

Linking Obligate Mutualism Models in an Extended Consumer-Resource Framework

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Keywords: Obligate mutualism;
Facultative mutualism;
Extended Consumer-resource;
Allee effect;
Limits to mutualism benefits;

Highlights: We propose an Extended Consumer-resource (ECR) framework
We note many models have similar vector fields and hence properties
The ECR model can transition from facultative to obligate mutualism and
between systems with and without Allee effects
The ECR framework identifies limits to mutualist benefits

Abstract

A simple model of obligate mutualist populations is presented in an extended consumer-resource (ECR) framework to resolve some of the deficiencies of traditional models. Varying parameters representing the costs of providing a mutualist benefit allows the model to smoothly and stably transition between many existing models of obligate mutualism. Varying density-independent mortality parameters allows us to include or exclude Allee effects, while varying an obligation parameter allows us to smoothly transition between facultative and obligate mutualism. Explicit and exact accounting of mutualism benefits, measured in terms of a finite total amount of cycling limiting resource, is shown to lead to population models that bridge between apparently incompatible models of obligate mutualism. This brings models of obligate mutualism into the Conservative Normal theoretical framework alongside models of competition, mixotrophy and predation.

1. Introduction

Mutualist interactions are thought to be ubiquitous, spanning all levels of biological organisation, and involving most species on Earth (Bronstein 2015c). However, in contrast to population interactions such as competition and predation, a succinct theoretical explanation of obligate mutualism at the population level has proved elusive. We use a heuristic model that represents obligation, mutualist benefits and mutualist costs in an Extended Consumer-Resource (ECR) framework to reveal that two quite different contemporary models of obligate mutualism are in fact extrema of a continuous spectrum of models. We show that this spectrum may be smoothly and simply transitioned by simple and intuitive cost parameter variations. By varying the obligation parameters, these systems can also change from facultative to obligate mutualists; the model may further transition between systems with and without Allee effects by variation of density-dependent and density-independent mortality parameters.

Obligate mutualism is a beneficial interaction between populations where in unidirectional obligate mutualism a population requires the presence of another to survive, and in bidirectional obligate mutualism neither population can survive in the absence of the other (Holland and DeAngelis 2010). Mutualist interactions may be central to the diversity of ecosystems (Gross 2008) and interactions such as pollination provide vital services to agriculture (Potts et al. 2010). Despite the importance and wide-spread occurrence of mutualism, the development of a population-level theory of mutualism has lagged behind that of other population interactions (May 1982, Ringel et al. 1996, Assaneo et al. 2013, Holland 2015). In contrast to obligate mutualism, competition and predation interactions are usefully modelled with Lotka-Volterra

equations (Lotka 1925, Volterra 1926) that despite their limitations provide useful heuristics to understand the basics of those interactions (May 1982, Pastor 2008), Lotka-Volterra models of obligate mutualism do not provide realistic answers (May 1981, Murray 2001).

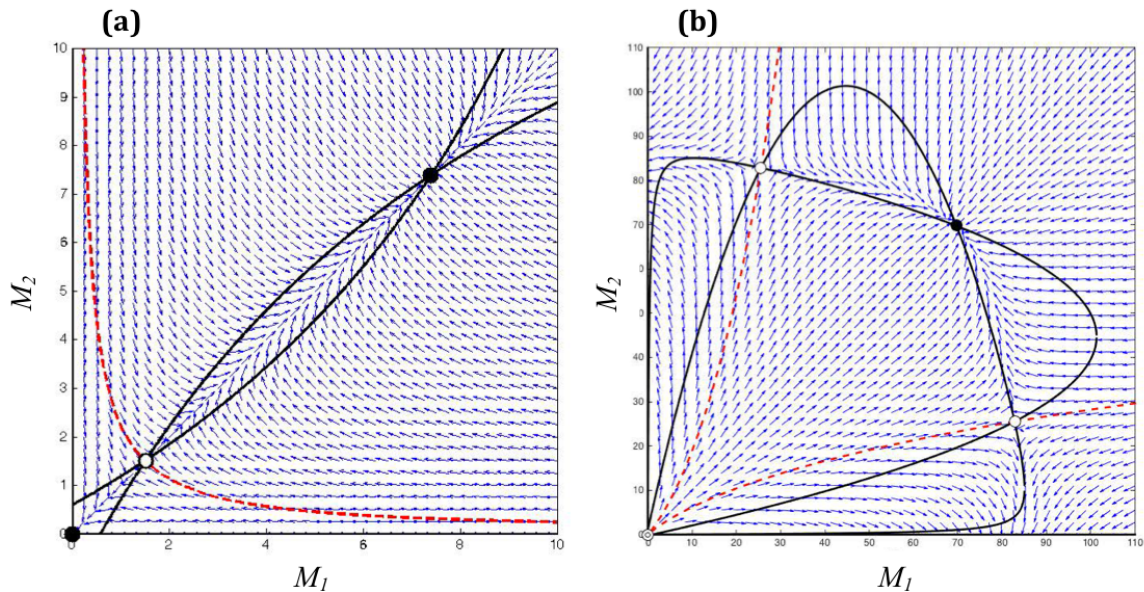


Figure 1. (a) The standard model: the vector field common to most models of obligate mutualism. (b) The HD2010 model: the vector field for the consumer-resource obligate mutualism model of Holland and DeAngelis (2010). The blue arrows in (a) and (b) show the vector fields, the solid black lines are the zero isoclines, and the dashed red lines are separatrices (see text for explanations).

Filled (open) circles show stable (unstable) equilibrium points.

The Lotka-Volterra equations were soon abandoned in the search for a theoretical explanation for mutualism, primarily it seems because they could not produce useful explanations for mutualism at the population level (Holland 2015), see also Murray (2001, p99); Loreau (2010, p80) suggests this may be because they ignored mass-

balance constraints. Instead, the “standard” model of mutualism (see Figure 1(a)) has been investigated by numerous authors (for example, May 1976, Case 2000, Kot 2001, Kang et al. 2011, Johnson and Amarasekare 2013). The only major model with apparently distinctly different ecological and dynamical properties to appear is the recent mutualism model HD2010 (Holland and DeAngelis 2009, 2010) (Figure 1(b)). This model emphasises the costs of providing mutualist benefits in a consumer-resource framework that dates back to MacArthur (1970). Here we describe an extension to the consumer-resource framework (ECR) that not only links the “standard model” to the HD2010 model of Holland and DeAngelis, but also smoothly bridges examples of facultative and obligate mutualism.

Using our extended model, we demonstrate that obligate mutualism only occurs in certain parameter regimes, why there is sometimes an Allee effect, how obligate mutualism models can arise from facultative mutualism, and the limits to mutualism. Both symmetric and asymmetric perturbations of parameters lead to transitions through various Allee and non-Allee families of stable coexistence solutions (Allee and Bowen 1932) depending on whether density-independent mortality is included

1.1 Outline of the Paper

Key general questions underpinning practical studies include to what extent are mutualist solutions robust to parameter variations (Rohr et al. 2014), and how do obligate mutualism interactions evolve (Aanen and Hoekstra 2007). We use an example model in the ECR framework to show how obligate mutualist populations can coexist, how mutualism systems can transition between various states (including from the standard model to the HD2010 model and from facultative to obligate mutualism), what

causes an Allee effect in the models, how robust the mutualism solutions are to parameter variations, and what identifies limits to obligate mutualism.

The example ECR model (although it is the framework, based on the Conservative Normal (CN) framework of (Cropp and Norbury 2015), rather than the particular model that is key to the results) smoothly and stably transitions through a spectrum of mutualism interactions, of which the standard model of Figure 1(a) and the HD2010 model of Figure 1(b) represent the extremities. The simplest examples of these transitions use interacting autotroph populations as these may be shown by two-dimensional figures. The ECR model is solved numerically using generic parameter values as it is too complicated for informative mathematical analysis. However, mathematical analysis of simpler models can provide useful heuristics for these obligate mutualism interactions.

Section 2 summarises the attributes of population interactions that involve obligate mutualism and introduce the example model in the extended consumer-resource (ECR) framework. Section 3 shows that the ECR model has mutualism solutions that smoothly and stably transition between the standard and the HD2010 models; between facultative and obligate; and from Allee to non-Allee by varying key parameters, and parameter ranges for families of stable obligate mutualist coexistence are discussed. Section 4 discusses the implications of the simple model in the context of the general ECR framework. The remainder of §1 explains the rationale for the ECR approach – some readers may prefer to skip to §2 where the model is detailed.

1.2 Early Mutualism Models: Obligation and Benefit

The historic failure of the Lotka-Volterra model to sensibly represent mutualism initially led to the introduction of density-dependent terms to describe the mutualism interactions. Models of obligate mutualism using this approach to explain many different practical examples of mutualism interactions include, for example, the theoretical models of May (1976), Dean (1983), Wright (1989), Bazykin (1998), Case (2000), and Graves et al. (2006), and the applied models of Neuhauser and Fargione (2004), plants, herbivores and ants (Morales et al. 2007), leaf-cutter ants and fungus (Kang et al. 2011), intra-guild consumers (Assaneo et al. 2013), and plants and animals (Johnson and Amarasekare 2013). However, such solutions have not generally been accepted as providing a generic explanation of population interactions involving obligate mutualism. Evidence of this may be found in many general texts in ecology, that discuss competition and predation interactions between populations with reference to mathematical models and graphs to explicate the theory, but present mutualism by solely discussing examples from nature (for example, Ricklefs and Relyea 2014). Some of the more mathematically-inclined ecology texts discuss the failings of the Lotka-Volterra model (for example, Bazykin 1998, Murray 2001, Pastor 2008), and a few texts aimed at mathematical ecologists consider the nonlinear standard model in some detail (for example, Kot 2001). Notwithstanding these, as a general rule the treatment of mutualism, and obligate mutualism in particular, remains cursory compared to the treatment of competition and predation in ecology textbooks.

