

Interactions among mutualism, competition, and predation foster species coexistence in diverse communities

Benedicte Bachelot · María Uriarte · Krista McGuire

Received: 23 December 2014 / Accepted: 2 January 2015
© Springer Science+Business Media Dordrecht 2015

Abstract In natural systems, organisms are simultaneously engaged in mutualistic, competitive, and predatory interactions. Theory predicts that species persistence and community stability are feasible when the beneficial effects of mutualisms are balanced by density-dependent negative feedbacks. Enemy-mediated negative feedbacks can foster plant species coexistence in diverse communities, but empirical evidence remains mixed. Disparity between theoretical expectations and empirical results may arise from the effects of mutualistic mycorrhizal fungi. Here, we build a multiprey species/predator model combined with a bidirectional resource exchange system, which simulates mutualistic interactions between plants and fungi. To reach population persistence, (1) the per capita rate of increase of all plant population must exceed the sum of the negative per capita effects of predation, interspecific competition, and costs of mycorrhizal association, and (2) the per capita numerical response of enemies to mycorrhizal plants must exceed the magnitude of the per capita enemy rate of mortality. These conditions reflect the balance between regulation and facilitation in the system. Interactions between plant natural enemies and mycorrhizal fungi lead to shifts in the strength and direction of net mycorrhizal effects on plants over time, with common plant species

deriving greater benefits from mycorrhizal associations than rare plant species.

Keywords Prey–predator model · Food web dynamics · Mutualism · Janzen-Connell · Mycorrhizal associations

Introduction

Interspecific interactions play a key role in driving population dynamics (Gause and Witt 1935). A large number of theoretical and empirical studies have focused on understanding the effects of competition and predation on population dynamics (Holling 1959; Rosenzweig and MacArthur 1963; Tilman 1982; Chesson 2000; Chesson and Kuang 2008). More recently, studies have also investigated the role of mutualisms in isolation (Bronstein 2001a; Holland et al. 2002; Bever 2003; Bruno et al. 2003). Two generalizations can be drawn from mutualism studies (Holland et al. 2002): mutualisms involve costs and benefits for both partners that are likely density-dependent (Roughgarden 1975; Addicott 1979; Morales 2000; Bronstein 2001b), and population stability requires that the positive feedbacks derived from mutualism are balanced by negative feedbacks (Gause and Witt 1935; Vandermeer and Boucher 1978; Chesson 2000; Bever 2003).

Stabilizing negative feedbacks can arise from multiple mechanisms such as resource limitation, competition, predation, or change in the net effects of mutualism (i.e., the balance between its costs and benefits) as population size increases (Holland et al. 2002; Schmitt and Holbrook 2003; Holland and DeAngelis 2010; Holland et al. 2013). Recent theoretical studies have enhanced our understanding of the joint role of mutualisms and negative feedbacks in stabilizing species interactions; however, they often remain limited to one or two

Electronic supplementary material The online version of this article (doi:10.1007/s12080-015-0251-2) contains supplementary material, which is available to authorized users.

B. Bachelot (✉) · M. Uriarte
Department of Ecology, Evolution and Environmental Biology,
Columbia University, 1200 Amsterdam Avenue, New
York, NY 10027, USA
e-mail: bmb2157@columbia.edu

K. McGuire
Department of Biology, Barnard College, Columbia University, New
York, NY 10027, USA

aspects of interspecific interactions. In natural systems, organisms are simultaneously involved in mutualism, competition, and predation. Each process interacts with each other, limiting our ability to understand their joint effects from studies that investigate them in isolation (Fontaine et al. 2011; Georgelin and Loeuille 2014). Therefore, it is important to combine mutualism and food web dynamics into our understanding of community dynamics and species coexistence (Rai et al. 1983; Addicott and Freedman 1984; Freedman et al. 1987; Ringel et al. 1996; Jang 2002; Bronstein et al. 2003; Melián et al. 2009; Loeuille 2010; Mougi and Kondoh 2012; Holland et al. 2013; Georgelin and Loeuille 2014; Mougi and Kondoh 2014). Recently, there has been a regained interest in combining interaction types such as mutualism and antagonism motivated by the recognition that indirect interactions can alter the effects of mutualism and antagonism (Holland et al. 2013; Tang et al. 2014), affect resilience of dynamical systems to perturbations (Georgelin and Loeuille 2014), and promote stability in complex systems (Mougi and Kondoh 2014), which tend to be unstable when investigating interaction types in isolation (Allesina and Tang 2012).

In this study, we investigate the joint role of predation, competition, and mutualistic associations with arbuscular mycorrhizal fungi for the dynamics of multiple plant species and for species coexistence. In highly diverse plant communities, such as tropical forests, negative density-dependent factors (also known as Janzen-Connell (J-C) effects; Janzen 1970; Connell 1971; Connell et al. 1984) are the most frequently studied mechanisms that could explain the tree species coexistence (reviewed in Wright 2002). Janzen-Connell effects operate through the attraction of species-specific enemies such as seed predators, herbivores, or pathogens to the seedlings of canopy trees, which reduce conspecific seedling survivorship near the adult trees at high conspecific seedling density, leaving ecological space for heterospecific seedlings to recruit. The prediction from the J-C hypothesis is that the per capita predation rate of a plant species increases with plant species abundance at local and community scales (Fig. 1a(1)).

In contrast to the large body of research on the importance of negative feedbacks for species coexistence in plant communities and of positive feedbacks for plant invasion (Eppstein et al. 2006; Levine et al. 2006; Eppstein and Molofsky 2007), the role of fluctuating positive and negative mycorrhizal feedbacks on plant community dynamics remains underexplored both theoretically (Bruno et al. 2003) and empirically (Booth and Hoeksema 2010). Yet, theoretical studies have shown the importance of fluctuating mutualisms in stabilizing interspecific interactions (Holland et al. 2013). Unlike soil pathogens, which only have negative effects on their host trees, mycorrhizal fungi can have variable impacts on their host plant along a continuum from mutualism to parasitism (Fig. 1a(2), Johnson et al. 1997; Johnson and Graham 2013). If recent theoretical studies have incorporated costs and

benefits in analysis of mutualism (Neuhauser and Fargione 2004; Holland and DeAngelis 2010; Holland et al. 2013), costs are usually lacking and mutualism is generally unidirectional in theoretical studies that combine mutualism and antagonism (Holland et al. 2013; Georgelin and Loeuille 2014; Mougi and Kondoh 2014).

The relative effect of mycorrhization on a plant is typically gauged in terms of the quantity of limiting resources extracted from soil versus the amount of carbon needed to maintain the symbiosis. Evidence for positive mycorrhizal effects on host plants is extensive and has been attributed to a variety of mechanisms including greater plant nutrient uptake (Smith and Read 2008), defense against enemies (Gange and West 1994), and drought resistance (Auge et al. 1987). The nutrient benefits a plant species derives from mycorrhizae increase with mycorrhizal fungal abundance as root colonization increases (Fitter 1991; Van der Heijden et al. 1998; Lekberg and Koide 2005; Hoeksema et al. 2010; Zhang et al. 2011) and saturates when all available roots have been colonized (Smith and Read 2008; Vannette and Hunter 2011; Fig. 1b(1)). Studies have also uncovered negative feedbacks to plants from mycorrhizal fungal associations, which result from greater carbon costs with higher fungal abundance (Vannette and Hunter 2011). However, the cost of mycorrhizal associations to the plant saturates with plant abundance (Leon and Tumpson 1975; Kiers et al. 2011; Fig. 1b(2)).

Additionally, mycorrhization has been repeatedly demonstrated to minimize the risk of infection by root pathogens (Newsham et al. 1995) and to maximize response efficiency of plant to natural enemies (Bi et al. 2007). Consequently, increased mycorrhizal colonization should be correlated with decreased vulnerability to enemies, potentially leading to weaker negative enemy-mediated density dependence and lower number of natural enemies (Fig. 1a(3)). Bi et al. (2007) provide an extensive review of the mechanisms underlying this effect, which include increased production of allelochemicals such as phenols by the plants, induction of plant defense genes, activation of the jasmonate pathway that is crucial to respond to attacks by plant enemies, and attraction of predators of plant natural enemies (Hoffman et al. 2011a, b).

Here, we present a mathematical model to explore the joint effects of negative enemy and mycorrhizal fungal feedbacks on plant community dynamics and species coexistence. We then interpret the results of our model in light of existing empirical work on several aspects of the feedbacks we examine. Specifically, we address the following questions:

1. How does the relative strength of negative feedbacks from natural enemies and the magnitude and direction of mycorrhizal effects vary over time within a plant species

