

# Consumer–resource dynamics of indirect interactions in a mutualism–parasitism food web module

J. Nathaniel Holland · Yuanshi Wang · Shan Sun · Donald L. DeAngelis

Received: 27 October 2012 / Accepted: 4 March 2013 / Published online: 19 March 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** Food web dynamics are well known to vary with indirect interactions, classic examples including apparent competition, intraguild predation, exploitative competition, and trophic cascades of food chains. Such food web modules entailing predation and competition have been the focus of much theory, whereas modules involving mutualism have received far less attention. We examined an empirically common food web module involving mutualistic ( $N_2$ ) and parasitic ( $N_3$ ) consumers exploiting a resource of a basal mutualist ( $N_1$ ), as illustrated by plants, pollinators, and nectar robbers. This mutualism–parasitism food web module is structurally similar to exploitative competition, suggesting that the module of two consumers exploiting a resource is unstable. Rather than parasitic consumers destabilizing the module through  $(-, -)$  indirect interactions, two mechanisms associated with the mutualism can actually enhance the persistence of the module. First, the positive feedback of mutualism favors coexistence in stable limit cycles, whereby  $(+, -)$  indirect interactions emerge in which increases in  $N_2$  have positive effects on  $N_3$  and increases in  $N_3$  have negative effects on  $N_2$ . This  $(+, -)$  indirect interaction

arising from the saturating positive feedback of mutualism has broad feasibility across many types of food web modules entailing mutualism. Second, optimization of resource exploitation by the mutualistic consumer can lead to persistence of the food web module in a stable equilibrium. The mutualism–parasitism food web module is a basic unit of food webs in which mutualism favors its persistence simply through density-dependent population dynamics, rather than parasitism destabilizing the module.

**Keywords** Community · Interaction strength · Model · Mutualism · Parasitism · Plant–pollinator–nectar robber

## Introduction

Our knowledge of the structure and dynamics of food webs has progressed by building up from pairwise interactions and food web modules to whole food webs and through analyses of community matrices of large ecological networks of interacting species (May 1974; Pimm 1982; Polis and Winemiller 1996; Allesina and Pascual 2008; Kondoh 2008; McCann 2012). Studies of food web modules common among communities have revealed the importance of both direct and indirect interactions in food webs (Paine 1980; Wootton 1994; Menge 1995; Werner and Peacor 2003; Peacor and Werner 2004; Kondoh 2008; McCann 2012). Classic indirect interactions in food web modules include apparent competition (Fig. 1a), trophic cascades in food chains (Fig. 1b), exploitative competition (Fig. 1c), and intraguild predation (Hairston et al. 1960; Holt 1977; Leon and Tumpson 1975; Hsu et al. 1978; Oksanen et al. 1981; Tilman 1982; Holt et al. 1994; Holt and Polis 1997). Compared with food web modules entailing predation and competition, the dynamics of food webs entailing mutualism are less well known. Indirect mutualisms are known to occur in food webs of competitive and predator–prey interactions

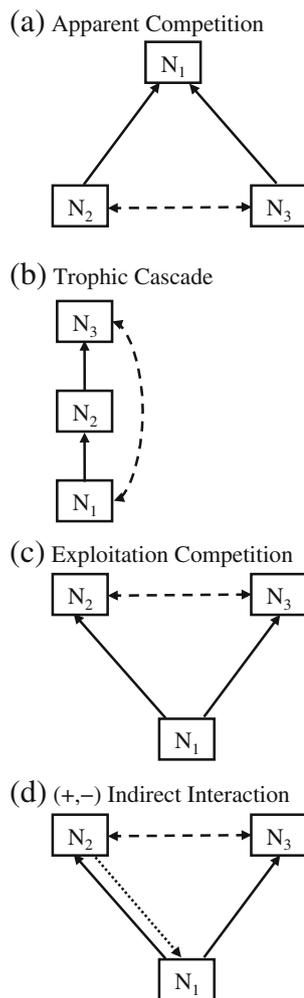
---

J. N. Holland (✉)  
Department of Biology and Biochemistry, University of Houston,  
Science and Research 2, Room 369, 4800 Calhoun Road,  
Houston, TX 77204, USA  
e-mail: jnhollandiii@gmail.com

Y. Wang  
School of Mathematics and Computational Science, Sun Yat-sen  
University, Guangzhou 510275, People's Republic of China

S. Sun  
Institute of Ecology, School of Life Science, Lanzhou University,  
Lanzhou 730000, People's Republic of China

D. L. DeAngelis  
US Geological Survey, Southeast Ecological Science Center,  
Department of Biology, University of Miami,  
Coral Gables, FL 33124, USA



**Fig. 1** Food web modules of indirect interactions characterized as **a** apparent competition, **b** food chain trophic cascade, **c** exploitative competition, and **d** (+,-) indirect interactions.  $N_1$ ,  $N_2$ , and  $N_3$  are species densities. *Solid lines* show direct interactions between consumer and resource species; *arrows* point from the resource to consumer species. *Dashed lines with double-sided arrows* show indirect interactions between  $N_2$  and  $N_3$  mediated by  $N_1$ . In **a**,  $N_1$  is a predator exploiting two prey species,  $N_2$  and  $N_3$ . In **b**,  $N_3$  is a predator,  $N_2$  is a herbivore, and  $N_1$  is the basal species. In **c**,  $N_2$  and  $N_3$  are consumers exploiting a shared resource,  $N_1$ . In **d**,  $N_2$  and  $N_3$  are mutualistic and parasitic consumers exploiting a basal mutualistic species,  $N_1$ . The *dotted arrow* in **d** depicts a non-trophic mutualistic service, pointing from the mutualistic consumer providing the service ( $N_2$ ) to the basal, resource mutualist receiving the service ( $N_1$ )

(Levine 1976; Vandermeer 1980; Stone and Roberts 1991; Kawanabe et al. 1993; Holland and DeAngelis 2010; Crowley and Cox 2011). Yet, direct mutualistic interactions have been mostly left out of food web studies due to difficulty integrating them into the consumer–resource network of food webs. Mutualism is now recognized as a consumer–resource interaction, aiding their inclusion in food webs alongside of predation and competition (Holland and DeAngelis 2009, 2010; Lee and Inouye 2010).

An empirically common subsystem of food webs involving mutualism is the mutualism–parasitism food web module in which both mutualistic ( $N_2$ ) and parasitic ( $N_3$ ) consumers exploit resources supplied by a basal mutualist ( $N_1$ ), resulting in indirect interactions between the two consumers (Fig. 1d). We do not distinguish parasitic consumers as “exploiters,” as both of the two consumers are exploiters of the basal mutualist. Examples of parasitic consumers that coexist in such food web modules are rhizobial bacteria exploiting plant photosynthates without fixing nitrogen; ants exploiting extrafloral nectar without defending plants against herbivores; and animals exploiting floral nectar without pollinating flowers (Bronstein 2001; Yu 2001). Consider plant ( $N_1$ ), pollinator ( $N_2$ ), and nectar robber ( $N_3$ ) interactions (Fig. 1d). Mutualistic pollinators consume floral nectar supplied by plants, depicted by a solid arrowed line pointing from  $N_1$  to  $N_2$ . Floral nectar attracts animals for the non-trophic service of pollination, shown by a dotted arrowed line pointing from  $N_2$  to  $N_1$ , which has a positive effect on the basal resource-supplying plant species. Parasitic nectar robbers exploit floral nectar, depicted by a solid arrowed line pointing from  $N_1$  to  $N_3$ . Nectar robbers do not pollinate, thus no  $N_3$  to  $N_1$  dotted line. Indirect interactions between  $N_2$  and  $N_3$  are shown by a dashed line with a double-sided arrow.

The plant–pollinator–nectar robber system is an example of a general class of mutualism–parasitism food web modules similar to exploitative competition in that two consumers ( $N_2, N_3$ ) exploit a resource ( $N_1$ ). Classic theory for exploitative competition predicts that two consumers cannot coexist on a shared resource if both consumers have identical prey-dependent functional responses and density-independent mortality (Leon and Tumpson 1975; Hsu et al. 1978; Tilman 1982). The consumer persisting at lower resource levels competitively excludes the other (the  $R^*$  rule). This basic result suggests that the mutualism–parasitism food web module is unstable, as mutualistic and parasitic consumers share a resource of the basal mutualist. Yet, mutualism–parasitism food web modules are common in nature (Genini et al. 2010), so it is important to understand mechanisms favoring its persistence.

Much attention has been given to the evolution of mutualisms and their mechanisms of retaliation against the effects of parasitic species (or cheater genotypes) (Axelrod and Hamilton 1981; Bull and Rice 1991; Bronstein 2001; Law et al. 2001; Yu 2001; Ferriere et al. 2002; Foster and Kokko 2006; Jones et al. 2009). Indeed, parasitic species are thought to exclude mutualistic ones, as it is assumed (though not empirically quantified) that the former does not have costs of the latter in reciprocating in the mutualism (Axelrod and Hamilton 1981; Bull and Rice 1991; Doebeli and Knowlton 1998). Here, we develop an ecological theory for the persistence of the mutualism–parasitism food web

module based on density-dependent population dynamics, rather than evolutionary mechanisms mutualists may use for retaliation against parasitic consumers. We first show that, even if both the mutualistic and parasitic consumers are complete competitors in having identical Michaelis–Menten (MM) functional responses (equivalent to a Holling Type II [HT2]), the positive feedback of mutualism can promote fluctuation-dependent persistence of the three species in stable limit cycles. We then examine optimization of resource exploitation by the mutualistic consumer, such as a pollinator, which can lead to a Beddington–DeAngelis (BD) rather than MM functional response (Beddington 1975; DeAngelis et al. 1975). The BD response allows for non-oscillating coexistence of parasitic and mutualistic consumers, a phenomenon amplified by the positive feedback of mutualism on the basal resource species. Overall, we report new community dynamics that arise from incorporating mutualism into food web modules, namely, the emergence of (+,–) indirect interactions between two consumers exploiting a shared resource. Rather than parasitic consumers destabilizing the module, aspects of mutualism enhance the persistence of the food web module, rather than parasitic consumers destabilizing it.

## Model formulations

We examine the dynamics of the mutualism–parasitism food web module, as exemplified by plant ( $N_1$ ), pollinator ( $N_2$ ), and nectar robber ( $N_3$ ) interactions. Any particular formulation of the mutualism–parasitism food web module is distinct from exploitative competition and other well-known food web modules. We first consider the following model, which is similar to the Rosenzweig–MacArthur model of consumer–resource interactions for two consumers and one resource, except that the ( $N_1, N_2$ )-mutualism leads to an additional positive-feedback term in the equation of the basal mutualist,  $N_1$ :

$$\frac{dN_1}{dt} = r_1 N_1 + c_1 \left( \frac{\alpha_{12} N_1 N_2}{h_1 + N_2} \right) - q_1 \left( \frac{\beta_1 N_1 N_2}{e_1 + N_1} \right) - q_2 \left( \frac{\beta_2 N_1 N_3}{e_2 + N_1} \right) - d_1 N_1^2 \quad (1)$$

$$\frac{dN_2}{dt} = c_2 \left( \frac{\alpha_{21} N_1 N_2}{e_1 + N_1} \right) - d_2 N_2 \quad (2)$$

$$\frac{dN_3}{dt} = c_3 \left( \frac{\alpha_{31} N_1 N_3}{e_2 + N_1} \right) - d_3 N_3 \quad (3)$$

Here,  $N_i$  is population density of species  $i$ . The first term in Eq. 1,  $r_1 N_1$ , is the population growth of the basal species

independent of species interactions. We assume  $r_1 > 0$ , as population growth of basal species are often positive in the absence of their consumers, such as population growth of plants in the absence of their pollinators due to selfing or vegetative reproduction. The last term in each of Eqs. 1, 2, and 3 describes mortality of species  $i$ , where  $d_i$  is the mortality rate of  $N_i$ ,  $d_i N_i^2$  is the density-dependent self-limitation, and  $d_i N_i$  is the density-independent mortality.

The second term in Eq. 1 is an MM functional response representing the positive feedback on  $N_1$ 's population growth due to mutualistic interactions with  $N_2$ . The MM function saturates with the density of the mutualistic consumer ( $N_2$ ) with a half-saturation coefficient of  $h_1$ . The interaction strength of the functional response,  $\alpha_{ij}$ , is the per-capita effect of species  $j$  on species  $i$ . The third and fourth terms of Eq. 1 decrease  $N_1$ 's population growth due to its supply of resources and consumption by  $N_2$  and  $N_3$ , respectively. The third and fourth MM functions of Eq. 1 represent losses of  $N_1$  through exploitation,  $\beta_i$  is the magnitude of the negative effects of resource supply and consumption, and  $e_i$  is the half-saturation constant. In Eqs. 2 and 3, the population growth of  $N_2$  and  $N_3$  depends on resource supply by  $N_1$ . Consumption by the mutualistic and parasitic consumers saturates with resource density ( $N_1$ ) according to an MM function, where  $\alpha_{ij}$  is the interaction strength and  $e_i$  is the half-saturation constant. We make the simplest assumption that decreases in  $N_1$ 's growth due to resource supply are a function of  $N_1$ , though it is feasible in other specific cases for consumers to alter resource supply in ratio-dependent forms (Abrams and Ginzburg 2000). Coefficients  $c_i$  and  $q_i$  convert functional responses and resource supply functions to numerical responses. For simplicity, we set them equal to unity without loss of generality. Consequently, the  $\alpha_{ij}$  parameters represent both the mutualistic effect on a species (of nectar or pollination) and its conversion to the numerical biomass of the species. In this model formulation, the mutualistic and parasitic consumers have identical prey-dependent MM functional responses, which are predicted to lead to instability based on theory of exploitative competition (Leon and Tumpson 1975; Hsu et al. 1978; Tilman 1982). Thus, the model formulation of Eqs. 1, 2, and 3 allows us to examine the role of mutualism in the dynamics of the food web module given its only difference with exploitative competition is the additional term for mutualism's positive feedback on the basal mutualist.

In contrast with the previous model formulation in which both consumers are described by MM functions, certain mutualistic interactions differ from the usual MM functional response. In accord, we consider a model formulation in which the mutualistic and parasitic consumers are characterized by different forms of functional responses. For example, some pollinators increase their foraging efficiency by avoiding previously visited flowers through behavioral cues

such as pheromones, scent marks, changes in attractive floral aromatics, trap-lining, and so on, whereas parasitic nectar robbers exploit flowers whether they were visited by pollinators or nectar robbers (Irwin et al. 2010). Fishman and Hadany (2010) analyzed flower avoidance behaviors, showing that pollinators increase their foraging efficiency by avoiding previously exploited resources, resulting in a functional response approximated by a BD rather than an MM function (Appendix 1).