Early studies of dynamical systems models of mutualism concluded that such interactions were destabilising (May 1973) - a recent theoretical analysis of random dynamical systems that include multiple types of population interactions suggests that

mutualism is the least likely of all population interactions to be stable and therefore mutualisms are unlikely to exist in large complex ecological networks (Allesina and Tang 2012). However, such results appear equivocal (Rohr et al. 2014), and contrary to the apparent widespread appearance of mutualist interactions in natural systems (Boucher 1985, Bronstein 2015a). Theoretical studies that support the commonly-observed mutualist behaviour in the natural world include, for instance, Umbanhowar and McCann (2005). These authors conclude from a modelling study of two competing plants and mycorrhizal fungi that the presence of a mutualist population can mediate competitive exclusion. Further, Assaneo et al. (2013) note that stable coexistence between two intra-guild mutualists is observed over a much larger parameter range than the equivalent system without mutualism. Similarly, Gross (2008) concludes from studies of defensively mutualist plant populations competing for shared resources that mutualisms can promote biodiversity. More generally, Hoeksema and Bruna (2000) observe that mutualism interactions often do not involve one organism consuming another (so benefits are more implicitly defined), and that the study of food webs using dynamical systems approaches may not be the most appropriate framework for studying mutualism. This theme of distinguishing direct transfers of resources from indirect transfers is a key feature of the ECR approach.

1.3 Recent Mutualism Models: Including Costs

Obligate mutualism is now widely believed to involve three distinct processes, that of obligation, benefits and costs, and theoretical models of obligate mutualism may be classified into three groups based on the mutualism processes they emphasise: first, (a) those that emphasise the obligation on another population to be able to grow, for example, the models of Dean (1983), Graves et al. (2006) and Gross (2008); second (b)

those that emphasise the benefits obtained by the mutualist population, for example, the models discussed by May (1976), Wright (1989) and Case (2000); and third (c) those that consider the costs of providing a mutualist benefit to a partner in addition to the benefits obtained from them (Holland and DeAngelis 2001, 2009, 2010, Holland 2015).

The approaches (a, b) that only include obligation or benefits produce the same generic model and solutions, the “standard model” which is succinctly described by the phase plane diagram in Figure 1(a). Despite representing very different scenarios of mutualism in the natural world, and despite the authors in (a) and (b) above making very different ecological process assumptions, and having very different equations, these models all have qualitatively the same phase planes, and consequently are effectively the same model.

The complete solutions for any particular parameter set for the usual differential equation models of two interacting populations may be visualised in phase plane diagrams such as Figure 1 that show the zero isoclines, equilibrium points and vector field of the model. Such diagrams form the basis of many theoretical discussions of obligate mutualism, for example Bazykin (1998), Case (2000), Kot (2001), Pastor (2008), Holland and DeAngelis (2009, 2010), and Holland (2015). The zero isoclines show locations in the phase plane where an individual population does not change in time, and the intersections of the isoclines define equilibrium points where the system does not change. Note that in most ecosystem models the axes are also zero isoclines, and hence equilibrium points at the origin are common. Equilibrium points are either stable (coloured black in Figure 1), in which case the system returns to them after a small perturbation, or unstable (coloured white in Figure 1), in which case the system

moves away from them after some, if not all, small perturbations. The vector fields in Figure 1 show how the systems evolve in time from any point (i.e. any initial population sizes) in the phase space, with the separatrices (the red dashed lines) denoting boundaries that trajectories cannot cross; for example, if a trajectory is initiated between the origin and the unstable equilibrium point in Figure 1(a) it cannot cross the red dashed line. These initial conditions lead to both populations going extinct as they never reach the stable equilibrium point where both populations coexist. This is an example of an Allee effect (Allee and Bowen 1932).

The standard model phase plane of Figure 1(a) is common to most theoretical and many applied models of obligate mutualism, see §1.2 references. The only model of obligate mutualism that appears to have a substantially different phase plane to Figure 1(a) is the consumer-resource model of Holland and DeAngelis (2010), which we refer to as HD2010, shown in Figure 1(b). This model explicitly includes the costs associated with providing mutualist benefits (Holland et al. 2002, Holland and DeAngelis 2010, Holland 2015), and it is high values of these costs that wrap the smooth isoclines of the standard model into a “Turk’s head knot” of interlacing curves and represents one of the few advances on the standard model. See Holland and DeAngelis (2010) for a description of over 20 ecological examples of both bidirectional and unidirectional mutualism and Holland et al. (2002), Holland et al. (2005), Holland and DeAngelis (2009, 2010), and Holland (2015) for further background to this approach.

The separatrices in Figure 1 reveal a further difference between the models: the standard model has an Allee effect while the HD2010 model does not in the usual sense. Allee effects are commonly observed in models of mutualisms, in particular those

involving plants (Morales et al. 2007, Lee and Inouye 2010, Lutscher and Iljon 2013). The Allee effect implies minimum population sizes below which the populations go extinct. The separatrix in Figure 1(a) shows that coexistence of obligate mutualist populations generally requires both populations to be present in “sufficient” quantities for stable coexistence to be possible. However, it also suggests that coexistence is possible if one population has a very high abundance associated with only a very few of its obligate mutualist population, perhaps a somewhat counterintuitive attribute.

1.4 Extended Consumer-Resource Modelling

The HD2010 model applies a consumer-resource approach to mutualism interactions (Jones et al. 2012). Consumer-resource approaches have a long history in ecology, commencing with the seminal paper of MacArthur (1970) that modified the Lotka-Volterra competition equations to explicitly represent resources (Chesson 1990). This to some extent alleviated the problem of unbounded solutions of the Lotka-Volterra equations noted by Kolmogorov (1936) for the predation version, and was consistent with the view of Bormann and Likens (1967) that population interactions had to be considered in the context of the limitations of their environment in order to be understandable. DeAngelis (1992, p xi) similarly suggested that understanding the interplay between the dynamics of food webs and the cycling of nutrients is pivotal to understanding ecosystems and synthesising the sub-disciplines of ecology, an approach also advocated by Loreau (2010).

The consumer-resource view of population interactions remains current, especially in the context of mutualism (Johnson 2015), and underpins the resource-based approach to modelling ecosystems (Cropp and Norbury 2015) that is used here. Both consumers

and resources are modelled explicitly, recognizing that limiting nutrients are tightly cycled within ecosystems (Loreau 2012), and that the cycling of resources within ecosystems in general exceeds inputs and outputs by at least an order of magnitude (Vitousek and Matson 2012). This approach formalises that ecosystem perspectives, in which the flows and limited availability of resources are central, is essential to understanding population interactions (Johnson 2015). This builds on the recent theoretical work of Holland and DeAngelis (2009, 2010) and applied modelling examples such as Kang et al. (2011).

The example ECR model that is considered here includes mutualist benefits and costs, similarly to Holland and DeAngelis (2010), and obligated growth, similarly to Dean (1983) and Graves et al. (2006), in a fully explicit consumer-resource framework. Competition for a finite limiting resource is included, and both density-dependent and density-independent mortality reflect self-limitation of populations and losses due to higher predation by populations that are not explicitly represented in the model. The model is able to bridge, smoothly and stably, the widely differing models of mutualism, including facultative and obligate forms.

2. The Extended Consumer-Resource (ECR) Obligate Mutualism Model

2.1. The Mutualist Food Web

The ECR model represents an extension of both the consumer-resource framework of MacArthur (1970) to include explicit modelling of the resource pool, and the approach of Holland and DeAngelis (2001, 2009, 2010) to include costs as well as the obligations

and benefits of obligate mutualism. A schematic of the ECR food web for two obligate mutualist populations, M_1 and M_2 , and their resource pool R is shown in Figure 2(a). In order to be consistent with the standard and HD2010 approaches, and to aid the presentation and interpretation of results, the multiple resource approach of Jones et al. (2012) is simplified, and a single resource for which the mutualists compete is modelled. Further, the mutualist benefits provided by one population to the other are not labelled as different resources. Note that the results of the analysis do not depend on these assumptions, and the ECR provides a generic framework for looking at many different population interactions, including competition, predation, mixotrophy and different forms of mutualism.

The abundances of the populations and the resource pool are measured in terms of the percentage of the total resource available in the environment that they contain or control (Franks 2002). The limiting resource may be food, nutrients, or similar, and is ‘conserved’, that is, for example, limiting nutrients that are lost by a population due to excretion or mortality are re-mineralised and recycled, and reappear in the resource pool (Vitousek and Matson 2012). For ease of discussion, the resource is food, and is measured in a common currency – in marine systems, for example, nitrogen is often used. This is a standard practice in ecosystem modelling, where the key limiting nutrient in the environment may be used as the currency (Franks 2002, Loreau 2010, Cropp and Norbury 2015). Alternatively, the resource might be shelter, in which case the environment only provides a finite amount of shelter, and shelter abandoned by one population becomes available to other populations, and this resource is also ‘conserved’ and ‘recycled’ (Holland and DeAngelis 2010).

Figure 2(a) shows a simple food web for two obligate mutualist populations and the limiting resource available in their environment. Note that exchanges of resources between the modelled system and the external environment are not shown in Fig. 2(a). This is because ecological systems recycle their limiting nutrients very tightly (usually greater than 90% of limiting nutrient is recycled (Vitousek and Matson 2012)) – the idealised case where 100% is recycled is considered here. Direct flows of limiting resource due to the growth and mortality of the populations are shown in Figure 2(a) by solid arrows between the resource pool and the populations, while the dotted arrows show indirect flows of limiting resource that result from mutualist interactions, which involve both benefits and costs. The increased fitness of a population that results from receiving a mutualist benefit is evidenced by the population increasing its share of overall limiting resources, and is represented in the diagram by an indirect transfer of limiting resource from the resource pool to the population. Similarly, the reduction in fitness of a population due to the cost of providing a mutualist benefit is evidenced by a reduction in the population's share of overall resources, and is represented in the diagram by an indirect transfer of limiting resource from the population to the resource pool.