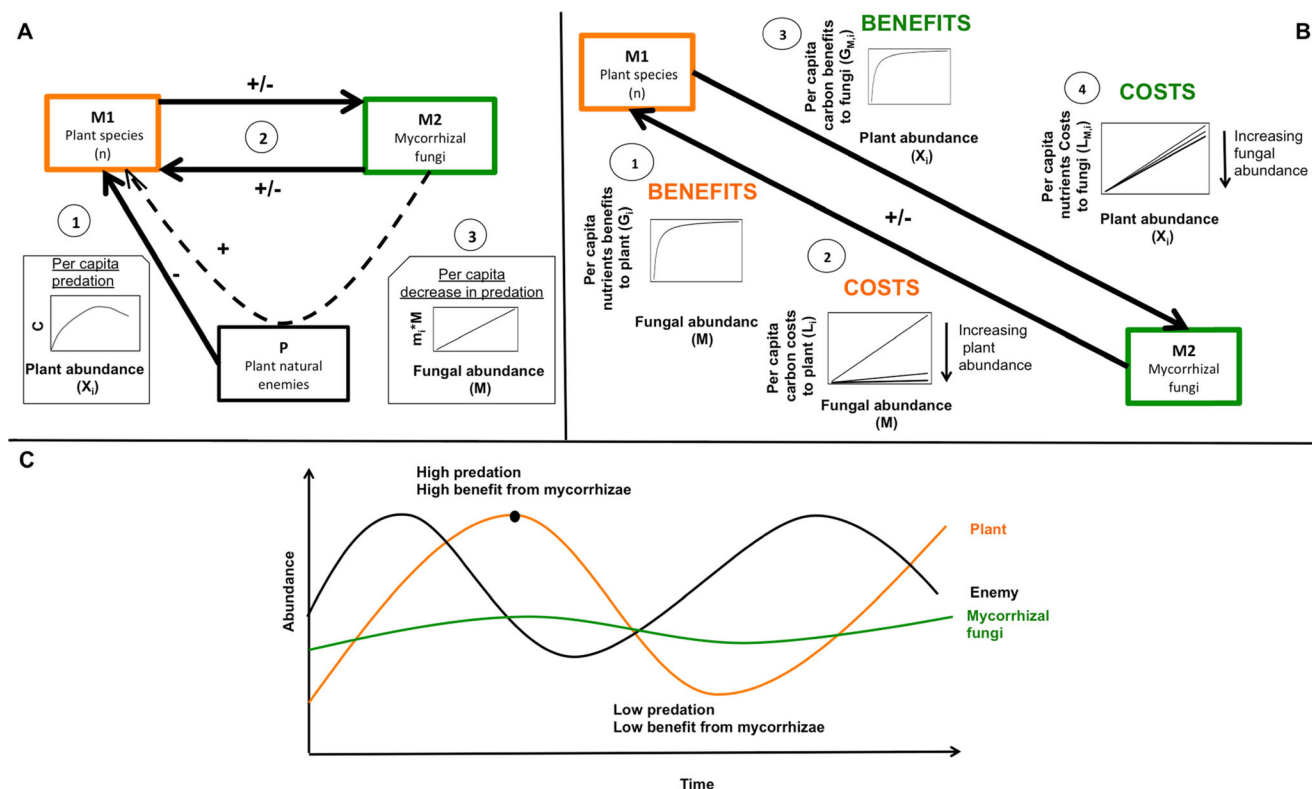


Fig. 1 Conceptual model showing the expected relationships between natural enemy, mycorrhizal fungi, and plant population dynamics. **a** 1 Per capita predation from enemies increases with plant abundance and saturates. We showed two possible forms in *plain* and *dashed* lines. 2 The effects of the fungi on the plants are both positive (nutrients provisioning) and negative (carbon costs). Similarly, the effects of the plants on the fungi are both positive (carbon gain) and negative (nutrients sink). These costs and benefits are further developed in **b**. 3 Per capita protection plants derive from mycorrhizal fungi linearly increases with the abundance of mycorrhizal fungi. **b** 1 Per capita nutrient benefits provided to the plants by the fungi increase (Fitter 1991; Van der Heijden et al. 1998; Lekberg and Koide 2005; Hoeksema et al. 2010; Zhang et al. 2011) and saturate with fungal abundance because mycorrhizal associations are limited by root surface and fungi control the amount of nutrients delivered to the plant (Smith and Read 2008; Vannette and Hunter 2011). 2 Per capita carbon costs of mycorrhizal associations to the plant increase with the abundance of the fungi (Vannette and Hunter 2011) but decrease with the abundance of the plant that can regulate the costs at the individual (Leon and Tumpson 1975; Tilman 1982; Koide 1991; Johnson et al. 1997; Smith and Read 2008; Johnson and Graham 2013; Koide 1991; Salzer et al. 1997) and

population levels (Selosse et al. 2006; van der Heijden and Horton 2009; Kiers et al. 2011). 3 Per capita carbon benefits the fungi gain from the plants increase and saturate with the plant abundance because mycorrhizal associations are limited by root surface. 4 Per capita costs of the mycorrhizal associations to the fungi increase with plant abundance but decrease with the abundance of the fungi. Fungi can regulate this cost by controlling mycelial growth and the extent of the common mycelial network (Selosse et al. 2006; van der Heijden and Horton 2009; Kiers et al. 2011). Recent evolutionary stable strategies analysis showed that regulation of costs and benefits of mutualistic association at the individual level leads to a cost and benefit control at the population level (Holland et al. 2004). Therefore, fungal populations control the costs of being associated with plants. **c** These interactions could result in the following patterns of population dynamics: at low density, a plant population experiences a predation release that allows it to increase in density despite low benefits from mycorrhizal fungi. At a specific flipping point (the *black dot*), the predation and the costs of supporting the mycorrhizal associations are not offset by the high mycorrhizal benefits, and the plant population density decreases. It is important to note that the net mycorrhizal effect (difference between benefits and costs) will be species-specific and in part controlled by the ratio of fungi and plant abundance

and what are the impacts of these fluctuations on the species' abundance?

2. How does the relative strength of negative feedbacks and mycorrhizal effects on rare and common plant species vary over time and what are the impacts of these fluctuations on plant species coexistence?

3. How do mycorrhizae alter the interactions between plants and natural enemies? Similarly, how do natural enemies affect the mutualistic interaction between plants and mycorrhizal fungi?

Model formulation

Our model assumes that plant species abundance fluctuates under pressure from three forces: the negative effects of inter-specific plant competition (X_i), the negative impacts of one natural enemies' population (Y) (i.e., pathogens and herbivores), and the effect of the mycorrhizal fungal population (M). Mycorrhizal fungi and plants interact according to a bi-directional resource exchange system; the fungi provide the plants with increasing nutrients, whereas the plants provide

the fungi with carbon (Smith and Read 2008). Furthermore, mycorrhizal colonization lowers predation from plant enemies by increasing plant defenses (Poza and Azcón-Aguilar 2007; Bi et al. 2007). To understand the dynamics that would result from these complex enemy–plant–fungal interactions, we

couple a multispecies, continuous, nonlinear prey–predator model (enemies–plant) with a bidirectional resource exchange model to represent the interactions between plants and fungi. The dynamics of plant species i (X_i) at time t are described by the following equation:

$$\frac{dX_i(t)}{dt} = X_i(t) \left[b_i + \alpha_i G_i(R_{M \rightarrow X_i}, t) - \beta_i L_i(R_{X_i \rightarrow M}, t) - [C_i(X, t) - m_i M(t)] Y(t) - \sum_{j=1}^n a_{i,j} X_j(t) \right] \quad (1)$$

where $X_i(t)$ and $Y(t)$ represent population abundance of plant species i (prey) and enemies, respectively, b_i represents the per capita exponential rate of increase of plant species i , $a_{i,j}$ designates the per capita interspecific competition among plant species, $a_{i,i}$ represents intraspecific competition (self-limitation), $M(t)$ is the abundance of the mycorrhizal fungal population, $X_i C_i(X, t)$ is the functional response of natural enemies to plant species i , and therefore $C_i(X, t)$ is the per capita rate of mortality from one enemy (Fig. 1a(1)). We used a classical Holling type III functional response (Holling 1959; Smout et al. 2010):

$$X_i C_i(X, t) = X_i(t) \frac{c_i X_i(t)}{1 + \sum_j w_j c_j X_j(t)^2}, \text{ with all } c_i \text{ and } w_i > 0 \quad (2)$$

where w_i is the handling time of plant species i , and c_i is the encounter rate of natural enemy with plant species i . This enables us to evaluate natural enemy behavior that causes density-dependent mortality (Janzen 1970; Connell 1971; Murdoch 1975; Pacala and Crawley 1992; Mordecai 2011), while acknowledging that natural enemies might satiate at high plant density (Silvertown 1980). Furthermore, it introduces the notion that natural enemy behavior might not be influenced by very low plant density (Real 1977; Krebs 1974; Jeschke et al. 2002). In a diverse community, very rare plant species might escape predation because natural enemies might not find them (Jaenike 1990; Pacala and Crawley 1992; Hierro et al. 2005) or not target them due to change in diet/host breadth with plant availability (Fox and Morrow 1981; Stephens and Krebs 1986). Therefore, a Holling type III functional response is the best choice to investigate the joint effect of natural enemies and mycorrhizal fungi on plant dynamics. Although we will present results for a type III response here, more general assumptions about functional responses yield similar qualitative results (see Appendix 1). The term $m_i \times M(t)$ in Eq. 1 modifies the functional response of the enemy because mycorrhizal fungi provide plants with increased per

capita protection (m_i) against enemies (Fig. 1a(3); Gange and West 1994; Poza and Azcón-Aguilar 2007; Bi et al. 2007). In order to prevent that a net positive effect arises from the interactions between natural enemies and fungi, we bounded the mycorrhizal fungal abundance so that $C_i(X, t) - m_i M(t) \geq 0$. Finally, the plant nutritionally benefits (Fig. 1a(2), b(1), $\alpha_i G_i(R_{M \rightarrow X_i}, t)$) and pays a carbon cost (Fig. 1a(2), b(2), $\beta_i L_i(R_{X_i \rightarrow M}, t)$) from the mycorrhizal associations (Smith and Read 2008; Johnson and Graham 2013). The functions $G_i(R_{M \rightarrow X_i}, t)$ represent the per capita increase in resource plants' gain from the mycorrhizal associations (Fig. 1b(1); Smith and Read 2008), whereas $L_i(R_{X_i \rightarrow M}, t)$ represents the per capita carbon losses to the associations (Fig. 1b(2); Olsson et al. 2010). The parameter α_i represents the conversion of the gain in a unit of resource per capita to a gain in abundance of the population of the plant species i . In contrast, β_i stands for the conversion of per capita loss in carbon to a loss in abundance of the population of the plant species i . We use the term net mycorrhizal effect for the plant species i to denote the difference between the benefits (nutrition and protection from enemies) and the costs (carbon): $\alpha_i G_i(R_{M \rightarrow X_i}, t) + m_i M(t) Y(t)$ and $\beta_i L_i(R_{X_i \rightarrow M}, t)$.

The dynamics of the mycorrhizal fungal population (M) directly depend on the balance between the carbon gains and nutrient losses they derive from plant species 1 to n (Koide and Elliott 1989; Fitter 1991). In an effort to increase model tractability, we did not account for different mycorrhizal fungal species. Growing evidence has shown that the specific community of mycorrhizal fungi associated with a plant rather than the identity of individual mycorrhizal fungi controls the outcomes of the associations (Johnson and Graham 2013; Toju et al. 2013). Therefore, considering the mycorrhizal fungal community rather than individual mycorrhizal fungal species does not dramatically hinder the realism of our model. The dynamics of the mycorrhizal fungal population are described by a consumer–resource (C-R) model (Rosenzweig and MacArthur 1963) similar to the bidirectional C-R model proposed by Holland and DeAngelis (2010) as follows (Fig. 1a(2)):

$$\frac{dM(t)}{dt} = M(t) \left(\sum_{i=1}^n [\alpha_{M,i} G_{M,i}(R_{X_i \rightarrow M}, t) - \beta_{M,i} L_{M,i}(R_{M \rightarrow X_i}, t)] - r_M \right) \quad (3)$$

where $G_{M,i}(R_{X_i \rightarrow M}, t)$ and $L_{M,i}(R_{M \rightarrow X_i}, t)$, respectively, represent the per capita resource gains and losses of the fungal population to plant species i , $\alpha_{M,i}$ represents the conversion of the gain in resource from plant species i to fungal population abundance (Smith and Read 2008), and $\beta_{M,i}$ modulates the per capita loss in resource to plant species i in loss in fungal abundance (respectively Fig. 1b(3, 4), and r_M is the per capita exponential rate of mortality of the mycorrhizal fungi in the absence of plants.

Studies have shown that the effects of mycorrhizal associations are context-specific, and the same mycorrhizal fungal species could have positive, negative, and neutral effects (Smith and Read 2008; Johnson and Graham 2013; Toju et al. 2013). To account for this level of variation in the effect of mycorrhizal fungi, we use plant species-specific resource gain and loss functions (G and L in Eqs. 1 and 3) and plant species-specific numerical responses (α and β in Eqs. 1 and 3). The mycorrhizal fungi are strictly obligate and cannot survive without the plants (Smith and Read 2008). Therefore, the dynamics of the fungi are solely controlled by the exchange of resources with the plants.

