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Competition for benefits can promote the persistence of mutualistic interactions

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HIGHLIGHTS

- We model mutualistic interactions in which individuals compete for benefits.
- We explicitly consider biologically-realistic trade-offs.
- Competition for benefits alone promotes persistence and community assembly.
- Trade-offs can facilitate or constrain persistence depending on their strength.

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ABSTRACT

Mutualistic interactions are characterized by positive density-dependence that should cause interacting species to go extinct when rare. However, data show mutualistic interactions to be common and persistent. Previous theory predicts persistence provided that mutualistic species are regulated by factors external to the mutualistic interaction (e.g., limiting background resources). Empirical data suggest that competition for the benefits provided by mutualistic partners could be a source of negative density-dependence that allows for population regulation, but there is little, if any, theoretical exploration of this mechanism. Here we develop mathematical models to investigate whether competition for benefits *alone* can allow the persistence of obligate mutualistic interactions. We consider the role of trade-offs in persistence, specifically, trade-offs between benefits acquired versus given and between competition for access to partners (competitive ability) and benefit acquisition. We find that competition for benefits alone is sufficient to promote the persistence of pairwise interactions and the assembly of a three-species community module from an initially pairwise interaction. We find that a trade-off between benefits acquired versus given reduces opportunities for cheating (because a species that acquires significantly more benefits than it gives drives its partner extinct), while a trade-off between competitive ability and benefit acquisition facilitates persistence when it is weak, but constrains persistence when it is strong. When both trade-offs operate simultaneously, persistence requires that each species acquire sufficient benefits to avoid being cheated by its partners, but not so much that it loses its competitive ability. The key finding is that competition for benefits provides a biologically-realistic mechanism for the long-term persistence of mutualistic interactions and the assembly of complex community modules from initially pairwise interactions.

1. Introduction

Mutualistic interactions are characterized by positive density-dependence (i.e., species' per capita growth rates decline with decreasing abundance), which should increase their risk of extinction and cause them to be quite rare in nature. Empirical data, however, suggest otherwise. Mutualisms are ubiquitous in nature, and many mutualistic interactions exhibit long-term persistence (Boucher et al., 1982; Bawa, 1990; Bronstein, 1994; Jordano, 2000; Bascompte and Jordano, 2007). This represents a paradox: long-term persistence suggests that negative density-dependent mechanisms, which cause the per capita growth rate to increase with decreasing abundance, are counteracting the positive density-dependent mechanisms that cause species to go extinct when rare. The challenge for theory has been to identify the sources of negative density-dependence that ensure long-term persistence. In previous models that do not consider stochasticity or spatial dynamics, negative density-dependence is incorporated via a self-limitation term that is independent of the mutualistic

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interaction, which is considered to arise from intra-specific competition for limiting background resources (e.g., nutrients, water, nest-sites, etc.) causing density-dependent mortality (Gauss and Witt, 1935; May, 1973; Vandermeer and Boucher, 1978; Goh, 1979; Travis, Post Iii, 1979; Heithaus et al., 1980; Addicott, 1981; Soberon and Martinez Del Rio, 1981; Gilpin et al., 1982; Wells, 1983; Wolin and Lawlor, 1984; Wolin, 1985; Pierce and Young, 1986; Wright, 1989; Hernandez, 1998; Ferrière et al., 2002, 2007; Holland et al., 2002; Bronstein et al., 2004; Okuyama and Holland, 2008; Bastolla et al., 2009; Holland and DeAngelis, 2009, 2010; Thébault and Fontaine, 2010; Fishman and Hadany, 2010; Lee and Inouye, 2010; Lee et al., 2011; Wang et al., 2011). Henceforth, we will refer to this source of negative density-dependence as intra-specific competition for background resources. In these models, therefore, the source of negative density-dependence (competition for background resources) is decoupled from the source of positive density-dependency (mutualism). As such, the theory is built on the assumption that population regulation occurs independently of the mutualistic interaction itself.

There is widespread empirical evidence that individuals compete for the benefits provided by mutualistic partners (see reviews by Addicott, 1985, Palmer et al., 2003 and Mitchell et al., 2009). Yet, very few studies have investigated whether competition for benefits *alone* can provide the negative density-dependence necessary for persistence (Jones et al., 2012). Nearly all the studies that consider competition for benefits also include a density-dependent mortality term attributed to competition for background resources. This makes it is difficult to disentangle the role of competition for benefits in promoting persistence from that of competition for background resources externally-induced self-regulation.

There are two recent studies of note that incorporate intra-specific competition for benefits. Ferrière et al. (2002) investigated the evolutionary dynamics of mutualism, in which different mutualist phenotypes (e.g., mutualist and ‘cheater’ phenotypes) engage in intra-specific competition for benefits. However, the model incorporates both competition for mutualistic benefits and competition for background resources. Therefore, it is difficult to determine what effect competition for benefits *per se* have on persistence. Morris et al. (2003) consider interactions between a plant and a pollinator/seed parasite and an exploiter species. The pollinator/seed parasite engages in intra-specific competition for benefits. However, the plant species engages in intra-specific competition for a background resource (suitable sites) and not for benefits. The model also incorporates inter-specific competition for benefits, but such competition occurs between a mutualist and an exploiter species rather than between mutualist species and competition is asymmetric: the mutualist has a competitive effect on the exploiter but not vice-versa. Because the model includes mutualistic–parasitic and consumer–resource interactions and because the nature of intra-specific competition is different for the two mutualistic species (e.g., competition for benefits vs. background resources), it is difficult to elucidate what role competition for benefits plays in promoting persistence. As this summary of previous work shows, there is no theory that explicitly investigates whether competition for benefits can allow the persistence of mutualistic interactions in the absence of competition for background resources or other species interactions.

Here, we investigate whether competition for benefits *alone* can provide sufficient negative density-dependence to allow the persistence of two- or three-species modules. While processes external to the mutualistic interaction (e.g., competition for limiting background resources) may play a role in regulating mutualistic interactions, our goal here is to investigate the role of competition within the context of the mutualistic interaction itself in promoting persistence. We explicitly consider trade-offs between acquiring versus giving benefits and between an individual's ability to compete for access to partners (competitive ability) and its ability to acquire benefits once it obtains a partner (benefit acquisition). Our approach yields testable predictions about the conditions under which competition for benefits *alone* can allow the persistence of pairwise interactions and the assembly of more complex community modules.

