/2\}$ into $f_1$ provides the condition on the parameter values that:

$$r_1 > 4m_1 + 2a_{12}. \tag{9}$$

Evaluating $f_1$ at the three vertices of $E$, where $R_1 = 0$, and (3) imposes additional constraints on the values that the parameters may take, using:

$$f_1|_{(0,0)} < 0 \Rightarrow m_1 > 0, \quad f_1|_{(1,0)} < 0 \Rightarrow m_1+a_{11} > 0, \quad \text{and} \quad f_1|_{(0,1)} < 0 \Rightarrow m_1+a_{12} > 0. \tag{10}$$

For $x_1$ to be a viable and realistic obligate mutualist, the parameter constraints in (9) and (10) must be satisfied. Similar constraints apply to $x_2$. Here $m_i$ are linear mortalities (positive), and $a_{ii}$ are quadratic mortalities, or closure terms, usually positive, which may have a limited negative range. In all cases $r_i > 2m_i > 0$. Note that (10) allows $a_{12} < 0$, which represents $x_1$ receiving a facultative mutualism benefit from the presence of $x_2$. Facultative mutualism occurs when $x_1$ just receives a benefit from the presence of $x_2$, but can survive in its absence, see [7]. Importantly, (10) places an upper bound on the amount of facultative mutualist benefit that $x_1$ can receive from $x_2$. This is constrained to be less than the natural mortality of $x_1$, and prevents the unrealistic scenario of a population existing with no resources (i.e. food) but surviving solely because it receives a benefit (perhaps shade) from another population.

3.2. Zero Isoclines (Nullclines). The autotroph mutualism system (7) has the usual zero isoclines (equivalently nullclines), $x_1 = 0$ and $x_2 = 0$, with the $f_1 = 0$ and $f_2 = 0$ isoclines being defined by:

$$f_1 = 0 : \quad -r_1x_2^2 + (r_1 - r_1x_1 - a_{12})x_2 - m_1 - a_{11}x_1 = 0,$$

$$f_2 = 0 : \quad x_2 = \frac{r_2x_1 - a_{21}x_1 - m_2 - r_2x_1^2}{a_{22} + r_2x_1}. \tag{11}$$

Throughout we use graphing conventions that when a denominator vanishes then the numerator also vanishes, unless there are asymptotes. The $f_1 = 0$ isocline is a curve that has the $x_2$–axis intercepts:

$$\left\{ \begin{array}{l} a_{12} - r_1 - \sqrt{(a_{12} - r_1)^2 - 4r_1m_1} \\ -2r_1 \end{array} \right\} \text{ and } \left\{ \begin{array}{l} a_{12} - r_1 - \sqrt{(a_{12} - r_1)^2 - 4r_1m_1} \\ -2r_1 \end{array} \right\}. \tag{12}$$

Similarly the $f_2 = 0$ isocline has the $x_1$–axis intercepts:

$$\left\{ \begin{array}{l} a_{21} - r_2 + \sqrt{(a_{21} - r_2)^2 - 4r_2m_2} \\ -2r_2 \end{array} \right\} \text{ and } \left\{ \begin{array}{l} a_{21} - r_2 - \sqrt{(a_{21} - r_2)^2 - 4r_2m_2} \\ -2r_2 \end{array} \right\}. \tag{13}$$

3.3. Equilibrium Points. The autotroph mutualist system (7) has the usual equilibrium point at the origin ($C_0$) defined by the intersection of the $x_1 = 0$ and $x_2 = 0$ isoclines. The stability of the equilibrium points is determined by the eigenvalues of
the Jacobian matrix $J$, the matrix of partial derivatives of $x_1 f_1$ and $x_2 f_2$. We define the Jacobian matrix and the eigenvalues of $J$ at any point in or on the boundary of $E$ in [7]. The eigenvalues of the Jacobian matrix at the origin are:

(14) \[ \lambda_1 = f_1|_{C_0} = -m_1 \quad \text{and} \quad \lambda_2 = f_2|_{C_0} = -m_2, \]

and reveal that the density independent mortality terms make this point locally stable. We readily check that \{x_1 = 0\} and \{f_2 = 0\} do not intersect in $0 \leq x_2 \leq 1$ (as they should not if $x_2$ is an obligate mutualist); and similarly that \{x_2 = 0\} and \{f_1 = 0\} do not intersect in $0 \leq x_1 \leq 1$.

The two interior (in $E$) equilibrium points of (7) where \{f_1 = 0\} intersects \{f_2 = 0\}, one stable and one unstable, are best found numerically. They are available analytically but generally the roots provide little insight due to their algebraic complexity.

3.4. Dynamical Properties. The zero isoclines, equilibrium points and vector fields of (7) are shown in Fig. 3 and summarise the basic dynamical properties of the obligate autotroph system. Fig. 3(a) shows obligate mutualists that interact only by facilitating each other’s growth. Neither provides a net mutualist benefit to the other in addition to this, consistent with Holland and DeAngelis’s[13] contention that in some mutualist interactions costs will exceed benefits. In this case although $x_1$ depends on $x_2$ to be able to grow, it outcompetes $x_2$ for the resource ($a_{21} = 0.375$) and consequently the populations coexist at parlously low levels which leave them susceptible to extinction through random environmental events. Note that Fig. 3(a) also reveals that the populations will simultaneously go extinct in a blue-sky (saddle-node) bifurcation if $x_2$ becomes a weaker competitor.

Fig. 3(b) shows the case where $x_2$ competes more effectively with $x_1$ ($a_{21} = 0.100$) and while the $x_2$ population has increased and both populations are less susceptible to random events, the outcome of the overall interaction is optimal for the $x_1$ population. The improvement in $x_2$’s competitive outcomes with $x_1$ is continued in Fig. 3(c), where $a_{21} = 0.030$ and the two populations have similar zero isoclines and coexist at similar equilibrium population levels, although they have very different properties as indicated by their parameter values.

Reducing $a_{21}$ to negative values (in Fig. 3(d) $a_{21} = -0.030$), so that $x_2$ now receives a mutualist benefit from $x_1$ in addition to $x_1$’s facilitation of $x_2$’s growth, produces an $x_2$ population that sequesters most of the resources despite its maximum photosynthetic growth rate being only half that of $x_1$ ($r_1 = 1.00$ vs $r_2 = 0.50$). This figure shows that relatively small mutualist benefit shifts ($a_{21}$ changes from 0.10 to 0.03 to -0.03 in panels (b), (c) and (d) respectively) enable $x_2$ to displace $x_1$ as the dominant population in the ecosystem: from panel (b) to (d) the $x_2/x_1$ ratio varies from approximately 1/5 to 5/1.