Quantifying the costs and benefits plants derive from mycorrhizal associations and vice versa remains challenging (Johnson et al. 1997; Johnson and Graham 2013). In our model, we used classical resource exchange functions such as the one described by Holland and DeAngelis (2010) (Fig. 1b(1, 2)):

$$G_i(R_{M \rightarrow X_i}, t) = \frac{g_i M(t)}{h_i + M(t)} \quad (4)$$

$$L_i(R_{X_i \rightarrow M}, t) = \frac{l_i M(t)}{k_i + X_i(t)} \quad (5)$$

In parallel, $G_{M,i}$ and $L_{M,i}$ for the fungi in Eq. 3 take the form (Fig. 1b(3, 4)):

$$G_{M,i}(R_{X_i \rightarrow M}, t) = \frac{g_{M,i} X_i(t)}{h_{M,i} + X_i(t)} \quad (6)$$

$$L_{M,i}(R_{M \rightarrow X_i}, t) = \frac{l_{M,i} X_i(t)}{k_{M,i} + M(t)} \quad (7)$$

where g_i and $g_{M,i}$ are the saturation levels of resource gains, and h_i and $h_{M,i}$ are the half saturation constants for plant

species i and for fungal population M , respectively. Similarly, l_i and $l_{M,i}$ are the saturation levels of the loss of resources, and k_i and $k_{M,i}$ are the half saturation constants. Parameters g and l represent the per capita interaction strength of one species on the other. We assumed per capita resource gain to plant species i (the G_i function in Eq. 1) a saturating (Michaelis-Menten) function of the abundance of fungi associated with each plant species $i=1$ to n (Fig. 1b(1)). Similarly, benefits to the mycorrhizal fungi (the $G_{M,i}$ function in Eq. 3) are described by Michaelis-Menten functions of the plant abundance associated with the fungal population (Fig. 1b(3)). This functional form captures the assumption that the benefits extracted by fungi and plants are limited by the extent of fine root surface area and that the two symbiotic partners (i.e., plants and fungi) can control these benefits. Per capita resources lost by plant species i (the L_i function in Eq. 1, Fig. 1b(2)) increase linearly with increasing fungal populations (Eq. 2), while resources lost by the fungi (the $L_{M,i}$ functions in Eq. 3) increase linearly with greater abundance of plant species i population (Eq. 7, Fig. 1b(4)). The per capita loss of resources functions saturates with the supplier species abundance (denominators in Eqs. 5 and 7, Fig. 1b(2, 4)). In Eq. 5 and Fig. 1b(2), the rationale for the denominator is that plants have the potential to control fungal colonization to maximize the benefits of the mycorrhizal associations while minimizing the costs (Koide 1991; Johnson et al. 1997; Smith and Read 2008; Johnson and Graham 2013). Similarly, the rationale for the denominator in Eq. 7 and Fig. 1b(4) is that fungi are able to overcome plant controls of the colonization (Johnson et al. 1997; Smith and Read 2008; Johnson and Graham 2013). In other words, plants and fungi can control the costs of the mycorrhizal associations at the individual level and thus at the population level due to evolutionary stable strategies of mutualism (Holland et al. 2004). Another motivation behind the denominator of the cost function arises from the fact that plants and mycorrhizal fungi are connected via common mycelial network, allowing them to share the costs of the mycorrhizal association with each other (Simard and Durall 2004). We acknowledge that the form we are using to represent the mycorrhizal effect is a simplification because we do not know the exact forms of per capita resource gains (the G_i and $G_{M,i}$ functions) and losses (the L_i and $L_{M,i}$ functions). These simple forms of consumer-resource interactions have been shown to be accurate in some biological systems (Holland 2002; Holland et al. 2002; Holland and DeAngelis 2006; Holland and DeAngelis 2010; Holland et al. 2013).

Finally, enemy dynamics (Y) are described as one population of enemies exhibiting host preferences rather than specialization. We assume that predation increases with plant abundance (Fig. 1a(1)). The assumption of host preferences can lead to the simulation of inappropriate population dynamics for the few plants that have species-specific interactions with specialist pathogens and herbivores. However, in these

associations between plants and specialist enemies, plant abundance dynamics are likely to be tightly dependent on the dynamics of their own specialist enemies and less dependent on other plant species present in the community. Therefore, ignoring the distinction between host-specific and generalist interactions in the system should not affect the validity of our conclusions especially given the low rates of host specialization of natural enemies in the tropics (Novotny et al. 2010). The dynamics of plant natural enemies are a function of plant species and mycorrhizal fungal abundances as follows:

$$\frac{dY(t)}{dt} = Y(t) \left[\sum_{i=1}^n [d_i(C_i(X, t) - m_i M(t)) X_i(t)] - eY(t) - r \right] \quad (8)$$

where $d_i C_i(X, t) X_i(t)$ represents the per capita numerical response of enemies to plant i , m_i the per capita protection against enemies provided by the mycorrhizal associations with plant species i (Fig. 1a(3)), M the abundance of the mycorrhizal fungal population, e is the per capita competition coefficient for the enemy species (self-limitation), and r the per capita exponential rate of mortality of the enemy species in the absence of plant (i.e., starvation rate). Therefore, the mycorrhizal fungi have two effects on the plant natural enemy population (Wootton 1994; Strauss and Irwin 2004; Koricheva et al. 2009; Bardgett and Wardle 2010; Barber et al. 2012): An indirect effect that arises from modifying plant population growth (depicted in the resource exchange functions, G and L), and a direct effect that emerges from change in natural enemy functional response due to increased plant protection ($-m_i M$).

We chose to co-model community dynamics in continuous time, which is more suitable to model populations of organisms with short life spans (natural enemies and mycorrhizal fungi) and very long-lived ones (trees, Wangersky 1978). The final system is a nonlinear prey–predator model that combines competition among plant species, predation, and potential facilitation by mycorrhizal fungi if the overall net mycorrhizal effect is positive. This last effect is a fluctuation-dependent mechanism (Chesson 2000). Over time, as plant abundance increases, the facilitation effect increases until a flipping point after which this facilitation effect levels off, eventually becoming a negative density-dependent effect driven by a growing enemy population and the carbon and other costs associated with the mycorrhizal symbiosis (Fig. 1c). The formulation of the net mycorrhizal effect via bidirectional resource/consumer system (Johnson et al. 1997; Holland and DeAngelis 2010) enables this effect to become negative and introduces an additional negative covariance between fitness and density similar to the one produced by the effect of predation (Chesson 2000). Our model is one of the first attempts to combine

mutualistic interactions and food web dynamics. Holland et al. (2013) used resource exchange functions to investigate the stability of a system that included one plant species, one mutualistic pollinator, and one nectar-parasite. In their system, the mutualistic pollinator gains benefits from the plant without paying a cost, and the nectar-parasite does not alter the behavior of the mutualistic pollinator (unidirectional mutualism). Our study expands on Holland et al. system (2013) and aims to explore community dynamics and coexistence of n plant species that are involved in bidirectional exchange with mycorrhizal fungi, where each plant and fungus experiences benefits and costs. Furthermore, natural enemies whose functional response is affected by mycorrhizae target the n plant species.

To evaluate the system, we assume that the mycorrhizal fungal population does not tend towards infinity but rather exhibits an upper bound (v). We defined this upper bound to ensure that the protection conveyed by mycorrhizal fungi does not result in a positive effect of natural enemies on plant population (for all plant species i , $m_i \leq \frac{C_i^l}{\max(M(t))} \frac{df}{dv}$). In other words, the mycorrhizal fungi might enhance plant protection against natural enemies, but this enhancement will not result in a total protection. If the mycorrhizal fungal population goes to extinction, then our model becomes a classical multispecies prey–predator type system. Therefore, in our work, we investigate the conditions to maintain plant species coexistence when the mycorrhizal fungal population remains between a strictly positive lower bound (λ) and an upper bound (v). The model was evaluated for n plant species (Appendix 1). Specifically, we analyzed the model to find conditions allowing the populations to remain between a positive lower abundance boundary and a finite upper abundance boundary. In other words, we evaluate the conditions enabling the coexistence of n plant species in the system. We also analyzed a simple version of the model involving one plant species and a fixed mycorrhizal fungal population in order to understand how mycorrhizal fungi alter the prey–predator dynamics (Appendix 2). Similarly, we investigated the case of a fixed natural enemy population to understand its effect on the mutualistic interactions (Appendix 2). We illustrated the important results of the model using simulation to represent fluctuations in abundance over time within one plant species and for two coexisting plant species: one rare and one common. In this paper, the distinction between a rare and a common plant species is a relative notion based upon the relative density of each plant species. Finally, we investigated the dynamics of one equilibrium by using simulations and changing the value of each parameter one by one (Tables 2 and 3 in Appendix 3). Specifically, we wanted to assess how small changes in each parameter of the model with two plant populations would change the dynamics of the equilibrium (stable, periodic, not periodic, or unstable). All simulations were accomplished using Mathematica v. 7.0. (Wolfram Research, Inc. 2008).

Results and discussion

Variability of the relative strength of negative feedbacks and net mycorrhizal effect on plant species

Our model shows that when a plant species reaches high abundance, its decline can occur via three mechanisms. First, at high density, it suffers greater per capita mortality from enemy ($Y(t)C_i(X,t)$ in Eq. 1) than at low density. Second, intraspecific competition ($a_{i,i}X_i(t)$ in Eq. 1) is stronger at high relative to low conspecific abundance. Third, the positive effect from mycorrhizal associations ($m_iM(t)Y(t) + \alpha_iG_i(R_{M \rightarrow X_i}, t)$) does not compensate for the negative effect of natural enemies as the mycorrhizal associations become more costly in term of carbon. These three factors then lead to a decline in plant abundance. The opposite scenario applies when a plant species reaches low abundance.