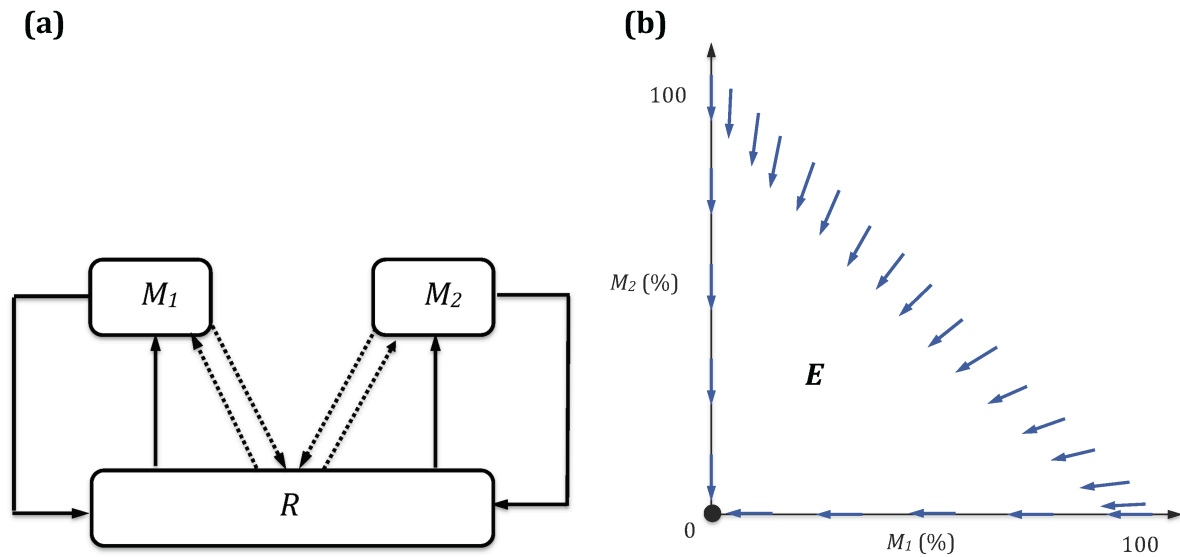


Figure 2. (a) Food web diagram showing flows of limiting resource between the non-living resource pool R and the obligate mutualist populations M_1 and M_2 . Solid arrows show flows due to direct interactions, and the dotted arrows show movement of resource due to mutualist interactions (benefits and costs). (b) The ecologically feasible solution space E showing the boundary of the vector field (blue arrows) controlling population dynamics for two obligate mutualist populations: the consequences of finite total amounts of limiting resources are the inward pointing arrows on the diagonal where $M_1 + M_2 = 100\%$, and the consequences of obligation are the arrows on the axes.

Figure 2(b) shows the boundary behaviour of a generic vector field for two obligate mutualist populations M_1 and M_2 (their resource pool R is implicit in the diagram). The vector field of a model describes all the population behaviours possible for the model, but in Figure 2(b) we show only two key elements of the vector field – the consequences of finite resources and the implications of obligation. The amount of resource in each living population M_1 and M_2 is measured as a percentage of the total cycling resource, as is the amount of resource in the nonliving resource pool R . When

337 the living populations have utilised all of the free resource in the environment (i.e.
 338 $M_1 + M_2 = 100\%$) then no non-living nutrient is left in the resource pool ($R = 0\%$), and
 339 no more limiting resource is available. It is unrealistic for these ecological models to
 340 have negative resources, so when $M_1 + M_2 = 100\%$ (i.e. along the diagonal from
 341 $M_1 = 100\%$, $M_2 = 0\%$ to $M_1 = 0\%$, $M_2 = 100\%$ in E , the space of feasible population states
 342 for M_1 and M_2) the combined population size can no longer increase. The amount of
 343 benefits of mutualism available to the populations when the resource pool is empty ($R =$
 344 0%), shown by the dotted arrows from R to M_1 and M_2 in Figure 2(a), are therefore
 345 limited to be less than or equal to the inflows to the resource pool. This ensures that the
 346 populations cannot “borrow” resources from their environment, and that the non-living
 347 resources can never be negative (an unrealistic state). As the living populations must
 348 reduce when there are no resources available to them, the vector field must point
 349 inwards everywhere along the diagonal whenever $M_1 + M_2 = 100\%$ (and $R = 0\%$), shown
 350 by the blue arrows in Fig. 2(b).

351

352 Obligation on another population means that each obligate population must die when
 353 the other population is zero. This means that the vectors along the obligated
 354 population’s axis must point towards the origin, an attribute shared by obligate
 355 mutualists and predators. This implies that the origin of the ecospace E , where both
 356 populations are extinct, must either be locally stable if the population has density-
 357 independent mortality, or neutrally stable (under linear stability theory) if it does not.
 358 An obligate mutualist system with a stable origin then usually has an Allee effect (Allee
 359 and Bowen 1932) where small populations go extinct but obligate mutualist populations
 360 coexist if they are initially present in sufficient amounts (see for example, Case (2000),

Kot (2001)). However, an obligate mutualist system with a linearly neutrally stable origin can rely on density-dependent growth terms to create outward-pointing vectors near the origin, and these allow population growth from small initial levels, and then coexistence (for example, Holland and DeAngelis 2010). Note that the vector fields of both the standard model and HD2010 (Figure 1(a, b)) are consistent with the properties of the generic vector field shown in Figure 2(b).

2.2. The Example ECR Model

The ECR model has two interacting obligate mutualist populations, M_1 and M_2 , and their resource pool R . We measure the populations in terms of the percentage of the total limiting resource cycling in the ecosystem that each population contains. We also explicitly model the percentage of the total limiting resource that is not in a living population – this is the resource pool R . For simplicity, we assume that the limiting resource is the cycling, available nitrogen, and the size of each population or the resource pool is measured in terms of the percentage of the total, finite and fixed, amount of nitrogen in the model domain (a closed ecosystem). The interactions between the populations and the resource pool are then expressed as movements of nitrogen. Each population has growth, interaction and mortality terms:

$$\begin{aligned} \frac{dM_1}{dt} &= M_1 \left(\mu_1 \left(\frac{M_2}{M_2 + \xi_2} \right) \left(\frac{R}{R + \kappa_1} \right) + \omega_1 \left(\frac{M_2}{M_2 + \zeta_2} \right) - \chi_1 \left(\frac{M_2}{M_1 + \varepsilon_1} \right) - \sigma_1 M_1 - \hat{\sigma}_1 \right) \\ \frac{dM_2}{dt} &= M_2 \left(\mu_2 \left(\frac{M_1}{M_1 + \xi_1} \right) \left(\frac{R}{R + \kappa_2} \right) + \omega_2 \left(\frac{M_1}{M_1 + \zeta_1} \right) - \chi_2 \left(\frac{M_1}{M_2 + \varepsilon_2} \right) - \sigma_2 M_2 - \hat{\sigma}_2 \right) \end{aligned} \quad (1)$$

In common with many other modelling approaches, including HD2010, we assume the growth, benefit and cost terms are saturating functions. The growth terms (the first terms in the two equations) have a maximum ‘per capita’ growth rate (μ_i), include a

dependence on the availability of resources ($\frac{R}{R+\kappa_i}$) and an obligation on the presence of the other population ($\frac{M_j}{M_j+\xi_i}$), where $i, j=1,2$ and $i \neq j$. The obligation terms function analogously to the saturating terms used by Dean (1983), Graves et al. (2006), Thompson et al. (2006), and Gross (2008). (We note that despite their similar functional forms and effects, these authors provide very different rationales for their use.) Note when $\xi_1 = 0 = \xi_2$ the growth of M_1 is not obligated on M_2 and *vice versa*: the mutualists are facultative. The terms follow the arguments of Dean (1983) and Graves et al. (2006) that obligation terms should saturate, but also act as a bridge from facultative to obligate mutualism (see Figure 4).

The second and third terms in equation (1) represent the mutualist benefits received by population M_i from population M_j ($\omega_i \left(\frac{M_j}{M_j+\xi_i} \right)$) and the costs to population M_i of providing mutualist benefits to population M_j ($\chi_i \left(\frac{M_j}{M_i+\zeta_i} \right)$). In this case we have used terms identical to those of Holland and DeAngelis (2010) which we note saturate respectively on the “giving” and “receiving” populations. Interested readers are referred to the detailed explanation of Holland and DeAngelis (2010) for the rationale for these forms. However, a key difference in the ECR approach is that when the resource pool is empty ($R = 0$) the mutualist benefit flows are controlled, as discussed for equation (2), so that benefit flows cannot exceed the inflows to the resource pool. (For a detailed explanation of the rationale behind the CN approach see Cropp and Norbury (2015).) Both density-dependent $\sigma_i M_i$ (Graves et al. 2006, Kang et al. 2011) and density-

independent $\hat{\sigma}_i$ (Wright 1989, Bazykin 1998) mortality terms are included in the model equations for completeness.