We examined a model formulation that incorporates differences in the forms of the functional responses of  $N_2$  and  $N_3$ . Equations 4, 5, and 6 describe the case of  $(N_1, N_2)$ -mutualism with BD functions and  $(N_1, N_3)$ -parasitism with MM functions:

$$\frac{dN_1}{dt} = r_1 N_1 + c_1 \left( \frac{\alpha_{12} N_1 N_2}{1 + a N_1 + b N_2} \right) - q_1 \left( \frac{\beta_1 N_1 N_2}{e_1 + N_1} \right) - q_2 \left( \frac{\beta_2 N_1 N_3}{e_2 + N_1} \right) - d_1 N_1^2 \quad (4)$$

$$\frac{dN_2}{dt} = c_2 \left( \frac{\alpha_{21} N_1 N_2}{1 + a N_1 + b N_2} \right) - d_2 N_2 \quad (5)$$

$$\frac{dN_3}{dt} = c_3 \left( \frac{\alpha_{31} N_1 N_3}{e_2 + N_1} \right) - d_3 N_3 \quad (6)$$

As with the MM formulation, coefficients  $c_i$  and  $q_i$  convert functional responses and resource supply functions to numerical responses. For simplicity, we set them equal to unity without loss of generality. The careful derivation of a BD function by Fishman and Hadany (2010) for a plant–pollinator mutualism motivated its use here for the  $(N_1, N_2)$ -mutualism. In the BD function,  $1/a$  is the half-saturation constant in its equivalent MM form and  $bN_2$  describes the effect of consumer density on the functional response and  $b$  sets the magnitude of this effect. If  $b=0$ , then BD reduces to an HT2 response, an equivalent expression to MM. The key aspect of the BD is that mutualistic consumers have high resource exploitation efficiencies at low densities, but low resource exploitation efficiencies at high densities (Appendix 1). As a result, some resources of  $N_1$  remain unexploited by  $N_2$ , even at high  $N_2$  density. The BD function is not restricted to plant–pollinator systems as analyzed by Fishman and Hadany (2010), but can occur more generally when consumer interference exists among individuals (Skalski and Gilliam 2001; Katrina et al. 2009). BD arises from indirect interference between mutualistic consumers, as the time spent directly exploiting resources (e.g., flowers) is small. Parasitic consumers (e.g., nectar robbers) do not have a  $bN_i$  term, as they exploit resources that have previously been exploited by pollinators and parasitic consumers

(Irwin et al. 2010). Parasitic consumers are thus less efficient foragers than mutualistic consumers at low mutualist densities, as parasitic consumers exploit low-quality resources as readily as high-quality resources, while mutualistic consumers only exploit high-quality (unexploited) resources. On the other hand, resource exploitation by parasitic consumers can exceed that of mutualistic consumers at high mutualist densities, as the high rate of low-quality resource avoidance can reduce mutualist exploitation of resources at high mutualist density.

## Model analyses and results

We examine community dynamics of the mutualism–parasitism food web module through phase-plane analysis, analytical proofs, and model simulations for sets of Eqs. 1, 2, and 3 and Eqs. 4, 5, and 6. Mathematical proofs are given in Appendix 2. We first review the population dynamics of the two consumer–resource subsystems of the food web module,  $(N_1, N_2)$ -mutualism and  $(N_1, N_3)$ -parasitism. We then examine the dynamics of the food web module as a whole, reporting on the stabilization of three-species coexistence that can occur when both consumers have MM functions and then when the mutualistic consumer has BD function.

Pairwise parasitism:  $(N_1, N_3)$ -subsystem of the food web module

For analyses of the  $(N_1, N_3)$ -parasitism, we dropped all terms in Eqs. 1 and 3 and Eqs. 4 and 6 that included  $N_2$ , as they are not a part of the pairwise parasitism. These equations are identical for the  $(N_1, N_3)$ -parasitism for both the MM and BD formulations. Phase-plane analysis of the  $(N_1, N_3)$ -parasitism of the food web module shows a humped-shaped prey curve, exhibiting classic Rosenzweig–MacArthur predator–prey dynamics (Rosenzweig and MacArthur 1963; Rosenzweig 1969, 1971). As these results are well founded, we only briefly summarize them in terms of the parasitic consumer’s exploitation of resources supplied by the basal mutualist. In sum, the parasitic consumer reduces the density of the resource-supplying mutualist, but, depending on interaction strengths of the parasitic consumer’s functional response ( $\alpha_{31}$ ), the  $(N_1, N_3)$ -parasitism can lead to a stable equilibrium or stable limit cycles. If  $\alpha_{31}$  is weak, such that a large density of  $N_1$  is required to sustain the parasitic consumer, a density beyond that of  $N_1$ ’s carrying capacity, then resources supplied by  $N_1$  are not sufficient, leading to the parasitic consumer’s extinction (Appendix 2). Yet, a stable equilibrium can occur if  $\alpha_{31}$  is neither too small nor too large, such that its zero-growth isocline intersects to the right of the hump of  $N_1$ ’s isocline (Appendix 2). If  $\alpha_{31}$  is

sufficiently large that its zero-growth isocline shifts to the left of the hump, then an unstable equilibrium occurs with stable limit cycles (Appendix 2).

Pairwise mutualism:  $(N_1, N_2)$ -subsystem of the food web module

For analyses of the  $(N_1, N_2)$ -mutualism, we dropped all terms in Eqs. 1 and 2 and Eqs. 4 and 5 that have  $N_3$ , as they are not a part of the pairwise mutualism. Contrary to the  $(N_1, N_3)$ -parasitism, Eqs. 1 and 2 and Eqs. 4 and 5 for the  $(N_1, N_2)$ -mutualism differ between the MM and BD formulations, but their dynamical properties are largely similar. We report the dynamics of the  $(N_1, N_2)$ -mutualism for the BD model (Eqs. 4 and 5), as the only difference with the MM formulation is that  $N_2$ 's zero-growth isocline is vertical. Phase-plane analysis of the population dynamics of the  $(N_1, N_2)$ -mutualism shows three equilibria (Fig. 2). The equilibrium at the origin,  $(0,0)$ , is a saddle point, and positive deviations of  $N_1$  and  $N_2$  move into positive phase-plane space due to the positive feedback of mutualism. The equilibrium on the  $N_1$  axis,  $(r_1/d_1, 0)$ , is the carrying capacity of the resource-supplying mutualist absent of interactions with its mutualistic consumer,  $N_2$ . This is a saddle point, as any  $N_2 > 0$  leads the transient dynamics of  $N_1$  and  $N_2$  to increase in phase-plane space. No such equilibrium occurs on the  $N_2$ -axis, as

$N_2$  depends on the resources supplied by  $N_1$ . Depending on parameter values, the nontrivial equilibrium is either stable, in which case the dynamics of  $N_1$  and  $N_2$  converge to the equilibrium, or it is an unstable focus, in which the dynamics of  $N_1$  and  $N_2$  result in stable limit cycles.

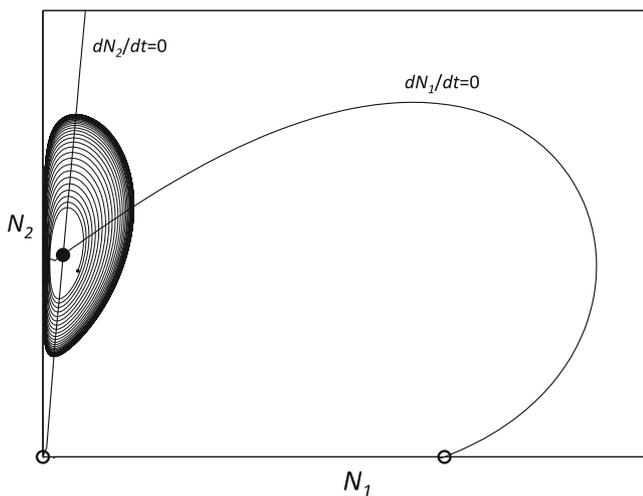
MM formulations of the food web module

We now examine the dynamics of the mutualism–parasitism food web module as a whole, in which identical MM functional responses characterize the mutualistic and parasitic consumers (Eqs. 1, 2, and 3). This formulation parallels classic exploitative competition in that two consumers ( $N_2, N_3$ ) exploit a shared resource ( $N_1$ ). Two equilibrium values occur for  $N_1$  based on Eqs. 2 and 3 for the mutualistic and parasitic consumers, respectively:

$$N_1^0 = \frac{e_1 d_2}{\alpha_{21} - d_2} \quad \text{and} \quad N_1^\# = \frac{e_2 d_3}{\alpha_{31} - d_3} \tag{7}$$

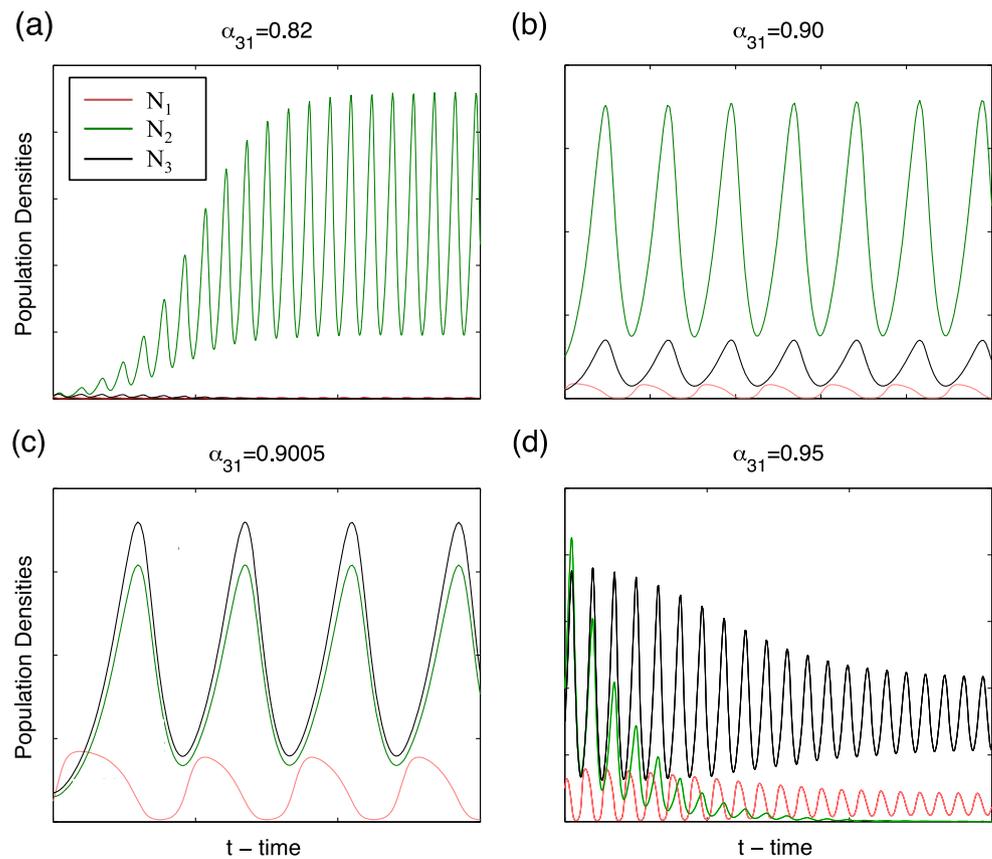
These equations are inconsistent. As in exploitative competition, one of the two consumers cannot have a non-oscillating equilibrium (Leon and Tumpson 1975; Hsu et al. 1978; Tilman 1982). We do not examine this razor-edge case in which  $N_1^0 = N_1^\#$ , as it is unrealistic with low feasibility in nature. Instead, we test the more biologically realistic case in which  $N_1^0 \neq N_1^\#$ . Specifically, we allowed the mutualistic consumer to persist at a lower resource level,  $R^*$ , than that of the parasitic consumer, that is  $N_1^0 = N_1^\#$ . Based on the  $R^*$  rule and  $N_1^0 = N_1^\#$ ,  $N_2$  should competitively exclude  $N_3$  through  $(-, -)$  indirect interactions. But the mutualism–parasitism food web module differs from exploitative competition in the second term of Eq. 1 for the positive feedback of mutualism on the basal resource species. While a stable equilibrium does not occur, we show that, under various scenarios of interaction strengths of the mutualistic and parasitic consumers on the basal resource mutualist, this positive feedback has key consequences for coexistence under endogenous (limit cycle) fluctuations.

We first examine food web dynamics for  $N_1^0 = N_1^\#$  for different interaction strengths of the parasitic consumer's functional response ( $\alpha_{31}$ ) on the basal mutualist. Module dynamics do vary with  $\alpha_{31}$ , including extinction of the parasitic consumer (Fig. 3a),  $(N_1, N_2, N_3)$ -coexistence in stable limit cycles in which  $N_2 > N_3$  (Fig. 3b),  $(N_1, N_2, N_3)$ -coexistence in stable limit cycles in which  $N_3 > N_2$  (Fig. 3c), and extinction of the mutualistic consumer (Fig. 3d). Transient dynamics and stable limit cycles of  $N_1, N_2$ , and  $N_3$  within each of Fig. 3a–d, along with shifts in densities of  $N_1, N_2$ , and  $N_3$  among Fig. 3a–d, exhibit a  $(+, -)$  indirect interaction, whereby increases in  $N_2$  have positive indirect effects on  $N_3$  by causing an increase in  $N_1$  and increases in  $N_3$  have negative indirect effects on  $N_2$  by causing a



**Fig. 2** Phase-plane diagram of the population dynamics of interactions between a resource-supplying mutualist ( $N_1$ ) and a mutualistic consumer providing a non-trophic service ( $N_2$ ), with their respective zero-growth isoclines labeled as  $dN_i/dt=0$ . The central, nontrivial equilibrium point ( $P_{12}$ ) labeled with a solid circle can be either a stable node or an unstable focus. Here, we have plotted the unstable focus, for which an example trajectory starting with the small filled circle leads to limit cycles. The two open circles, one at the origin and the other on the  $N_1$ -axis, are saddle points which lead to the nontrivial equilibrium. Note that the  $y$ -intercept of the  $N_2$  isocline is negative. Parameter values for this particular solution are  $r_1=1.0, d_2=0.7, d_1=0.01, \alpha_{12}=2.55, a=0.35, b=0.2, \beta_1=0.9, \beta_2=4.8, \alpha_{21}=1.9, e_1=20$ , and  $e_2=23.4$