Temporal fluctuations in negative feedbacks and the strength and direction of the net mycorrhizal effect correlate with fluctuations in the abundance of the plant and enemy populations. The fluctuations in the abundance of the plant population can be stable and stationary or periodic in the case of periodic or constant parameters (for example parameters that fluctuate seasonally) (step 3 in Appendix 1). The simultaneous analysis of the dynamics of plants, enemies, and mycorrhizal fungi provides insights into the mechanisms underlying plant population dynamics. If the per capita benefits from mycorrhizal fungi to the plant is high relative to the per capita costs ($m_iM(t)Y(t) + \alpha_iG_i(R_{M \rightarrow X_i}, t) > \beta_iL_i(R_{X_i \rightarrow M}, t)$), the dynamics of the net mycorrhizal effect and plant populations will be positively correlated and the net mycorrhizal effect and enemy population will be negatively correlated (Fig. 2a). In other words, mycorrhizal fungi will have a large impact of the dynamics of plants and enemies by enhancing plant population

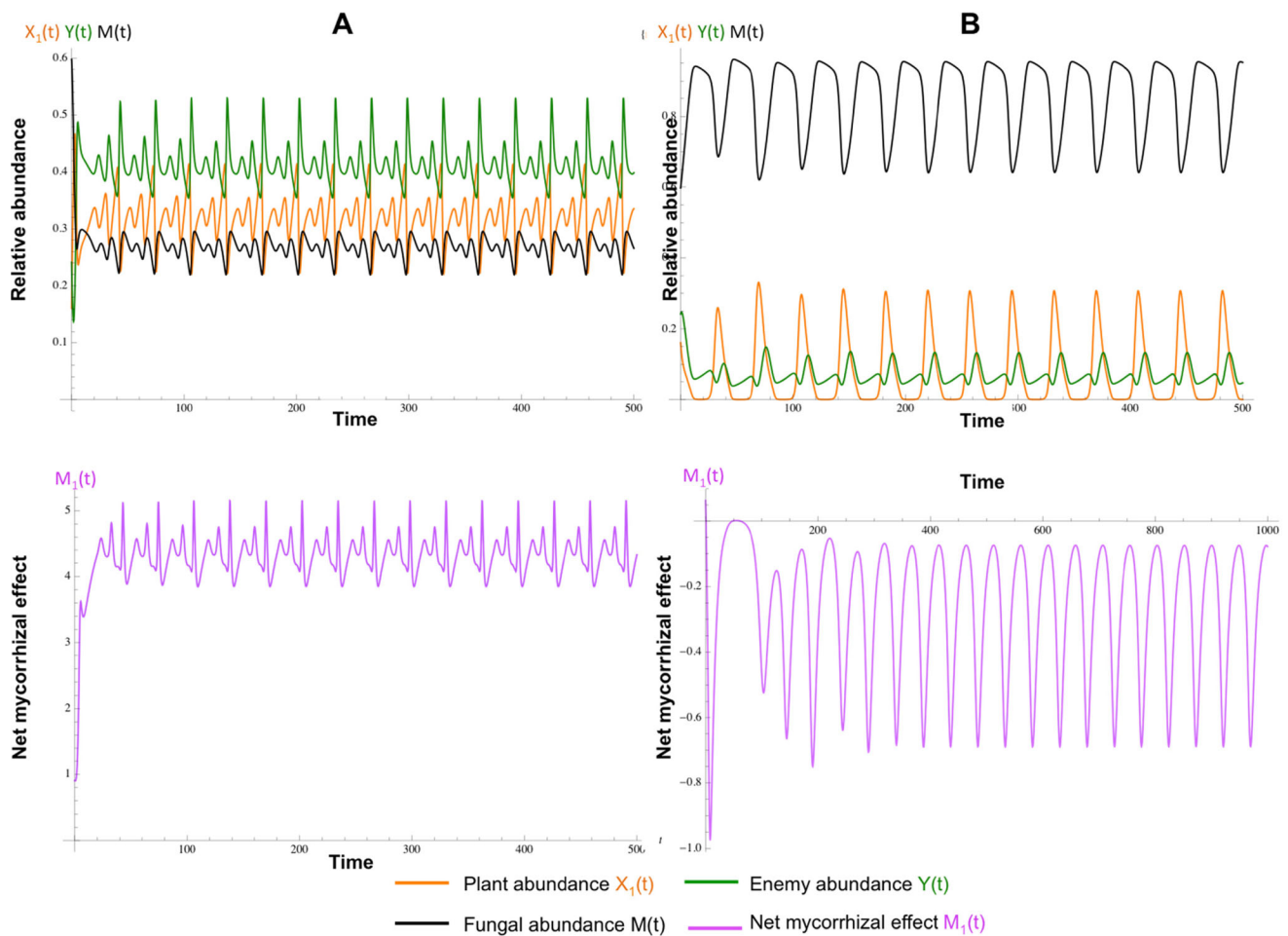


Fig. 2 Model simulations for one plant species (X) with constant parameters in the presence of natural enemies (Y) and mycorrhizal fungi (M). M_i represents the net effect of mycorrhizal associations for the plant species. Panel **a** represents a situation where the benefits of the mycorrhizal symbiosis are greater than the costs ($m_iM(t)Y(t) + \alpha_iG_i(R_{M \rightarrow X_i}, t) > \beta_iL_i(R_{X_i \rightarrow M}, t)$). In this case, there is a mismatch between plant and mycorrhizal fungal

dynamics. Panel **b** represents the opposite situation where the costs of the mycorrhizae are greater than their benefits ($m_iM(t)Y(t) + \alpha_iG_i(R_{M \rightarrow X_i}, t) < \beta_iL_i(R_{X_i \rightarrow M}, t)$). In this case, plant and mycorrhizal fungal dynamics are synchronous. Parameter values used for the simulations are provided in Appendix 2

growth and impeding predation from enemies. Conversely, if the per capita benefits from mycorrhizal associations are lower than its per capita costs for both fungi and plant populations ($m_i M(t) Y(t) + \alpha_i G_i(R_{M \rightarrow X_i}, t) < \beta_i L_i(R_{X_i \rightarrow M}, t)$ and $m_i M(t) Y(t) + \alpha_{M,i} G_{M,i}(R_{X_i \rightarrow M}, t) < \beta_{M,i} L_{M,i}(R_{M \rightarrow X_i}, t)$), the net mycorrhizal effect to the plants and the plant population size will remain positively correlated, but the net mycorrhizal effect to the plants and the enemy population might become positively correlated (Fig. 2b). In other words, the mycorrhizal fungi will not be beneficial to the plants but rather they might indirectly enhance the enemy population. In other words, this could occur if by enhancing plant growth, mycorrhizal fungi indirectly benefit plant enemies. If the net mycorrhizal effect fluctuates between positive and negative (The sign of $m_i M(t) Y(t) + \alpha_i G_i(R_{M \rightarrow X_i}, t) - \beta_i L_i(R_{X_i \rightarrow M}, t)$ will change over time due to fluctuating plant and fungal populations, similar to the parasitism/mutualism continuum proposed by Johnson and Graham 2013), the dynamics will exhibit a variety of patterns ranging from positive to negative correlations between the net

mycorrhizal effect and the natural enemy population size (Fig. 3).

Our model shows that the joint impacts of enemies and mycorrhizal fungi can lead to temporal fluctuations in the abundance of a single plant species. The impacts of these combined feedbacks on plant dynamics have received scant attention (Van der Putten et al. 2009; Bardgett and Wardle 2010). While these interactions are complex and likely to be species-specific (Wardle 2002), evidence from herbivory studies suggests that mycorrhizal fungi and plant natural enemies are interacting (Bi et al. 2007). The various dynamic patterns obtained with our model suggest that the interactions between plant natural enemies and mycorrhizal fungi are often but not always negative. In support of our findings, a number of empirical studies have uncovered negative correlations between herbivory and the abundance, phenology, and colonization of mycorrhizal fungi, lending support to the idea that top-down effects can modulate the strength and direction of mycorrhizal effects on plants. For example, Gehring and Whitham (1994)

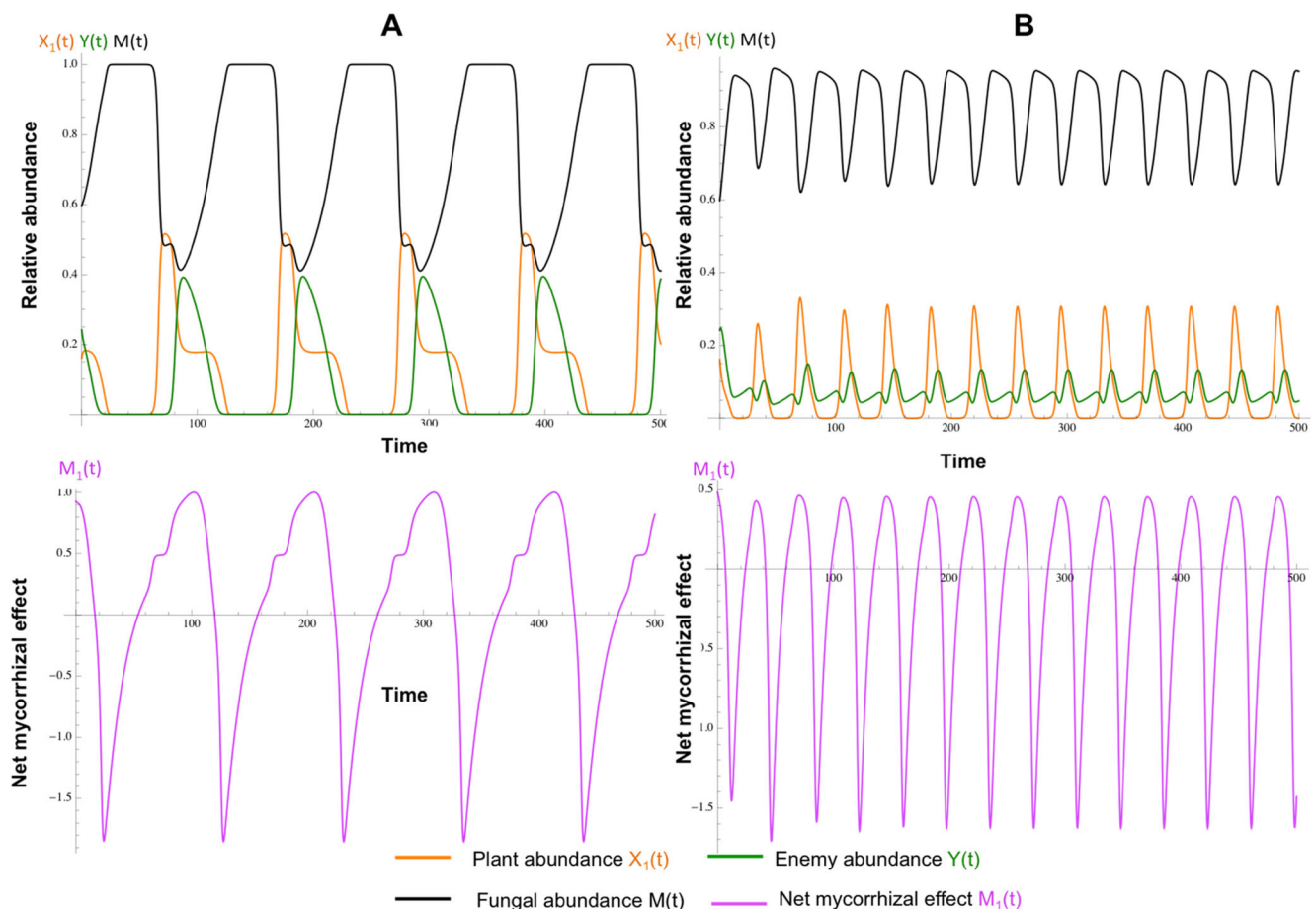


Fig. 3 Model simulations for one plant species (X) in the presence of natural enemies (Y) and mycorrhizal fungi (M) with constant parameters. M_i represents the net effect of mycorrhizal associations for the plant species. Panels **a** and **b** illustrate two situations where over time the net

effect of mycorrhizal associations is fluctuating between positive and negative. Parameter values used for the simulations are provided in [Appendix 2](#)

found a decrease in mycorrhizal colonization following defoliation for 23 of 37 studied plants. Recent reviews, however, highlight how the complex interaction between plant enemies and mycorrhizal fungi can vary with the frequency, timing, and type of herbivory (Klironomos et al. 2004; Saravesi et al. 2008).