2. Background

Previous models of mutualistic interactions are based on either modified Lotka–Volterra competition models or, more recently, modified consumer–resource models (e.g., Holland et al., 2002, Okuyama and Holland, 2008, Bastolla et al., 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine, 2010, Fishman and Hadany, 2010 and Wang et al., 2011). In both cases (but see Dean, 1983 and Morris et al., 2003), the dynamics of obligate pairwise interactions (e.g., between a plant and animal species) are given by the following generalized model:

$$
\begin{aligned}
\frac{dP}{dt} &= P(r_P - I_P P + f_P(A,P)) \\
\frac{dA}{dt} &= A(r_A - I_A A + f_A(P,A)) \qquad (1)
\end{aligned}
$$

where P and A are, respectively, the abundances of the plant and animal species; r_i is the intrinsic growth rate of species i ($i = P,A$); I_i is the strength of density-dependent mortality (assumed to arise via intra-specific competition for background resources), and the function f_i, which is akin to a functional response in consumer–resource interactions, describes the rate at which species i acquires benefits from species j.

The model given by Eq. (1) has three features of note. First, the obligate nature of the interaction is represented in terms of a negative intrinsic growth rate (i.e., $r_i < 0$). Hence, species go extinct if they cannot acquire sufficient benefits to overcome the deficit between births and deaths. Second, persistence requires both a source of negative density-dependence (depicted by the density-dependent mortality term) *and* non-linear rates of benefit acquisition (see Appendix B). Without a source of negative density-dependence, the interior equilibrium is unstable (Fig. 1a) and species either increase without bound (if $f_P(A,P) > |r_P|$ and $f_A(P,A) > |r_A|$) or go extinct. Likewise, if species experience self-limitation (via competition for background resources), but acquire benefits at a constant rate (i.e., f_i is linear), the interior equilibrium is unstable and the only outcomes are unbounded growth (if $f_P(A) > |r_P| + I_P P$ and $f_A(P) > |r_A| + I_A A$) or extinction (Fig. 1a; e.g., Gauss and Witt, 1935, May, 1973, Vandermeer and Boucher, 1978, Goh, 1979, Travis, Post Iii, 1979, Heithaus et al., 1980, Addicott, 1981, Gilpin et al., 1982, Wolin and Lawlor, 1984 and Wolin, 1985). Modified competition models with self-limitation and non-linear rates of benefit acquisition result in non-linear zero-growth isoclines and two interior equilibria: an unstable equilibrium (a saddle) at low density and a stable equilibrium at high density (Fig. 1b; e.g., Addicott, 1981, Wolin and Lawlor, 1984, Wolin, 1985, Pierce and Young, 1986, Hernandez, 1998, Ferrière et al., 2002, 2007 and Bronstein et al., 2004). Likewise, modified consumer–resource models with self-limitation and saturating rates of benefit acquisition (i.e., f_i is a declining function of partner density) result in a stable equilibrium at high density (Fig. 1b; e.g., Soberon and Martinez Del Rio, 1981, Wells, 1983, Wright, 1989, Okuyama and Holland, 2008, Bastolla et al., 2009, Thébault and Fontaine, 2010 and Fishman and Hadany, 2010). Several recent models have modified the functional response (f_i) to capture the costs of mutualism, which results in one or two unstable interior equilibria

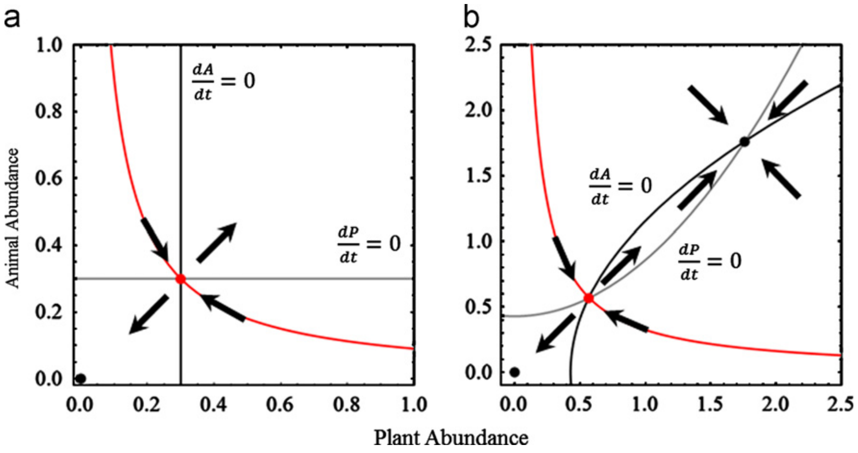

Fig. 1. Phase plots for pairwise mutualistic dynamics (Eq. (3)). The gray line is the zero growth isocline for the plant species and the black line is the zero growth isoclines of the animal species. The black circles represent stable equilibria and red circles represent unstable equilibria. The red line is the separatrix that represents the Allee threshold. (a) Without a source of negative density-dependence parameter, extinction is the only stable equilibrium. (b) When competition is for benefits, stable persistence is possible provided the abundances of both speces exceed the Allee threshold. Other parameter values: $r_P = r_A = -0.3$; $m_{PA} = m_{AP} = 1$; $\tau_P = \tau_A = 1$; and $\alpha_P = \alpha_A = 1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

(depending on whether mutualism is uni-directional or bi-directional), but these models still require a density-dependent mortality term to obtain a stable interior equilibrium (e.g., Holland et al., 2002, Holland and DeAngelis, 2009, 2010 and Wang et al., 2011). The important point is that persistence is impossible without the density-dependent mortality term, which phenomenologically represents intra-specific competition for background resources.

The third feature of note is that the source of negative density-dependence (density-dependent mortality) is decoupled from the source of positive density-dependence (mutualism). This decoupling means that persistence is determined by the strength of density-dependent mortality arising from factors external to the mutualistic interaction, rather than by the properties of the mutualistic interaction. If the mutualistic interaction is itself a source of negative density-dependence, persistence will not be contingent on self-limitation induced by external factors such as competition for resources. This is the issue that we investigate here.

3. Mathematical framework

We use the mathematical framework for consumer–resource interactions (e.g., Holland et al., 2002, Okuyama and Holland, 2008, Bastolla et al., 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine, 2010, Fishman and Hadany, 2010 and Wang et al., 2011) as a starting point to develop a framework in which competition for mutualistic benefits is the only source of negative density-dependence. We begin with a pairwise interaction because it represents the basic building-block of mutualistic communities and serves as a starting point for investigating how more complex communities are assembled. We consider obligate, rather than facultative, mutualisms because they represent the 'worst-case scenario', i.e., species go extinct in the absence of their mutualistic partners. We envision an interaction between a plant species and its pollinator or seed-disperser for illustrative purposes, but our model applies broadly to other mutualistic interactions.