**Fig. 3** Representative trajectories of Eqs. 1, 2, and 3 for the dynamics of the mutualism–parasitism food web module with MM functional responses describing both the  $(N_1, N_2)$ -mutualism and  $(N_1, N_3)$ -parasitism, for which  $N_1^0 < N_1^\#$  (see Eq. 7). Here, the interaction strength ( $\alpha_{31}$ ) of the parasitic consumer's functional response was varied, resulting in **a** parasitic consumer extinction, **b** three-species coexistence in stable limit cycles in which  $\alpha_{31} < \alpha_{21}$ , **c** three-species coexistence in stable limit cycles in which  $\alpha_{31} = \alpha_{21}$  (approximating  $N_1^0 = N_1^\#$ ), and **d** mutualistic consumer extinction. Densities of  $N_1$ ,  $N_2$ , and  $N_3$  are expressed over time in red, green, and black, respectively. Parameter values for solutions of Eqs. 1, 2, and 3 are  $r_1 = 1.5$ ,  $d_1 = 0.01$ ,  $d_2 = d_3 = 0.45$ ,  $\alpha_{12} = 0.55$ ,  $\alpha_{21} = 0.9005$ ,  $\beta_1 = 0.005$ ,  $\beta_2 = 0.03$ , and  $e_1 = e_2 = 50$ . Similar results occur for variation in other parameter values

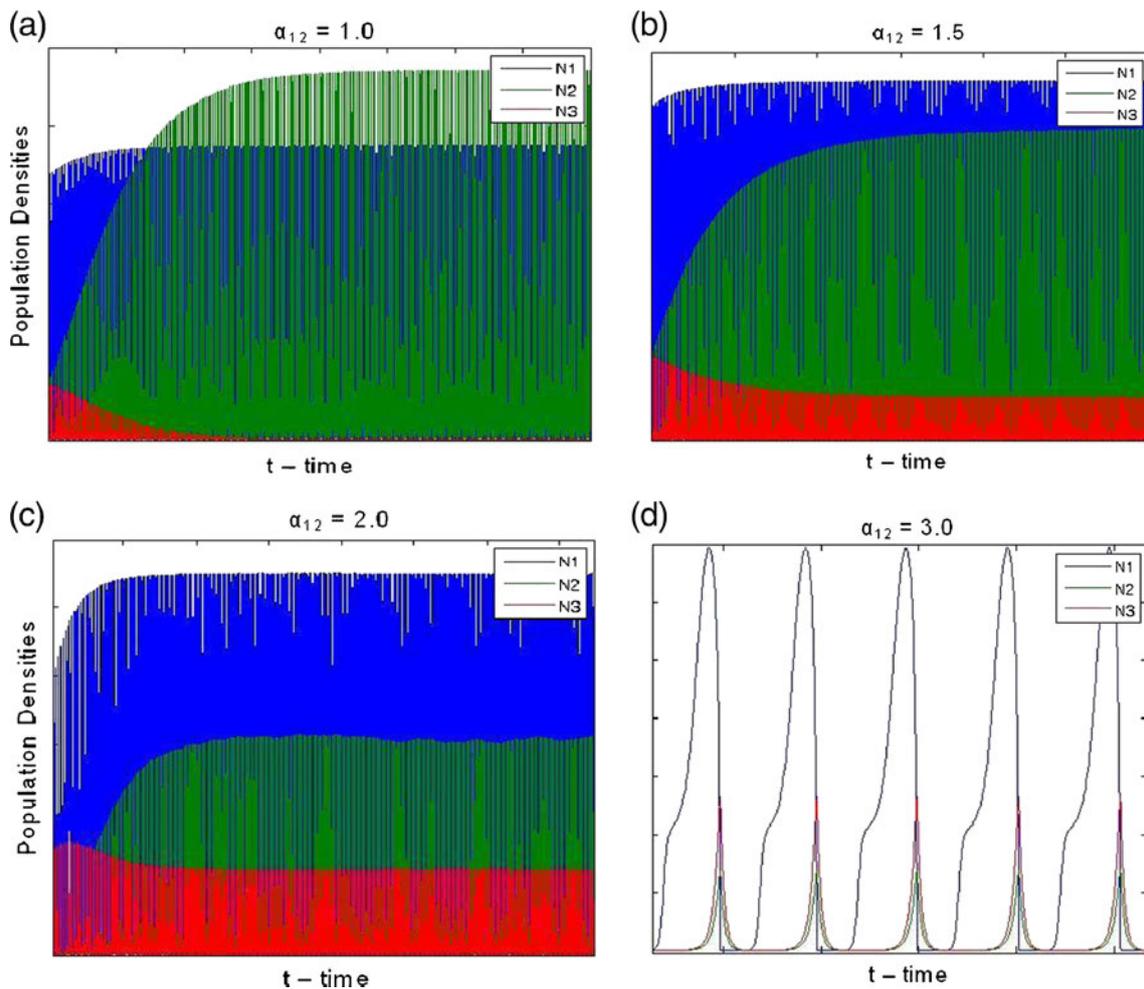


decrease in  $N_1$ . The stable limit cycles show periodic oscillations with increases in  $N_2$  having positive indirect effects on  $N_3$  through increases in  $N_1$  and increases in  $N_3$  having negative indirect effects on  $N_2$  through decreases in  $N_1$ .

The (+, -) indirect interaction facilitates  $(N_1, N_2, N_3)$ -coexistence, rather than competitive exclusion through (-, -) indirect interactions. The interaction strength for the positive feedback on the basal mutualist,  $\alpha_{12}$ , plays a key role in whether or not coexistence occurs. For small values of this feedback ( $\alpha_{12} = 0.5$ ), the parasitic consumer is excluded by the mutualistic consumer (Fig. 4a), while for sufficiently large values, three-species coexistence occurs (Fig. 4b–d). Such  $(N_1, N_2, N_3)$ -dynamics conditional upon  $\alpha_{12}$  are further exemplified by bifurcation plots (Fig. 5). The three-species coexistence for larger values of  $\alpha_{12}$  represents an example of fluctuation-dependent persistence (Chesson 2000) and a case of relative nonlinearity of competition (Armstrong and McGehee 1976). The basis for this mechanism is in the growth rates of  $N_2$  and  $N_3$  varying with  $N_1$ , showing that the former has a higher growth rate for smaller values of  $N_1$  and the latter has a higher growth rate for larger values of  $N_1$  (Fig. 6). This implies, as shown in Fig. 6, that the growth curves for  $N_2$  and  $N_3$ ,  $\alpha_{21}N_1/(e_1 + N_1) - d_2$  and  $\alpha_{31}N_1/(e_2 + N_1) - d_3$ , respectively, cross for intermediate values of  $N_1$ . This occurs for the parameter values in Fig. 4; that is, for small values of  $N_1$ , the per capita growth rates for  $N_2$  and  $N_3$  obey the inequality

$\alpha_{21}N_1/e_3 - d_2 > \alpha_{31}N_1/e_3 - d_3$ , whereas for large values of  $N_1$ , the growth rates are  $\alpha_{21} - d_2 < \alpha_{31} - d_3$ . For simplicity, we have set  $d_2 = d_3$ , but in general, these will be different and will contribute to differences in growth rates. Theory shows that coexistence is possible if the fluctuation amplitude is such that each of the two consumer species has some period of time in which it is competitively superior to the other and is more limited by its own density than that of the other consumer. Coexistence occurs only for values of  $\alpha_{12}$  higher than some minimum threshold, whereas extinction of the parasitic consumer occurs below this threshold  $\alpha_{12}$ . These alternatives occur because the amplitude of the oscillations of  $N_1$  depends on the positive feedback from  $N_2$  on  $N_1$ , whose strength depends on  $\alpha_{12}$ . Large fluctuations favor the persistence of the parasite,  $N_3$ , because it is superior to  $N_2$  at high densities of  $N_1$ .

However, in contrast with the case in which  $N_1^0 < N_1^\#$ , a remarkable phenomenon occurs when the inequality is reversed such that  $N_1^0 < N_1^\#$ . Quasi-stable persistence or co-occurrence occurs over a long time period, but this fluctuation-dependent persistence eventually undergoes a sudden shift to competitive exclusion of one consumer, for example, the mutualistic consumer for  $\alpha_{12} = 2.55$  (Fig. 7a) and the parasitic consumer for  $\alpha_{12} = 2.57$  (Fig. 7b). This apparent sudden “regime shift” is due to the positive feedback effect of  $N_2$  on  $N_1$ . When this feedback is strong, the oscillations in  $N_1$  are very strong, favoring the mutualistic



**Fig. 4** Representative trajectories of Eqs. 1, 2, and 3 for the dynamics of the mutualism–parasitism food web module with MM functional responses describing both the  $(N_1, N_2)$ -mutualism and  $(N_1, N_3)$ -parasitism, for which  $N_1^0 < N_1^\#$  (Eq. 7). Here, the interaction strength ( $\alpha_{12}$ ) of the positive feedback on the basal mutualist was varied, resulted in **a** parasitic consumer extinction ( $\alpha_{21}=1.0$ ), **b** three-species coexistence in stable limit cycles ( $\alpha_{21}=1.5$ ), **c** three-species coexistence in stable limit

cycles ( $\alpha_{21}=2.0$ ), and **d** three-species coexistence in stable limit cycles ( $\alpha_{21}=3.0$ ). The scale of this last panel is blown up to show the oscillations more clearly. Densities of  $N_1$ ,  $N_2$ , and  $N_3$  are expressed over time in blue, green, and red, respectively. Parameter values for solutions of Eqs. 1, 2, and 3 are  $r_1=1.0$ ,  $d_1=0.01$ ,  $d_2=d_3=0.5$ ,  $\alpha_{31}=0.92$ ,  $\alpha_{21}=0.90$ ,  $\beta_1=0.90$ ,  $\beta_2=4.8$ ,  $e_1=20$ , and  $e_2=23.4$

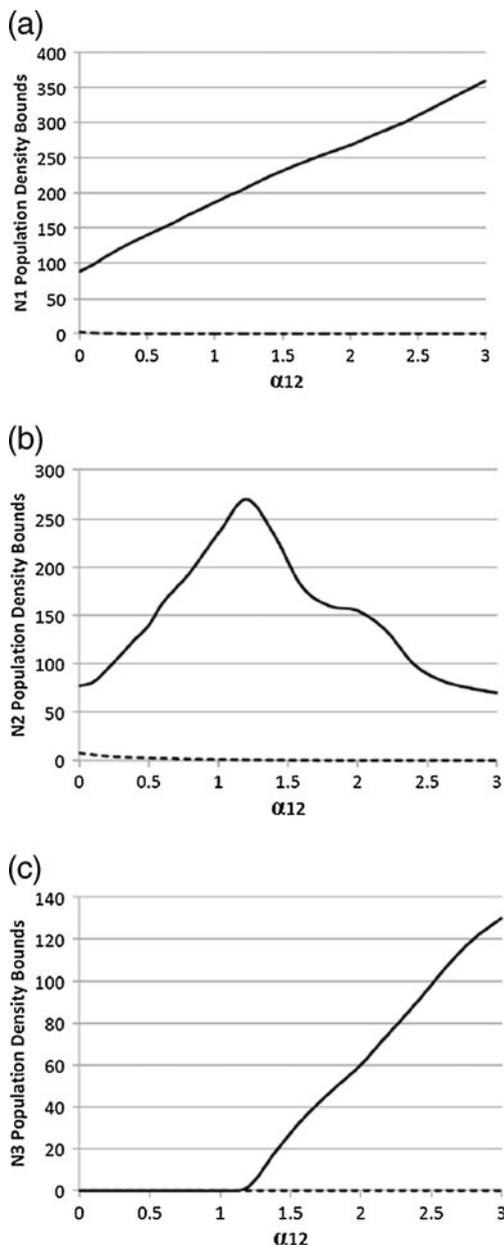
consumer, which has a higher growth rate at larger values of  $N_1$ . An initially imperceptibly slow change in the amplitude of the limit cycle of  $N_1$  may suddenly accelerate to smaller or larger values due to the positive feedback, leading to an extinction that was not easy to predict. When the parasitic consumer is a superior competitor and can persist at a lower  $R^*$  level than the mutualistic consumer, that is  $N_1^0 > N_1^\#$ , then after a long period of time, three-species persistence under endogenous limit cycles degrades into competitive exclusion of the mutualistic consumer if its interaction strength and positive feedback on the basal mutualist is sufficiently strong.

**BD formulations of the food web module**

While fluctuations in the densities of the interacting species facilitate coexistence of the mutualistic and parasitic

consumers in stable limit cycles when both have MM responses, three-species coexistence may also occur in a stable (non-oscillating) equilibrium when the consumers have different functional responses. We examine this for Eqs. 4, 5, and 6 with BD and MM functional responses for mutualism and parasitism (Appendix 2). The module now shows a single stable  $(N_1, N_2, N_3)$ -equilibrium,  $P^*$ , for many parameter values (Fig. 8). For densities of  $N_1$ ,  $N_2$ , and  $N_3 > 0$ , the module converges to this stable equilibrium. In the absence of  $N_2$ , trajectories lead to an alternative saddle point,  $P_{13}$ , in the  $(N_1, N_3)$ -plane, which is unstable to invasion of  $N_2$ , which leads to  $P^*$  (Fig. 7). Equilibria of Eqs. 4, 5, and 6 are:

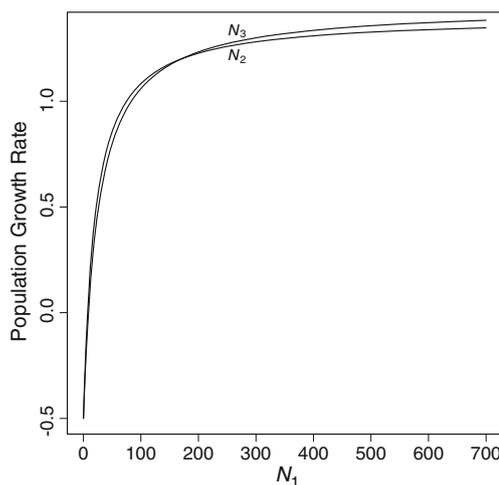
$$N_1^* = \frac{d_3 e_2}{\alpha_{31} - d_3} \tag{8}$$



**Fig. 5** Bifurcation diagrams showing lower (*dashed lines*) and upper (*solid lines*) bounds on the oscillations of  $N_1$ ,  $N_2$ , and  $N_3$  (**a**, **b**, and **c**, respectively) as functions of parameter  $\alpha_{12}$  from Eqs. 1, 2, and 3 for the dynamics of the mutualism–parasitism food web module, based on MM functional responses for both the  $(N_1, N_2)$ -mutualism and  $(N_1, N_3)$ -parasitism, for which  $N_1^0 < N_1^\#$  (Eq. 7). Note the shift from stable limit cycles of  $N_1$  and  $N_2$  to stable limit cycles of  $N_1$ ,  $N_2$ , and  $N_3$  as  $\alpha_{12}$  exceeds a value of about 1.2. Parameter values for solutions of Eqs. 1, 2, and 3 are  $r_1=1.0$ ,  $d_1=0.01$ ,  $d_2=d_3=0.5$ ,  $\alpha_{31}=0.92$ ,  $\alpha_{21}=0.90$ ,  $\beta_1=0.90$ ,  $\beta_2=4.8$ ,  $e_1=20$ , and  $e_2=23.4$

$$N_2^* = \frac{(\alpha_{21} - ad_2)N_1^* - d_2}{bd_2} \tag{9}$$

$$N_3^* = \frac{e_2 + N_1^*}{\beta_2} \left[ r_1 + \frac{\alpha_{12}N_2^*}{1 + aN_1^* + bN_2^*} - \frac{\beta_1 N_2^*}{e_1 + N_1^*} - d_1 N_1^* \right] \tag{10}$$