The key difference between the ECR model and previous consumer-resource models of obligate mutualism is that a finite total amount of limiting resource that cycles in the food web is imposed, and a resource pool R is explicitly modelled. Equation (2) is used to monitor the amount of resource available to fuel the growth of the mutualist populations by accounting for all inputs and outputs of the resource pool:

$$\begin{aligned} \frac{dR}{dt} = & \hat{\sigma}_1 M_1 + \hat{\sigma}_2 M_2 + \sigma_1 M_1^2 + \sigma_2 M_2^2 + \chi_1 \left(\frac{M_2}{M_1 + \varepsilon_1} \right) M_1 + \chi_2 \left(\frac{M_1}{M_2 + \varepsilon_2} \right) M_2 \\ & - \mu_1 \left(\frac{M_2}{M_2 + \xi_2} \right) \left(\frac{R}{R + \kappa_1} \right) M_1 - \mu_2 \left(\frac{M_1}{M_1 + \xi_1} \right) \left(\frac{R}{R + \kappa_2} \right) M_2 \\ & - \omega_1 \left(\frac{M_2}{M_2 + \zeta_2} \right) M_1 - \omega_2 \left(\frac{M_1}{M_1 + \zeta_1} \right) M_2 \end{aligned} \quad (2)$$

Here the flows into the resource pool due to mortality and the cost of providing mutualist benefits are included. These positive contributions to the resource pool may reflect direct flows, in the case of mortality, or indirect flows that reflect a reduction in fitness of a population that provides an opportunity for another population to increase its fitness and hence indirectly draw additional resource from the pool. The negative terms in equation (2) also include direct uptake of resources by the populations to fuel growth.

Equation (2) is an important addition to most of the usual models of mutualism, as we assume that the receipt of a mutualist benefit improves the fitness of the recipient population, and that improved fitness is represented in models such as (1), that are written in a currency of limiting resource, as the population increasing its share of the

total resource. The resource that represents this increased fitness in these heuristic models does not come from the benefactor population (which determines the quantum of benefaction) but from the resource pool. Similarly, costs incurred by a population in providing a mutualist benefit to another population reduce its fitness, which is represented by a reduction in the share of the total resource that the population sequesters. This reduction, the quantum of which may be related to or determined by the recipient population, occurs via a loss of resource to the resource pool. These exchanges between the populations and the resource pool may represent any form of mutualism interaction (transport, protection, pollination, etc. (Holland and DeAngelis 2009, 2010, Vannette and Hunter 2011, Jones et al. 2012, Courchamp et al. 2015) and see Bronstein (2015b) for a review) and point to the central role of the resource pool and explicit resource accounting in understanding obligate (and facultative) mutualism.

Equations (1) and (2) describe a generic model that may represent pure competition between autotrophs ($\xi_1 = 0 = \xi_2, \omega_1 = 0 = \omega_2$ and $\chi_1 = 0 = \chi_2$), facultative mutualism ($\xi_1 = 0 = \xi_2, \omega_1 > 0 < \omega_2$ and $\chi_1 > 0 < \chi_2$), obligate mutualism ($\xi_1 > 0 < \xi_2, \omega_1 > 0 < \omega_2$ and $\chi_1 > 0 < \chi_2$), or any combination of these. Mutualism and competition are commonly considered in such models (Lee and Inouye 2010, Johnson and Amarasekare 2013). Full definitions of parameters and the base set of parameter values used to draw the diagrams of the vector fields, etc. for the ECR model are provided in Table 1. Variations to the base parameter set values used to represent different interactions and to create each Figure are provided in the figure legends.

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Table 1. Parameter definitions and base values for the ECR model. ^{1,2}

Parameter	Definition	Value
μ_i	Maximum population growth rate	1.00
κ_i	Half-saturation constant for resource-limited population growth	2.00
ξ_i	Half-saturation constant for obligated population growth	0.10
ω_i	Maximum mutualism benefit	0.50
ζ_i	Half-saturation constant for mutualism benefit	0.10
χ_i	Maximum mutualism cost	0.10
ε_i	Half-saturation constant for mutualism cost	0.10
σ_i	Density-dependent mortality rate	0.50
$\hat{\sigma}_i$	Density-independent mortality rate	0.15

450 ¹ As the dynamics of both populations are described by analogous equations, in
 451 keeping with standard practice we show symmetric solutions; the definitions and
 452 values in this table apply to both populations and are not repeated.

453 **2. The parameter set in the table complies with the requirements for valid**
 454 **ecosystem models (Cropp and Norbury 2015) and the requirement for mutualism**
 455 **models that $dR/dt \geq 0$ when $R = 0$. These conditions are rechecked whenever the**
 456 **values used to create the different vector fields of Figures 4-7 below are varied.**

457

458 The parameter values in Table 1 produce the vector field for the ECR model shown in
 459 Figure 3. This has elements of both the standard model, with its Allee effect, the
 460 arrangement of equilibrium points and the classic Allee separatrices; and HD2010 in the
 461 shape and arrangement of the zero isoclines. The arrangement of isoclines is also not

dissimilar to those described by Lutscher and Iljon (2013) for Allee effects in plant-pollinator systems.

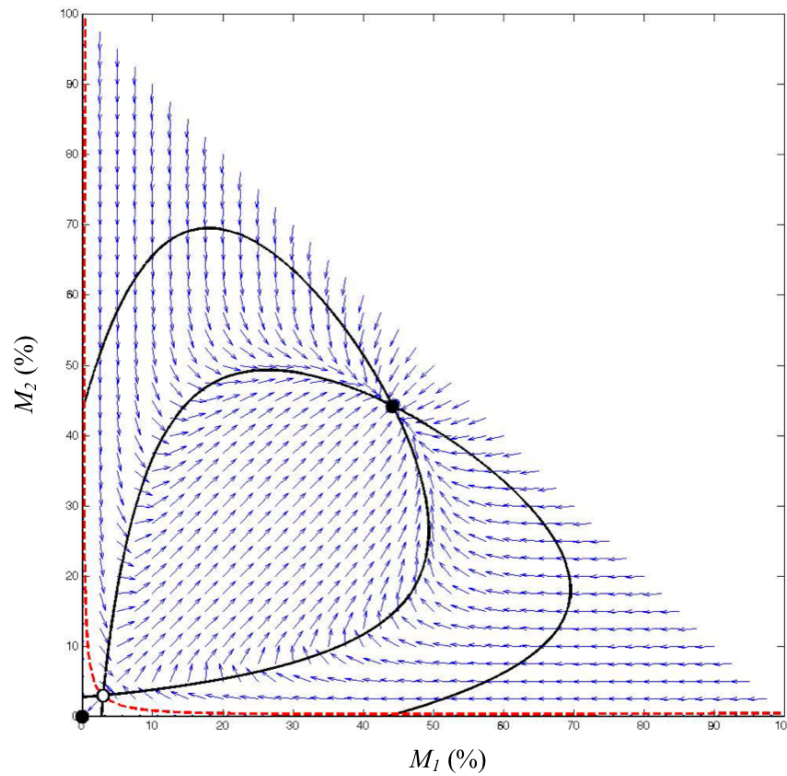


Figure 3. The vector field, zero isoclines, equilibrium points and separatrices of the ECR model with the parameter values listed in Table 1. This parameter set describes an intermediate model with properties of both the standard and HD2010 models. Details as for Figure 1 except that these populations, and the populations in all further figures are measured in terms of the percentage of the total nutrient in the system that they have sequestered.

Note that the phase plane shown in Figure 3 is not dependent on using saturating terms in the ECR model equations (1) and (2) - similar phase plane solutions can result if non-saturating functions are used. This extended model can explain why obligate mutualism

only occurs in certain parameter regimes, why there is sometimes an Allee effect, how obligate mutualism models can arise from facultative mutualism, and identify the limits to mutualism. Both symmetric and asymmetric perturbations of parameters lead to transitions through various Allee and non-Allee families of stable coexistence solutions, as are shown in the next sections, and in particular in Figure 4.

Finally, note that only mutualism interactions that involve indirect transfers of mass, where a mutualist population facilitates the acquisition of an increased share of the total mass by the beneficiary population rather than directly providing it, are considered in the model. Such transfers may occur through one population improving the fitness of the other, for example in the common goby – shrimp mutualism, where the shrimp provides signals to the goby that there are no predators present and it may leave the burrow to forage for food (Thompson et al. 2006, Lyons 2013). Such interactions form the foundation of many examples of the standard model and are the sole mutualism interactions modelled in both the standard model and HD2010. Other mutualisms, such as pollination, do involve direct transfers of mass between the interacting mutualist populations; however, these are not considered here as in these simple, heuristic models they are analogous to predator-prey interactions, that are well-understood

3. Results

Results from the ECR model reveal that the standard and HD2010 views of obligate mutualism, that essentially differ in whether they explicitly include functions describing the costs to a population of providing mutualist benefits to another population, are actually extreme cases of assumptions of the costs of mutualism. In fact, the standard model and HD2010 may be bridged by a more general model that explicitly includes

both obligated growth and changes in population fitness associated with benefits obtained from and costs associated with mutualism interactions, in an extended consumer-resource (ECR) framework that recognises that resources are finite and must be accounted for explicitly in models of mutualist population interactions. This bridging is demonstrated by independently varying single parameters: the cost half-saturation parameter ε_i to transition from the standard model to HD2010; the obligation half-saturation parameter ξ_i to transition between facultative and obligate mutualism; and the density independent mortality parameter $\hat{\sigma}_i$ to transition between Allee and non-Allee solutions.

3.1. Transition from the Standard to the HD2010 Model

The vector fields of the standard and HD2010 models appear different (Figure 1) and, in particular, the separatrices that separate populations that can coexist from populations that go jointly extinct appear fundamentally different. However, Figure 3, showing the ECR model solution for its base parameter set (Table 1) suggests that the standard and HD2010 models may just be extreme cases of a general model of obligate mutualism. Figure 4 shows that this is indeed the case, where a single parameter, the half-saturation constant for the mutualist cost term ε_i , transitions from the standard model to the HD2010 model. This reflects the contention of Holland and DeAngelis (2010) that previous models had not appropriately considered the importance of the costs of providing mutualist benefits.