4. Pollination. Our second example is the well-known mutualism of obligate pollination, which occurs between certain plants and their pollinators, usually insects or birds. Pollination may be a bi-directional mutualism, but is often a uni-directional mutualism, and as contrast to the previous example of bi-directional obligation, we now consider the uni-directional case of pollination. Here an autotroph (plant) population consumes inorganic nutrient $N$ as its resource to fuel growth, but depends on the presence of a pollinator population to reproduce. This pollinator consumes
Fig. 3. Ecospace diagrams with vector fields, zero isoclines, and equilibrium points for obligate mutualism between autotrophs. Both $x_1$ and $x_2$ feed on inorganic nutrient $N$ and require the presence of the other population to grow. Panel: (a) $x_1$ has a strong negative net direct interaction effect on $x_2$ ($a_{21} = 0.375$); (b) $x_1$ has a weak negative net direct interaction effect on $x_2$ ($a_{21} = 0.100$); (c) $x_1$ has a very weak negative net direct interaction effect on $x_2$ ($a_{21} = 0.030$); (d) $x_1$ has a very weak positive net direct interaction (mutualist) effect on $x_2$ ($a_{21} = -0.030$). The other (constant) parameter values used to draw this figure are provided in Table 1 of the Appendix. Here, as $a_{21}$ decreases from panel (a) to panel (d), $x_2$ increases its equilibrium share of the cycling limiting nutrient from less than 5% to more than 70%; note that the $a_{21}$ variation is relatively small in magnitude during $x_2$’s increasing dominance of the ecosystem.

resource (nectar or similar) provided by the plant, and then moves pollen acquired during feeding from one plant to another. The heterotroph pollinator population acts purely as a predator, albeit one that provides a service to its prey. Then the autotroph (plant) population, although a prey additionally obtains a benefit from, and is obligate upon, the predator.

We represent the interaction of the plant $x_1$ and the pollinator $x_2$ by the LV CN equations extended by the nonlinear saturating obligate growth term with the obli-
gation parameter $\epsilon_2$ positive. We separate out the usual net growth term $r_1$ into the growth component, that is dependent on the presence of $x_2$ and nutrient $N$, and the linear mortality component $m_1$ that is not:

\begin{align}
\dot{x}_1 &= x_1 f_1(x_1, x_2; N) = x_1 (r_1 \frac{x_2}{x_2 + \epsilon_2} - N - m_1 - a_{11} x_1 - a_{12} x_2), \\
\dot{x}_2 &= x_2 f_2(x_1, x_2) = x_2 (r_2 - a_{21} x_1 - a_{22} x_2),
\end{align}

where $N = 1 - x_1 - x_2$. The implication of this expression for $N$ is that the system has a finite and limiting quantity of at least one resource, in this case a nutrient that is recycled within the system. Although the growth of the plant and pollinator are constrained by the availability of different resources (inorganic nutrient for the plant, and nectar provided by the plant for the pollinator), these resources are measured in the same finite currency. The currency available to represent any resource is limited by the amount of currency sequestered in other populations and/or resources. (In teaching terms the obligation part of the model in §3 is simpler mathematically (see equation (7)), and lecturers may prefer to use the simpler form for obligation in (15) first to explain the procedure to mathematically weaker students.)

Here, $\epsilon_2 > 0$ captures the extent of the obligation of $x_1$ on $x_2$. When $\epsilon_2 = 0$, we replace the obligation coefficient $x_2/(x_2 + \epsilon_2)$ by 1; then $x_1$ can reproduce independently of $x_2$, and we describe the interaction as facultative mutualism if $a_{12} < 0$. When $\epsilon_2$ is 'small' (say 0.001), $x_1$ only requires a 'small' $x_2$ population (say 1-2% of the total resource pool) to achieve near maximum reproduction, whereas if $\epsilon_2$ is 'larger', a 'larger' $x_2$ population is required, and $x_1$’s reproductive success depends on it providing sufficient nectar to support the larger pollinating population $x_2$.

The pollinator $x_2$ acts as a simple predator in this example as it directly consumes nectar and/or pollen produced by the plant (i.e. $a_{21} < 0$), and this interaction is subject to a local mass balance constraint $-a_{21} < a_{12}$, so that the pollinator cannot consume more than the plant provides. As is usual for a heterotroph population, $r_2$ is negative and represents density-independent mortality, and conventionally $a_{22} > 0$ represents density-dependent mortality.

### 4.1. Parameter Sign Conditions for Obligate Mutualism.

To ensure that $x_1$ is a viable obligate mutualist we identify the point $\{0, x_2^*\}$ where $\hat{R}_{1}^{**}$, the value of the maximum possible pseudo-resource, occurs in, or on the boundary of, $E$. We use the pseudo-resource function with $N = 1 - x_2$,

\begin{equation}
\phi_1(N, x_2; \epsilon_2) = N \left( \frac{x_2}{x_2 + \epsilon_2} \right) = (1 - x_2) \left( \frac{x_2}{x_2 + \epsilon_2} \right), \quad \epsilon_2 > 0,
\end{equation}

and ensure that $f_1 > 0$ at $\{0, x_2^*\}$. To find the maximum of $\phi_1(N, x_2; \epsilon_2)$ on $N = 1 - x_2$, $0 \leq x_2 \leq 1$, we evaluate the derivative:

\begin{equation}
\frac{d\phi_1}{dx_2} = \frac{\epsilon_2 - 2\epsilon_2 x_2 - x_2^2}{(x_2 + \epsilon_2)^2}.
\end{equation}

The point of maximum possible pseudo-resource $\hat{R}_{1}^{**}$ is then given by:

\begin{equation}
x_2^{**} = +\sqrt{\epsilon_2 + \epsilon_2^2} - \epsilon_2 \approx \sqrt{\epsilon_2} - \epsilon_2 \text{ for } \epsilon_2 \text{ small}.
\end{equation}
We take the positive square root, as the negative square root gives \( x_2^{**} < 0 \), and is not ecologically relevant. It is left as an exercise to show that \( \lim_{\epsilon_2 \to \infty} (\sqrt{\epsilon_2 + \epsilon_2^2} - \epsilon_2) = \frac{1}{2} \), but we note that this function asymptotes to \( \frac{1}{2} \) very quickly as \( \epsilon_2 \) increases. For example, \( \epsilon_2 = 1 \) gives \( x_2^{**} = 0.4142 \), that is, the function achieves over 80\% of its value at \( \epsilon_2 = \infty \) at just \( \epsilon_2 = 1 \). This suggests that plants that are obligate on a pollinator might survive with relatively small pollinating populations. We discuss the more ecologically interesting limit of \( \epsilon_2 \) small later.