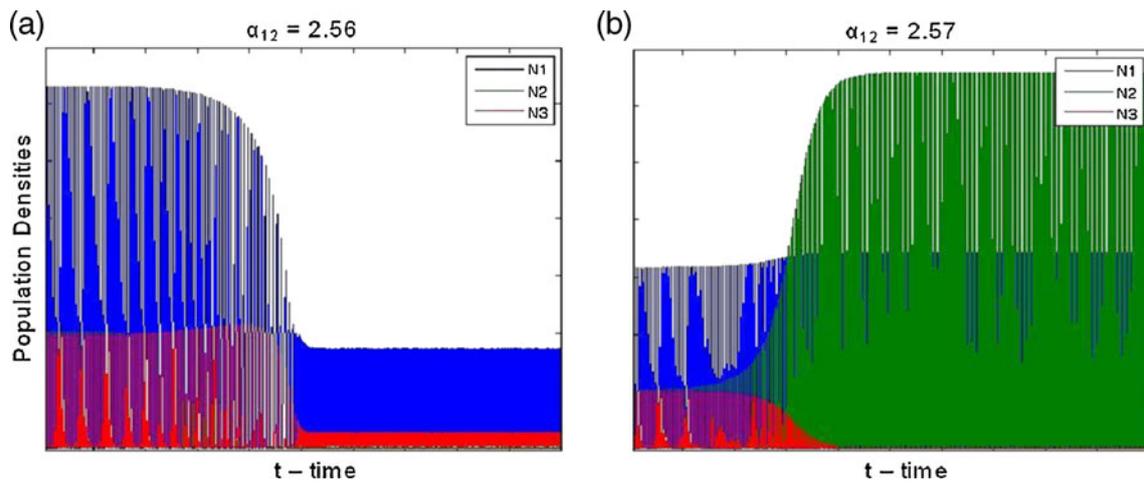
**Fig. 6** Growth rates of the mutualistic consumer ( $N_2$ )  $a_{21}N_1/(e_1 + N_1) - d_2$  and the parasitic consumer ( $N_3$ )  $a_{31}N_1/(e_2 + N_1) - d_3$  as a function of the density of the basal resource mutualist ( $N_1$ ). The growth rate of  $N_2$  exceeds that of  $N_3$  for small values of  $N_1$ , while the growth rate of  $N_3$  exceeds that of  $N_2$  for large values of  $N_1$ . Parameter values for these solutions include  $d_2=d_3=0.5$ ,  $\alpha_{21}=1.90$ ,  $\alpha_{31}=1.95$ ,  $e_1=20$ , and  $e_2=25.0$ . The parameter values here are slightly different from those of Fig. 4 to demonstrate the differences in growth rates with  $N_1$

These solutions show the feasible existence of a positive  $(N_1^*, N_2^*, N_3^*)$ -equilibrium and can be used to determine the range of parameters for this solution.

In Eq. 8, we see that  $N_3$  controls  $N_1^*$ .  $N_2^* > 0$  can occur for parameter ranges in which  $N_2$  is more efficient than  $N_3$  in exploiting resources of  $N_1$  when the density of  $N_2$  is low. This is seen by first renaming  $N_1^*$  in Eq. 9 as  $N_{1,p}^*$ , as this value is determined by the parasitic consumer (Eq. 6). Then, rearrange the terms in Eq. 10 as follows:

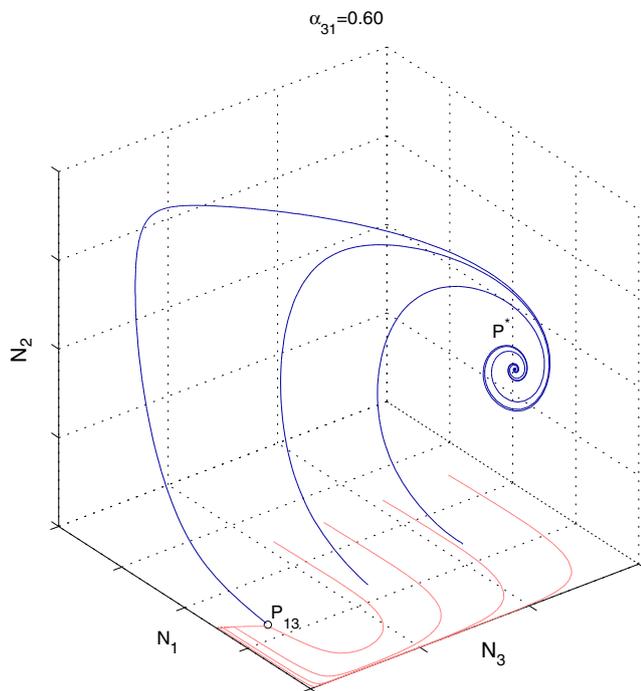
$$N_2^* = \frac{1}{b} \left[ N_{1,p}^* \frac{(\alpha_{21} - ad_2)}{d_2} - 1 \right] = \frac{1}{b} \left[ \frac{N_{1,p}^*}{N_{1,m}^*} - 1 \right] \tag{11}$$

where  $N_{1,m}^* = d_2 / (a_{21} - ad_2) \cdot N_{1,p}^*$  is the level at which  $N_1$  would be held by the mutualistic consumer, if the parasitic consumer was not present and the effect of the  $bN_2$  term in Eq. 5 was negligible at equilibrium. For  $N_2^*$  to be positive in Eq. 11, it requires that  $N_{1,m}^* < N_{1,p}^*$ , that is, the mutualistic consumer is more efficient than the parasitic consumer at exploiting the resource-supplying mutualist when the mutualistic consumer is at low densities. Existence of a positive non-oscillating  $(N_1^*, N_2^*, N_3^*)$ -equilibrium distinguishes the mutualism–parasitism food web module from that of exploitative competition. This positive non-oscillating  $(N_1^*, N_2^*, N_3^*)$ -equilibrium arises from the negative density dependence of the BD functional response, but is also enhanced by the positive feedback of the  $(N_1, N_2)$ -mutualism.  $N_2$  increases  $N_1$ 's density, which in turn increases resources of  $N_1$  that are available to  $N_3$ . Density effects of  $bN_2$  of the



**Fig. 7** Representative trajectories of Eqs. 1, 2, and 3 for the dynamics of the mutualism–parasitism food web module with MM functional responses describing the  $(N_1, N_2)$ -mutualism and  $(N_1, N_3)$ -parasitism, but now with  $N_1^0 > N_1^\#$  due to the switching of the values of  $\alpha_{21}$  and  $\alpha_{31}$  and of  $e_1$  and  $e_2$  in Fig. 4. Here, the interaction strength ( $\alpha_{12}$ ) of the positive feedback on the basal mutualist was varied, resulting in **a** quasi-stable three-species limit cycle coexistence ( $\alpha_{12}=2.56$ ) that eventually underwent a switch in which the mutualist consumer was

eliminated (it is difficult to distinguish the mutualist consumer in the early part of this plot, but it is coexisting stably) and **b** quasi-stable three-species limit cycle coexistence ( $\alpha_{12}=2.57$ ) that eventually underwent a switch in which the parasitic consumer was eliminated. Densities of  $N_1$ ,  $N_2$ , and  $N_3$  are expressed over time in *blue*, *green*, and *red*, respectively. Parameter values are the same as in Fig. 4. Long-term persistence of the three-species coexistence appears to be difficult or perhaps impossible in this situation

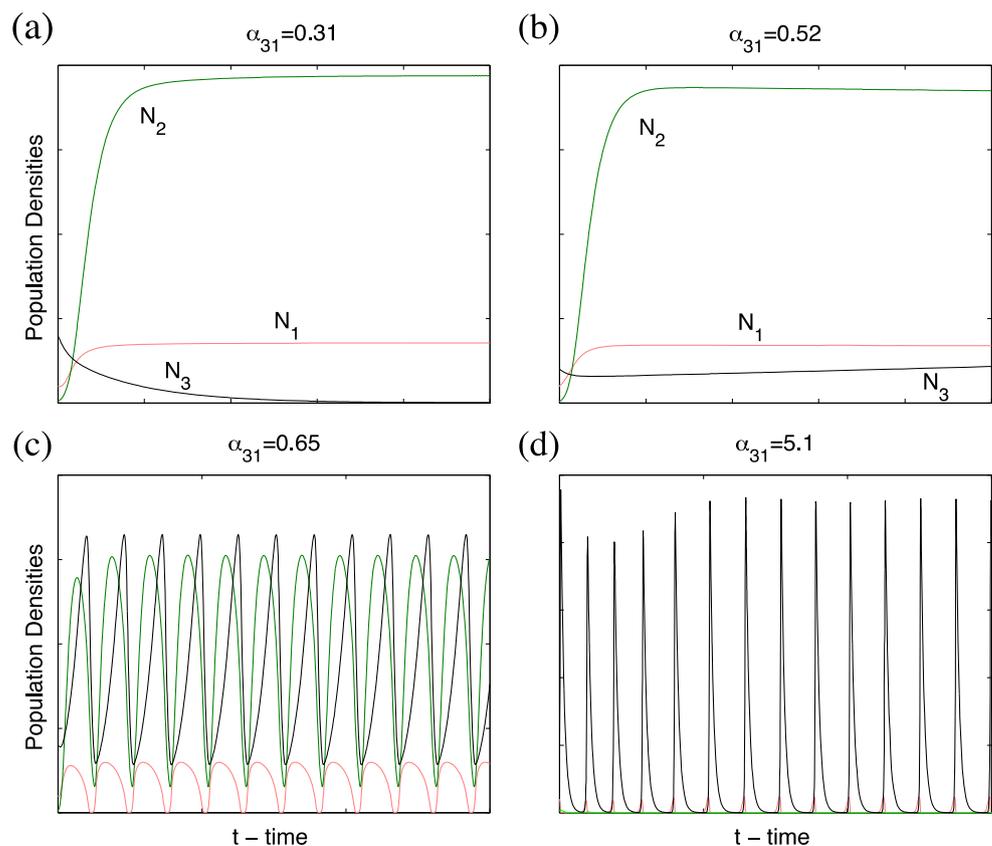


**Fig. 8** Phase-plane diagram of the community dynamics of the mutualism–parasitism food web module, including direct and indirect interactions between mutualistic ( $N_2$ ) and parasitic ( $N_3$ ) consumers exploiting resources supplied by another mutualist ( $N_1$ ). With initial densities of  $(N_1, N_2, N_3) > (0, 0, 0)$  and an intermediate interaction strength of  $N_3$ , community dynamics converge to the stable  $(N_1, N_2, N_3)$ -equilibrium,  $P^*$ , as shown by three example trajectories in *blue*. In the absence of  $N_2$ , for example, the dynamics differ, such as the saddle point,  $P_{13}$ , as shown by four example trajectories in *red*. Parameter values are  $r_1=1.5$ ,  $d_1=0.01$ ,  $d_2=0.45$ ,  $d_3=0.45$ ,  $\alpha_{12}=0.55$ ,  $\alpha_{21}=0.65$ ,  $a=0.35$ ,  $b=0.2$ ,  $\beta_1=\beta_2=0.005$ , and  $e_1=e_2=50$

BD functional response of  $N_2$  lead to incomplete resource exploitation by  $N_2$  at high  $N_2$  densities, resulting in resources available for  $N_3$  to persist.

The stable  $(N_1^*, N_2^*, N_3^*)$ -equilibrium of the BD formulation also exhibits the  $(+, -)$  indirect interaction: increases in  $N_2^*$  have positive indirect effects on  $N_3^*$  by increasing  $N_1^*$  and increases in  $N_3^*$  have negative indirect effects on  $N_2^*$  by decreasing  $N_1^*$ . Representative dynamics of the food web module show that different scenarios of  $(N_1, N_2, N_3)$ -interactions can arise with changes in interaction strengths of the parasitic consumer’s functional response ( $\alpha_{31}$ ) relative to that of the mutualistic consumer ( $\alpha_{21}$ ) (Fig. 9). Shifts in  $N_1$ ,  $N_2$ , and  $N_3$  among Fig. 9a–d exhibit the  $(+, -)$  indirect interactions. If  $\alpha_{31}$  of the parasitic consumer’s functional response is small, then  $N_3$  tends towards extinction (Fig. 9a). A sufficient increase in  $\alpha_{31}$  leads to  $(N_1^*, N_2^*, N_3^*)$ -coexistence in a stable equilibrium (Fig. 9b). A further increase in  $\alpha_{31}$  continues to lead to  $(N_1, N_2, N_3)$ -coexistence, but in a stable limit cycle (Fig. 9c). The stable limit cycle exhibits dynamics of the  $(+, -)$  indirect interactions, whereby increases in the density of the mutualistic consumer increase the density of the resource-supplying mutualist, which increases the density of the parasitic consumer. On the other hand, increasing the density of the parasitic consumer reduces the density of resource-supplying mutualists and in turn the density of the mutualistic consumer. Ongoing changes in the densities of  $N_2$  and  $N_3$  lead to periodic oscillations, whereby increases in  $N_3$  have negative effects on  $N_2$  through decreases in  $N_1$  and increases in  $N_2$  have positive effects on  $N_3$  through increases in  $N_1$  (Fig. 9c). Peaks and troughs in the densities of  $N_1$ ,  $N_2$ , and  $N_3$  are out of phase

**Fig. 9** Representative trajectories of Eqs. 4, 5, and 6 for the dynamics of the mutualism–parasitism food web module with BD functional responses describing the  $(N_1, N_2)$ -mutualism and MM functional responses describing the  $(N_1, N_3)$ -parasitism. Here, the interaction strength ( $\alpha_{31}$ ) of the parasitic consumer functional response was varied, resulting in **a** parasitic consumer extinction, **b** three-species coexistence in stable equilibrium, **c** three-species coexistence in stable limit cycles, and **d** mutualistic consumer extinction. The densities of  $N_1$ ,  $N_2$ , and  $N_3$  in red, green, and black, respectively, are expressed over time. For solutions of Eqs. 8, 9, and 10, parameter values are  $r_1 = 1.5$ ,  $d_1 = 0.01$ ,  $d_2 = d_3 = 0.45$ ,  $\alpha_{12} = 0.55$ ,  $\alpha_{21} = 0.65$ ,  $a = 0.35$ ,  $b = 0.2$ ,  $\beta_1 = \beta_2 = 0.005$ , and  $e_1 = e_2 = 50$ . Similar results occur for variation in other parameter values



due to the (+,−) indirect interactions between  $N_2$  and  $N_3$ . With strong interaction strengths ( $\alpha_{31}$ ) of the parasitic consumer, it is feasible for the parasitic consumer to overexploit the resource-supplying mutualist and cause extinction of the mutualistic consumer (Fig. 9d). In this case, the (+,−) indirect effect is prevalent only in the  $(N_1, N_2, N_3)$ -transient dynamics toward a  $(N_1, N_3)$ -stable limit cycle (Fig. 9d). However, this latter change in  $\alpha_{31}$  was exceedingly large relative to other parameter values of  $\alpha_{31}$  and  $\alpha_{21}$ .