Impact of negative feedbacks relative strength and net mycorrhizal effect fluctuations on species abundance and coexistence

Our model predicts coexistence of n plant species under the joint effects of mycorrhizal fungi, plant natural enemies, and plant competition, which together establish lower and upper abundance constraints, offering an additional mechanism to explain the high diversity of plant species in diverse communities such as tropical forests. This result is the first theoretical evidence showing that the joint effects of plant natural enemies and mycorrhizal fungi can lead to plant species coexistence. This result is consistent with theoretical work showing that mutualism alone cannot lead to species coexistence (McGill 2005) unless mutualistic populations are regulated by other mechanisms (e.g., plant natural enemies in our model, Simonsen and Stinchcombe 2014).

Our model predicts that each plant species will fluctuate between low and high abundance constraints that depend on the magnitude of negative feedbacks from natural enemies, plant, and mycorrhizal fungi. In order to reach coexistence, the parameters of the model must satisfy three conditions (Appendix 1). First, the per capita exponential rate of growth of the plant population i (b_i) must be greater than the sum of (1) the negative per capita effects due to predation ($C_i^u q$, where q is the upper bound of enemy population and C_i^u is the maximum value of the per capita mortality of plant species i from enemy, see Appendix 1), (2) the per capita interspecific competition ($\sum_{j=1, j \neq i}^n [a_{i,j} p_j]$, where p_j is the upper limit of plant species j population size), and (3) the per capita costs of mycorrhizal associations ($\beta_i \frac{l_i v}{k_i}$, where v is the upper bound of mycorrhizal fungal population) (step 2), that is:

$$b_i > C_i^u q + \sum_{j=1, j \neq i}^n [a_{i,j} p_j] + \beta_i \frac{l_i v}{k_i} \quad (9)$$

This first condition ensures that plant populations avoid extinction. Second, the persistence of plant species requires that the enemy population does not become overdominant and that this upper limit of natural enemy population is biologically reachable (in other words, it is not an infinite or a negative number). This condition requires that the per capita enemy exponential rate of mortality (r) is strictly lower than the total

of the maximum value of the per capita numerical responses of enemies to plants ($\sum_{i=1}^n d_i C_i^u p_i$) (step 1 in Appendix 1):

$$r < \sum_{i=1}^n d_i C_i^u p_i \quad (10)$$

This condition ensures the existence of an upper bound (q) for the enemy population that depends only on the per capita enemy numerical responses ($\sum_{i=1}^n d_i C_i^u p_i$), the per capita competition among enemies (e), and the per capita enemy exponential rate of mortality (r), as follows:

$$Y(t) \leq \frac{\sum_{i=1}^n d_i C_i^u p_i - r}{e} \underline{\text{def}} q \quad (11)$$

A third condition required to prevent enemy population extinction is that the total of the minimum value of the per capita numerical responses of enemies to plants ($\sum_{i=1}^n (d_i C_i^l \tilde{p}_i)$, where \tilde{p}_i is the lower limit of plant species i population size) protected by mycorrhizal fungi ($\sum_{i=1}^n (-d_i m_i v p_i)$, where v is the upper bound of mycorrhizal fungal population) must be greater than the per capita enemy exponential rate of mortality (r) (step 2 in Appendix 1):

$$\sum_{i=1}^n (d_i C_i^l \tilde{p}_i - d_i m_i v p_i) > r \quad (12)$$

If this condition is met (Eq. 12), then the condition to prevent enemies from becoming overdominant (Eq. 10) is also met. Thus, we found that two necessary conditions must be met to maintain species coexistence: (1) the per capita exponential rate of growth of the plant population must be greater than the sum of the negative effects due to per capita predation, per capita interspecific competition, and the per capita costs of mycorrhizal associations, and (2) the total of the minimum value of the per capita numerical responses of enemies to plants protected by mycorrhizal fungi must be greater than the per capita enemy exponential rate of mortality. In other words, the protection conveyed by the mycorrhizal association is not strong enough to dramatically decrease the enemy population (food web cascade; Bruno et al. 2003; Cantrell and Cosner 2001; McGill 2005). Overall, these two conditions reflect the balance between regulation and facilitation in the system. More empirical and experimental work is required to evaluate the realism of these two conditions.

If the two conditions described in inequalities Eqs. 9 and 12 are met, the abundance of plant species i (X_i) will fluctuate between the following upper (p_i) and lower (\tilde{p}_i) limits (see Appendix 1 for more details):

$$\tilde{p}_i \stackrel{\text{def}}{=} \frac{b_i - \beta_i \frac{l_i v}{k_i} - \sum_{j=1, j \neq i}^n [a_{i,j} p_j] - C_i^u q}{a_{i,i}} \leq X_i \leq \frac{b_i + \alpha_i g_i}{a_{i,i}} \stackrel{\text{def}}{=} p_i \quad (13)$$

The parameters q and v represent the upper boundary of enemy and mycorrhizal fungal abundance, respectively (Appendix 1). The upper limit of plant abundance depends on the per capita benefits to the plant species i ($\alpha_i g_i$) associated with the mycorrhizal associations and the per capita exponential rate of increase of plant species i (b_i), whereas the lower boundary is a function of the maximum per capita costs of mycorrhizal associations to the plant species i ($\beta_i \frac{l_i v}{k_i}$), the per capita competition among plants (a_{ij}), and the maximum per capita predation effect (C_i^u). Different parameters will lead to different model outputs: If the per capita benefits gained via mycorrhizal fungi are lower in rare relative to common plant

species ($\alpha_r g_r < \alpha_c g_c$) as expected in light of empirical work (Moora et al. 2004), given similar per capita intraspecific competition ($a_{i,i}$) and per capita growth rate (b_i), the maximum abundance of a rare plant species (p_r) will remain lower than that of a common plant species (p_c):

$$p_r = \frac{b_r + \alpha_r g_r}{a_{r,r}} \leq \frac{b_c + \alpha_c g_c}{a_{c,c}} = p_c \quad (14)$$

Therefore, inequality Eq. 14 predicts that lower frequency of association with beneficial fungi could explain the relative rarity of a plant species. Alternatively, lower growth rate or higher intraspecific competition in rare relative to common plant species could explain rarity.

The lower limit of plant abundance can take a lower value for common species than for rare species when the effects of per capita predation ($C_c^u q$) plus the per capita costs of mycorrhizal associations ($\beta_c \frac{l_c v}{k_c}$) are greater in a common relative to a rare plant species ($\beta_c \frac{l_c v}{k_c} + C_c^u q > \beta_r \frac{l_r v}{k_r} + C_r^u q$), given similar per capita intraspecific and interspecific competition ($a_{i,j}$) and per capita growth rate (b_i):

$$\tilde{p}_c = \frac{b_c - \beta_c \frac{l_c v}{k_c} - \sum_{j=1, j \neq c}^n [a_{c,j} p_j] - C_c^u q}{a_{c,c}} \leq \frac{b_r - \beta_r \frac{l_r v}{k_r} - \sum_{j=1, j \neq r}^n [a_{r,j} p_j] - C_r^u q}{a_{r,r}} = \tilde{p}_r \quad (15)$$

Greater effect of natural enemies on common relative to rare plant species is predicted by the J-C hypothesis (Janzen 1970; Connell 1971; Connell et al. 1984). Furthermore, several empirical studies supported this prediction (Bachelot and Kobe 2013; Bagchi et al. 2014). However, if plant natural enemies equally target common and rare plant species ($C_c^u q = C_r^u q$), then the costs that arise from mycorrhizal associations could explain rarity (if rare species pay greater per capita costs for the association than common species) or large fluctuations in common plant species abundance (if common plant species experiences greater per capita costs than rare plant species).

Overall, variation in the strength and direction of enemy and mycorrhizal fungal feedbacks confines the population of each plant species between an upper limit p_i and a lower limit \tilde{p}_i , ensuring plant species coexistence because no species will go extinct or become overdominant. Furthermore, common plant species are likely to reach higher abundance and can experience greater fluctuations in abundance over time than rare plant species (Fig. 4).

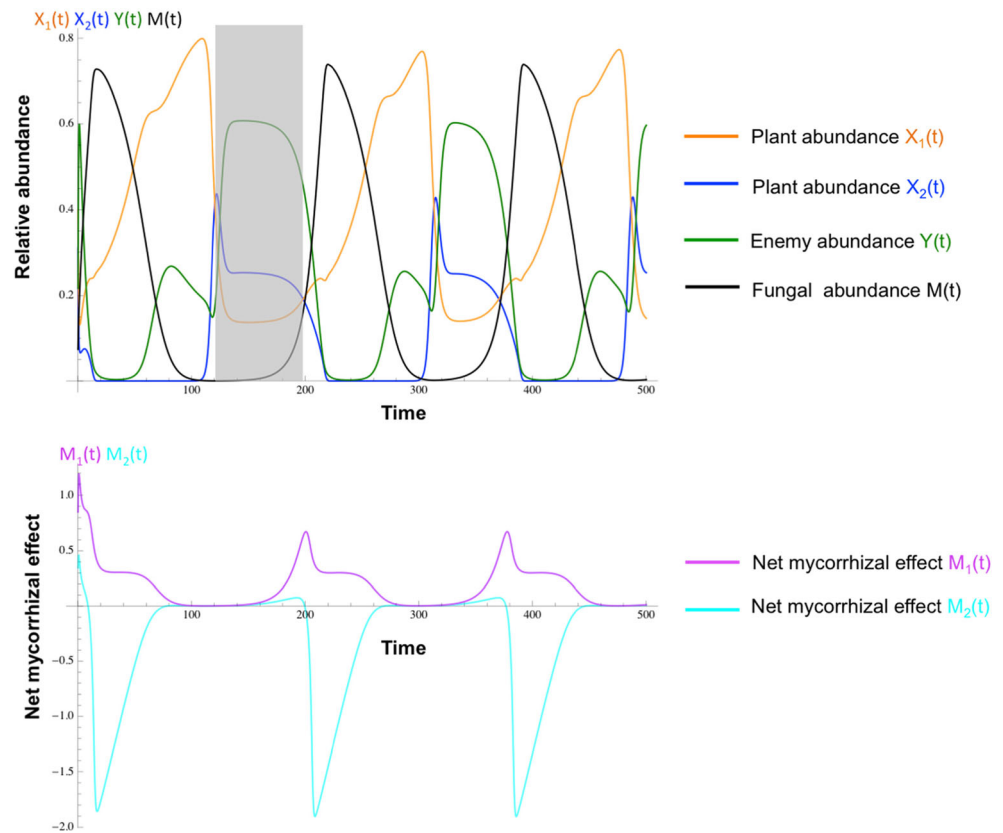
Beside change in the strength of various interactions among species, the hierarchical structure of the interactions can greatly impact species coexistence (Kondoh et al. 2010; Mougi and Kondoh 2012; Suweis et al. 2014; Mougi and Kondoh 2014). In our model, however, we did not incorporate hierarchical structure since each species interact with every

other species. Future work should investigate how network structure would affect natural enemies–plants–mycorrhizal fungi interactions.