The maximum possible amount of pseudo-resource is:

\[
R_1^{**} = 1 - 2\sqrt{\epsilon_2 + \epsilon_2^2} + 2\epsilon_2 = 1 - 2x_2^{**},
\]

reflecting that as the dependency of the plant population on a pollinating population increases, the amount of resource in the system potentially available to the plant population to grow upon is reduced. Note that for small \( \epsilon_2 \), \( x_2^{**} \) is small and \( R_1^{**} \) is almost one; but when \( \epsilon_2 \) is large, \( x_2^{**} \) is nearly \( \frac{1}{2} \) and \( R_1^{**} \) is small. This indicates that obligate pollination mutualisms involve a trade-off between a reliance on a large pollinator population (using (19)):

\[
\hat{R}_1 = 1 - \frac{2x_2^{**}}{1 - 2x_2^{**}}.
\]

As \( 0 < x_2^{**} < 1/2 \), the "best case" scenario for \( x_2 \), in which it has no natural mortality (\( m_1 \)) and \( x_2 \) has no net direct detrimental effect on it (\( a_{12} = 0 \)), always has \( f_1 \) positive somewhere in \( E \) for \( r_1 > 0 \), so that \( x_1 \) can always grow. As \( m_1 \), \( a_{12} \), and \( \epsilon_2 \) increase, so must \( r_1 \) increase for \( x_1 \) to remain a viable population. The ecological interpretation of either increasing mortality \( m_1 \), increasing the net mutualism cost \( a_{12} \) for decreasing the pollination efficiency is naturally to require a higher growth rate coefficient to ensure the survival of the population.

Pollination where the obligate mutualist autotroph does not receive any net mutualist benefit from the pollinator other than transport of gametes between plants appears to be a common, if not the most common, form [3]. This suggests a trade-off between the pollinator population size required to ensure reproductive success, and competition with that population for a share of the overall resources. As \( x_1 \) becomes dependent on increasingly large populations of \( x_2 \) for pollination (i.e. \( x_2 \) is an inefficient pollinator) its survival may depend on it adapting to its environment and reducing its natural mortality rate \( m_1 \) and/or receiving a net mutualism benefit (such
as a protection mutualism that reduces its natural mortality rate) from $x_2$ in addition to its pollination services. Similarly, if $x_2$ is an inefficient pollinator and $x_1$ requires a large population to ensure maximum reproduction ($\epsilon_2$ 'large') then both populations are at risk of extinction via the blue-sky (equivalently saddle-node) bifurcation that occurs at $\epsilon_2^2 = 0.0872$. This may be avoided by moving the intercept of the $f_2$ isocline with the $x_1$ axis to the left, for example by increasing the magnitude of $a_{21}$, that represents the growth rate of the $x_2$ population as a result of grazing on nectar provided by $x_1$. However, the requirement for $\epsilon_2$ to be small to enable stable coexistence of populations provides the testable prediction that plants rely on relatively small populations of obligate pollinators for survival.

The parameter profile for $x_2$ is that of a predator \[7\], so that here the linear mortality coefficient is smaller in magnitude than the grazing coefficient $a_{21} < r_2 < 0$; this satisfies $f_2|\mu_2 = 1 > 0$ and ensures the viability of $x_2$. We usually take the quadratic mortality coefficient to be positive $a_{22} \geq 0$, as increases in populations beyond their Allee point \[1\] generally have detrimental effects on themselves. However, we note that $r_2 < a_{22} < 0$ is also a valid choice and may be appropriate in some ecologies. The bidirectional mutualism case, defined by $a_{12} < 0$, is also left as a further interesting exercise.

4.2. Zero Isoclines (Nullclines). The pollination system \(15\) has the usual $x_1 = 0$ and $x_2 = 0$ zero isoclines common to all CN systems, with the $f_1 = 0$ and $f_2 = 0$ zero isoclines being defined by:

$$f_1 = 0 : -(r_1 + a_{12})x_2^2 + (r_1(1 - x_1) - m_1 - a_{11}x_1 - a_{12}\epsilon_2)x_2 - \epsilon_2m_1 - \epsilon_2a_{11}x_1 = 0,$$

\(22\)

$$f_2 = 0 : x_2 = \frac{r_2}{a_{22}} - \frac{a_{21}}{a_{22}}x_1, \text{ for } a_{22} \neq 0.$$

The $f_1 = 0$ isocline is a quadratic in $x_2$ for fixed $x_1$ that has the $x_2$ axis intercepts:

\(23\)

$$\left\{ 0, -\frac{b - \sqrt{b^2 - 4ac}}{2a} \right\} \text{ and } \left\{ 0, -\frac{b + \sqrt{b^2 - 4ac}}{2a} \right\},$$

where $a = r_1 + a_{12}$, $b = -r_1 + m_1 + a_{12}\epsilon_2$ and $c = \epsilon_2m_1$. When $\epsilon_2 = 0$, with $a_{11}, a_{12} \geq 0$, the isocline is a straight line with axis intercepts:

\(24\)

$$\left\{ \frac{r_1 - m_1}{r_1 + a_{11}}, 0 \right\} \text{ and } \left\{ 0, \frac{r_1 - m_1}{r_1 + a_{12}} \right\}.$$

It is left as an exercise to investigate the effect of $a_{12}$ becoming negative (when mutualist benefits outweigh mutualist costs), which modifies the following discussion. In particular, $a_{12} < 0$ requires a consistency check to ensure that $\dot{N} > 0$ when $N = 0$.