BD formulations of the food web module with  $(N_1, N_2)$  limit cycles

The above BD results apply to the situation in which the  $(N_1, N_2)$ -mutualism has a stable equilibrium. Yet, as in Fig. 2, the  $(N_1, N_2)$ -mutualism, as with the  $(N_1, N_3)$ -parasitism, can persist in stable limit cycles. When concurrent stable limit cycles occur between the  $(N_1, N_2)$ -mutualism and  $(N_1, N_3)$ -parasitism, then the positive equilibrium  $P^*$  (Fig. 8) shifts to an unstable focus with  $(N_1, N_2, N_3)$ -coexistence in stable limit cycles that exhibit (+,−) indirect interactions. When interaction strengths ( $\alpha_{31}$ ) of the parasitic consumer's functional response are large, then  $N_3$  leads to the extinction of  $N_2$  and the  $(N_1, N_3)$ -parasitism persists in stable limits cycles. When  $\alpha_{31}$  is small, then  $N_3$  goes to extinction and  $(N_1, N_2)$ -mutualism persists in limits cycles. Thus, results of Fig. 9 are not restricted to the  $(N_1, N_2)$ -mutualism having a stable equilibrium, but

are consistent with  $(N_1, N_2)$ -mutualism limit cycles interacting with limit cycles of the  $(N_1, N_3)$ -parasitism.

## Discussion

Food web modules exemplify many basic ways in which direct and indirect interactions between species can shape community dynamics. We studied the consequences of direct and indirect interactions for the ecological dynamics of mutualism–parasitism food web modules in which mutualistic ( $N_2$ ) and parasitic ( $N_3$ ) consumers exploit shared resources of a basal mutualist ( $N_1$ ), as exemplified by plant ( $N_1$ ), pollinator ( $N_2$ ), and nectar robber ( $N_3$ ) interactions. Our approach differs from earlier work in that we constructed a mutualism–parasitism module by employing consumer–resource theory to build up from individual species and their pairwise interactions to the food web module (Holt 1977; Paine 1980; McCann 2012). This approach of building up to the food web module has provided mechanistic insights at each level, including, as we discuss in the succeeding paragraphs, how incorporating mutualism into food web modules can lead to previously not well-recognized community dynamics such as (+,−) indirect interactions; how the density-dependent dynamics of the food web module alone can lead to persistence of the module, rather than parasitic (cheater) species destabilizing the

module; and how differences in foraging biology and resource exploitation between mutualistic and parasitic species can alter their functional responses (e.g., BD vs MM), resulting in stability of mutualism–parasitism modules.

At the level of the food web module as a whole, we report fundamental dynamics of food webs previously not well established, namely, the emergence of (+,–) indirect interactions. That is, increases in the density of the mutualistic consumer ( $N_2$ ) increase the parasitic consumer's density ( $N_3$ ) through positive feedback on the density of the basal mutualist ( $N_1$ ); increases in the density of the parasitic consumer ( $N_3$ ) decrease the mutualistic consumer's density ( $N_2$ ) through negative feedback on the density of the basal mutualist ( $N_1$ ). For instance, increasing pollinator density has a positive indirect effect on nectar robber density by increasing plant density, and increasing nectar robber density has a negative indirect effect on pollinator density by decreasing plant density. While it has been suggested that food web modules involving predation and competition may lead to (+,–) indirect interactions (Menge 1995), here, we report that density-mediated (+,–) indirect interactions arise from food web modules involving mutualism. In fact, the (+,–) indirect interaction is a key property of the mutualism–parasitism food web module, akin to apparent competition, apparent mutualism, and exploitative competition, in which two consumer species of the same guild interact indirectly. In this way, the mutualism–parasitism food web module reveals basic insights into density-mediated indirect interactions in food webs.

Structural similarity between the mutualism–parasitism module (Fig. 1d) and that of exploitative competition (Fig. 1c), in which two consumers ( $N_2, N_3$ ) exploit a shared resource ( $N_1$ ), implies that mutualistic and parasitic consumers may not coexist. Yet, we have shown that density-dependent food web dynamics alone can lead to the persistence of the food web module, in contrast to prior studies that have focused on evolutionary mechanisms by which mutualistic species can control the parasitic (cheater) species. Instead of the parasitic consumer destabilizing the module through (–,–) indirect interactions, the ( $N_1, N_2$ )-mutualism actually favors persistence of the parasitic consumer in two general ways. First, if both pairwise interactions are governed by MM functional responses, for which stable limit cycles ensue, then the positive feedback of mutualism contributes to the size of the fluctuations of  $N_1$ , which in turn favors persistence of the parasitic consumer. Strong interaction strengths of mutualism ( $\alpha_{21}, \alpha_{12}$ ) enhance the persistence of parasitic consumers and the food web module as a whole. Saturating positive feedback of the functional responses of mutualism can enhance persistence of the mutualism–parasitism food web module through fluctuation-dependent stable limit cycles when both consumers have MM functional responses. A mutualism

described by its consumer–resource interactions is capable of supporting stable limit cycles, just like predator–prey systems, as shown in Fig. 2. In these limit cycles, the amplitude of the basal mutualist's cycle is increased by the positive feedback of the mutualism, which promotes two consumer persistence through the mechanism of fluctuation-dependent persistence (Fig. 4), specifically the relative nonlinearity of competition (Armstrong and McGehee 1976; Chesson 2000). This occurs when the mutualistic consumer is the superior competitor (i.e.,  $N_1^0 < N_1^\#$ ), as it has a higher growth rate for low densities of the basal mutualist and the parasitic consumer has a higher growth rate for higher values of the basal mutualist (Fig. 6). Yet, when these differences in the growth rates of the two consumers are reversed, such that the parasitic consumer is the superior competitor (i.e.,  $N_1^0 > N_1^\#$ ), the parasitic consumer is excluded for high values of  $\alpha_{12}$  and the mutualistic consumer is excluded for low values of  $\alpha_{12}$ . For values of  $\alpha_{12}$  close to a threshold between these two outcomes, quasi-stable persistence of the three species can occur. Nevertheless, imperceptibly slow changes in the amplitude of the basal mutualist are eventually amplified rapidly by the positive feedback, such that one of the two coexisting consumers may suddenly go to extinction (Fig. 7).

Second, rather than fluctuation-dependent persistence arising from both the mutualistic and parasitic consumers having MM functional responses, some mutualisms may have functional responses other than the MM or HT2. For BD functional responses, mutualistic consumers avoid previously exploited resources such as flowers by pollinators, so that the mutualist's foraging strategy leads to highly efficient resource exploitation at low to intermediate densities of itself, but self-limitation at high densities. As a result, resource exploitation by the parasitic consumer exceeds that of the mutualist at high densities of the mutualistic consumer. These attributes of resource exploitation arising from a BD function for the mutualistic consumer enables three-species coexistence in a stable equilibrium (Fig. 9b), for which positive feedback of mutualism increases parameter space over which the equilibrium exists. For example, the BD formulation requires very large (and possibly biologically unrealistic) interaction strengths ( $\alpha_{31}$ ) of parasitic consumers for the mutualistic consumer to become extinct (Fig. 9d) compared to MM formulations (Figs. 3 and 4). In addition to the BD form, other functional responses for the mutualistic consumer, such as ratio dependence, can lead to enhanced stability of the mutualism–parasitism food web module. For simplicity, we set other parameters for the effects of the two consumers on the resource to the same values. This situation should be explored for a wider range of parameters.

Ecological dynamics of the mutualism–parasitism food web module are consistent with the few other ecological studies that have examined the dynamics of three-species

coexistence in mutualism–parasitism interactions (Bronstein et al. 2003; Morris et al. 2003; Wilson et al. 2003; Lee and Inouye 2010). Morris et al. (2003) show that high intraspecific and interspecific competition facilitate coexistence between pollinating seed-eating mutualists and non-pollinating parasites. Competition leads to unexploited resources by one species which favors coexistence of the other without extinction arising from (–,–) indirect interactions. Wilson et al. (2003) show how spatial structure enhances coexistence of mutualistic and parasitic consumers through patch dynamics; unexploited resource patches make resources available to consumers preventing extinction. Lee and Inouye (2010) show coexistence between two mutualistic consumers (competitors) and a resource species. Both mutualistic consumers coexist through indirect interactions that arise via mutualistic feedbacks on resource attributes beyond that of density alone. Our results and these other recent studies of food web modules involving mutualism illustrate the importance of not extrapolating well-known results from one situation (exploitative competition) to another (mutualism–parasitism module) without taking into account the biology of the system of interest.

Key efforts have been made to integrate mutualism into community and ecosystem ecology (e.g., Odum and Biever 1984; Jordano 1987; Oksanen 1988; Polis and Strong 1996; Ringel et al. 1996; Stanton 2003; Agrawal et al. 2007; Goudard and Loreau 2008). Yet, we know little of mutualism's influence on community dynamics, as it has been largely omitted from traditional studies of food webs. The food web module approach remains relatively unexplored for mutualism, though a few other recent studies have provided some insights. In addition to the previously mentioned studies, Knight et al. (2005, 2006) showed that food chains with mutualism can lead to trophic cascades that deviate from standard top-down effects. In a three-species food chain, a top predator can decrease rather than increase the basal species by reducing the positive feedback of mutualism at the intermediate trophic level (pollination) on the basal species (plant). In a four-species food chain, mutualism can increase rather than decrease the basal trophic level, as shown by a fish reducing dragonfly abundance by consuming their larvae, which reduces dragonfly predation on insect pollinators and thereby increases plant pollination.

In addition to the food web module approach, there is the classic approach of examining large community matrices of species interactions (May 1974; Pimm 1982). Recent application of network theory in ecology has renewed interest in this approach to the many interactions (edges) among large numbers of species (nodes) comprising a community (network). One such study has shown that parasitic consumers of the mutualism–parasitism food web module are

common in networks (Genini et al. 2010). While the dynamics of food web modules may not be consistent with large community matrices, McCann (2012) and others have effectively shown that there is congruence between the two approaches, though the degree of congruence may vary with the extent to which modules are represented in community matrices (Bascompte and Melian 2005; Allesina and Pascual 2008; Kondoh 2008; Williams 2008; Stouffer and Bascompte 2010). The (+,–) indirect interactions of mutualism–parasitism food web modules may well contribute to the overall persistence of communities. Network analyses are certainly providing new insights into ecological communities in general and mutualistic ones in particular (e.g., Bascompte et al. 2003; Jordano et al. 2003; Bascompte and Jordano 2007; Okuyama and Holland 2008; Ings et al. 2009; Vázquez et al. 2009; Fontaine et al. 2011; Pires et al. 2011). We are only beginning to integrate mutualism with other forms of interaction within food webs and community matrices (Ings et al. 2009; Thebault and Fontaine 2010; Fontaine et al. 2011; Allesina and Tang 2012; Kefi et al. 2012). Yet, it is clear that, at both the level of the food web module and large complex networks, new structural and dynamical properties can emerge through the inclusion of mutualism.

**Acknowledgments** We thank W.F. Morris, S. Schreiber, and the anonymous reviewers for their comments which have improved this study. S.S. acknowledges support by the National Natural Science Foundation of China grant no. 31100277 and the Fundamental Research Funds for the Central Universities (lzujbky-2013-99). Y.W. acknowledges the support by NSFC of China grant no. 60736028, NSFC grant no. 11171355, and NSF of Guangdong Province S2012010010320. D.L.D. was supported by the US Geological Survey's Southeastern Ecological Science Center. J.N.H. and D.L.D. acknowledge the support from NSF grants DEB-0814523 and DEB-1147630.

#### **Appendix 1: derivation of Beddington–DeAngelis functional response for plant–pollinator interactions (Fishman and Hadany 2010)**

Fishman and Hadany (2010) modeled the interaction between plants and central place pollinators. They modeled the interactions on three time scales: handling of individual flowers on the scale of seconds, foraging bouts and nectar recovery on the scale of tens of minutes, and plant and pollinator population densities on the scale of years. The specific pollinator modeled, bees, are known to leave scent markers on visited plants. Until the scent wears off, bees reject the marked flowers. This has the benefit of preventing pollinators from wasting time on flowers in which the resources are depleted. Starting from an analysis of individual bee–flower interactions, and using the method of separation of time scales (Segel and Slemrod 1989) to derive equations for the long-term population dynamics of the pollinators and plants, Fishman and Hadany (2010) found the approximate

spatially implicit equations for plant–pollinator interactions, with a Beddington–DeAngelis (BD) functional response:

$$\frac{dx}{dt} = \left[ \frac{\eta\alpha y}{1 + \alpha x + \alpha\beta y} - B(x) \right] x \tag{12}$$

$$\frac{dy}{dt} = \left[ \frac{\mu\alpha x}{1 + \alpha x + \alpha\beta y} - D(y) \right] y \tag{13}$$

where  $x$  is the plant population size;  $y$  is the pollinator population size;  $\alpha = \frac{k_f k_a}{(k_p + k_u)(k_a + k_d)}$ ;  $\beta = k_p/k_r$ ;  $\eta$  is the rate constant describing the plant’s efficiency in translating plant–pollinator interactions into fitness;  $\mu$  is the rate constant describing the pollinator’s efficiency in translating plant–pollinator interactions into fitness;  $k_a$  is the rate constant with which pollinators arrive at the foraging patch ( $\approx 1/h$ );  $k_d$  is the rate constant with which pollinators depart the foraging patch ( $\approx 1/\text{tens of minutes}$ );  $k_f$  is the rate constant for the pollinator’s visits to individual flowers ( $\approx 1/s$ );  $k_m$  is the rate constant for pollinators rejecting a marked flower ( $\approx 1/s$ );  $k_p$  is the rate constant for productive plant–pollinator interaction proportional to the inverse of the flower-handling time ( $\approx 1/s$ );  $k_r$  is the rate coefficient of nectar recovery and fading of marks ( $\approx 1/\text{tens of minutes}$ );  $k_u$  is the rate constant for nonproductive plant–pollinator interactions, wherein a pollinator departs from an unmarked flower without collecting a reward ( $\approx 1/s$ ); and,  $B(x)$  and  $D(y)$  are the loss rates.