3.1. Pairwise mutualistic interaction

Consider a plant species that relies on an animal species for pollination and/or seed dispersal and provides the animal species with a resource that it cannot otherwise obtain (e.g., nectar, fruit). The dynamics of such an obligate interaction are given by the following generalized model:

$$\begin{aligned}\frac{dP}{dt} &= P(r_P + g(P,\ A))\\ \frac{dA}{dt} &= A(r_A + h(A,P))\end{aligned} \qquad (2)$$

where P and A are, respectively, the abundances of the plant and animal species; r_i is the intrinsic growth rate of species i (i=P,A), and $g(P,\ A)$ and $h(A,P)$ are, respectively, the per capita rates at which the plant and animal species acquire benefits.

In nature, the benefits available to a given mutualist (e.g., the amount of nectar available to pollinators) are limited. Because our goal is to disentangle the role of intra-specific competition for benefits from intra-specific competition for background resources, we assume that species are limited primarily by mutualistic benefits rather than by external resources. Let m_{AP} be the per capita rate at which the animal species acquires benefits from an individual plant; thus, $m_{AP}P$ quantifies the per capita rate at which benefits are acquired from the plant population at any given time. We consider the per capita rate of benefit acquisition to be a saturating function of the abundance of the species that gives the benefits, i.e., $m_{AP}P/(1+m_{AP}\tau_A P)$ where τ_A is the benefit handling time. Intra-specific competition for benefits reduces the rate at which individuals acquire benefits. Let $\propto_A$ quantify the competitive effect of a single animal individual on another animal individual in a population (measured in units of per individual animal squared). Thus, $\alpha_A A$ gives the competitive effect of a single animal individual on the animal population and $\alpha_A A^2$ gives the cumulative strength of intra-specific competition for benefits within the animal species. The per capita rate at which the animal species acquires benefits from the plant species is therefore given by $h(A,P) = m_{AP}P/(1+m_{AP}\tau_A P+\alpha_A A^2)$. We can use the same argument to derive the per capita rate at which the plant species acquires benefits from the animal species as $g(P,A) = m_{PA}A/(1+m_{PA}\tau_P A+\alpha_P P^2)$.

These functions are qualitatively similar to the Beddington–DeAngelis functional response (Beddington, 1975; DeAngelis et al., 1975), which describes interference competition in consumer–resource interactions. The key difference is that the term describing competition for benefits is a function of mutualist abundance squared, while the consumer interference term in the Beddington–DeAngelis functional response is a linear function of consumer abundance. Thus, the terms describing intra-specific competition for benefits (i.e.,$\alpha_A A^2$ and $\alpha_P P^2$) are more akin to intra-specific competition terms in Lotka–Volterra competition models, in which species compete for implicit resources. The functional responses (i.e., $g(P, A)$ and $h(A, P)$), however, are based on consumer–resource theory. Hence, our framework incorporates competition for benefits without within the same framework of recent models of mutualistic interactions (e.g., Holland et al., 2002, Okuyama and Holland, 2008, Bastolla et al., 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine, 2010, Fishman and Hadany, 2010 and Wang et al., 2011).

Our model has three key features. First, each species' intrinsic growth rate is negative (i.e., $r_i < 0$) due to the obligate nature of the interaction. Because the magnitude of r_i describes the rate at which species *i* goes extinct in the absence of the benefits it receives from species *j*, we refer to r_i as the extinction tendency of species *i*. Second, note that m_{ij} is a trait of both species (i.e., it includes both the rate at which species *j* produces benefits and the rate at which species *i* acquires benefits), and is analogous to an attack rate in consumer–resource interactions. For brevity, we refer to m_{ij} as the benefits acquired by species *i*. Third, competition for benefits is incorporated into the species' benefit acquisition response (akin to a functional response in consumer–resource models). The dynamics of a pairwise mutualistic interaction with competition for benefits is given by

$$\frac{dP}{dt} = P\left(r_P + \frac{m_{PA}A}{1 + m_{PA}\tau_P A + \alpha_P P^2}\right)$$
$$\frac{dA}{dt} = A\left(r_A + \frac{m_{AP}P}{1 + m_{AP}\tau_A P + \alpha_A A^2}\right) \qquad (3)$$

The key feature of our model that distinguishes it from previous work is that intra-specific competition for benefits is the only source of negative density-dependence. Hence, the mutualistic interaction is the source of both positive and negative density-dependence.

We first investigate whether competition for benefits alone is sufficient to allow the persistence of obligate pairwise interactions. We then determine the conditions under which a new species can invade the pairwise interaction, leading to a three-species community module.

3.2. Assembly of community modules

The invading species can be a plant or an animal species. Without loss of generality, we consider a plant species that invades and competes with a resident plant over the benefits provided by a shared animal partner. For example, the invasive dandelion (*Taraxacum officinale*) competes with the native dandelion (*T. japonicum*) for the attention of shared pollinators (Kandori et al., 2009). Similarly, fireweed aphids (*Aphis varians*) compete with ant-tended aphids (*Cinara sp.*) for protection by ants (*Formica fusca* and *F. cinerea*) (Addicott, 1978; Cushman and Addicott, 1989; Breton and Addicott, 1992). The dynamics of the three-species interaction are given by

$$\frac{dP_R}{dt} = P_R\left(r_{P_R} + \frac{m_{P_R A}A}{1 + m_{P_R A}\tau_{P_R}A + \alpha_{P_R}{P_R}^2 + \alpha_{P_R P_I}P_I}\right)$$
$$\frac{dP_I}{dt} = P_I\left(r_{P_I} + \frac{m_{P_I A}A}{1 + m_{P_I A}\tau_{P_I}A + \alpha_{P_I}{P_I}^2 + \alpha_{P_I P_R}P_R}\right)$$
$$\frac{dA}{dt} = A\left(r_A + \frac{m_{AP_R}P_R + m_{AP_I}P_I}{1 + m_{AP_R}\tau_{AP_R}P_R + m_{AP_I}\tau_{AP_I}P_I + \alpha_A A^2}\right) \qquad (4)$$

where P_I, P_R, and A are, respectively, the abundances of the invader plant species, the resident plant species, and the animal species scaled by their respective carrying capacities. There are two features to note. First, all species have negative intrinsic growth rates ($r_i < 0$; $i = P_R, P_I, A$). This is because the two plant species are completely dependent on the animal partner and the animal species' persistence requires that at least one plant species be present in the community. Second, there is now intra- *and* inter-specific competition for benefits; with $\alpha_{P_i P_j}$ specifying the competitive effect of plant species *j* on plant species *i* (measured in units of per individual of species *j*). The population-level effect of inter-specific competition for benefits of plant species *j* on plant species *i* is given as the product of the per capita competition coefficient and the abundance of species *j* (i.e., $\alpha_{P_i P_j}P_j$), as is the standard form in competition models.