Impacts of mycorrhizal associations on a plant–enemy dynamics

Consistent with recent work (Holland et al. 2013; Georgelin and Loeuille 2014), the third analysis of the system showed that adding mutualism to a prey–predator system could stabilize or destabilize the interactions. Specifically, our analysis revealed complex changes in the dynamics of the system with increasing mycorrhizal fungal abundance (Appendix 2). If the protection conveyed by the fungi to the plants is small enough, mutualism stabilizes the interactions between plants and natural enemies, suggesting that mutualism can dampen the interactions between plants and natural enemies (Figs. 5 and 6). However, as mycorrhizal fungal abundance continues to increase, the natural enemy population can be pushed to extinction, resulting in the collapse of the system (Fig. 6). When protection conveyed by mycorrhizal fungi to plants is large, mutualism destabilizes the system, which can introduce cycle dynamics and collapse (Fig. 6). Similar potential stabilization and destabilization effects of mutualism were also detected in pollinator–herbivore–plant systems involving unidirectional

Fig. 4 Model simulations for two plant species (X_1 and X_2). The dynamics of the dominant plant species and associated net mycorrhizal effect are shown in orange and dark blue, rare species in purple and light blue. Fluctuations in enemy (green) and mycorrhizal (black) effects lead to sporadic changes in the abundance status of the two plant species, with periods when the common plant species becomes less abundant than the rare plant species (*area shaded in*). M_1 and M_2 represent the net effect of mycorrhizal associations for the plant species X_1 and X_2 . Parameter values used for the simulations are provided in Appendix 1



mutualism (Mougi and Kondoh 2012; Georgelin and Loeuille 2014).

Overall, stabilization was more likely at intermediate mycorrhizal fungal population, which is somewhat consistent with a recent study of “hybrid” community (Mougi and Kondoh 2014). In this study, the authors asked which composition of interactions (mutualism, antagonism, and

competition) could lead to the stability of many interacting species. They found that a moderate mixing of the three types of interactions enhanced stability in diverse systems. However, they assume functional type I interactions between each species simplifying dramatically the system.

Interestingly, the costs and benefits of mycorrhizal fungal associations have a similar effect on the Jacobian matrix, suggesting that both costs and benefits could stabilize prey–predator interactions (Appendix 2). However, the upper and lower boundaries of the population abundance set some limits to the costs and benefits. If benefits tend to infinity, the system is destabilized because plant population obtains an infinite growth rate. In contrast, if costs tend to infinity, the plant population dies off. Therefore, within the limit of coexistence, increasing costs and benefits tend to stabilize the systems but outside of the domain of coexistence, enhanced costs, and benefits destabilize the system.

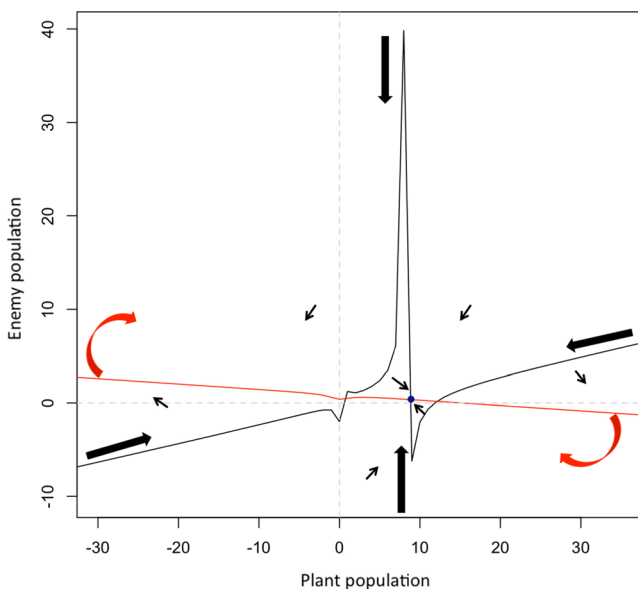


Fig. 5 Figures representing the effects of mycorrhizal fungi on the null isoclines of the prey–predator model

Impacts of plant natural enemies on a plant–fungi dynamics

Consistent with previous work, antagonist interactions (such as plant–enemy) can stabilize mutualism, by introducing negative feedbacks (Holland et al. 2002). Analysis of the system with a fixed natural enemy population showed that if the costs of mycorrhizal associations to the fungi are high enough, then an increase in natural enemy population could stabilize the system (Fig. 7, Appendix 2). However, the increase in natural

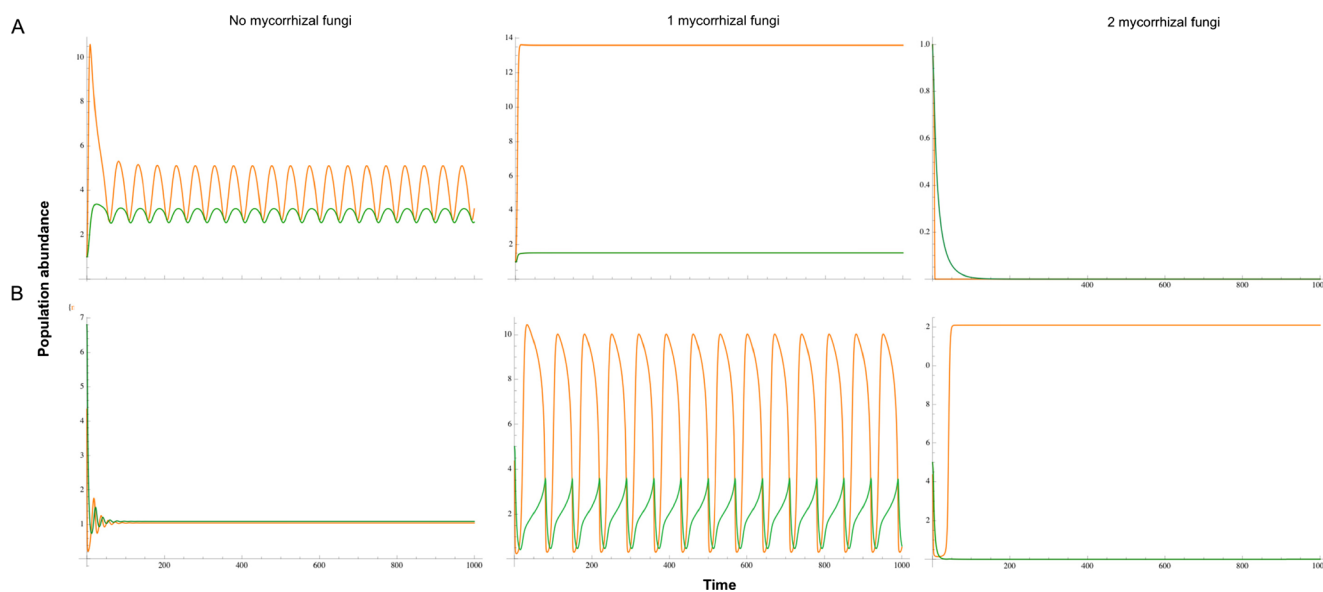


Fig. 6 Model simulations for one plant species (X) in the presence of natural enemies (Y) and with fixed mycorrhizal fungal population (M) and parameters. Panels **a** and **b** illustrate two situations where mycorrhizal fungi, respectively, stabilize and destabilize the prey–predator dynamics

enemy population needs to remain in the domain of coexistence defined in the analysis of the full system (Appendix 1). If natural enemy population becomes too abundant, it will push plant population to extinction (Fig. 7).

It is interesting to note that in the absence of the natural enemy population, the model represents a bidirectional consumer–resource interaction between a facultative host (plant) that undergo intraspecific competition and an obligate mutualist (mycorrhizal fungi). Holland and DeAngelis (2010) studied a similar model in depth without competition, and they showed that mutualism described in such a way was generally stable. Furthermore, they demonstrated that the range of dynamics predicted by this type of mutualistic interactions was similar to prey–predator interactions. In particular, cycles and dampen oscillations towards the equilibrium were two possible outcomes. Consistent with their findings, our simulations led to similar dynamics (Fig. 7).

Effect of the environment on complex dynamic systems

An important consideration is that the effects of microbial feedbacks on plant community dynamics could be endogenous (depend solely on the fungal–plant associations) or driven by exogenous temporal variability in the physical environment (e.g., precipitation or soil fertility). In particular, previous research suggests an increase in the costs of mycorrhizal associations with increasing soil fertility and shade, with a potential shift from mutualistic to parasitic associations (Neuhauser and Fargione 2004). In our model, mycorrhizal fungal associations result in costs and benefits for the plants similarly to Neuhauser and Fargione (2004). However, Neuhauser and Fargione incorporated the benefits of mutualism

as an increase in carrying capacity of the host (2004), rather than an increase in growth rate as we did. It would be interesting to expand upon our model to test if an increase in soil fertility would enhance parasitism. Furthermore, exogenous fluctuations in plant–enemy and mycorrhizal fungal feedbacks might follow non-random patterns. For example, the accumulation of pathogens over time might result in an increase in negative feedbacks from natural enemies (Klironomos 2002; Diez et al. 2010). In contrast, host specificity in mycorrhizal fungal might lead to an increase in positive feedbacks over time (Kardol et al. 2006). Although important for understanding natural variation in community dynamics, such exogenous variation in enemy and mycorrhizal fungal effects would not change the results concerning plant species coexistence of our model as we included this level of variation in the mathematical analyses (Appendix 1).

