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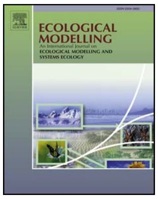

Linking obligate mutualism models in an extended consumer-resource framework

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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).

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 Fig. 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) (Fig. 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.

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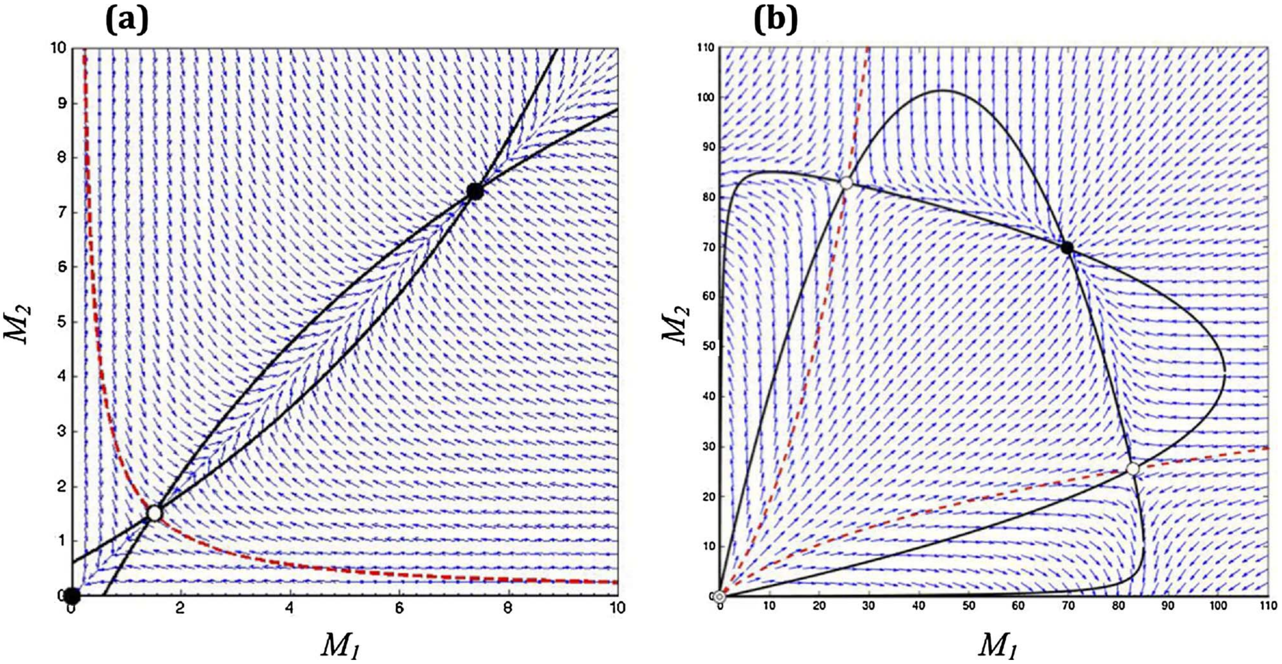

Fig. 1. (a) The standard model: the vector field common to most models of obligate mutualism. (b) The HD2010 model: the vector field for the consumer-resource obligate mutualism model of Holland and DeAngelis (2010). The blue arrows in (a) and (b) show the vector fields, the solid black lines are the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

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 Fig. 1(a) and the HD2010 model of Fig. 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