3.3. The role of trade-offs on persistence and community assembly

In many species, energetic, physiological, and/or other constraints lead to trade-offs between life history traits. We investigate how persistence is influenced by two types of trade-offs that are likely to be important in mutualistic species: a trade-off between (i) benefits acquired and benefits given and (ii) between competitive ability and benefit acquisition.

3.3.1. Trade-off between benefits acquired and benefits given

For mutualistic species in nature, producing benefits (e.g., nectar) comes at an energetic cost. One could envision a situation in which providing benefits to a mutualistic partner comes at the cost of reduced survival and/or reproduction (Ferrière et al., 2002, 2007; Bronstein et al., 2004; Holland et al., 2004). We incorporate this trade-off into the model (Eqs. (3) and (4)) by making the intrinsic growth rate of each species a function of the ratio of benefits given versus received, i.e., $\hat{r}_i = r_i(\sum_j m_{ji}/\sum_j m_{ij})$ where $\hat{r}_i$ is the intrinsic growth rate with the trade-off. Thus, an increase in the rate at which a species gives benefits to its partner (i.e., m_{ji} increases), comes at the cost of an increased extinction tendency (i.e., $r_i^{'}$ becomes more negative). We use a linear form for purposes of illustration, but more complex forms can easily be incorporated into the model. This trade-off can arise in the pairwise interaction and three-species community module. Note that because this trade-off does not depend on species' abundances, it is not a source of negative density-dependence.

3.3.2. Trade-off between benefit acquisition and competitive ability

In mutualistic species, greater energy allocation to competition for access to partners may come at the cost of acquiring fewer benefits (or vice-versa). For example, a plant species may allocate energy towards large, colorful flowers to attract pollinators away from competitors, thus increasing its competitive ability, at the cost of reduced energy allocation towards pollen production, thus reducing the rate at which it acquires benefits (pollen transfer). We incorporate this trade-off into the three-species community module (Eq. (4)) by modifying the rate of benefit acquisition of plant species *i* ($m_{P_i A}$). For this trade-off to occur, the rate of benefit acquisition must first be directly related to the strength of inter-specific competition for benefits. We assume that $m_{P_i A}$ decreases as the strength of inter-specific competition for benefits increases (i.e., $\hat{m}_{P_i A} = m_{P_i A}(1 - \alpha_{P_i P_j}P_j)$ where $\hat{m}_{P_i A}$ is the rate of benefit acquisition with the trade-off). The trade-off is incorporated into this function by making inter-specific competition a function of the rate at which species *i* acquires benefits relative to that of its competitor *j* (i.e., $m_{P_i A}/m_{P_j A}$). Thus, this trade-off is incorporate into the model as: $\hat{m}_{P_i A} = m_{P_i A}(1 - (m_{P_i A}/m_{P_j A})\alpha_{P_i P_j}P_j)$. Hence, when species *j* allocates more towards acquiring benefits relative to species *i* (i.e., $m_{P_i A}/m_{P_j A}$ decreases), its competitive effect on species *i* becomes weaker and species *i* is able to acquire more benefits. Because it involves inter-specific competition, this trade-off can only operate in community modules of three or more species.

4. Results

4.1. Pairwise mutualistic interaction

We find that competition for benefits alone is sufficient to allow the persistence of obligate pairwise mutualistic interactions. We first report results in the absence of any trade-offs. In the absence of any negative density-dependence, the tight interdependence between species leads to an Allee effect. If the initial species' abundances are below a critical threshold defined by an unstable interior equilibrium (a saddle; Fig. 1a; Appendix A), positive density-dependence (i.e., per capita growth rates decrease with declining abundance) causes extinction. If the initial abundances exceed this threshold, species abundances increase indefinitely. Thus, when there are no negative density-dependent mechanisms operating, extinction is the only stable outcome.

With competition for benefits, an interior equilibrium becomes feasible such that there now exist alternative stable states (extinction and persistence) separated by a saddle (Fig. 1b). This occurs because competition for benefits causes benefit acquisition rates (functions g and h in Eq. (2)) to decline with increasing species abundance, which causes each species' per capita growth rate to decrease as its abundance increases and leads to a non-linearity in the species' zero-growth isoclines (Fig. 1b). Importantly, this non-linearity in species' zero-growth isoclines is an outcome of the model that arises naturally from the negative density-dependent mechanism (competition for benefits). Whether species can persist in the long-term depends on their initial abundances. Below we explain how this dependence can lead to different long-term outcomes.

When both partners are rare, competition for benefits is weak and negative density-dependence is insufficient to overcome positive density-dependence. Because neither species can acquire sufficient benefits from its rare partner to overcome its extinction tendency (r_i), species' per capita growth rates decline as their abundances decrease and both partners go extinct.

When both species are abundant, intra-specific competition for benefits is strong and causes each species' per capita growth rate to decline as its abundance increases. Thus, the negative density-dependence due to intra-specific competition for benefits outweighs the positive density-dependence due to the Allee effect, allowing both partners to attain a steady state with positive abundances (Fig. 1b; Appendix A).

An interesting outcome ensues when one species is abundant and the other is rare. In this case, competition for benefits is intermediate in strength and the outcome depends on the tension between positive density-dependence in the rare partner and negative density-dependence in the abundant partner. Because of this tension, the interaction stands on the knife-edge between persistence and extinction and a small difference in the initial abundances of the partners can lead to fundamentally different outcomes (Fig. 2a,b). The initially rare partner increases in abundance due to weak intra-specific competition for the large amount of benefits provided by the abundant partner. As the rare partner increases, increased intra-specific competition leads to stronger negative density-dependence. At the same time, the initially abundant partner decreases in abundance due to strong intra-specific competition for the small amount of benefits provided by the rare partner. As the abundant partner declines, decreased intra-specific competition leads to weaker negative density-dependence. Persistence occurs when the rare partner increases above a level that allows the abundant partner to increase (Fig. 2a). Above this threshold, negative density-dependence is stronger than positive density-dependence for each partner, allowing them both to persist. Extinction occurs when the abundant partner declines below a level that prevents the rare partner from increasing (Fig. 2b). Below this threshold, positive density-dependence is stronger than negative density-dependence and both species go extinct.

As the above analyses show, the relative strengths of positive and negative density-dependence when species are abundant versus rare is the key to understanding how competition for benefits alone allows for the persistence of pairwise mutualistic interactions.