Conclusion

Our model considers the simultaneous effects of mycorrhizal fungi and negative feedbacks from enemies as mechanisms driving fluctuations in plant species abundance and fostering species coexistence. Previous work examining the role of plant–soil feedbacks in plant species coexistence concluded that diversity could be maintained by negative but not positive feedbacks (Bever et al. 1997). Other modeling efforts have demonstrated that the joint effects of competition, mutualism, and predation could lead to species coexistence (Neuhauser and Fargione 2004; Holland et al. 2013; Georgelin and Loeuille 2014; Mougi and Kondoh 2014). Our model

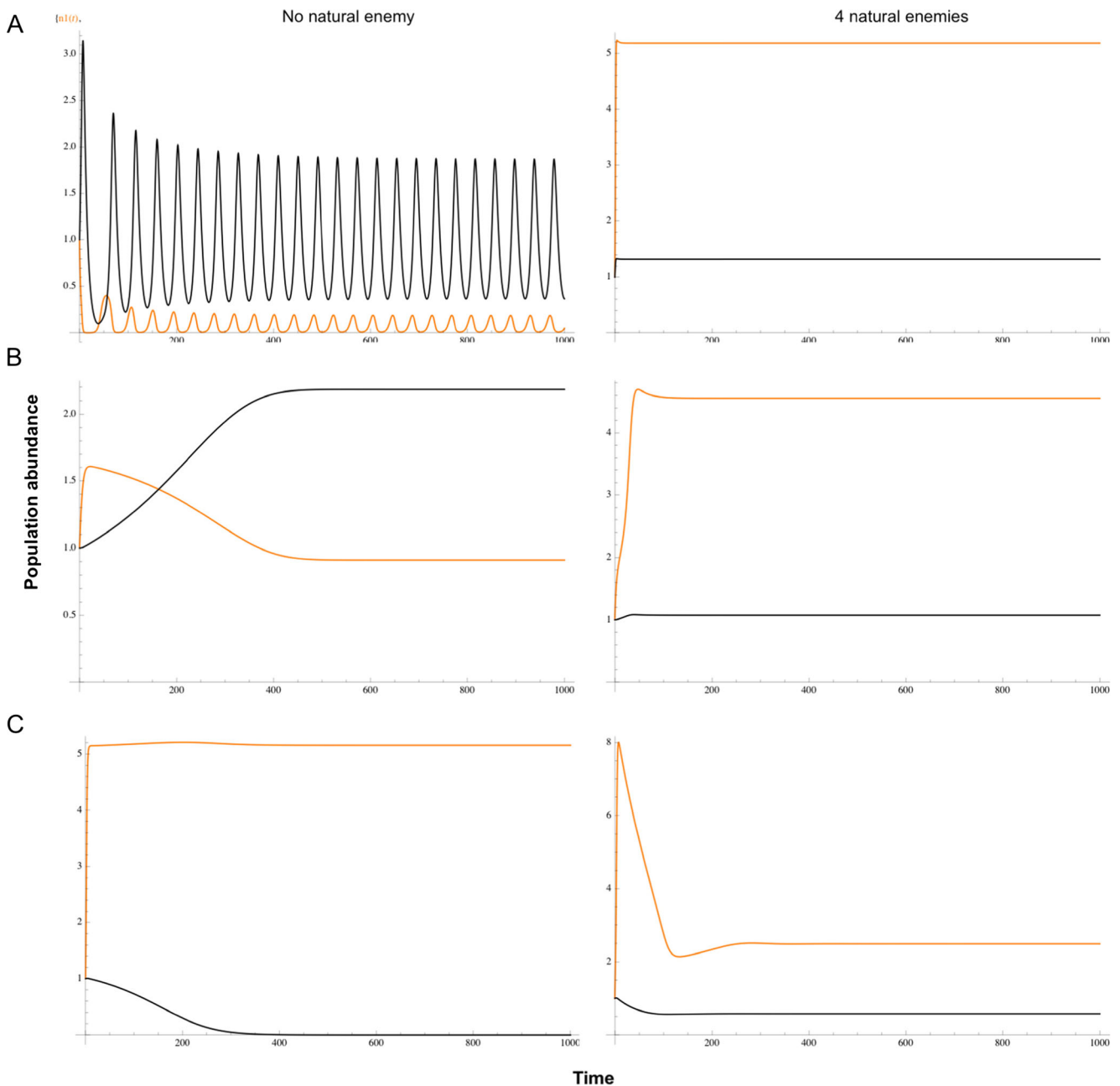


Fig. 7 Model simulations for one plant species (X) in the presence of mycorrhizal fungi (M) and with fixed natural enemy population (Y) and parameters. Panels **a**, **b**, and **c** illustrate three situations where natural

enemy population stabilizes a mutualism system that exhibits cycles (**a**), that is stable (**b**), or that is unstable (**c**)

synthesizes these efforts by considering the joint effects of mutualism, predation, and competition. Furthermore, we added an explicit interaction between mutualism and predation. By combining these three important dynamics and their interactions, our approach is more ecologically realistic than previous models.

Specifically, our analysis addresses the effects of these complex trophic dynamics on plant species coexistence, further developing the integration of mutualisms in food web and community dynamics (Rai et al. 1983; Addicott and Freedman

1984; Freedman et al. 1987; Ringel et al. 1996; Jang 2002; Bronstein et al. 2003; Melián et al. 2009; Loeuille 2010; Mougi and Kondoh 2012; Holland et al. 2013; Georgelin and Loeuille 2014; Mougi and Kondoh 2014). Early work in this area typically includes only two species (May 1976; Christiansen and Fenchel 1977; Vandermeer and Boucher 1978; Addicott 1981). Subsequently, the focus shifted towards three-species interactions in which a mutualist would arise from a prey–predator or a competitor system (Rai et al. 1983; Addicott and Freedman 1984; Freedman et al. 1987).

These studies found that different types of mutualisms stabilize or destabilize a community: mutualisms that deter predators, compete with a predator, or decrease competitive interactions can stabilize interspecific interactions, whereas mutualisms that increase prey availability or asymmetric competition might destabilize interactions (Addicott and Freedman 1984; Thébault and Fontaine 2010). Consistent with these studies, Holland et al. (2013) concluded that a mutualistic pollinator could maintain the stability of the system involving a plant, a mutualistic pollinator (unidirectional mutualism), and a nectar-parasite. Similarly, our work shows that n plant species can coexist with enemy and mycorrhizal fungal populations because the mycorrhizal fungi and natural enemy stabilize each other interactions with plants. Our system expands on previous work by combining competition, predation, and bidirectional mutualism with density-dependent costs and benefits involving $n+2$ species. However, our model lacks network structure, which can have dramatic effects on community diversity (Mougi and Kondoh 2014; Suweis et al. 2014). Future work should aim at combining network structure, trophic interactions, and community dynamics.

Acknowledgments Benedicte Bachelot was partially supported with funds from National Science Foundation DEB-524989 to MU. We are grateful to Dr. Agnes Bachelot, Dr. Alain Bachelot, Dr. Duncan Menge, Dr. Jason Hoeksema, Dr. Stefano Allesina, Dr. Samir Suweis, Dr. Charlotte Lee, Rachael Eaton, Benton Taylor, Bob Muscarella, Naomi Schwartz, and anonymous reviewers for useful comments on the manuscript. In particular, we are grateful to Axios Review that greatly helped us improve our manuscript.

References

- Addicott JF (1979) A multispecies aphid–ant association: density dependence and species-specific effects. *Can J Zool* 57:558–569
- Addicott JF (1981) Properties of 2-species models of mutualism: simulation studies. *Oecologia* 49:42–49
- Addicott JF, Freedman HI (1984) On the structure and stability of mutualistic systems: analysis of predator–prey and competition models as modified by the action of a slow-growing mutualist. *Theor Popul Biol* 26:320–339
- Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483:205–208
- Auge RM, Schekel KA, Wample RL (1987) Leaf water and carbohydrate status of VA mycorrhizal rose exposed to drought stress. *Plant Soil* 302:291–302
- Bachelot B, Kobe RK (2013) Rare species advantage? Richness of damage types due to natural enemies increases with species abundance in a wet tropical forest. *J Ecol* 101:846–856
- Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, Freckleton RP, Lewis OT (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85–90
- Barber NA, Adler LS, Theis N, Hazzard RV, Kiers ET (2012) Herbivory reduces plant interactions with above- and belowground antagonists and mutualists. *Ecology* 93:1560–1570
- Bardgett RD, Wardle DA (2010) Aboveground-belowground linkages. Oxford University Press, Oxford
- Bever JD (2003) Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol* 157:465–473
- Bever JD, Westover KM, Antonovics J (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J Ecol* 85:561–573
- Bi HH, Song YY, Zeng RS (2007) Biochemical and molecular responses of host plants to mycorrhizal infection and their roles in plant defence. *Allelopathy J* 20:15–27
- Booth MG, Hoeksema JD (2010) Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* 91:2294–2302
- Bronstein JL (2001a) The exploitation of mutualisms. *Ecol Lett* 4:277–287
- Bronstein JL (2001b) The costs of mutualism. *Am Zool* 41:825–839
- Bronstein J, Wilson W, Morris W (2003) Ecological dynamics of mutualist/antagonist communities. *Am Nat* 162:S24–S39
- Bruno J, Stachowicz J, Bertness M (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
- Cantrell RS, Cosner C (2001) On the dynamics of predator–prey models with the Beddington–DeAngelis functional response. *J Math Anal Appl* 257:206–222
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Chesson P, Kuang JJ (2008) The interaction between predation and competition. *Nature* 456:235–238
- Christiansen FB, Fenchel T (1977) Theories of populations in biological communities. Springer
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312. In: Boer P J, Graadwell G R (eds) Dynamics of numbers in populations
- Connell JH, Tracey JG, Webb LJ (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest. *Ecol Monogr* 54:141–164
- Diez JM, Dickie I, Edwards G, Hulme PE, Sullivan JJ, Duncan RP (2010) Negative soil feedbacks accumulate over time for non-native plant species. *Ecol Lett* 13:803–809
- Eppstein MJ, Molofsky J (2007) Invasiveness in plant communities with feedbacks. *Ecol Lett* 10:253–263
- Eppstein MJ, Bever JD, Molofsky J (2006) Spatio-temporal community dynamics induced by frequency dependent interactions. *Ecol Model* 197:133–147
- Fitter A (1991) Costs and benefits of mycorrhizas: implications for functioning under natural conditions. *Experientia* 47:350–355
- Fontaine C, Guimarães PR, Kéfi S, Loeuille N, Memmott J, van der Putten WH, van Veen FJF, Thébault E (2011) The ecological and evolutionary implications of merging different types of networks. *Ecol Lett* 14:1170–1181
- Fox L, Morrow P (1981) Specialization: species property or local phenomenon? *Science* 211:887–893
- Freedman HI, Addicott JF, Rai B (1987) Obligate mutualism with a predator: stability and persistence of three-species models. *Theor Popul Biol* 342:157–175
- Gange A, West HM (1994) Interactions between arbuscular mycorrhizal fungi and foliar-feeding insects in *Plantago lanceolata* L. *New Phytol* 128:79–87
- Gause G, Witt A (1935) Behavior of mixed populations and the problem of natural selection. *Am Nat* 69:596–609
- Gehring CA, Whitham TG (1994) Comparisons of ectomycorrhizae on pinyon pines (*Pinus edulis*; Pinaceae) across extremes of soil type and herbivory. *Ecology* 81:1509–1516
- Georgelin E, Loeuille N (2014) Dynamics of coupled mutualistic and antagonistic interactions, and their implications for ecosystem management. *J Theor Biol* 346:67–74

- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Ecology* 93:5–15
- Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Umbanhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol Lett* 13:394–407
- Hoffmann D, Vierheilig H, Schausberger P (2011) Mycorrhiza-induced trophic cascade enhances fitness and population growth of an acarine predator. *Oecologia* 166:141–9
- Hoffmann D, Vierheilig H, Peneder S, Schausberger P (2011) Mycorrhiza modulates aboveground tri-trophic interactions to the fitness benefit of its host plant. *Ecological Entomology* 36:574–581
- Holland JN (2002) Benefits and costs of mutualism: demographic consequences in a pollinating seed-consumer interaction. *Proc Biol Sci R Soc* 269:1405–1412
- Holland J, DeAngelis DL (2006) Interspecific population regulation and the stability of mutualism: fruit abortion and density-dependent mortality of pollinating seed-eating insects. *Oikos* 3:563–571
- Holland JN, DeAngelis DL (2010) A consumer-resource approach to the density-dependent population dynamics of mutualism. *Ecology* 91:1286–1295
- Holland J, DeAngelis D, Bronstein J (2002) Population dynamics and mutualism: functional responses of benefits and costs. *Am Nat* 159:231–244
- Holland JN, DeAngelis DL, Schultz ST (2004) Evolutionary stability of mutualism: interspecific population regulation as an evolutionarily stable strategy. *Proc R Soc Biol Sci* 271:1807–1814
- Holland JN, Wang Y, Sun S, DeAngelis DL (2013) Consumer–resource dynamics of indirect interactions in a mutualism–parasitism food web module. *Theor Ecol* 6:475–493
- Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can Entomol* 91:293–320
- Jaenike J (1990) Host specialization in phytophagous insects. *Annu Rev Ecol Syst* 21:243–273
- Jang SRJ (2002) Dynamics of herbivore-plant-pollinator models. *J Math Biol* 44:129–149
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jeschke J, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. *Ecol Monogr* 72:95–112
- Johnson ANC, Graham JH (2013) The continuum concept remains a useful framework for studying mycorrhizal functioning. *Plant Soil* 363:411–419
- Johnson ANC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol* 135:575–586
- Kardol P, Bezemer TM, Van der Putten WH (2006) Temporal variation in plant-soil feedback controls succession. *Ecol Lett* 9:1080–1088
- Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A, Palmer TM, West SA, Vandenkoornhuyse P, Jansa J, Bücking H (2011) Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333:880–882
- Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70
- Klironomos J, McCune J, Moutoglou P (2004) Species of arbuscular mycorrhizal fungi affect mycorrhizal responses to simulate herbivory. *Appl Soil Ecol* 26:133–141
- Koide R (1991) Tansley review no. 29: nutrient supply, and nutrient to plant response mycorrhizal infection. *New Phytol* 117:365–386
- Koide R, Elliott G (1989) Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. *Funct Ecol* 3:252–255
- Kondoh M, Kato S, Sakato Y (2010) Food webs are built up with nested subwebs. *Ecology* 91:3123–3130
- Koricheva J, Gange AM, Jones T (2009) Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology* 90:2088–2097
- Krebs JR (1974) Behavioral aspects of predation. In: Bateson HG, Klopfer P (eds) *Perspectives in ethology*. Plenum, New York, pp 73–111
- Lekberg Y, Koide RT (2005) Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytol* 168:189–204
- Leon JA, Tumpson DB (1975) Competition between two species for two complementary or substitutable resources. *J Theor Biol* 50:185–201
- Levine JM, Pachepsky E, Kendall BE, Yelenik SG, Lambers JHR (2006) Plant-soil feedbacks and invasive spread. *Ecol Lett* 9:1005–1014
- Loeuille N (2010) Influence of evolution on the stability of ecological communities. *Ecol Lett* 13:1536–1545
- May RM (1976) Models for two interacting populations. In: May RM (ed) *Theoretical ecology*. Saunders, Philadelphia, pp 49–70
- McGill B (2005) A mechanistic model of a mutualism and its ecological and evolutionary dynamics. *Ecol Model* 187:413–425
- Melián CJ, Bascompte J, Jordano P, Krivan V (2009) Diversity in a complex ecological network with two interaction types. *Oikos* 118:122–130
- Moora M, Opik M, Sent R, Zobel M (2004) Native arbuscular fungal communities mycorrhizal influence the seedling performance of rare differentially and common *Pulsatilla* species. *Funct Ecol* 18:554–562
- Morales M (2000) Mechanisms and density dependence of benefit in an ant-membracid mutualism. *Ecology* 81:482–489
- Mordecia E (2011) Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. *Ecol Monogr* 81:429–441
- Mougi A, Kondoh M (2012) Diversity of interaction types and ecological community stability. *Science* 337:349–351
- Mougi A, Kondoh M (2014) Stability of competition-antagonism-mutualism hybrid community and the role of community network structure. *J Theor Biol* 360:54–58
- Murdoch W (1975) Diversity, complexity, stability and pest control. *J Appl Ecol* 12:795–807
- Neuhauser C, Fargione JE (2004) A mutualism–parasitism continuum model and its application to plant–mycorrhizae interactions. *Ecol Model* 177:337–352
- Newsham KK, Fitter AH, Watkinson AR (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends Ecol Evol* 10:407–411
- Novotny V, Miller SE, Baje L, Balagawi S, Basset Y, Cizek L, Craft KJ, Dem F, Drew RAI, Huler J, Leps J, Lewis OT, Pokon R, Stewart AJA, Samuelson GA, Weiblen GD (2010) Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest. *J Anim Ecol* 79:1193–1203
- Olsson PA, Rahm J, Aliasgharzad N (2010) Carbon dynamics in mycorrhizal symbioses is linked to carbon costs and phosphorus benefits. *FEMS Microbiol Ecol* 72:125–131
- Pacala S, Crawley M (1992) Herbivores and plant diversity. *Am Nat* 140:243–260
- Pozo MJ, Azcón-Aguilar C (2007) Unraveling mycorrhiza-induced resistance. *Curr Opin Plant Biol* 10:393–398
- Rai B, Freedman H, Addicott LJ (1983) Analysis of three species models of mutualism in predator–prey and competitive systems. *Math Biosci* 50:13–50
- Real L (1977) The kinetics of functional response. *Am Nat* 111:289–300
- Ringel MS, Hu HH, Anderson G (1996) The stability and persistence of mutualisms embedded in community interactions. *Theor Popul Biol* 50:281–297
- Rosenzweig M, MacArthur R (1963) Graphical representation and stability conditions of predator–prey interactions. *Am Nat* 97:209–223

- Roughgarden J (1975) Evolution of marine symbiosis—a simple cost-benefit model. *Ecology* 56:1201–1208
- Salzer P, Hübner B, Sirrenberg A, Hager A (1997) Differential effect of purified spruce chitinases and beta-1, 3-glucanases on the activity of elicitors from ectomycorrhizal fungi. *Plant Physiol* 114:957–968
- Saravesi K, Markkola A, Rautio P, Roitto M, Tuomi J (2008) Defoliation causes parallel temporal responses in a host tree and its fungal symbionts. *Oecologia* 156:117–123
- Schmitt RJ, Holbrook SJ (2003) Mutualism can mediate competition and promote coexistence. *Ecol Lett* 6:898–902
- Selosse MA, Richard FHX, Simard SW (2006) Mycorrhizal networks: des liaisons dangereuses? *Trends Ecol Evol* 21:621–628
- Silvertown JW (1980) The evolutionary ecology of mast seeding in trees. *Biol J Linn Soc* 14:235–250
- Simard S, Durall D (2004) Mycorrhizal networks: a review of their extent, function, and importance. *Can J Bot* 82:1140–1165
- Simonsen AK, Stinchcombe JR (2014) Herbivory eliminates fitness costs of mutualism exploiters. *New Phytol*
- Smith SE, Read DJ (2008) *Mycorrhizal symbiosis*, 3rd edn. Academic, London
- Smout S, Asseburg C, Matthiopoulos J, Fernández C, Redpath S, Thirgood S, Harwood J (2010) The functional response of a generalist predator. *PLoS One* 5:e10761
- Stephens DW, Krebs JR (1986) *Foraging theory*, vol 1. Princeton University Press, Princeton, pp 1–100
- Strauss S, Irwin R (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu Rev Ecol Syst* 35:435–466
- Suweis S, Grilli J, Maritan A (2014) Disentangling the effect of hybrid interactions and of the constant effort hypothesis on ecological community stability. *Oikos* 123:525–532
- Tang S, Awar SP, Allesina S (2014) Correlation between interaction strengths drives stability in large ecological networks. *Ecol Lett* 17:1094–1100
- Thébault 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
- Toju H, Sato H, Yamamoto S, Kadowaki K, Tanabe AS, Yazawa S, Nishimura O, Agata K (2013) How are plant and fungal communities linked to each other in belowground ecosystems? A massively parallel pyrosequencing analysis of the association specificity of root-associated fungi and their host plants. *Ecol Evol* 3:1–13
- Van der Heijden MGA, Horton TR (2009) Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J Ecol* 97:1139–1150
- Van der Heijden MGA, Klironomos J, Ursic M, Moutoglou P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396:69–72
- Van der Putten WH, Bardgett RD, de Ruiter PC, Hol WHG, Meyer KM, Bezemer TM, Bradford MA, Christensen S, Eppinga MB, Fukami T, Hemerik L, Molofsky J, Schädler M, Scherber C, Strauss SY, Vos M, Wardle DA (2009) Empirical and theoretical challenges in aboveground-belowground ecology. *Oecologia* 161:1–14
- Vandermeer JH, Boucher DH (1978) Varieties of mutualistic interaction in population models. *J Theor Biol* 74:549–558
- Vannette R, Hunter MD (2011) Plant defense theory re-examined: nonlinear expectations based on the costs and benefits of resource mutualisms. *J Ecol* 99:66–76
- Wangersky PJ (1978) Lotka-Volterra population models. *Annu Rev Ecol Syst* 9:189–218
- Wardle DA (2002) *Communities and ecosystems: linking the aboveground and belowground components*. Princeton University Press, Princeton
- Wolfram Research, Inc. (2008) *Mathematica*, Version 7.0, Champaign
- Wootton J (1994) The nature and consequences of indirect effects in ecological communities. *Annu Rev Ecol Syst* 25:443–466
- Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14
- Zhang Q, Xu L, Tang J, Bai M, Chen X (2011) Arbuscular mycorrhizal mediation of biomass-density relationship of *Medicago sativa* L. under two water conditions in a field experiment. *Mycorrhiza* 21:269–277