The ECR model produces a vector field, isoclines and separatrices very similar to the standard model when it has high values of ε_i (around 20 times the maximum population size, Figure 4(a)), reflecting that the ‘per capita’ costs to M_i of providing

mutualist benefits to M_j in this case are relatively low (approximately χ_i/ε_i , which is 0.005 in this case) and linearly scales with M_j . This is consistent with the standard view that mutualism costs were less important relative to mutualism benefits when explaining obligate mutualism, as most models that produce the standard vector field (Figure 1(a)) do not include the costs of providing mutualist benefits. In contrast, Holland and DeAngelis (2009, 2010) considered that such costs were fundamental to models of mutualism, and Figure 4(d) shows this. Here, the ECR model has a very low value of ε_i , approximately 1/2,000 of the maximum population size, reflecting that costs of providing mutualist benefits are relatively high and saturate at very low population sizes. In this case, the costs to M_i of providing mutualist benefits to M_j scale linearly with the ratio of the populations, $\chi_i\left(\frac{M_j}{M_i}\right)$. Figure 4(d) identifies coexistence of obligate mutualists in the region between the two separatrices where $\frac{M_j}{M_i} > \frac{1}{4}$, where in this example, the ‘per capita’ costs of obligate mutualism exceed 0.025. The boundary between coexistence and co-extinction in Figure 4(d) is then defined by a per capita cost of providing a mutualist benefit that is approximately five times that of the standard model in Figure 4(a).

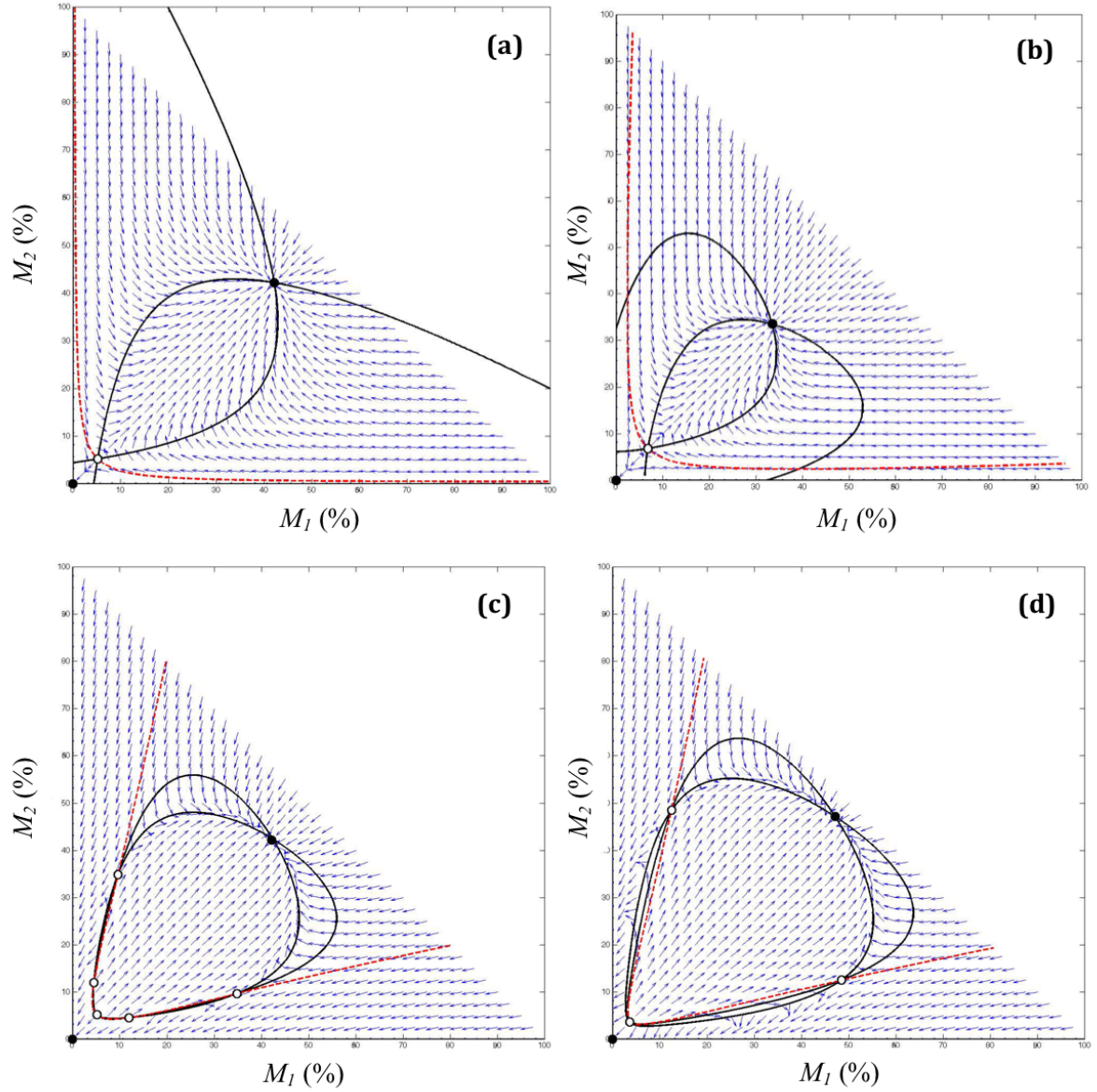


Figure 4. The four panels show the transition of the obligate mutualism vector fields of the ECR model from the standard model to the HD2010 model. All panels were drawn using the parameter values listed in Table 1 except density independent mortality was increased to show the Allee effect more clearly ($\hat{\sigma}_1 = 0.25 = \hat{\sigma}_2$). The transition between panels is achieved by varying a single parameter pair: $\varepsilon_1 = 20 = \varepsilon_2$ in (a) through $\varepsilon_1 = 0.05 = \varepsilon_2$ in (b), $\varepsilon_1 = 0.00075 = \varepsilon_2$ in (c) to $\varepsilon_1 = 0.0005 = \varepsilon_2$ in (d).

Reducing the values of the ε_i from the large values of the standard models to very small values transitions the model solutions smoothly from the standard picture (Figure 4(a)) to the HD2010 picture (Figure 4(d)). Large increases in the cost function are required to move the separatrices from the standard model towards the HD2010 form, with the ε_i reduced by a factor of 400 to transition from Figure 4(a) to 4(b). Although this change has had a relatively minor impact on the Allee effect and its separatrices it has had a major impact on the zero isoclines, bending them dramatically and approaching the Turk's head knot form of HD2010. A further reduction in ε_i by factor of 67 has a more noticeable effect on the separatrices, moving their outer regions further from the axes, and a subtler effect on the zero isoclines. These no longer intercept the axes, but have created the Turk's head knot, with multiple intersections and their unstable equilibrium points lying along the separatrices.

Figure 4 reveals that the transition between the standard and HD2010 models involves some complex changes near the origin, with equilibrium points appearing and disappearing in response to small changes in parameter values. The ECR model solution for relatively high costs of mutualism (Figure 4(d)) differs from that of HD2010 (Figure 1(b)) in that it has a stable equilibrium at the origin and an Allee effect, whereas the solution of Holland and DeAngelis (2010) does not have an Allee effect and has a neutrally stable origin. This does not imply a fundamental difference between the two models – the HD2010 model produces a stable origin and an Allee effect if r_1 and r_2 are negative. Further, the isoclines of the ECR model form a similar 'Turk's head knot' to those of Holland and DeAngelis, and the separatrices are fundamentally similar, suggesting that this model captures the essence of the Holland and DeAngelis (2010) model. In the next section, we consider the transition from solutions without an Allee

effect to solutions with by including density-independent mortalities, as this is the most straight-forward way of introducing the change. However, the important result that this figure demonstrates is that a smooth transition between the two models exists, and that the seemingly incompatible separatrices of the standard and HD2010 models are in fact consistent.

3.2. Transition from Facultative to Obligate Mutualism

The transition from facultative to obligate mutualism is demonstrated using the half-saturation constant for obligation ξ_i in equation (1). Two examples are shown: using the ECR model emulating the standard model (Figure 5); and using the ECR model in its intermediate form (Figure 6). The parameter set of Table 1 is used as the basis to draw both figures, but in Figure 5 set $\omega_1 = 5 = \omega_2$, $\zeta_1 = 5 = \zeta_2$, $\chi_1 = 4 = \chi_2$, and $\varepsilon_1 = 4 = \varepsilon_2$ to emulate the standard form.

Setting $\xi_1 = 0 = \xi_2$ produces facultative mutualism (Figure 5(a)), with each population's ability to exist independently of the other revealed by the existence of an unstable equilibrium point on its axis. Each of these points is stable if the other facultative mutualist population is absent. Increasing the half-saturation constants to positive values, for example $\xi_1 = 0.0001 = \xi_2$, causes these equilibrium points to immediately slide down their respective axes to the origin, making the populations obligate upon each other (Figure 5(b)). Note that very small values of ξ_1 and ξ_2 result in very little change to most of the vector field – although the disappearance of the equilibrium points on the axes is a fundamental change in the properties of the system on and near the axes, the effects of this change are not apparent in most of the ecospace (cf. Figure 5, (a) and (b)). The majority of the vector field is unaffected by this change, suggesting a

smooth transition from facultative to obligate mutualism is possible for most population starting values, even though population growth becomes dependent on very small numbers of an obliging population. As the obligated population's growth requires increasing numbers of the obliging population (i.e. ξ_1 and ξ_2 increase) its zero isoclines become more smoothly curved and affect the dynamics of the populations throughout the ecospace (cf. Figure 5, (c) and (d)).