4.2. Role of trade-offs on the persistence of pairwise interactions

An important question is how a trade-off between benefits acquired versus given alters the above results for pairwise interactions (Ferrière et al., 2002, 2007; Bronstein et al., 2004; Holland et al., 2004). The main difference is that the trade-off causes the

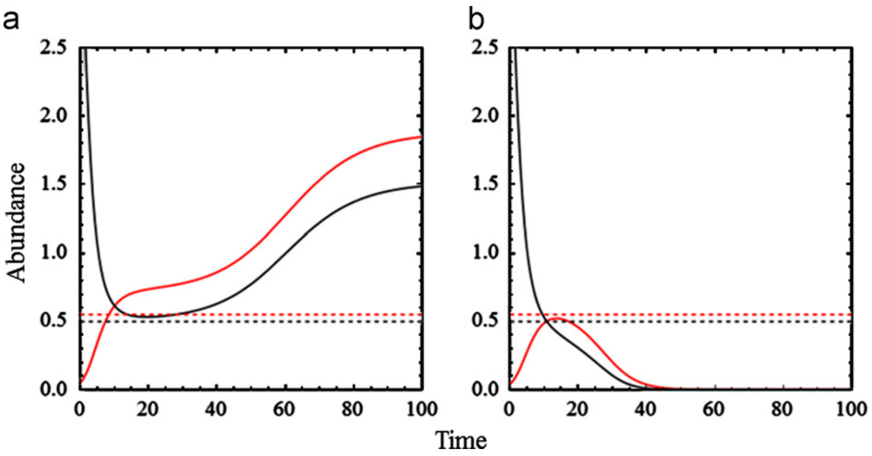

Fig. 2. Time series plots for the pairwise mutualistic interaction when one partner is rare and the other is abundant. The red line is the initially rare partner and the black line is the initially abundant partner. The dashed red line is the threshold abundance of the rare partner. If the rare species exceeds this threshold, the abundant species can increase. The dashed black line is the threshold abundance of the abundant species. If the abundant species delines below this threshold, the rare species cannot increase. The initial abundance of the rare partner is only 1% greater in panel (a) than in panel (b). (a) When the rare partner increases above its threshold, negative density-dependence is stronger than positive density-dependence for both partners and the species persist. (b) When the abundant partner declines below its threshold, positive density-dependence is stronger than negative density-dependence for both partners and the species go extinct. Parameter values: $r_P = -0.2$; $r_A = -0.3$; $m_{PA} = m_{AP} = 0.75$; $\tau_P = \tau_A = 1$; and $\alpha_P = \alpha_A = 1$. Initial abundances: (a) $P = 0.05$ and $A = 3$; (b) $P = 0.04$ and $A = 3$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

extinction of interactions in which one species gains significantly more benefits than does its partner (i.e., a 'cheater'; Fig. 3). Here, cheaters are species that acquire significantly more benefits than they give, as opposed to species that acquire benefits without reciprocating at all (e.g., Morris et al., 2003; Bronstein et al., 2003). Extinction occurs because the cheater causes the abundance of its partner to fall below the Allee threshold. This suggests that a trade-off between benefits acquired versus given should reduce opportunities for cheating. Note that the trade-off between competitive ability and benefit acquisition can only operate in interactions involving three or more species.

4.3. *Assembly of community modules*

The key finding is that competition for benefits alone is sufficient to allow the assembly of more complex community modules from simple pairwise interactions. Below we explain how this result comes about.

4.3.1. *Invasibility*

The conditions under which a second plant species can invade the pairwise interaction between a resident plant and animal species are as follows. The invader can increase from initially small numbers if it can maintain a positive per capita growth rate when the resident plant–animal pair is at equilibrium. Invasion occurs when $m_{P_IA}A^* > |r_{P_I}|(1 + m_{P_IA}\tau_{P_I}A^* + \alpha_{P_IP_R}P_R^*)$ where P_R^* and A^* are, respectively, the equilibrium abundances of the resident plant and animal species (Fig. 4a). The invading plant species will increase when rare if it acquires sufficient benefits to overcome both its extinction tendency (i.e., $r_{P_I} < 0$) *and* the effects of inter-specific competition for benefits from the resident plant (i.e., $\alpha_{P_IP_R}P_R^*$), despite the saturating rate at which it acquires benefits (i.e., $1 + m_{P_IA}\tau_{P_I}A^*$). Otherwise, the initial pairwise plant–animal interaction cannot be invaded by a second plant (or by extension, an animal) species. The invader species is more likely to establish with an increase in its benefit acquisition rate relative to its extinction tendency (i.e., m_{P_IA}/r_{P_I}) and/or a reduction in its handling time (τ_{P_I}) or the strength of inter-specific competition for benefits of the resident species ($\alpha_{P_IP_R}$).

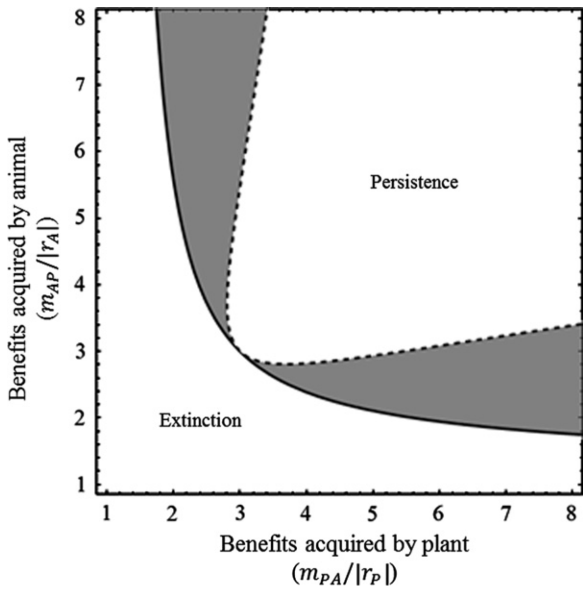

Fig. 3. Effect of a trade-off between benefits acquired versus given on the persistence of an obligate pairwise mutualistic interaction (Eq. (3)), plotted as the ratio of the benefit acquisition rate to the intrinsic growth tendency (i.e., $m_{ij}/|r_i|$) of the animal species against that of the plant species. The solid line divides the parameter space into regions where exinction and persistence occur without the trade-off. The dashed line is the threshold above which persistence occurs with the trade-off and the gray area is the region of the parameter space eleminated by the trade-off. The trade-off constrains persistence by eliminating interactions in which one species (i.e., a cheater) acquires more benefits from its partner than it gives in return. Other parameter values: $r_P = r_A = -0.2$; $\tau_P = \tau_A = 1$; and $\alpha_P = \alpha_A = 1$.