The efficiency of individual pollinators,  $\mu$ , is enhanced by their avoiding marked flowers. At high pollinator densities, however, the efficiency of the population decreases because the  $\alpha\beta y$  term, which is larger the slower the rate of fading of the marker, effectively acts like mutual interference. Hence, by using a device that allows the individual pollinators to avoid flowers that are relatively depleted in resources, individual bees gain efficiency. At low bee numbers, that efficiency is shared by all of the foragers, but as the number of foragers increases, the  $\alpha\beta y$  term decreases the rate at which the foragers land on flowers. This has implications for coexistence of a pollinator with another consumer population that does not discriminate among resources. Consider the two species system invaded by a third species, whose density is  $z$ . If the invader does not discriminate in exploitation of resources, then the equations describing the system are:

$$\frac{dx}{dt} = \left[ \frac{\eta\alpha y}{1 + \alpha x + \alpha_1\beta_1 y} - B(x) \right] x \tag{14}$$

$$\frac{dy}{dt} = \left[ \frac{\mu_1\alpha_1 x}{1 + \alpha_1 x + \alpha_1\beta_1 y} - D_1(y) \right] y \tag{15}$$

$$\frac{dz}{dt} = \left[ \frac{\mu_2\alpha_2 x}{1 + \alpha_2 x} - D_2(z) \right] z \tag{16}$$

Following Fishman and Hadany (2010), the time spent on individual flowers by individual foragers is so small that there is no direct interference of either forager species with itself or with the other forager species, so only forager density-dependent terms in the denominators comes from the discrimination of flowers. Foraging on nectar-rich flowers, the pollinator, at low densities, is more efficient than the invading forager, i.e.,  $\mu_1 > \mu_2$ . It is a well-known result that, if  $\beta_1 = 0$ , then at equilibrium, Eqs. 15 and 16 can be solved to give different values for  $x$ :

$$x_1^* = \frac{D_1}{\alpha_1(\mu_1 - D_1)} \quad x_2^* = \frac{D_2}{\alpha_2(\mu_2 - D_2)}.$$

Because  $\mu_1 > \mu_2$ , we have  $x_1^* < x_2^*$ , which means that  $x_2$  goes to extinction. This does not necessarily happen, however, when  $\beta_1 > 0$ , as shown in the main text.

Literature cited

Fishman MA, Hadany L (2010) Plant–pollinator population dynamics. *Theoretical Population Biology* 78:270–277

Segel LA, Slemrod M (1989) The quasi-steady state assumption: a case study in perturbation. *SIAM Review* 31:446–477

**Appendix 2: analytical solutions and mathematical proofs for the community dynamics of the parasitism–mutualism food web module**

In the paper, we presented formulations of the mutualism–parasitism food web module with Eqs. 1, 2, and 3 based on MM functions describing the mutualistic and parasitic consumers and Eqs. 4, 5, and 6 based on BD functions for the  $(N_1, N_2)$ -mutualism. Here, we first present the analytical solutions and mathematical proofs for Eqs. 4, 5, and 6 and then those for Eqs. 1, 2, and 3, as it was easier to derive the simpler solutions of Eqs. 1, 2, and 3 from those of Eqs. 4, 5, and 6.

BD formulations of the food web module

For the system as a whole, we examined initial value conditions of  $N_1(0) \geq 0$ ,  $N_2(0) \geq 0$ , and  $N_3(0) \geq 0$ , for which the solutions are non-negative. It follows from Eq. 4 that  $dN_1/dt \leq N_1(r_1 + \alpha_{12}/b - d_1N_1)$ , thus the comparison principle (Cosner 1996) implies that  $\limsup_{t \rightarrow \infty} N_1(t) \leq (br_1 + \alpha_{12})/bd_1$ . Then for  $\delta > 0$  small,

we have  $N_1(t) \leq [(br_1 + \alpha_{12})/bd_1] + \delta$  when  $t$  is sufficiently large. Let,  $d_0 = \min\{d_2, d_3\}$ . By Eqs. 4, 5, and 6, we have:

$$\begin{aligned} & \frac{d}{dt} \left( N_1 + \frac{\alpha_{12}}{\alpha_{21}} N_2 + \frac{\beta_2}{\alpha_{31}} N_3 \right) \\ &= N_1 \left( r_1 - d_1 N_1 \right) + \left( \frac{2\alpha_{12} N_1 N_2}{1 + aN_1 + bN_2} \right) - \left( \frac{\beta_1 N_1 N_2}{e_1 + N_1} \right) - \frac{\alpha_{12}}{\alpha_{21}} d_2 N_2 - \frac{\beta_2}{\alpha_{31}} d_3 N_3 \\ &\leq N_1 \left( r_1 \frac{2\alpha_{12}}{b} \right) - d_0 \left( \frac{\alpha_{12}}{\alpha_{21}} N_2 + \frac{\beta_2}{\alpha_{31}} N_3 \right) \\ &\leq \left( \frac{br_1 + \alpha_{12}}{bd_1} + \delta \right) \left( d_0 + r_1 + \frac{2\alpha_{12}}{b} \right) - d_0 \left( N_1 + \frac{\alpha_{12}}{\alpha_{21}} N_2 + \frac{\beta_2}{\alpha_{31}} N_3 \right). \end{aligned}$$

Again, using the comparison theorem of Cosner (1996), we have:

$$\limsup_{t \rightarrow \infty} \left( N_1 + \frac{\alpha_{12}}{\alpha_{21}} N_2 + \frac{\beta_2}{\alpha_{31}} N_3 \right) \leq \frac{1}{d_0} \left( \frac{br_1 + \alpha_{12}}{bd_1} + \delta \right) \left( d_0 + r_1 + \frac{2\alpha_{12}}{b} \right)$$

which implies that solutions of Eqs. 4, 5, and 6 are bounded. It follows from Eq. 5 that  $dN_2/dt \leq 0$  if  $d_2 \geq \alpha_{21}/a$ . By the Lyapunov Theorem (Hofbauer and Sigmund 1998), we have  $\lim_{t \rightarrow \infty} N_2(t) = 0$  and  $\lim_{t \rightarrow \infty} N_3(t) = 0$  if  $d_3 \geq \alpha_{31}$ . For this reason, we focused persistence of the system by assuming  $d_2 < \alpha_{21}/a$  and  $d_3 > \alpha_{31}$ . In the absence of  $N_1$ , both  $N_2$  and  $N_3$  go to extinction, thus we first examine the two subsystems of the  $(N_1, N_2)$ -mutualism and the  $(N_1, N_3)$ -parasitism, and then the persistence of the  $(N_1, N_2, N_3)$  food web module as a whole.

$(N_1, N_2)$ -mutualism

The  $(N_1, N_2)$ -mutualism, independent of the parasitism, is described by the two equations:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 + \left( \frac{\alpha_{12} N_1 N_2}{1 + aN_1 + bN_2} \right) - \left( \frac{\beta_1 N_1 N_2}{e_1 + N_1} \right) - d_1 N_1^2 \\ \frac{dN_2}{dt} &= \left( \frac{\alpha_{21} N_1 N_2}{1 + aN_1 + bN_2} \right) - d_2 N_2 \end{aligned}$$

Let  $l_i$  denote the zero-growth isoclines of  $N_i$  in the positive region, where  $i=1, 2$ :

$$\begin{aligned} l_1 : f_1(N_1, N_2) &= r_1 + \left( \frac{\alpha_{12} N_2}{1 + aN_1 + bN_2} \right) - \left( \frac{\beta_1 N_2}{e_1 + N_1} \right) - d_1 N_1 \\ l_2 : f_2(N_1, N_2) &= \left( \frac{\alpha_{21} N_1}{1 + aN_1 + bN_2} \right) - d_2 \end{aligned}$$

$l_1$  and the  $N_1$ -axis intersect at  $O_1(r_1/d_1, 0)$ .  $O_1$  is an equilibrium of the  $(N_1, N_2)$ -mutualism and is stable on the  $N_1$ -axis.  $l_1$  and the  $N_2$ -axis intersect at  $Q(0, N_2)$ , which satisfies:

$$0 = \frac{b\beta_1}{e_1} N_2^2 + \left( \frac{\beta_1}{e_1} - \alpha_{12} - br_1 \right) N_2 - r_1$$

As  $b\beta_1/e_1 > 0$  and  $-r_1 < 0$ , one root of the  $(N_1, N_2)$ -mutualism is positive and the other is negative, which correspond to the two intersection points  $Q^+(0, q^+)$  and  $Q^-(0, q^-)$ .  $l_2$  and the  $N_1$ -axis intersect at  $(N_1^0, 0)$  with  $N_1^0 = d_2/(\alpha_{21} - ad_2) = N_{1,m}^* \cdot l_2$  and the  $N_2$ -axis intersect at  $(0, -1/b)$ .

Because we focus on parasitic nectar robbers' invasion into plant–pollinator systems, we assume that the pollinators (i.e., pollination mutualism) can persist in the plant–pollinator system when there are no nectar robbers, that is,  $N_1^0 < r_1/d_1$ . Similar reasoning can also be applied to the situation in which  $N_1^0 < r_1/d_1$  when the pollinators with high initial densities can survive in the plant–pollinator system. When  $N_1^0 < r_1/d_1$ , there is a unique positive equilibrium  $E_{12}(N_1^+, N_2^+)$  of the  $(N_1, N_2)$ -mutualism. Let  $E_{12}(N_1, N_2)$  be the intersections of  $l_1$  and  $l_2$ . By  $f_2(N_1, N_2)=0$ , we obtain  $N_1 = N_1^0(bN_2 + 1)$ . By  $f_1(N_1, N_2)=0$ , we obtain:

$$g(N_2) = AN_2^3 + BN_2^2 + CN_2 + E = 0$$

where  $A = d_1 b_3 N_1^{03}$  and  $E = -(r_1 - d_1 N_1^0) N_1^0 (e_1 + N_1^0)$ . Since  $A > 0$  and  $E < 0$ , there is at least one positive root of  $g(N_2)$ , and as will be shown next, there is a negative root  $g(N_2)$ , indicating that the third root is also negative and the positive root is unique. As  $g(0)=E < 0$  and  $g(q^+) = g(q^-) = 0$ ,  $O(0, 0)$  is between  $Q^+$  and  $Q^-$  on the  $N_2$ -axis. By  $g(-1/b) = -\alpha_{12}/b < 0$ , the point  $(0, -1/b)$  is also between  $Q^+$  and  $Q^-$ . The isocline  $l_1$  can be rewritten as:

$$\begin{aligned} l_1^0 : (r_1 - d_1 N_1)(e_1 + N_1)(1 + aN_1 + bN_2) + a_{12} N_2 (e_1 + N_1) \\ - \beta_1 N_2 (1 + aN_1 + bN_2) = 0. \end{aligned}$$

Thus, the points  $(-e_1, 0)$  and  $(-e_1, (ae_1 - 1)/b)$  are on  $l_1^0 \cdot l_1^0$  is a continuous line linking the points  $(-e_1, 0)$  and  $Q^-$ . Because  $(0, 1/b)$  is above  $Q^-$ , there is an intersection point of  $l_1$  and  $l_2$  in the region  $N_1 < 0, N_2 < 0$ . Thus, there is a negative root of  $g(N_2)$ , and the positive equilibrium of the  $(N_1, N_2)$ -mutualism is unique.

On the  $N_1, N_2$ -plane, the equilibrium  $O(0, 0)$  is a saddle with eigenvalues  $r_1$  and  $-d_2$ . When  $N_1^0 < r_1/d_1$  holds, we obtain  $f_2(r_1/d_1, 0) > f_2(N_1^0, 0) = 0$ . Thus,  $O_1$  is a saddle with eigenvalues  $-r_1$  and  $f_2(r_1/d_1, 0) > 0$ . Solutions of the  $(N_1, N_2)$ -mutualism are bounded. Hence, every positive solution of the  $(N_1, N_2)$ -mutualism either converges to  $E_{12}$  or to a periodic orbit  $E_\Phi(\phi_1(t), \phi_2(t))$ . It follows from the Poincaré–Bendixson Theorem that there is a periodic orbit when  $E_{12}$  is unstable. Since the right-hand side of the equations for the  $(N_1, N_2)$ -mutualism is analytic, the number of periodic orbits  $E_\Phi$  is limited. While the number of  $E_\Phi$  is not determined here, constraints on  $E_\Phi$  in the following analyses are effective for each of the periodic orbits.

$(N_1, N_3)$ -parasitism

The  $(N_1, N_3)$ -parasitism, independent of mutualism, is described by the two equations:

$$\frac{dN_1}{dt} = r_1 N_1 - \left( \frac{\beta_2 N_1 N_3}{e_2 + N_1} \right) - d_1 N_1^2$$

$$\frac{dN_3}{dt} = \left( \frac{\alpha_{31} N_1 N_3}{e_2 + N_1} \right) - d_3 N_3$$

The dynamics of this parasite–host system are well understood and follow classic Rosenzweig–MacArthur predator–prey dynamics, including having a positive globally stable  $(N_1, N_3)$ -equilibrium, extinction of the parasitic species, a globally stable equilibrium of the host, and an unstable equilibrium with limit cycles (Rosenzweig and MacArthur 1963; Rosenzweig 1971, Kuang and Freedman 1988). Briefly, these proofs include the following. There is a positive equilibrium  $E_{13}(N_1^\#, N_3^\#)$  if  $d_3 < r_1 \alpha_{31} / (r_1 + d_1 e_2)$ , where  $N_1^\# = d_3 e_2 / (\alpha_{31} - d_3)$  and  $N_3^\# = \alpha_{31} N_1^\# (r_1 - d_1 N_1^\#) / \beta_2 d_3$ . Second, if  $d_3 \geq r_1 \alpha_{31} / (r_1 + d_1 e_2)$ , then the equilibrium  $(r_1/d_1, 0)$  is globally stable. Third,  $E_{13}$  is globally stable if:

$$\frac{(r_1 - d_1 e_2) \alpha_{31}}{r_1 + d_1 e_2} \leq d_3 \leq \frac{r_1 \alpha_{31}}{r_1 + d_1 e_2}.$$

Yet, if:

$$d_3 < \frac{(r_1 - d_1 e_2) \alpha_{31}}{r_1 + d_1 e_2},$$

then  $E_{13}$  is unstable and there is a unique globally stable limit cycle,  $E_\Psi(\psi_1(t), \psi_3(t))$  (except for the stable equilibrium  $E_{13}$ ).