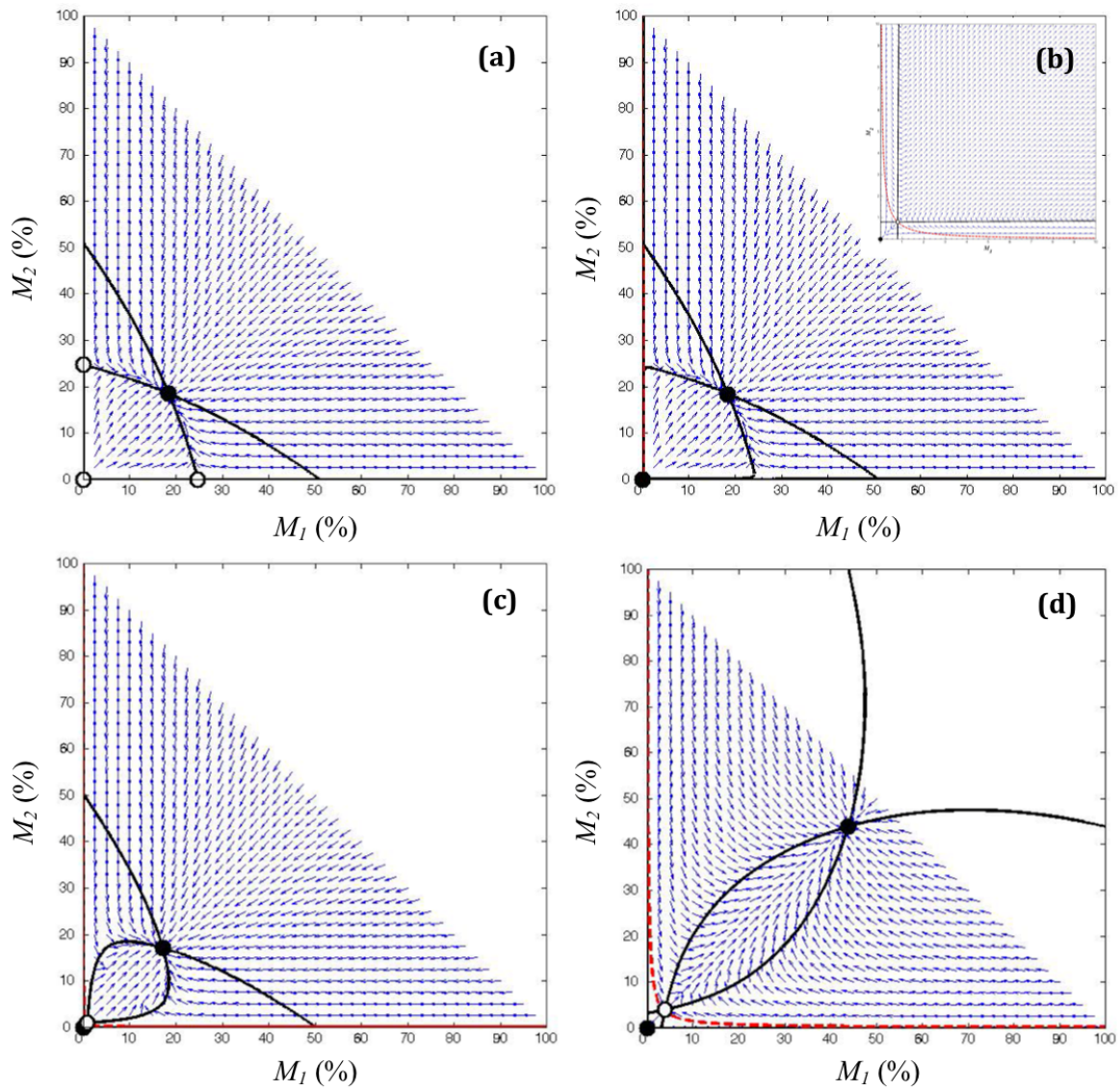


Figure 5. The transition from facultative mutualism to obligate mutualism using the ECR model emulating the standard model solution. This uses the parameter set of Table 1 with $\omega_1 = 5 = \omega_2$, $\zeta_1 = 5 = \zeta_2$, $\chi_1 = 4 = \chi_2$, and $\varepsilon_1 = 4 = \varepsilon_2$. (a) Facultative mutualism with $\xi_1 = 0 = \xi_2$. (b) Minimal obligate mutualism using $\xi_1 = 0.0001 = \xi_2$. (Note: inset shows the unstable equilibrium point near the origin associated with the Allee effect). (c) Moderate obligate mutualism with $\xi_1 = 0.01 = \xi_2$. (d) Approximating the standard model with $\xi_1 = 0.05 = \xi_2$ (note $\varepsilon_1 = 20 = \varepsilon_2$ in this case to reveal the detail of the figure).

The change from facultative ($\xi_1 = 0 = \xi_2$) to obligate ($\xi_1 > 0 < \xi_2$) mutualism does have a profound effect on the vector field near the origin that is not obvious in Figure 5(b) but becomes more apparent as the degree of obligation increases (Figure 5 (c, d)). Two fundamental changes occur at the origin when ξ_1 and ξ_2 become positive: the equilibrium points slide down the axes and collide with the origin, making the origin stable; and an unstable equilibrium point, with associated separatrices, simultaneously pops out of the origin to create an Allee effect. This same process is evident in the ECR model in its intermediate form (Figure 6): again, the transition from facultative to obligate when ξ_1 and ξ_2 become positive affects the vector field near the axes and the origin, indicating a smooth transition is possible irrespective of the nature of the isoclines. The creation of an unstable point and separatrices associated with an Allee effect is also evident in Figure 6(b). We consider Allee effects in more detail in the following section.

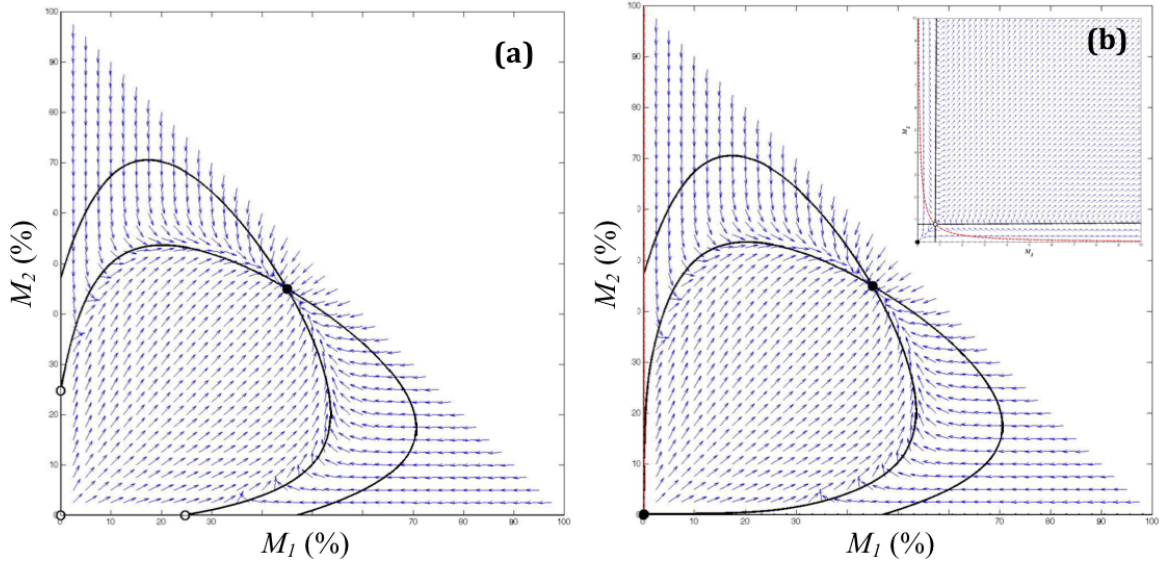


Figure 6. The transition from facultative mutualism to obligate mutualism in the ECR model in its intermediate form (using the parameter values listed in Table 1) but with $\xi_1 = 0 = \xi_2$ for the facultative case (a) and with $\xi_1 = 0.001 = \xi_2$ for the obligate case (b). Note: case (a) does not have an Allee effect and the inset in (b) shows the unstable equilibrium point near the origin associated with the effect.

Figures 5 and 6 further demonstrate the consistency of the standard and HD2010 models of obligate mutualism, in that with subtle parameter variations we are able to smoothly transition the ECR model from the relatively straight isoclines and characteristic Allee effect separatrices of the standard model through to the Turk's head knot isoclines and wrapped separatrices of the HD2010 model. We note a subtle difference between the isoclines and separatrices of the HD2010 model and the equivalent ECR model near the origin. The Allee effect is discussed further in the next section.

3.3. Transition from Allee to non-Allee Models of Obligate Mutualism

The presence of an Allee effect in the standard model of obligate mutualism (Figure 1(a)) is well-known but the absence of an Allee effect in the HD2010 model raises the issue of whether this represents a fundamental difference between the two models, which as is shown above, are at opposite ends of a spectrum of obligate mutualism models as a result of the importance they allocate to the costs of providing mutualist benefits. The generic vector field for obligate mutualism (Figure 1(b)) suggests that the origin is either linearly stable, which implies there must be an Allee effect to enable the stable coexistence of obligate mutualists, or linearly neutral, in which case the system relies on density-dependent growth terms exceeding density-dependent loss terms to enable stable coexistence of obligate mutualists. The standard model implements the former option, with typically a linear mortality term ensuring that the origin is stable, while the HD2010 model implements the latter, with parameters chosen so that the mutualist benefit term is over four times the magnitude of the loss terms (the cost of providing a mutualist benefit plus density dependent mortality) when the populations are near the origin and have similar sizes (i.e. not near an axis, where the relevant population must reduce). The implications of such an arrangement for the limits to mutualism are considered in the next section.

The transition from a form of obligate mutualism that includes an Allee effect to a form that does not in the ECR model may be achieved by changing the coefficient of density-independent mortality $\hat{\sigma}_i$ or any other density-independent loss term. Setting this coefficient to zero produces an HD2010-like solution (Figure 7(a)), while setting it to positive values creates an Allee effect with its unstable equilibrium point and associated

separatrices (Figure 7(b)). Increasing the magnitude of the $\hat{\sigma}_i$ moves the unstable equilibrium point farther from the origin, and increases the minimum size of populations of obligate mutualists that can coexist.