The $f_2 = 0$ isocline is a straight line that has the axis intercepts:

\(25\)

$$\left\{ \frac{r_2}{a_{21}}, 0 \right\} \text{ and } \left\{ 0, \frac{r_2}{a_{22}} \right\}.$$

Note that for a predator (for which $a_{21} < r_2 < 0 < a_{22}$) $0 < (r_2/a_{21}) < 1$ and $(r_2/a_{22}) < 0$, and predator-prey coexistence occurs when $(r_2/a_{21}) < (r_1/a_{11}).$ This
Fig. 4. The ecospace diagram with vector fields, zero isoclines, and equilibrium points for a pollination mutualism. \( x_1 \) is an autotroph population that feeds on inorganic nutrient \( N \) and is pollinated by the predator population \( x_2 \) as it feeds on \( x_1 \). Panel: (a) the plant is not obligate on the pollinator and the pollinator effectively functions as a predator (\( \epsilon_2 = 0 \)); (b) obligate pollination mutualism dependent on a small pollinator population (\( \epsilon_2 = 0.001 \)); (c) obligate pollination mutualism dependent on a moderate pollinator population (\( \epsilon_2 = 0.05 \)); (d) obligate pollination mutualism dependent on a large pollinator population at the point of blue sky bifurcation (\( \epsilon_2 = \epsilon^*_2 = 0.087225 \)). The parameter values used to draw this figure are provided in Table 1 of the Appendix.

The coexistence condition is modified when the plant becomes obligate on the predator. Then the \( f_1 = 0 \) isocline bends markedly near the \( x_1 \) axis for small positive \( \epsilon_2 \) (Fig. 4) but the coexistence condition remains as a useful heuristic for small values of \( \epsilon_2 \) in this simple obligate scenario.

4.3. Equilibrium Points. The pollinator system (15) has the usual equilibrium point at the origin (\( C_0 \)) defined by the \( x_1 = 0 \) and \( x_2 = 0 \) isoclines. The eigenvalues of the Jacobian matrix, where in [7] we describe the matrix of partial derivatives \( J \) and its eigenvalues, of the rhs of (15) at the origin are:
\[ \lambda_1 = \begin{cases} r_1 - m_1 > 0 & \text{when } \epsilon_2 = 0 \\ -m_1 < 0 & \text{when } \epsilon_2 > 0 \end{cases}, \quad \text{and} \quad \lambda_2 = r_2 < 0. \]

When \( \epsilon_2 = 0 \) the opposing signs at the origin imply an unstable saddle where the plant population grows and the pollinator population dies. The system has a further equilibrium point \( (C_1) \) when \( \epsilon_2 = 0 \), where the \( f_1 = 0 \) and \( x_2 = 0 \) isoclines intersect, located at:

\[ \left\{ x_1^* = \frac{r_1 - m_1}{r_1 + a_{11}}, x_2^* = 0 \right\}. \]

This autotroph point, where only plants survive, has the eigenvalues:

\[ \lambda_1 = -(r_1 - m_1) < 0 \quad \text{and} \quad \lambda_2 = r_2 - a_{21} \frac{r_1 - m_1}{r_1 + a_{11}}. \]

When the \( x_1 \) axis intercept \( (r_1 - m_1)/(r_1 + a_{11}) \) of \( f_1 \) lies to the right of the \( x_1 \) axis intercept \( r_2/a_{21} \) of \( f_2 \), as in Fig. 4(a), \( \lambda_2 > 0 \) and \( C_1 \) is also an unstable saddle point, which implies that any \( x_2 \) population will grow in this neighbourhood.

For \( \epsilon_2 > 0 \) (Fig. 4(b-d)) the system has equilibrium points defined by the intersections of the \( f_1 = 0 \) and \( f_2 = 0 \) isoclines at:

\[ \left\{ x_1^* = \frac{r_2 - a_{22}x_2^*}{a_{21}}, x_2^* = -\beta \pm \frac{\sqrt{\beta^2 - 4\alpha\gamma}}{2\alpha} \right\}, \]

where \( \alpha = a_{22}(r_1 + a_{11}) - a_{21}(r_1 + a_{12}), \beta = a_{21}(r_1 - m_1) - r_2(r_1 + a_{11}) + \epsilon_2(a_{11}a_{22} - a_{12}a_{21}) \) and \( \gamma = -\epsilon_2(a_{11}r_2 + a_{21}m_1) \). Obtaining such expressions is of limited use analytically, but is useful to check numerically to confirm the accuracy of plots of zero isoclines and vector fields.

Fig. 4 reveals that when \( \epsilon_2 = 0 \) (29) produces a single equilibrium point; when \( \epsilon_2 \) becomes non-zero the location of the existing equilibrium point is modified slightly, and a second interior point near \( \{x_1 = r_2/a_{21}, x_2 = 0\} \) is non-continuously created. These two interior equilibrium points move closer together as \( \epsilon_2 \) increases, until the interior point disappears in a blue-sky, or saddle-node, bifurcation when the solution to equation (29) becomes complex at \( \beta^2 - 4\alpha\gamma = 0 \). This value is best calculated numerically for each parameter combination.

The direct interpretation of the limit to the obligate mutualist dependence of the plant \( x_1 \) population on its pollinator/predator population \( x_2 \) is not clear from equation (29), but as it involves all the parameters in the model it does reveal that obligation is a system-level property rather than a property of the plant or the pollinator alone. Further, examination of the ecospaces diagrams for various values of \( \epsilon_2 \) (Fig. 4) reveals that both the plant and the predator/pollinator populations appear to do better when \( \epsilon_2 \) is small, with all else the same, when only a relatively small biomass of pollinators is required for the plant to achieve close to maximum reproduction.

If we fix \( \epsilon_2 \) small (say \( \epsilon_2 = 0.001 \)), and vary the plant and pollinator growth parameters so as to move both isoclines in the increasing \( x_1 \) direction, we find that the plant-pollinator system does better. Improving the plants' lot by moving the
$f_1 = 0$ isocline to the right provides a better outcome for both the plant and the pollinator, whereas improving the pollinators’ lot by moving the $f_2 = 0$ isocline up improves the pollinators’ outcome but is detrimental to the plant population.

Many students enjoy, and find it helps their understanding of modelling, varying parameters in such simple models, examining their output graphically, and interpreting what this means for the modelled populations.

4.4. Consistency Check. The consistency check ($\dot{N}|_{N=0} > 0$) of the CN framework is satisfied for the above parameters ranges when $a_{12} \geq 0$. When $a_{12} < 0$, and mutualist benefits occur, we need to check that the parameter choices lead to consistent models with $N$ positive. We demonstrate the importance of this check in §5.