$(N_1, N_2, N_3)$ -mutualism–parasitism food web module

We examined the persistence of the food web module of Eqs. 4, 5, and 6, showing that community dynamics have boundaries and equilibria in the positive octant. Let  $F(N_1, N_2, N_3)$ ,  $G(N_1, N_2, N_3)$ , and  $H(N_1, N_2, N_3)$  denote functions on the right-hand side of Eqs. 4, 5, and 6, respectively, such that the Jacobian matrix is as follows:

$$J(N_1, N_2, N_3) = \begin{pmatrix} F_1 & F_2 & F_3 \\ G_1 & G_2 & 0 \\ H_1 & 0 & H_3 \end{pmatrix}, \text{ where}$$

$$F_1 = r_1 - 2d_1 N_1 + \frac{\alpha_{12} N_2}{1 + aN_1 + bN_2} - \frac{\beta_1 N_2}{e_1 + N_1} - \frac{\beta_2 N_3}{e_2 + N_1} + N_1 \left[ -\frac{a\alpha_{12} N_2}{(1 + aN_1 + bN_2)^2} + \frac{\beta_1 N_2}{(e_2 + N_1)^2} \right]$$

$$F_2 = \frac{\alpha_{12} N_2 (1 + aN_1)}{(1 + aN_1 + bN_2)^2} - \frac{\beta_1 N_1}{e_1 + N_1}$$

$$F_3 = \frac{\beta_2 N_1}{e_2 + N_1}$$

$$G_1 = \frac{\alpha_{21} N_2 (1 + bN_2)}{(1 + aN_1 + bN_2)^2}$$

$$G_2 = -d_2 + \frac{\alpha_{21} N_1}{1 + aN_1 + bN_2} + \frac{b\alpha_{21} N_1 N_2}{(1 + aN_1 + bN_2)^2}$$

$$H_1 = \frac{e_2 \alpha_{31} N_3}{(e_2 + N_1)^2}$$

$$H_3 = -d_2 + \frac{\alpha_{31} N_1}{e_2 + N_1}$$

Equilibria and periodic orbits can occur within the boundaries of the positive octant. First, equilibrium  $O(0,0,0)$  is a saddle point with eigenvalues  $r_1, -d_2$ , and  $-d_3$ . The  $(N_2, N_3)$ -plane is the stable subspace and the  $N_1$ -axis is the unstable subspace. Second, equilibrium  $P_1(r_1/d_1, 0, 0)$  always exists with eigenvalues:

$$\lambda_1^{(1)} = -r_1 < 0, \quad \lambda_2^{(1)} = -d_2 + \frac{\alpha_{21} r_1}{d_1 + ar_1}, \quad \lambda_3^{(1)} = -d_3 + \frac{\alpha_{31} r_1}{r_1 + d_1 e_2}.$$

Here,  $\lambda_i^{(j)}$  denotes the eigenvalue of equilibrium  $P^{(j)}$  in the  $N_i$ -axis. If  $\lambda_2^{(1)} > 0$  and  $\lambda_3^{(1)} > 0$ , then  $P_1$  is a saddle point for which the  $N_1$ -axis is the stable subspace and the  $(N_2, N_3)$ -plane is the unstable subspace.

Third, the equilibrium  $P_{12}(N_1^+, N_2^+, 0)$  exists if  $\lambda_2^{(1)} > 0$ . Its eigenvalue in the  $N_3$ -axis is:

$$\lambda_3^{(12)} = -d_3 + \frac{\alpha_{31} N_1^+}{e_2 + N_1^+}$$

where  $N_1^+$  is the unique positive solution of  $g(N_2)$ . When there is a periodic orbit  $P_\Phi(\phi_1(t), \phi_2(t))$  on the  $(N_1, N_2)$ -plane, its stability is determined by Floquet multipliers (Klausmeier 2008) of the variational system:

$$\frac{d\Phi(t)}{dt} = J(\phi_1(t), \phi_2(t), 0)\Phi(t), \quad \Phi(0) = I$$

where  $J(N_1, N_2, N_3)$  is given above and  $I$  is the  $3 \times 3$  identity matrix. Let  $T$  denote the period of  $P_\Phi(t)$ . The Floquet multiplier in the  $N_3$ -axis is:

$$\exp \left[ \frac{1}{T} \int_0^T \left( -d_3 + \frac{\alpha_{31} \phi_1(t)}{e_2 + \phi_1(t)} \right) dt \right].$$

Thus, if:

$$\lambda_3^{(\Phi)} = -d_3 + \frac{1}{T} \int_0^T \frac{\alpha_{31} \phi_1(t)}{e_2 + \phi_1(t)} dt > 0,$$

then  $P_\Phi(t)$  is unstable in the  $N_3$ -axis direction. Fourth, equilibrium  $P_{13}(N_1^\#, 0, N_3^\#)$  exists if  $\lambda_3^{(1)} > 0$ , where  $N_1^\#$  and  $N_3^\#$  are given previously. The eigenvalue of  $P_{13}(N_1^\#, 0, N_3^\#)$  in the  $N_2$ -axis is:

$$\lambda_2^{(13)} = -d_2 + \frac{\alpha_{21}N_1^\#}{1 + aN_1^\#}.$$

Thus, if  $\lambda_2^{(13)} > 0$  and the following condition holds:

$$\frac{(r_1 - d_1e_2)\alpha_{31}}{r_1 + d_1e_2} \leq d_3 \leq \frac{r_1\alpha_{31}}{r_1 + d_1e_2},$$

then  $P_{13}$  is a saddle point for which the  $(N_1, N_3)$ -plane is the stable subspace and the  $N_2$ -axis is the unstable subspace.

Yet, if  $\lambda_2^{(13)} > 0$  and the following condition holds:

$$d_3 < \frac{(r_1 - d_1e_2)\alpha_{31}}{r_1 + d_1e_2},$$

then  $P_{13}$  is an unstable node, for which  $(N_1, N_3)$ -plane and  $N_2$ -axis are both unstable subspaces.

The periodic orbit  $P_\Psi(\psi_1(t), 0, \psi_3(t))$  exists when the second of the two previous conditions holds, where  $\psi_1(t)$  and  $\psi_3(t)$  are given previously. Because  $P_\Psi(t)$  is stable in the  $(N_1, N_3)$ -plane, we only need to consider its stability in the  $N_2$ -axis, which is determined by the Floquet multipliers of the variational system:

$$\frac{d\psi(t)}{dt} - J(\psi_1(t), 0, \psi_3(t))\Psi(t), \quad \Psi(0) = 1,$$

where  $J(N_1, N_2, N_3)$  is given previously and  $I$  is the  $3 \times 3$  identity matrix. Let  $T$  denote the period of  $P_\Psi(t)$ . The Floquet multiplier in the  $N_2$ -axis is:

$$\exp\left[\frac{1}{T} \int_0^T \left(-d_2 + \frac{\alpha_{21}\psi_1(t)}{1 + a\psi_1(t)}\right) dt\right]$$

Thus, if:

$$\lambda_2^{(\Psi)} = -d_2 + \frac{1}{T} \int_0^T \frac{\alpha_{21}\psi_1(t)}{1 + a\psi_1(t)} dt > 0,$$

then  $P_\Psi(t)$  is unstable in the  $N_2$ -axis direction. If  $\lambda_2^{(\Psi)} < 0$ , then it is asymptotically stable. The persistence of the  $(N_1, N_2, N_3)$ -mutualism–parasitism food web module can be described as follows. When  $\lambda_2^{(1)} > 0$  and  $\lambda_3^{(1)} > 0$ , then  $P_1$  is a saddle point and equilibria  $P_{12}$  and  $P_{13}$  exist. If  $\lambda_3^{(12)} > 0$  and  $\lambda_3^{(\Phi)} > 0$  for each  $P_\Phi$ , then  $P_{12}$  and  $P_\Phi$  are unstable in the  $N_3$ -axis. If  $\lambda_2^{(13)} > 0$  and the following condition holds:

$$\frac{(r_1 - d_1e_2)\alpha_{31}}{r_1 + d_1e_2} \leq d_3 \leq \frac{r_1\alpha_{31}}{r_1 + d_1e_2},$$

then  $P_{13}$  is a saddle point where the  $(N_1, N_3)$ -plane is the stable subspace and the  $N_2$ -axis is the unstable subspace. If  $\lambda_2^{(13)} > 0, \lambda_2^{(\Psi)} > 0$ , and the following holds:

$$d_3 < \frac{(r_1 - d_1e_2)\alpha_{31}}{r_1 + d_1e_2},$$

then  $P_{13}$  and  $P_\Psi(t)$  are unstable, where the  $(N_1, N_3)$ -plane is the stable subspace and the  $N_2$ -axis is the unstable subspace. Thus, the boundary equilibria and periodic orbits cannot form a heteroclinic cycle. It follows from the Acyclicity Theorem (Butler et al. 1986, Butler and Waltman 1986) that the persistence of the  $(N_1, N_2, N_3)$ -mutualism–parasitism food web module is guaranteed, as will be shown next.

Assuming  $\lambda_2^{(1)} > 0$  and  $\lambda_3^{(1)} > 0$ , then the  $(N_1, N_2, N_3)$ -mutualism–parasitism food web module is uniformly persistent if one of the two following conditions is satisfied. First,  $\lambda_2^{(13)} > 0, \lambda_3^{(12)} > 0, \lambda_3^{(\Phi)} > 0$ , and the following holds:

$$\frac{(r_1 - d_1e_2)\alpha_{31}}{r_1 + d_1e_2} \leq d_3 \leq \frac{r_1\alpha_{31}}{r_1 + d_1e_2}.$$

Second,  $\lambda_2^{(13)} > 0, \lambda_3^{(12)} > 0, \lambda_3^{(\Phi)} > 0, \lambda_2^{(\Psi)} > 0$ , and the following holds:

$$d_3 < \frac{(r_1 - d_1e_2)\alpha_{31}}{r_1 + d_1e_2}.$$

It follows from the boundedness of the solutions and uniform persistence that there is a positive equilibrium  $P^*(N_1^*, N_2^*, N_3^*)$  (Butler et al. 1986), where:

$$N_1^* = \frac{d_3e_2}{\alpha_{31} - d_3} (= N_1^\#)$$

$$N_2^* = \frac{(\alpha_{21} - ad_2)N_1^* - d_2}{bd_2}$$

$$N_3^* = \frac{e_2 + N_1^*}{\beta_2} \left[ r_1 - d_1N_1^* + \frac{\alpha_{12}N_2^*}{1 + aN_1^* + bN_2^*} - \frac{\beta_1N_2^*}{e_1 + N_1^*} \right]$$

The Jacobian matrix of  $P^*$  is:

$$J^* = \begin{pmatrix} F_1^* & F_2^* & F_3^* \\ G_1^* & G_2^* & 0 \\ H_1^* & 0 & 0 \end{pmatrix}, \text{ where}$$

$$F_1^* = N_1^* \left[ -d_1 - \frac{a\alpha_{12}N_2^*}{(1 + aN_1^* + bN_2^*)^2} + \frac{\beta_1N_2^*}{(e_1 + N_1^*)^2} + \frac{\beta_2N_3^*}{(e_2 + N_1^*)^2} \right]$$

$$F_2^* = \frac{\alpha_{12}N_2^*(1 + aN_1^*)}{(1 + aN_1^* + bN_2^*)} - \frac{\beta_1N_1^*}{e_1 + N_1^*}$$

$$F_3^* = \frac{\beta_2N_1^*}{e_2 + N_1^*} < 0$$

$$G_1^* = \frac{\alpha_{21}N_2^*(1 + bN_2^*)}{(1 + aN_1^* + bN_2^*)^2} > 0$$

$$G_2^* = -\frac{b\alpha_{21}N_1^*N_2^*}{(1 + aN_1^* + bN_2^*)^2} < 0$$

$$H_1^* = \frac{e_2\alpha_{31}N_3^*}{(e_2 + N_1^*)^2} > 0$$

The characteristic equation is  $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ , where:

$$a_1 = -(F_1^* + G_2^*), \quad a_2 = F_1^*G_2^* - H_1^*F_3^* - G_1^*F_2^*, \quad a_3 = H_1^*G_2^*F_3^* > 0$$

Because  $a_3 > 0$ , it follows from the Routh–Hurwitz criteria that the stability of  $P^*$  can be determined. If:

$$a_1 = -(F_1^* + G_2^*) > 0,$$

$$a_1a_2 - a_3 = F_1^*(H_1^*F_3^* + G_1^*F_2^* - F_1^*G_2^*) + G_2^*(G_1^*F_2^* - F_1^*G_2^*) > 0,$$

then the positive equilibrium  $P^*$  is asymptotically stable.

### MM formulations of the food web module

Having presented solutions for the mathematically more complex scenario involving BD functions, we now present the analytical solutions and mathematical proofs for Eqs. 1, 2, and 3 based on MM functions describing the  $(N_1, N_2)$ -mutualism. Note that the dynamics of Eqs. 1, 2, and 3 on the  $(N_1, N_3)$ -plane are the same as those presented previously, and all orbits on the  $(N_2, N_3)$ -plane converge to  $(0, 0)$ . Thus, we only present the solutions for the  $(N_1, N_2)$ -mutualism and the  $(N_1, N_2, N_3)$  food web module as a whole for Eqs. 1, 2, and 3).

#### $(N_1, N_2)$ -mutualism

The  $(N_1, N_2)$ -mutualism is described by the two equations:

$$\frac{dN_1}{dt} = N_1 \left( r_1 - d_1N_1 + \frac{\alpha_{12}N_2}{h_1 + N_2} - \frac{\beta_1N_2}{e_1 + N_1} \right)$$

$$\frac{dN_2}{dt} = N_2 \left( -d_2 + \frac{\alpha_{21}N_1}{e_1 + N_1} \right)$$

We denote the isoclines in the positive region as follows:

$$l_1 : r_1 - d_1N_1 + \frac{\alpha_{12}N_2}{h_1 + N_2} - \frac{\beta_1N_2}{e_1 + N_1} = 0, \quad l_2 : -d_2 + \frac{\alpha_{21}N_1}{e_1 + N_1} = 0.$$

Then, the  $l_1$  and the  $N_1$ -axis intersect at  $(r_1/d_1, 0)$  and the  $l_2$  and the  $N_1$ -axis intersect at  $(N_1^{**}, 0)$  with

$N_1^{**} = d_2e_1/(\alpha_{21} - d_2)$ , where we assume  $\alpha_{21} - d_2 > 0$  previously for Eqs. 4, 5, and 6. As we focus on parasitic consumers invading pairwise mutualism, we assume the persistence of the mutualistic consumers ( $N_2$ ), that is,  $N_1^{**} < r_1/d_1$ . Indeed, when  $N_1^{**} < r_1/d_1$ , equilibrium  $(r_1/d_1, 0)$  is locally asymptotically stable and the mutualistic consumers with low initial densities go to extinction.  $l_1$  and  $l_2$  intersect at  $(N_1^{**}, N_2^{**})$ , where  $N_2^{**}$  satisfies:

$$\frac{\beta_1}{e_1 + N_1^{**}}N_2^2 + \left[ \frac{\beta_1h_1}{e_1 + N_1^{**}} - \alpha_{12} - (r_1 - d_1N_1^{**}) \right] N_2 - (r_1 - d_1N_1^{**})h_1 = 0.$$

Since  $(r_1 - d_1N_1^{**})h_1 < 0$ , there is a unique positive root of the equation. Thus, there is a unique positive equilibrium  $E_{12}(N_1^{**}, N_2^{**})$  of the model on the  $(N_1, N_2)$ -plane.