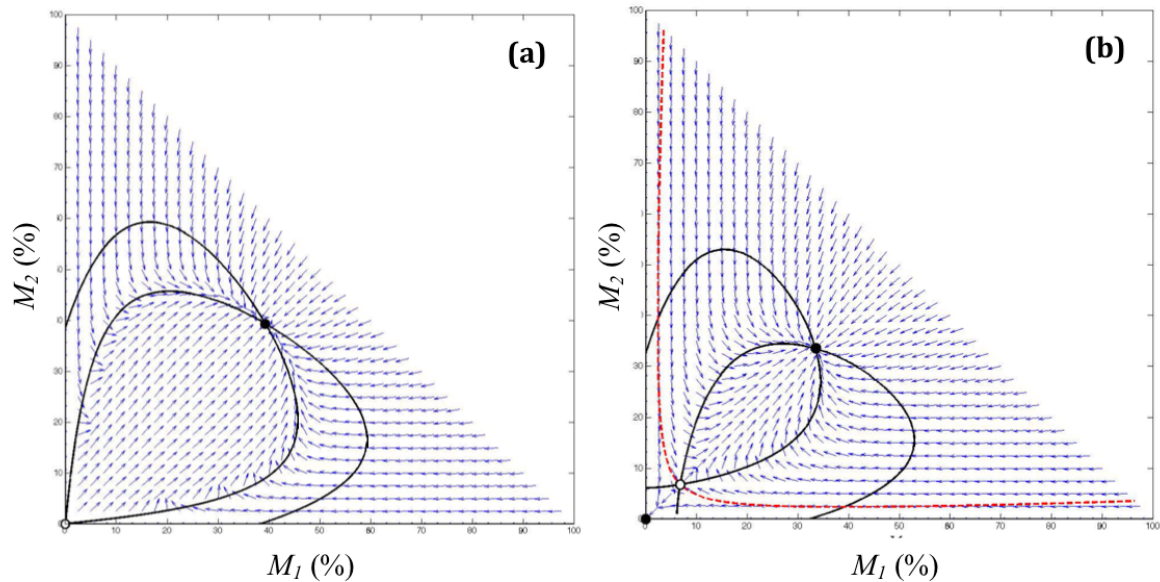


Figure 7. The transition of the ECR model in intermediate form from a parameterisation that does not have an Allee effect to a parameterisation that does. Both panels were drawn using the parameter values listed in Table 1 except density-independent mortalities were set to zero in (a) to remove the Allee effect ($\hat{\sigma}_1 = 0 = \hat{\sigma}_2$), and mutualist benefits reduced commensurately ($\omega_1 = 0.25 = \omega_2$) to ensure that the coexistence equilibrium point was an ecologically feasible solution. Density-independent mortalities were increased to $\hat{\sigma}_1 = 0.25 = \hat{\sigma}_2$ in panel (b) to show the Allee effect more clearly with mutualist benefits reset to Table 1 values.

As in Bazykin (1998), Case (2000), Graves et al. (2006) and Kang et al. (2011) a sufficiently strong obligate growth/benefit effect is needed to balance the loss/mortality

(past the Allee-threshold in Figure 1(a)) in order for stable coexistence of the mutualist populations. Notice that we can also decrease the flow of benefits to M_1 until it becomes unidirectional from M_1 to M_2 , but coexistence is still possible in this situation when M_1 grows in an obligate manner and the mortalities are not too large. Thus, we get (-, +) population interactions where the + is not predation of M_1 on M_2 , but is facilitated mutualistic flow from the resource pool. This may also occur in facultative mutualism when the M_1 mutualist changes from + to - and suggests (-, +) population interactions need to be considered depending whether the signs represent an indirect benefit, as in mutualism, or a direct transfer of mass, as in predation. It is important whether the populations are on the same trophic level or not –all predators gain benefit from the presence of their prey and are obligate on them (as a group if not individually), so that the “between trophic level” population interactions are of a different type to those where populations occupy the same trophic level. The standard “compass rose” of heuristic interaction types, which usually ignores trophic levels and whether interactions are direct or indirect, may be better represented by a helix, where interaction signs within a level have a different interpretation to interaction signs between levels.

3.4. Limits to Obligate Mutualism

A limit to obligate mutualism in the ECR model arises from the fundamental constraint that the benefits of mutualism may not accrue to a population faster than new resource is supplied to the resource pool when it is empty. This provides an upper bound on the quantum of mutualist benefit that might be obtained by either population in any parameterisation of the model. Parameter values that do not comply with this fundamental requirement produce mathematically sound results, but have populations

that have sequestered more than the total amount of resources in the environment and are ecologically unrealistic. The constraints on parameter values imposed by the positive resource condition ensure ecologically realistic answers by placing an upper bound on the mutualist benefits available in the ecosystem.

The ECR model responds quite differently to reductions in the quantum of mutualist benefit depending on whether an Allee effect is present. If an Allee effect is present (Figure 8(a)) the stable population coexistence equilibrium point and the unstable Allee equilibrium point approach each other as the net mutualist benefit is reduced until they meet in a bistable equilibrium point as shown in Figure 8(b). The cost of providing mutualist benefits was increased to a critical level ($\chi_1 = 18 = \chi_2$ in this case) to produce Figure 8(b). The populations can coexist at such a point, and will recover if they experience a perturbation that increases their population sizes, but will go extinct if they suffer a perturbation that reduces their population sizes. Any further reduction in net mutualist benefits results in the immediate co-extinction of the populations, from seemingly sustainable levels.

The HD2010 case of the ECR model behaves in a similar manner to the standard model case if it includes an Allee effect (Figure 8(c)), which is easily achieved by making r_1 and r_2 negative rather than zero. Reduction in net mutualist benefits, in this example by reducing the mutualist benefit parameter ω_i , again causes the unstable Allee equilibrium point to increase and the stable coexistence equilibrium point to decrease until they meet, in this case when $\omega_1 = 0.21 = \omega_2$, and the populations are again on the brink of catastrophic extinction.

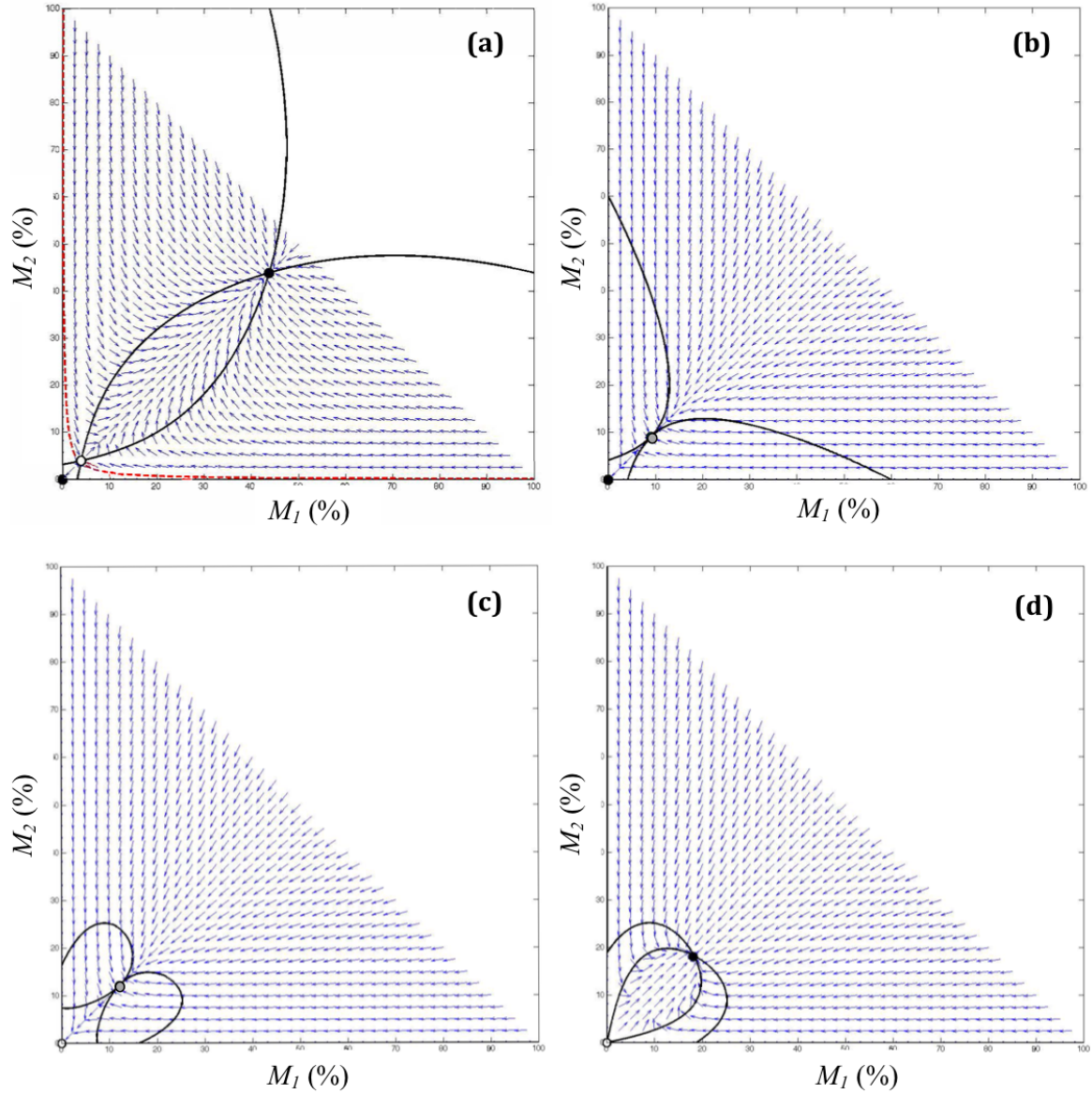


Figure 8. The effects of reducing the benefits obtained from mutualism on the populations of ECR model for three cases: the standard case (a, b), the HD2010 case with an Allee effect (c) and the HD2010 case without an Allee effect (d). Table 1 parameter values are used to draw the figures except where noted. (a) The standard case ($\omega_1 = 5 = \omega_2$, $\zeta_1 = 5 = \zeta_2$, $\chi_1 = 4 = \chi_2$, and $\varepsilon_1 = 20 = \varepsilon_2$). (b) The end of obligate mutualism in the standard case with $\chi_1 = 18 = \chi_2$. In this panel $\varepsilon_1 = 20 = \varepsilon_2$ to improve the clarity of the figure. (c) The HD2010 case with an Allee effect where the mutualist benefits have been reduced to a level ($\omega_1 = 0.21 = \omega_2$) where

the populations are on the brink of co-extinction, analogous to (b). (d) The limit of mutualism benefits ($\omega_1 = 0 = \omega_2$) in the HD2010 case without an Allee effect ($\hat{\sigma}_1 = 0 = \hat{\sigma}_2$). The coexistence point (grey) at this key point of transition is bistable (see text).