4.5. Dynamical Properties. The zero isoclines, equilibrium points and vector fields of (15) are shown in Fig. 4 and summarise the basic dynamical properties of the pollination system as the plant transitions from a prey with no mutualism interaction Fig. 4(a) to an obligate mutualist dependent on a small pollinating population Fig. 4(b), through dependence on a pollinating population of moderate size Fig. 4(c) to the limiting case where if the system depends on a pollinating population any larger then it will collapse and both plant and pollinator populations $x_1^*$ and $x_2^*$ will go extinct in a blue-sky bifurcation (known mathematically as a saddle-node bifurcation), Fig. 4(d). This behaviour has been documented for much more detailed and complex models of pollination [16].

A straightforward ecological interpretation of Fig. 4 suggests that, all else remaining the same, the dependence of a plant on an increasingly large biomass of pollinators produces worse outcomes for both populations in an obligate pollination mutualism. Note that the stable equilibrium populations of both $x_1^*$ and $x_2^*$ are reduced in Figs. 4(b)-4(d), and that these are smaller than the equilibrium populations for the facultative case Fig. 4(a). At first sight we might argue that small $x_2$ (the relative biomass of the pollinators), together with small $\epsilon_2$ and reduced $x_1$ levels compared to the facultative mutualist case, suggests obligate mutualism might be less common. Instead, these facts can be interpreted as the co-evolutionary outcome of many (smaller) pollinating individuals with a relatively small total biomass, compared to the plant biomass, and this is often observed in practice.

Co-evolution of plants and pollinators is a cornerstone of adaptation, mentioned by Darwin in the Introduction to "On the Origin of Species" [8], and provides an appropriate perspective from which to investigate these systems. Roughgarden [25] provides a more recent introduction to evolutionary ecology, and comments that a framework such as the above extended CN system, with continuously varying stable equilibrium points, would help in developing a theory where competitor populations might co-adapt: we comment that this could be into a mutualist or even a predator population.

An eco-evolutionary perspective suggests that exploration of the parameter space and associated dynamics of the pollination model might best be undertaken with an evolutionary algorithm, such as a genetic algorithm [12, 20] that allows some/all parameters to vary simultaneously and searches a fitness landscape for optimal outcomes. It is beyond the scope of this manuscript to delve into the implications of co-evolution in these systems, but exploring the behaviour of the system as parameters vary can provide useful and insightful projects for students to pursue in numerical studies. In summary, this extended CN framework allows description of smoothly varying families of ecological models where the differing mass and energy transfers can be compared
using the limiting resource as an exchange currency.

5. Obligate Mutualism between Heterotrophs. Obligate mutualisms between heterotrophs are common, for example protection obligations such as the sea anemone and the clown fish or the goby and shrimp; see [18] for an example of experiments in the Bahamas. Protection mutualisms may serve to facilitate growth or reduce mortality, which can produce analogous obligation terms in model equations. Both Holland and DeAngelis [13] and Thompson et al. [28] give surveys of well-documented examples of these mechanisms and models, listing around forty examples of obligate/facultative and bi/uni-directional mutualisms.

We consider two heterotrophs $x_2$ and $x_3$, that in this example feed on a common resource the autotroph $x_1$, and that depend upon each other to be able to grow:

$$
\dot{x}_1 = x_1 f_1(x_1, x_2, x_3) = x_1 (r_1 - a_{11} x_1 - a_{12} x_2 - a_{13} x_3),
$$

$$
\dot{x}_2 = x_2 f_2(x_1, x_2, x_3) = x_2 (r_2 - a_{21} \frac{x_3}{x_3 + \epsilon_3} x_1 - a_{22} x_2 - a_{23} x_3),
$$

$$
\dot{x}_3 = x_3 f_3(x_1, x_2, x_3) = x_3 (r_3 - a_{31} \frac{x_2}{x_2 + \epsilon_2} x_1 - a_{32} x_2 - a_{33} x_3).
$$

Here, $\epsilon_3$ and $\epsilon_2$ are (relatively small) positive parameters that represent the degree of obligation on $x_3$ and $x_2$ respectively of the growth of $x_2$ and $x_3$, which growth is by directly consuming $x_1$ so that $a_{21}, a_{31} < 0$. (Note: lecturers may also prefer to initially use the simpler form for obligation used in the first example (7) in this example to explain the procedure to mathematically weaker students.)

As is usual in the notation convention we use throughout this manuscript, $r_1$ reflects how $x_1$ interacts with the inorganic nutrient pool, and is the net of linear growth minus linear mortality. This is positive for a viable autotroph as growth exceeds mortality. Similarly, $r_2$ and $r_3$ reflect how $x_2$ and $x_3$ interact with the inorganic nutrient pool; as these are heterotrophs that cannot grow on inorganic nutrient the growth component is zero and $r_2$ and $r_3$ are negative and are interpreted as net linear mortality terms for heterotrophs. The $a_{ij}$ coefficients are usually positive and represent quadratic (density-dependent) mortality, although mathematically they are sometimes called closure coefficients. While $a_{12}, a_{13}$ are positive, and $a_{21}, a_{31}$ are negative, as $x_2, x_3$ consume $x_1$, we note that $a_{23}, a_{32}$ may take either sign. Positive values represent the usual competition between the heterotrophs whereas negative values represent net mutualist benefits in addition to the obligation.

5.1. Parameter Sign Conditions. The parameter sign conditions for the autotroph $x_1$, which is not involved in any mutualistic interactions, are the usual constraints on the sign of the life function at maximum and minimum resources ($f_1|_{R_1=1} > 0 > f_1|_{R_1=0}$, equation (3)) . We apply these conditions and determine parameter relationships consistent with the usual autotroph parameter profile (see [7]):

$$
0 < r_1 < a_{11}, a_{12}, a_{13}.
$$

We also obtain parameter constraints imposed by considering the trophic strategy of each population and evaluating (3) at the origin of $E$:

$$
0 = f_1|_{(0,0,0)} > 0 \Rightarrow r_1 > 0, \quad f_2|_{(0,0,0)} < 0 \Rightarrow r_2 < 0, \quad \text{and} \quad f_3|_{(0,0,0)} < 0 \Rightarrow r_3 < 0.
$$
These growth/mortality conditions hold for all mutualism strategies of \( x_2 \) and \( x_3 \).