4.3.2. *Stable coexistence*

In order for a third species to successfully integrate into an existing two-species community, it must invade *and* coexist with the resident species. Coexistence requires mutual invasibility, i.e., each plant species must be able to increase in abundance when it is rare and its competitor is at equilibrium with the animal species. Mutual invasibility occurs when $m_{P_IA}A^* > |r_{P_I}|(1 + m_{P_IA}\tau_{P_I}A^* + \alpha_{P_IP_R}P_R^*)$ and $m_{P_RA}A^* > |r_{P_R}|(1 + m_{P_RA}\tau_{P_R}A^* + \alpha_{P_RP_I}P_I^*)$, where P_I^* is the equilibrium abundance of the invader plant. Mutual invasibility is possible when both species acquire sufficient benefits to overcome their respective extinction tendencies *and* the effects of inter-specific competition for benefits, despite saturating rates of benefit acquisition. Coexistence occurs when inter-specific competition for benefits in both species is relatively weak compared to the rates at which each species acquires benefits and is more likely to occur with a reduction in both species' handling times. The resident excludes the invader when its inter-specific competitive ability is relatively strong compared to the rate at which the invader acquires benefits (Fig. 4a). However, if the invader acquires sufficient benefits to increase in abundance when rare *and* is a relatively strong competitor for benefits, the invader excludes the resident and forms a new pairwise interaction with the animal species. Coexistence further requires that all species' abundances exceed their respective Allee thresholds (i.e., species are locally, but not globally, stable to perturbations of their equilibrium abundances).

An interesting point to note is that coexistence can occur even when the invader acquires fewer benefits than does the resident (i.e., $m_{P_IA} < m_{P_RA}$). In extreme cases, the invader can even persist in a three-species web when it would go extinct in a pairwise interaction. This occurs because the resident plant keeps the animal sufficiently abundant to compensate for the low rate at which the invader plant acquires benefits. Hence, the resident may indirectly facilitate the invader and thus promote coexistence.

4.4. *Role of trade-offs in community assembly*

We next investigate how the above results on invasibility and coexistence are influenced by trade-offs between (i) benefits acquired and given and (ii) competitive ability and benefit acquisition both when they operate separately versus simultaneously. When there is a fitness cost to giving benefits, the invader must acquire greater benefits to become established than it would in the absence of the trade-off (Fig. 4b vs. a). This is because the invader must acquire sufficient benefits to overcome competition from the resident as well as its greater extinction tendency (i.e., $r_{P_I} \ll \lambda 0$) due to providing more benefits than it receives.

When a trade-off between competitive ability and benefit acquisition operates, invasion is much less likely to occur compared to when there is no trade-off (Fig. 4c vs. a). When inter-specific competition from the resident is relatively weak, however, we get a counter-intuitive result: the invader is more likely to establish when the trade-off is weak than when it is strong. This is because the strength of competition for benefits from the resident (i.e., $\alpha'_{P_IP_R}$) determines the outcome of invasion. When the trade-off is relatively weak, coexistence is possible because the resident species is superior at acquiring benefits, but the invader species is the superior competitor for benefits. For instance, the invader is better at competing for the attention of the shared partner species, but the resident is able to acquire greater benefits per interaction with the shared partner species. When the trade-off is relatively

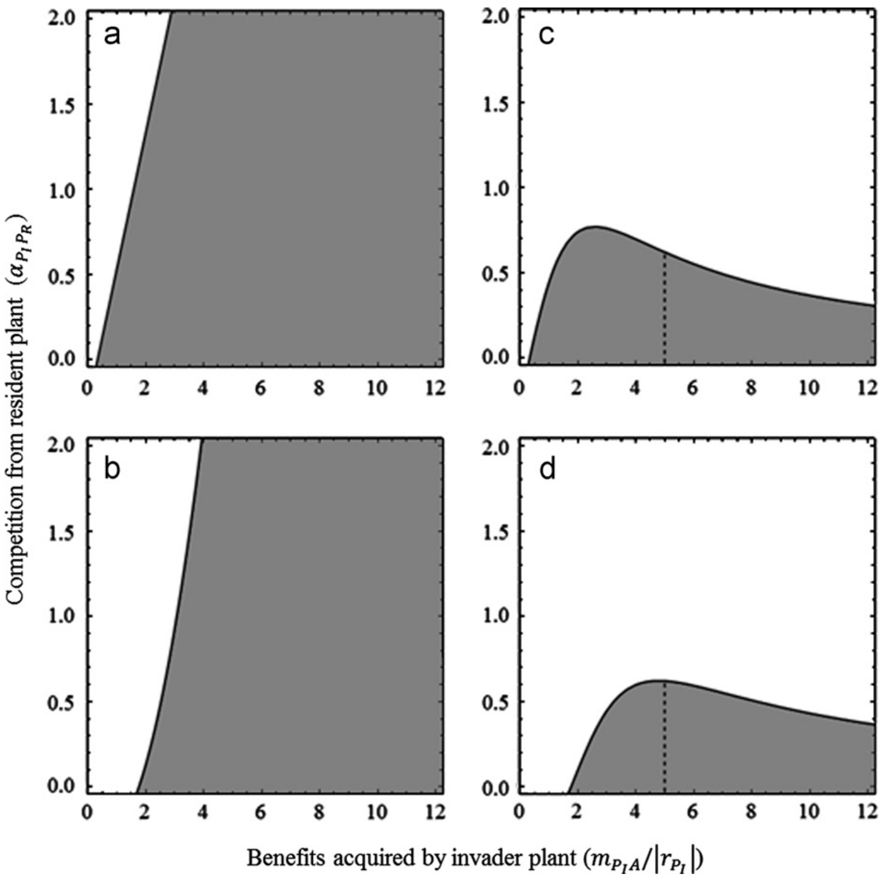

Fig. 4. Effects of a trade-off between (i) benefits acquired versus given (panels b and d) and (ii) benefit acquisition and competitive ability (panels c and d) on community assembly (Eq. (4)), plotted as the strength of inter-specific competition for benefits on the invader plant species from the resident plant species (i.e., $\alpha_{P_I P_R}$) against ratio of the benefit acquisition rate to the intrinsic growth rate of the invader plant species (i.e., $m_{P_I A}/|r_{P_I}|$). The black line divides the parameter space into regions where invasion (gray region) and exinction (white region) occur. The dashed lines in panels (c) and (d) show the benefits acquired by the resident plant for comparison purposes. (a) In the absence of any trade-off, invasion occurs if inter-specific competition for benefits from the resident species is relatively weak compared to the rate at which the invader species acquires benefits from the shared animal parnter. (b) A trade-off between benefits acquired versus given contrains persistence because the invader must acquire greater benefits to invade than without the trade-off. (c) A trade-off between benefit acquisition and competitive ability facilitates persistence at intermediate levels of benefit acquisition, but constrains persistence at high levels of benefit acquisition. (d) When both trade-offs operate, persistence is constrained to intermediate levels of benefit acquisition. Other parameter values: $r_{P_R} = r_{P_I} = r_A = -0.2$; $m_{P_R A} = m_{AP_R} = m_{AP_I} = 1$; $\tau_{P_R} = \tau_{P_I} = \tau_A = 1$; and $\alpha_{P_R} = \alpha_{P_I} = \alpha_A = \alpha_{P_R P_I} = 1$.