The ECR model in HD2010 form without an Allee effect (Figure 8(d)) has a similar initial behaviour but a quite different final outcome. As net mutualism benefits decrease, again by reducing the mutualist benefit parameter ω_i , the coexistence equilibrium point moves toward the origin. However, somewhat surprisingly, reducing the benefits obtained from mutualism to zero ($\omega_1 = 0 = \omega_2$) is not sufficient to extinguish the populations. This is due to the lack of density-independent mortality in the model. In this case, a smooth reduction in ω_i produces a smooth and predictable reduction in the populations, until they reach levels determined by the relative magnitudes of the density-dependent growth and loss terms. This will always result in non-zero equilibrium populations as the density-dependent grow terms had to exceed the density-dependent loss terms in order for this solution to exist.

4. Discussion

The ECR framework allows the development of a model of obligate mutualism that provides a transition between the standard model of obligate mutualism and the HD2010 model, and indicates that these are at opposite ends of a spectrum of models of stable obligate mutualism. These apparently different solutions, that have very different separatrices dividing population combinations that can coexist from those that can't and consequently differ in the presence or absence of an Allee effect, are in fact consistent.

The example ECR model smoothly transitions between these extremes with just the variation of the half-saturation constant of the term representing the cost of providing a mutualist benefit to another population, ε_i . Large values of this parameter (20 times the maximum possible population size) make the cost of providing a mutualist benefit very small compared to the benefit of receiving one, and produce the standard model solution. If the parameter is reduced to extremely small values (1/2,000 of the maximum population size) the function value is relatively large, saturating at very small population sizes. The costs then effectively scale with the ratio of the giving to the receiving population, and produce the HD2010 solution. Intermediate values of the parameter, that might be considered more 'realistic' (say, 10% of the maximum population size), produce solutions that sit between these extremes, with attributes of both the standard and the HD2010 solutions. The novel 'Turk's head knot' pattern of coiling zero isoclines of the HD2010 model can be smoothly wrapped and unwrapped by reducing or increasing the half-saturation constant ε_i of the cost of providing a mutualist benefit, which reduces the per-capita cost of providing the benefit.

The example ECR model also allows a smooth transition from the coexistence of facultative mutualists to the coexistence of obligate mutualists by varying a single quantity – the dependence of each population on the other. Facultative mutualism is represented in the ECR model when the half-saturation constant of obligation (ξ_i) is zero, and unstable boundary equilibrium points, that are stable in the absence of the other population, exist on each axis. As the ξ_i are increased from zero, and each facultative population becomes obligate on the presence of just a very few of its mutualist benefactor population to be able to grow, the boundary equilibrium points

immediately move to the origin. Although this is a discontinuous change exactly on the axis, the vector field near the axis changes very smoothly. The assumption central to population/ecosystem modelling, that we can ignore individuals, does not hold in the regions very close to the axes where one population has an infinitesimally small percentage of the resources, representing just a few individuals. The discontinuity in the transition from facultative to obligate mutualism that occurs exactly on each axis when the ξ_i become non-zero consequently does not represent an unrealistic property of the model.

The third key transition demonstrated with the example ECR model is from systems without an Allee effect, such as HD2010, to systems such as the standard model that have Allee effects. The Allee effect arises from the presence of density-independent mortality, and Allee effects may be introduced into systems without them by increasing the density-independent mortality coefficients $\hat{\sigma}_i$ from zero. As these parameters increase, an unstable equilibrium point with associated separatrices that divide population combinations that can coexist from those that can't, appears at the origin and smoothly moves away from it as the parameter values increase.

All obligate mutualist populations in the example ECR model that are subject to density-independent mortality processes have stable equilibrium points at the origin of their ecospace where all populations are zero, and rely on an Allee effect, the existence of an unstable equilibrium point near the origin, to enable stable coexistence. This is the standard solution as discussed in Case (2000, p287), Kot (2001), and a number of other texts. Obligate mutualist populations that are not subject to density-independent mortality processes have a neutrally stable origin (under linear stability theory, but

unstable considered in a nonlinear context) and rely on density-dependent growth rates to exceed density-dependent loss processes to enable coexistence of obligate mutualists, as in (Holland and DeAngelis 2009, 2010, Holland 2015). Arguably all ecosystem models should contain both density-dependent and density-independent mortality processes (Pastor 2008). The HD2010 model is unusual among models of obligate mutualism in that it does not have an Allee effect, however, recent applications of the HD2010 consumer-resource framework to specific examples, such as leaf-cutter ants and the moulds that they farm (Kang et al. 2011), do have an Allee effect. Similarly, the ECR form of HD2010 does have an Allee effect, suggesting that the lack of an Allee effect is not central to the HD2010 solution.

Models with Allee effects have an unstable equilibrium point near the origin with associated separatrices that divide the ecospace into regions where obligate mutualists can stably coexist and regions where they can't. In the standard model the separatrices asymptote towards the axes at large population sizes, allowing very disparate population ratios between obligate mutualists to ultimately result in stable coexistence. In the HD2010 formulation, the separatrices move away from the axes as the populations increase, suggesting that relatively large or small population ratios do not result in stable coexistence. This may be related to the formulation of the term describing the costs of providing a mutualism benefit, which in this case increase approximately linearly with the ratio of the populations. Recall that the solutions shown are for symmetric systems in which the populations have identical properties. This does not suggest that neutral theory is in any way involved in obligate mutualism, but is done solely to improve the clarity of the diagrams. Dissimilar obligate mutualist populations

are much more likely than similar ones, and will have skewed vector fields and asymmetric separatrices.

The generality of the ECR framework allows us to compare the response of systems with Allee effects to those without when the benefits obtained from mutualism are reduced, and reveal that the systems respond very differently. As the benefits obtained from mutualism reduce in systems with Allee effects, in the example shown by reducing the maximum mutualism benefit ω_i , the coexisting populations reduce in size as the stable equilibrium point moves towards the origin until it meets the unstable point moving out from the origin and they both disappear in a 'blue sky' bifurcation in the middle of the ecospace. Here, relatively large, apparently stable populations suddenly disappear in catastrophic extinctions as mortalities and the costs of supplying mutualist benefits overwhelm the benefits of obligate mutualism. The potential for such catastrophic extinctions may present a significant problem for large-scale computer simulations of populations subject to environmental change.

Reductions in the maximum mutualism benefit ω_i have a much less dramatic effect in systems without Allee effects. Reducing the maximum mutualism benefit ω_i in these systems moves the zero isoclines apart and causes the stable equilibrium point to move towards the origin, reflecting a reduction in population sizes as the benefits of mutualism reduced. The populations in the intermediate form of the ECR model are able to coexist even when the mutualist benefits were zero, however, increasing the loss terms (density-dependent mortality or the cost of providing mutualist benefits) moves the equilibrium point closer to the origin until it eventually meets it when the populations can no longer grow. In this case, the populations evidence a smooth and

predictable decline to extinction, in contrast to the cataclysmic extinction of the system with density-independent mortality.

5. Conclusion

The example model constructed in the ECR framework unifies many previous models of obligate mutualism and shows how mutualist interactions integrate with, and smoothly bridge, other population interactions. This reveals how a single ECR model can smoothly transition from facultative to obligate mutualism, from Allee to non-Allee mutualisms, and from the standard obligate mutualism solution (for example Case (2000)) to the solution of Holland and DeAngelis (2009, 2010). A range of values of the cost parameters are identified that allow a spectrum of stably coexisting mutualist populations - note that the standard and HD2010 solutions are at opposite extremes of this spectrum. The role of density independent mortality as a key factor in producing an Allee effect is also confirmed.

Further, this analysis shows how explicitly monitoring the resource available in the environment keeps a bound on the amount of available mutualist interactions, and restricts mutualist benefits to be less than the supply of recycled resources to or in the resource pool. Implementing the simple ecological axioms of the CN framework (Cropp and Norbury 2015) such as ensuring populations can't grow when they have no resources, and preventing negative resource levels in the resource pool, ensures that the models cannot produce ecologically nonsensical answers. Greedy populations, that seek excessive mutualist benefits, become extinct. This simple constraint on the mutualist benefit determines what are ecologically reasonable parameter value combinations in models of mutualism, and also ensures that ecologically reasonable solutions may be

differentiated from solutions that are mathematically possible but represent scenarios that are not ecologically possible.

Finally, the example model of obligate mutualism in the ECR framework includes only principles and processes that have been commonly used to represent obligate mutualism. Many authors have built models that include saturating explicit mutualist benefits (for example, Bazykin 1998, Holland and DeAngelis 2010, Kang et al. 2011), and some authors have built models that include saturating explicit costs (for example, Holland and DeAngelis 2010, Kang et al. 2011). Others have included terms that explicitly represent obligation, on either growth (Dean 1983, Graves et al. 2006, Thompson et al. 2006) or mortality terms (Gross 2008). In many respects, there is nothing new in this modelling approach – it is a synthesis of many existing ideas that allows the unification of apparently disparate models of obligate mutualism.

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