For the obligate heterotroph populations \( x_2 \) and \( x_3 \) we identify the points of maximum pseudo-resources, for \( x_2 \), \( \phi_2(x_3, x_1; \epsilon_3) = \left( \frac{x_3}{x_3 + \epsilon_3} \right)x_1 \), and for \( x_3 \), \( \phi_3(x_2, x_1; \epsilon_2) = \left( \frac{x_2}{x_2 + \epsilon_2} \right)x_1 \). We evaluate these terms on the lines where \( x_1 + x_3 = 1 \) and \( x_1 + x_2 = 1 \) respectively, so look for the maximums of the functions \( \left( \frac{x_3}{x_3 + \epsilon_3} \right)(1-x_3) \) and \( \left( \frac{x_2}{x_2 + \epsilon_2} \right)(1-x_2) \) respectively, analogous to the pseudo-resource function for an autotroph in §4.1 above. Taking the appropriate derivatives gives:

\[
\frac{d\phi_2}{dx_3} = \frac{\epsilon_3 - 2\epsilon_3 x_3 - x_3^2}{(x_3 + \epsilon_3)^2} \quad \text{and} \quad \frac{d\phi_3}{dx_2} = \frac{\epsilon_2 - 2\epsilon_2 x_2 - x_2^2}{(x_2 + \epsilon_2)^2}.
\]

The locations of the points of maximum possible pseudo-resource \( \hat{R}_2^{**} \) and \( \hat{R}_3^{**} \) for the heterotrophs \( x_2 \) and \( x_3 \) are analogous to that for the autotroph \( x_1 \) in §4.1:

\[
x_3^{**} = \sqrt{\epsilon_3^2 + \epsilon_3 - \epsilon_3} \text{ with } x_2^{**} = 0, \quad \text{and} \quad x_2^{**} = \sqrt{\epsilon_2^2 + \epsilon_2 - \epsilon_2} \text{ with } x_3^{**} = 0,
\]

with the maximum possible amounts of pseudo-resource being:

\[
\hat{R}_2^{**} = 1 - 2\sqrt{\epsilon_3 + \epsilon_3^2 + 2\epsilon_3} = 1 - 2x_3^{**} \quad \text{and} \quad \hat{R}_3^{**} = 1 - 2\sqrt{\epsilon_2 + \epsilon_2^2 + 2\epsilon_2} = 1 - 2x_2^{**}.
\]

Evaluating the sign conditions \( f_2|\hat{R}_2^{**} > 0 \) and \( f_3|\hat{R}_3^{**} > 0 \), that ensure that the \( x_2 \) and \( x_3 \) populations can always grow at their point of maximum pseudo-resource, provide the relations:

\[
r_2 > a_{21}\hat{R}_2^{**} + a_{23}x_3^{**} \quad \text{and} \quad r_3 > a_{31}\hat{R}_3^{**} + a_{32}x_2^{**}.
\]

Substituting for the maximum resources (35) into (36) provides the relations (noting \( a_{21}, a_{31} < 0 \)):

\[
x_3^{**} < \frac{-a_{21} + r_2}{-2a_{21} + a_{23}} \quad \text{and} \quad x_2^{**} < \frac{-a_{31} + r_3}{-2a_{31} + a_{32}}
\]

if we assume that \( -2a_{21} + a_{23} > 0 \) and \( -2a_{31} + a_{32} > 0 \). Then \( -a_{j1} > r_j > 0 \) ensures \( x_j^{**} > 0 \) for \( j = 2, 3 \). The "usual" scenario, that despite \( x_3 \) facilitating \( x_2 \)’s growth it sequesters resources that are then not available to \( x_2 \), has \( a_{23} > 0 \) with \( a_{21} < 0 \) by definition (and similarly for \( x_3 \)), so the assumptions are generally satisfied. Further, the usual condition for \( x_2 \) and \( x_3 \) populations that are not obligate upon each other, but coexist in an ecosystem where they both prey upon \( x_1 \), has \( a_{21} < r_2 < 0 \) and \( a_{31} < r_3 < 0 \) (see [7] for details). We expect this condition to remain valid after such populations became obligate, in which case (37) provides constraints upon the maximum size of the obligating populations for the viability of each population. These constraints are relaxed (i.e. larger obliging populations are permitted) if the obliging population also provides a mutualist benefit in addition to facilitating growth, when \( a_{23} \) and/or \( a_{32} \) become negative.

Hence, \( x_2 \) can only function as an obligate mutualist heterotroph if it depends on populations of \( x_3 \) up to a specific size. If \( x_2 \) requires larger populations of \( x_3 \) to grow then \( x_3 \) needs to become a less-efficient competitor for resources, or \( x_2 \) needs to
receive a net mutualist benefit from $x_3$, in addition to its role in facilitating growth. These scenarios are captured by a reduction of $a_{23}$. Similar conditions hold for $x_3$. We note that these conditions are analogous to those obtained for bilateral obligate autotrophs in §3 and the unilateral obligate autotroph-heterotroph interaction in §4.

5.2. Zero Isosurfaces (Null surfaces). The autotroph-heterotroph system (30) has the usual $x_1 = 0$, $x_2 = 0$, and $x_3 = 0$ zero isosurfaces, with the $f_1 = 0$, $f_2 = 0$, and $f_3 = 0$ isosurfaces being defined by:

\begin{align*}
    f_1 = 0 : & \quad x_3 = \frac{r_1}{a_{13}} - \frac{a_{11}}{a_{13}} x_1 - \frac{a_{12}}{a_{13}} x_2, \\
    f_2 = 0 : & \quad x_3 = -\left(r_2 - a_{21} x_1 - a_{22} x_2 - \epsilon_3 a_{23}\right) \pm \sqrt{\left(r_2 - a_{21} x_1 - a_{22} x_2 - \epsilon_3 a_{23}\right)^2 + 4 \epsilon_3 a_{23} (r_2 - a_{22} x_2)}, \\
    f_3 = 0 : & \quad x_3 = \frac{r_3}{a_{33}} - \frac{a_{31}}{a_{33}} x_2 + \epsilon_2 x_1 - \frac{a_{32}}{a_{33}} x_2.
\end{align*}

The $f_1 = 0$ isosurface is a plane that has the axis intercepts:

\begin{equation}
\left\{ \frac{r_1}{a_{11}}, 0, 0 \right\}, \quad \left\{ 0, \frac{r_1}{a_{12}}, 0 \right\}, \quad \text{and} \quad \left\{ 0, 0, \frac{r_1}{a_{13}} \right\},
\end{equation}

the $f_2 = 0$ isosurface has the axis intercepts:

\begin{equation}
\left\{ 0, \frac{r_2}{a_{22}}, 0 \right\}, \quad \text{and} \quad \left\{ 0, 0, \frac{r_2}{a_{23}} \right\},
\end{equation}

and the $f_3 = 0$ isosurface has the axis intercepts:

\begin{equation}
\left\{ 0, \frac{r_3}{a_{32}}, 0 \right\}, \quad \text{and} \quad \left\{ 0, 0, \frac{r_3}{a_{33}} \right\}.
\end{equation}

Note that as $\epsilon_2$ and $\epsilon_3$ are greater than zero neither of the heterotroph zero isosurfaces intersect the $x_1$ axis, and since usually $r_2, r_3 < 0 \leq a_{22}, a_{33}$ these isosurfaces intercept the other axes in $0 \leq x_i \leq 1$ only in rare circumstances.