strong, the species that is the superior competitor for benefits deprives the other species of its advantage in acquiring benefits, resulting in competitive exclusion. The superior competitor, because of its greater ability to attract the mutualistic partner, preempts the benefits that the inferior competitor (who is more efficient at acquiring benefits once an encounter with a partner ensues) could have otherwise acquired. Thus, the trade-off leads to a priority effect where the species that is better able to attract a mutualistic partner gains an initial advantage by depriving its competitor from sufficient access to the mutualistic partner.

When both trade-offs operate simultaneously, the invader cannot establish when it acquires significantly fewer benefits or greater benefits than the resident (Fig. 4d). When the invader acquires significantly fewer benefits than the resident, the trade-off between benefits acquired versus given dominates and extinction occurs because the invader experiences a greater deficit between benefits acquired versus given, and thus a greater extinction tendency (i.e., r_{P_I} is more negative). In other words, the invader is unable to acquire sufficient benefits to compensate for the benefits it gives to the partner species and is thus ‘cheated’ by its partner. In this case, the invader is eliminated by its partner. Thus, this trade-off reduces both the persistence of pairwise partners and the coexistence of species competing for shared partner species. When the invader acquires more benefits than the resident, the trade-off associated with competitive ability and benefit acquisition dominates and extinction occurs because the resident is the superior competitor for benefits and competitively excludes the invader. In contrast to the previous case, the invader is now eliminated by its competitor. The key result is that coexistence requires that a species acquire an intermediate level of benefits such that it is neither cheated by its partner nor competitively excluded by a superior competitor for benefits.

4.5. Comparison with previous work

In previous models, negative density-dependence arises from a density-dependent mortality term, which is attributed to intraspecific competition for background resources. Hence, negative density-dependence arises from a source external to the mutualistic interaction and is therefore decoupled from the positive density-dependence that is inherent in the mutualistic interaction. In contrast, when competition is for benefits, positive and negative density-dependence arise from the mutualistic interaction itself.

We illustrate this point by comparing our framework with a model in which negative density-dependence arises from external factors (Eq. (1)) with $f_P(A,P) = m_{PA}A/(1+A)$ and $f_A(P,A) = m_{AP}P/(1+P)$; e.g., Holland et al., 2002, Okuyama and Holland, 2008, Bastolla et al., 2009, Holland and DeAngelis, 2009, 2010, Thébault and Fontaine, 2010, Fishman and Hadany, 2010 and Wang et al., 2011). The key finding is that for a given intrinsic growth rate

(r), species requires greater rates of benefit acquisition (m) to persist when self-limitation arises from a process external to the mutualistic interaction, such as competition for background resources (i.e., I in Eq. (1)), than when self-limitation arises from competition for benefits (i.e., α in Eqs. (3) and (4)), even when $I=\alpha$ (Fig. 5). We illustrate this difference by considering the plant species in a pairwise interaction. We derive the minimum value of $m_{PA}A$ (i.e., the total benefits acquired from the animal species) required for the per capita growth rate of the plant species to be positive (i.e., $(dP/dt)/P>0$). We do this by solving $r_P - I_P P + m_{PA}A/(1+m_{PA}\tau_P A)>0$ (competition for background resources) and $r_P + m_{PA}A\,/(1+m_{PA}\tau_P A+\alpha_P P^2)>0$ (competition for benefits) for $m_{PA}A$. When competition is for background resources, this condition is: $m_{PA}A>(|r_P|+I_P P)/(1-\tau_P I_P P-|r_P|\tau_P)$. When competition is for benefits, it is: $m_{PA}A>|r_P|(1+\alpha_P P^2)/(1-|r_P|\tau_P)$. The difference in outcomes can be illustrated as follows. If the minimum value of $m_{PA}A$ is equal in both models, then: $(|r_P|+I_P P)/(1-\tau_P I_P P-|r_P|\tau_P)=|r_P|(1+\alpha_P P^2)/(1-|r_P|\tau_P)$, which simplifies to: $I_P/(1-\tau_P I_P P-|r_P|\tau_P)=|r_P|\alpha_P P$ (note that the left-side of this condition is when competition is for background resources and the right-side is when competition is for benefits; see Appendix C). The plant species can persist only if it can acquire sufficient benefits to increase when rare (i.e., when $P\approx 0$). Thus, for the minimum value of $m_{PA}A$ to be equal in both models *and* be sufficient for the plant species to increase when rare, requires that: $I_P/(1-|r_P|\tau_P)\approx 0$. Since $I_P\neq 0$, the minimum value of $m_{PA}A$ must always be greater when competition is for background resources (as in previous models) than when competition is for benefits (as in our framework).

This is because, in previous models, self-limitation via intraspecific competition for background resources is decoupled from the mutualistic interaction *and* persistence requires the inclusion of a saturating function for benefit acquisition (Appendix B). In our model, competition for benefits is intrinsic to the mutualistic interaction and thus directly leads to the decline in the rate of benefit acquisition as species increase in abundance. It should be noted that saturating rates of benefit acquisition are an input in previous models that is necessary to generate non-linear zero growth isoclines and a stable interior equilibrium, while in our case, non-linear zero growth isoclines are a natural outcome of the model resulting from the interplay between competition and mutualism.