Similar to the previous discussion for Eqs. 8, 9, and 10, equilibria  $(0, 0)$  and  $(r_1/d_1, 0)$  are saddles and every positive solution of the  $(N_1, N_2)$ -mutualism either converges to  $E_{12}$  or to a periodic orbit  $E_\Phi(\varphi_1(t), \varphi_2(t))$  and the number of periodic orbits  $E_\Phi$  is limited. These dynamical properties of the  $(N_1, N_2)$ -mutualism are similar to those in Fig. 2, while the unique difference is that the isocline  $l_2$  here is a vertical line.

#### $(N_1, N_2, N_3)$ -mutualism–parasitism food web module

We focused on the persistence of Eqs. 1, 2, and 3, while properties of equilibria  $O(0, 0, 0)$  and  $P_1(r_1/d_1, 0, 0)$  are the same as those for Eqs. 4, 5, and 6. First, the equilibrium  $P_{12}(N_1^{**}, N_2^{**}, 0)$  exists if  $N_1^{**} < r_1/d_1$ . Its eigenvalue in the  $N_3$ -axis direction is:

$$\lambda_3^{(12)} = -d_3 + \frac{\alpha_{31}N_1^*}{e_2 + N_1^*} = \frac{(\alpha_{31} - d_3)(N_1^* - N_1^\#)}{e_2 + N_2^*}$$

where  $N_1^\#$  is given previously for Eqs. 8, 9, and 10. When there is a periodic orbit  $P_\Phi$  on the  $(N_1, N_2)$ -plane, its stability is determined by its Floquet multiplier in the  $N_3$ -axis direction. That is, if:

$$\lambda_3^{(\Phi)} = -d_3 + \frac{1}{T} \int_0^T \frac{\alpha_{31}\Phi_1(t)}{e_2 + \Phi_1(t)} dt > 0,$$

then  $P_\Phi$  is unstable in the  $N_3$ -axis direction. Second, equilibrium  $P_{13}(N_1^\#, 0, N_2^\#)$  exists if  $\lambda_3^{(1)} > 0$  as shown for Eqs. 8, 9, and 10. The eigenvalue of  $P_{13}$  in the  $N_2$ -axis direction is:

$$\lambda_2^{(13)} = -d_2 + \frac{a_{21}N_1^\#}{e_1 + N_1^\#} = \frac{(\alpha_{21} - d_2)(N_1^\# - N_1^*)}{e_1N_1^\#}.$$

When  $N_1^{**} = N_1^\#$ , a direct computation shows that:

$$\frac{dN_3}{dN_2} = \frac{(e_1 + N_1)}{(e_2 + N_1)_2} \leq C_2$$

Because the plants ( $N_1(t)$ ) always persist in the three-species system, there exist positive constants  $C_1$  and  $C_2$  such that:

$$C_1 \leq \frac{(e_1 + N_1)}{(e_2 + N_1)_2} \leq C_2.$$

That is:

$$c_0 N_2^{d_3 C_1 / d_2} \leq N_3 \leq c_0 N_2^{d_3 C_2 / d_2}, \quad c_0 > 0,$$

which means that  $N_2$  and  $N_3$  always coexist, as shown in Fig. 3.

On the other hand, when  $N_1^{**} \neq N_1^\#$ , we have  $\lambda_3^{(12)} \lambda_2^{(31)} < 0$ . That is, either  $P_{12}$  or  $P_{13}$  has a stable manifold in the positive cone, which means that the three-species system cannot persist when their initial densities are on the stable manifold. In this situation, the three species can coexist when limit cycles occur on the coordinate planes and initial densities of the three species are not on the stable manifold, as shown in Fig. 6. Since the boundary equilibrium  $P_{12}$  or  $P_{13}$  has stable manifold in the positive cone, species coexistence depends on initial densities and limit cycle stability. Analyzing such coexistence is not within persistence theory and is not easy to prove.

#### Literature cited

Butler GJ, Waltman P (1986) Persistence in dynamical systems. *Journal of Differential Equations* 63:255–263

Butler GJ, Freedman HI, Waltman P (1986) Uniformly persistent systems. *Proceedings of the American Mathematical Society* 96:425–430

Cosner C (1996) Variability, vagueness and comparison methods for ecological models. *Bulletin of Mathematical Biology* 58:207–246

Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge

Klausmeier CA (2008) Floquet theory: a useful tool for understanding nonequilibrium dynamics. *Theoretical Ecology* 1:153–161

Kuang Y, Freedman HI (1988) Uniqueness of limit cycles in Gause-type predator–prey systems. *Mathematical Biosciences* 88:67–84

Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387

Rosenzweig ML, MacArthur RH (1963) Graphical representation and stability conditions of predator–prey systems. *American Naturalist* 97:209–223

#### References

Abrams PA, Ginzburg LR (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol Evol* 15:337–341

Agrawal AA, Ackerly DD, Adler F, Arnold AE, Cáceres C, Doak DF, Post E, Hudson PJ, Maron J, Mooney KA, Power M, Schemske DW, Stachowicz J, Strauss SY, Turner MG, Werner E (2007) Filling key gaps in population and community ecology. *Front Ecol Environ* 5:145–152

Allesina S, Pascual M (2008) Network structure, predator–prey modules, and stability in large food webs. *Theor Ecol* 1:55–64

Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483:205–208

Armstrong RA, McGehee R (1976) Coexistence of species competing for shared resources. *Theoretical Population Dynamics* 9:317–328

Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211:1390–1396

Bascompte J, Melian CJ (2005) Simple trophic modules for complex food webs. *Ecology* 86:2868–2873

Bascompte J, Jordano P (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annu Rev Ecol Evol Syst* 38:567–593

Bascompte J, Jordano P, Melianand CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. *Proc Natl Acad Sci USA* 100:9383–9387

Beddington JR (1975) Mutual interference between parasites or predators and its effect on searching efficiency. *J Anim Ecol* 44:331–430

Bronstein JL (2001) The exploitation of mutualisms. *Ecol Lett* 4:277–287

Bronstein JL, Wilson WG, Morris WF (2003) Ecological dynamics of mutualist/antagonist communities. *Am Nat* 162:S24–S39

Bull JJ, Rice WR (1991) Distinguishing mechanisms for the evolution of cooperation. *J Theor Biol* 149:63–74

Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366

Crowley PH, Cox JJ (2011) Intraguild mutualism. *Trends Ecol Evol* 26:627–633

DeAngelis DL, Goldstein RA, O'Neill RV (1975) A model for trophic interaction. *Ecology* 56:881–892

Doebeli M, Knowlton N (1998) The evolution of interspecific mutualism. *Proc Natl Acad Sci USA* 95:8676–8680

Ferriere R, Bronstein JL, Rinaldi S, Law R, Gauduchon M (2002) Cheating and the evolutionary stability of mutualisms. *Proc R Soc Lond B* 269:773–780

Fishman MA, Hadany L (2010) Plant–pollinator population dynamics. *Theor Popul Biol* 78:270–277

Fontaine C, Guimaraes PR Jr, Kefi S, Loeuille N, Memmott J, van der Putten WH, van Veen FJF, Thebault E (2011) The ecological and evolutionary implications of merging different types of networks. *Ecol Lett* 14:1170–1181

Foster KR, Kokko H (2006) Cheating can stabilize cooperation in mutualisms. *Proc R Soc Biol Sci B* 273:2233–2239

Genini J, Morellato LPC, Guimaraes PR Jr, Olesen JM (2010) Cheaters in mutualism networks. *Biol Lett* 6:494–497

Goudard A, Loreau M (2008) Nontrophic interactions, biodiversity, and ecosystem functioning: an interaction web model. *Am Nat* 171:91–106

Hairton NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425

Holland JN, DeAngelis DL (2009) Consumer–resource theory predicts dynamic transitions between outcomes of interspecific interactions. *Ecol Lett* 12:1357–1366

Holland JN, DeAngelis DL (2010) A consumer–resource approach to the density-dependent population dynamics of mutualism. *Ecology* 91:1286–1295

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol* 12:197–229

Holt RD, Grover J, Tilman D (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am Nat* 144:741–771

- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- Hsu SB, Hubbell SP, Waltman P (1978) A contribution to the theory of competing predators. *Ecol Monogr* 48:337–349
- Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, Dormann CF, Edwards F, Figueroa D, Jacob U, Jones JL, Lauridsen RB, Ledger ME, Lewis HM, Olesen JM, Frank van Veen FJ, Warren PH, Woodward G (2009) Ecological networks—beyond food webs. *J Anim Ecol* 78:253–269
- Irwin RE, Bronstein JL, Manson JS, Richardson L (2010) Nectar robbing: ecological and evolutionary perspectives. *Annu Rev Ecol Syst* 41:271–292
- Jones EI, Ferriere R, Bronstein JL (2009) Eco-evolutionary dynamics of mutualists and exploiters. *Am Nat* 174:780–794
- Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal—connectance, dependence asymmetries and co-evolution. *Am Nat* 129:657–677
- Jordano P, Bascompte J, Olesen JM (2003) Invariant properties in eco-evolutionary networks of plant–animal interactions. *Ecol Lett* 6:69–81
- Katrina P, Vos M, Bateman A, Anholt BR (2009) Functional responses modified by predator density. *Oecologia* 159:425–433
- Kawanabe H, Cohen JE, Iwasaki K (1993) Mutualism and community organization: behavioural, theoretical, and food-web approaches. Oxford University Press, Oxford
- Kefi S, Berlow E, Wieters E, Navarrete S, Petchey O, Wood S, Boit A, Joppa L, Lafferty K, Williams R, Martinez N, Menge B, Blanchette C, Iles A, Brose U (2012) More than a meal... Integrating non-feeding interactions into food webs. *Ecol Lett* 15:291–300
- Knight TM, McCoy MW, Chase JM, McCoy KA, Holt RD (2005) Trophic cascades across ecosystems. *Nature* 437:880–883
- Knight TM, Chase JM, Hillebrand H, Holt RD (2006) Predation on mutualists can reduce the strength of trophic cascades. *Ecol Lett* 9:1173–1178
- Kondoh M (2008) Building trophic modules into a persistent food web. *Proc Natl Acad Sci of the USA* 105:16631–16635
- Law R, Bronstein JL, Ferriere R (2001) On mutualists and exploiters: plant–insect coevolution in pollinating seed–parasite systems. *J Theor Biol* 212:373–389
- Lee CT, Inouye BD (2010) Mutualism between consumers and their shared resource can promote coexistence. *Am Nat* 175:277–288
- Leon JA, Tumpson DB (1975) Competition between two species for two complementary or substitutable resources. *J Theor Biol* 50:185–201
- Levine SH (1976) Competitive interactions in ecosystems. *Am Nat* 110:903–910
- May RM (1974) Stability and complexity in model ecosystems. Princeton University Press, Princeton
- McCann KS (2012) Food webs. Princeton University Press, Princeton
- Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol Monogr* 65:21–74
- Morris WF, Bronstein JL, Wilson WG (2003) Three-way coexistence in obligate mutualist–exploiter interactions: the potential role of competition. *Am Nat* 161:860–875
- Odum EP, Biever LJ (1984) Resource quality, mutualism, and energy partitioning in food webs. *Am Nat* 124:360–376
- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240–261
- Oksanen L (1988) Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence. *Am Nat* 131:424–444
- Okuyama T, Holland JN (2008) Network structural properties mediate the stability of mutualistic communities. *Ecol Lett* 11:208–216
- Paine RT (1980) Food webs: linkage, interaction strength, and community infrastructure. *J Anim Ecol* 49:667–685
- Peacor SD, Werner EE (2004) How dependent are species pair interaction strengths on other species in the food web? *Ecology* 85:2754–2763
- Pimm SL (1982) Food webs. University of Chicago Press, Chicago
- Pires MM, Prado PI, Guimaraes PR (2011) Do food web models reproduce the structure of mutualistic networks? *PLoS One* 6:e27280
- Polis GA, Strong DR (1996) Food web complexity and community dynamics. *Am Nat* 147:813–846
- Polis GA, Winemiller KO (1996) Food webs: integration of patterns and dynamics. Chapman and Hall, New York
- Ringel MS, Hu HH, Anderson G (1996) The stability and persistence of mutualisms embedded in community interactions. *Theor Popul Biol* 50:281–297
- Rosenzweig ML (1969) Why the prey curve has a hump. *Am Nat* 103:81–87
- Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387
- Rosenzweig ML, MacArthur RH (1963) Graphical representation and stability conditions of predator–prey systems. *Am Nat* 97:209–223
- Skalski GT, Gilliam JF (2001) Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology* 82:3083–3092
- Stanton ML (2003) Interacting guilds: moving beyond the pairwise perspective on mutualisms. *Am Nat* 162:S10–S23
- Stone L, Roberts A (1991) Conditions for a species to gain advantage from the presence of competitors. *Ecology* 72:1964–1972
- Stouffer DB, Bascompte J (2010) Understanding food web persistence from local to global scales. *Ecol Lett* 13:154–161
- Thebault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton
- Vandermeer J (1980) Indirect mutualism: variations on a theme by Stephen Levine. *Am Nat* 116:441–448
- Vázquez DP, Blüthgen N, Cagnolo L, Chacoff NP (2009) Uniting pattern and process in plant–animal mutualistic networks: a review. *Ann Bot* 103:1445–1457
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100
- Williams RJ (2008) Effects of network and dynamical model structure on species persistence in large model food webs. *Theor Ecol* 1:141–151
- Wilson WG, Morris WF, Bronstein JL (2003) Coexistence of mutualists and exploiters on spatial landscapes. *Ecol Monogr* 73:397–413
- Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. *Annu Rev Ecol Syst* 25:443–466
- Yu DW (2001) Parasites of mutualisms. *Biol J Linn Soc* 72:529–546