5.3. Equilibrium Points. The heterotroph mutualist system (30) has the usual equilibrium point at the origin ($C_0$) defined by the intersection of the $x_1 = 0$, $x_2 = 0$, and $x_3 = 0$ isosurfaces. The eigenvalues of the Jacobian matrix at the origin are:

\begin{equation}
\lambda_1 = f_1|_{C_0} = r_1 > 0, \quad \lambda_2 = f_2|_{C_0} = r_2 < 0, \quad \text{and} \quad \lambda_3 = f_3|_{C_0} = r_3 < 0,
\end{equation}

where the signs of the eigenvalues are determined by (32). The origin is always a saddle point in these systems as the autotroph population is always able to grow.

The system also has an autotroph (plant only) equilibrium point where the $f_1 = 0$, $x_2 = 0$, and $x_3 = 0$ isosurfaces intersect, at:

\begin{equation}
C_1 = \left\{ \frac{r_1}{a_{11}}, 0, 0 \right\}.
\end{equation}
Fig. 5. Ecospace diagram with vector fields, zero isoclines, and equilibrium points for obligate mutualism between heterotrophs $x_2$ and $x_3$ where each is obligated to the other in order to feed on the autotroph $x_1$ (equation (30)). Each of $x_2$ and $x_3$ receives a strong net mutualist benefit from the other population ($a_{23} = -1 = a_{32}$), for instance as a mutual protection. Panels are: (a) $f_1 = 0$ 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 $x_1 = x_1^*$. The parameter values used to draw this figure are provided in Table 2 of the Appendix.

The eigenvalues of the Jacobian matrix at this point are:

\begin{equation}
\lambda_1 = \frac{\partial f_1}{\partial x_1}|_{C_1} = -a_{11}x_1^* = -r_1 < 0, \quad \lambda_2 = f_2|_{C_1} = r_2 < 0, \quad \text{and} \quad \lambda_3 = f_3|_{C_1} = r_3 < 0.
\end{equation}

This point is always stable, suggesting that if the interior coexistence point $C_7$ is stable, then a separatrix dividing the basins of attraction of the two points must exist.
Hence the presence of linear mortality terms introduces an Allee effect [1], which we discuss in the next section.

The equilibrium points $C_2, C_3, C_4, C_5,$ and $C_6$ of three-population LVCN systems (see [7]) all lie outside the ecospace in this obligation example, so the only other equilibrium point relevant to the model dynamics is the coexistence point $C_7$ defined by the intersection of the $f_1 = 0$, $f_2 = 0$, and $f_3 = 0$ isosurfaces. Equation (38) reveals that evaluating the location of this point algebraically is complicated and likely to be uninformative, so we calculate it numerically when its location is needed.

5.4. Dynamical Properties. The zero isosurfaces, equilibrium points and vector fields shown in Fig. 5 summarise the dynamical properties of the obligate heterotroph system (30) for the case where each heterotroph population is dependent on the other to be able to grow ($\epsilon_2 = 0.01 = \epsilon_3$), and in which the obligate heterotroph populations each receive a strong net mutualist benefit from each other in addition to the obligate populations facilitating growth ($a_{23} < r_2 < 0$ and $a_{32} < r_3 < 0$).

Fig. 5(a) shows that as expected the heterotroph zero isosurfaces do not intersect the axes of the ecospace. The system trajectories in Fig. 5(b) demonstrate that the equilibrium point $C_7$ where all populations coexist is stable, and the section of the heterotroph zero isosurface in Fig. 5(c) shows two stable equilibrium points $C_1$ and $C_7$. This and the intersection of the heterotroph zero isosurfaces further from the origin in Fig. 5(d) reveals an Allee effect [1], indicating that the heterotrophs require minimum population sizes to avoid extinction. A separating surface must exist between the regions of the ecospace where the initial conditions lead to the stable coexistence equilibrium point $C_7$ and the regions of the ecospace where the initial conditions lead to the stable extinction equilibrium point $C_1$. While separatrices may be reasonably easily computed in two-population systems, computing separating surfaces in three dimensions is significantly more difficult and we do not show it here.

We can see from the arrangement of the $f_2$ and $f_3$ zero isosurfaces that the Allee effect introduces the potential for the $x_2$ and $x_3$ populations to go extinct in blue-sky (saddle-node) bifurcations as $\epsilon_2$ and $\epsilon_3$ are increased and the isosurfaces move apart in the $x_2 - x_3$ plane. Reducing the values of the density-independent mortality parameters $r_2$ and $r_3$ reduces the magnitude of the Allee effect until it disappears when these parameters are zero, and the populations then can only go extinct in a transcritical bifurcation at $C_1$.

This section with its three-population model shows how we generalise the framework of §3 and §4 to models with three or more populations. We finish this section by relating the model described by (30) to the conventional carrying capacity based models where the dependence of the model on both $N$ and $x_1$ is suppressed and the $x_2, x_3$ populations are related to their environment by using carrying capacities. This is conceptually equivalent to assuming $x_3$ is fixed at its stable $C_7$ equilibrium value. We frame this discussion as examples in the use of the lid condition (4).

5.5. Cautionary Examples. We end this introductory examination of the dynamics of some simple obligate heterotroph systems with two brief examples that provide salutary lessons:

- Models that look wrong are not necessarily wrong; and,
- Models that look right are not necessarily right.

This rubric emphasises the importance of having a rigorous framework within which to construct the models and checks such as the lid consistency condition to ensure that parameter sets do not introduce unrealistic behaviour into otherwise realistic models.
The first example (Fig. 6) considers the case of the obligate mutualist heterotroph model defined by equation (30) with a changed parameter set (Appendix Table 2) where the vector field in Fig. 6(d) looks wrong in that it implies that the lid condition is violated and populations could go to infinity, or negative nutrient masses could be predicted. The vector field in this panel is a section through the ecospace at the level of a constant resource, and is identical to the vector fields that convinced theoreticians using Lotka-Volterra models of obligation mutualism (using negative carrying capacities) that these models produced unrealistic solutions where the populations either go extinct or go to infinity. Fig. 6(d) reproduces the classic phase-plane diagram of Lotka-Volterra obligation models that assume a carrying capacity, that suggests the model is invalid. However, in this case the system is not constrained to a constant $x_1$ plane, as the classic example using carrying capacity effectively does.

We see from Fig. 6(b) that in fact the model produces a stable equilibrium point in the ecospace. Further, checking the lid condition confirms that the model with this parameter set can never violate conservation of mass, and that Fig. 6(d) in that context is quite misleading. Two salient points arise from this example:

• Scaling vectors, which is commonly done so that the direction that small magnitude vectors are pointing can be more easily seen, and has been done in all figures in this manuscript, can be quite misleading. The three-dimensional vector sum of the vectors in Fig. 6(c and d) in fact points into the ecospace $E$, as the magnitudes of the horizontal vectors pointing out of $E$ (that suggest the lid condition is violated) are small compared to the magnitudes of the vertical vectors pointing into $E$ at that location; and

• The explicit representation of all resources in a system can be fundamental to obtaining a useful solution. Many years were spent trying to obtain sensible representations of obligation mutualism interactions between populations using models in which the resources upon which the populations relied were modelled implicitly. These models gave rise to vector fields like Fig. 6(d), causing the models to be derided as ‘too simplistic’. In fact, it was not the simplicity of the model that was the problem, but the omission of explicit resource accounting.

The second example (Fig. 7) shows the time series of a parameterisation of equation (30) that looks right: we don’t include a phase space figure for this, as it is qualitatively the same as (in fact, almost identical to) Fig. 5. However, when we numerically check the lid condition for this parameter set, we find that it is not satisfied. Although the model can produce plausible solutions for the populations (as in Fig. 5) the lid condition indicates that for integrations that are initiated in the region near to where the lid condition is violated, in this example near $x_1 = 0.428$ and $x_2 = 0.268 = x_3$, negative nutrient masses will be predicted before the system re-enters the ecospace and returns to sensible answers (Fig. 7(d)).

While the model in Fig. 7 generally produces solutions that appear plausible, our analysis techniques reveal that such a model is flawed as it can also produce solutions, albeit perhaps only temporarily, that are physically unrealistic. Such unphysical behaviour might not be readily apparent in numerical explorations of the model, the common analysis tool for ecosystem models with three or more equations. The consequences of using a model with undiscovered basic flaws for applications such as to predict biological carbon dioxide exchange between the ocean and the atmosphere in a complicated, and often large, climate model, for example, could be profound.
6. Discussion. Heuristic Lotka-Volterra models, that represent interactions between populations with simple linear functions that produce linear or planar zero isolines or surfaces, arguably initiated the field of mathematical ecology in the 1920s, and have provided the basis for much of the ecology theory we have today. Competition, predation and mutualism are considered the tripod of population interactions upon which ecological analysis of communities rests [3, 13]. Linear per capita growth functions have been especially successful in establishing a solid theoretical basis for competition and predation interactions, but have not provided a similarly useful theory for mutualist interactions, in particular obligate mutualism. Cropp and Norbury [7] showed that LVCN models could represent competition, predation, mixotrophy and facultative mutualism seamlessly in simple models with two populations. However, it appears that the representation of obligate mutualism in models may require
curved isoclines, as suggested by Holland and DeAngelis [13], and we have taken this approach.

We consider a closed system for the cycling limiting nutrient in the food web, which is as usual open to flows of energy and many other materials; then each population has explicit finite resources within the food web. These assumptions allow obligate mutualism to be included in a single synthesising theoretical framework that unites the other population interactions when we treat obliging populations as catalysts. This extended LVCN framework can then represent all population interactions from competition between autotrophs, through various forms of mixotrophy and facultative mutualism, through predation where the predators occupy a new trophic level, and then to obligate mutualism between heterotrophs. This framework identifies near-smooth transitions between what were previously perceived to be distinct, unrelated population interactions, and allows adaptation, represented by single-parameter variations, to take populations from one interaction extreme to any other, all the time maintaining stable coexistence [7].

Obligate mutualism systems are continuously and stably related to facultative mutualist systems for both autotroph and heterotroph populations. This uses models of obligate mutualism that are relatively simple in both mathematical analysis and ecological interpretation. While we have focused here on simple generic models for their heuristic value, in particular for their teaching efficacy, the (extended) CN framework also provides a bridge between theoretical and applied models. Even complex CN models are amenable to a certain amount of mathematical analysis and suggest appropriate ways to measure real systems in terms of a common currency, the limiting nutrient. They are useful for undergraduate and postgraduate teaching in mathematical ecology and biology, for comparison with experimental outcomes and data, and for the general theoretical understanding of mutualism between interacting
populations. Further analysis of the pollination model’s results suggest systems with small obligation saturation effects, and partial or smaller shares of the total cycling nutrient for the pollinators, appear to create effective mutualist niches for these populations to stably exist in larger ecosystems. The CN framework effectively resolves the issues that were encountered by earlier efforts to use Lotka-Volterra models to understand obligate mutualism between heterotrophs, by considering the role of mutualism for the beneficiary population. This suggests that interesting insights into the reasons for the ubiquity of mutualist population interactions in the natural world might be obtained by considering how model populations respond to simulated evolutionary pressures. Such questions provide an avenue for the further development and application of these simple models.

7. Acknowledgements. The authors thank two anonymous reviewers: their thoughtful and constructive comments substantially improved this manuscript.


Table 1: Parameter values used to draw the vector fields in Figs. 3 and 4.

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<th>Value</th>
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<td>3(a)</td>
<td>r₁, r₂, ϵ₂, m₁, m₂, a₁₁, a₁₂, a₂₁, a₂₂</td>
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<td>3(c)</td>
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<td>3(d)</td>
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<td>4(a)</td>
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Table 2: Parameter values used to draw the vector fields in Figs. 5, 6 and 7.

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REFERENCES