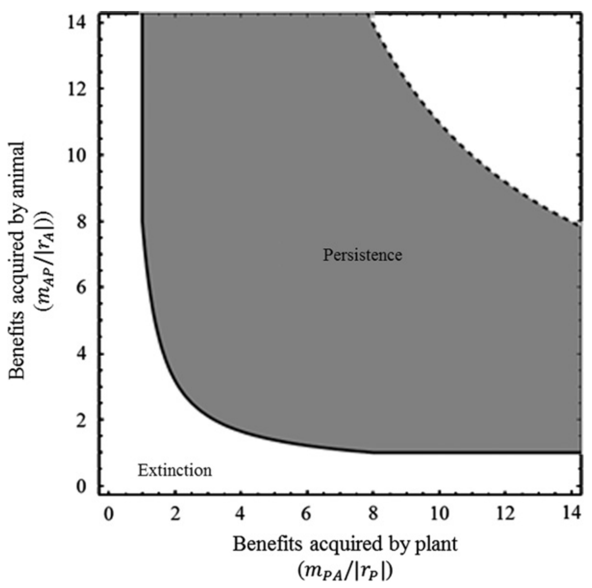

Fig. 5. Persistence of pairwise mutualistic interactions in our model and in previous models, plotted as the ratio of the benefit acquisition rate to the intrinsic growth rate (i.e., $m_{ij}/|r_i|$) of the animal species against that of the plant species. In previous models (Eq. (1)), persistence occurs in the region above the dashed line, while extinction occurs in the region below the dashed line. In our model (Eq. (3)), persistence occurs in the region above the solid line, while extinction occurs in the region below the solid line. The key point is that for a given intrinsic growth rate (r), our model allows for the persistence of species with lower rates of benefit acquisition (m) than in previous models (gray region). Note that for comparison purposes, the strength of competition for background resources in previous models is eqivalent to the strength of competition for benefits in our model (i.e., $I=\alpha$); hence, *all parameters are the same in both models*. Other parameter values: $r_P=r_A=-0.2$; $\tau_P=\tau_A=1$; and $\alpha_P=I_P=\alpha_A=I_A=1$.

5. Discussion

Mutualistic interactions represent a paradox: they are characterized by positive density-dependence, but data demonstrate long-term persistence, suggesting that negative density-dependent mechanisms are at play. The challenge for theory has been to identify biologically-realistic sources of negative density-dependence. One source of negative density-dependence which theory has not adequately explored is competition for the benefits provided by mutualistic partners (Jones et al., 2012). Here we develop a mathematical model to investigate the role of competition for benefits in the persistence of mutualistic interactions. Our approach differs from previous work in that we consider intra- *and* inter-specific competition, both of which occur for the benefits received from a mutualistic partner. Inter-specific competition ensures that inferior competitors for benefits are excluded, but the fact that both positive and negative density-dependence arise from the mutualistic interaction itself ensures that even weakly interacting partners (i.e., those that acquire relatively few benefits from one another) can persist in the long-term. While it is possible that factors such as competition for background resources play a role in regulating mutualistic interactions, our work shows that mechanisms external to the mutualistic relationship are not necessary for persistence. Indeed, we find that competition for benefits alone can allow the long-term persistence of pairwise mutualistic interactions as well as the assembly of more complex community modules. Thus, our model provides a parsimonious resolution to the paradox of how mutualistic species persist despite their inherent tendency to go extinct when rare.

An important aspect of our framework is the explicit consideration of trade-offs that affect both persistence and community assembly. This analysis leads to two key results. First, a trade-off between benefits acquired and benefits given can reduce persistence by eliminating cheaters (partners that acquire far more benefits that they give). This trade-off is interesting because it imposes an ecological constraint on the evolution of cheating (e.g., Ferrière et al., 2002, 2007, Bronstein et al., 2004 and Holland et al., 2004). It also suggests the possible role of indirect interactions in more complex community modules that may lead to a transition between mutualism and antagonism (Holland et al., 2002; Holland and DeAngelis, 2009, 2010; Wang et al., 2011).

A second key result is that when a trade-off between benefit acquisition and competitive ability operates, invasion is more likely when the trade-off is weak than when the trade-off is strong. Coexistence occurs when the trade-off is weak because one species is slightly better at competing for access to partners, while the other species is slightly better at acquiring benefits once an interaction with a partner ensues. Competitive exclusion occurs when the trade-off is strong because of an asymmetry in the trade-off: the superior competitor has an extra advantage because it exerts a preemptive effect, i.e., by attracting more mutualistic partners it undermines its competitor's advantage in acquiring greater benefits once a partner is encountered.

When the two trade-offs operate simultaneously, coexistence requires that a species acquire sufficient benefits relative to those it gives to overcome its extinction tendency, but not in such excess that it is excluded by a superior competitor for benefits. A key insight to emerge from this analysis is that persistence is most likely at intermediate levels of benefit acquisition. This result offers an intriguing parallel to consumer–resource models in which biodiversity is maximized at intermediate productivity (e.g., Holt and Polis, 1997). In consumer–resource models, biodiversity is reduced by limited resources at low productivity and by strong consumer control at high productivity. In our model, persistence is reduced by limited benefits at low levels of benefit acquisition and by strong competition for benefits at high levels of benefit acquisition.

An important question in applying these ideas to real communities is how prevalent competition for benefits is likely to be in nature and how relevant our results are to real mutualistic communities. Empirical evidence suggests that competition is quite common (see reviews by Addicott, 1985, Palmer et al., 2003 and Mitchell et al., 2009). Examples include competition for pollinators (e.g., Levin and Anderson, 1970, Mosquin, 1971, Waser, 1978, Bawa, 1980, Zimmerman, 1980, Campbell, 1985, Campbell and Motten, 1985, Waser and Fugate, 1986, Bell et al., 2005 and Pauw and Bond 2011), seed dispersers (e.g., Ruhren and Dudash, 1996, Alcantara et al., 1997, Alcantara and Rey, 2003, Saracco et al., 2005 and Rodriguez-Perez and Traveset, 2010), or ant protectors (e.g., Addicott, 1978, Cushman and Addicott, 1989, Cushman and Whitham, 1991, Breton and Addicott, 1992, Fischer and Shingleton, 2001, Ness and Bronstein 2004, Morris et al., 2005, Ness et al., 2009). It also suggests that natural mutualistic communities are characterized by weak interactions (Bascompte et al., 2006; Bascompte and Jordano, 2007). For instance, Bascompte et al. (2006) analyzed the distribution of interaction strengths (termed 'mutual dependence') of 26 plant–animal networks, quantified by the fraction of all visits to a plant species from a given animal species (quantified here by m_{PA}) and the fraction of all visits from an animal species to a given plant species (quantified here by m_{AP}). Regardless of the type of mutualism, the frequency distribution of interaction strength (dependences) shows mostly weak interactions with only a few strong interactions (Bascompte et al., 2006). A key outcome of our mathematical framework is that mutualistic species can persist even when there are low rates of benefit acquisition (m) for a given intrinsic growth rate (r). This is because competition for benefits occurs within the mutualistic interaction itself, while competition for background resources is decoupled from the mutualistic interaction. Thus, our framework, based on competition for mutualistic benefits, provides a potential explanation for the preponderance of weakly interacting mutualistic communities in nature.

Indeed, the biological significance of our theory lies in its ability to generate testable predictions about the conditions under which persistence verses competitive exclusion may arise in natural mutualistic communities. As illustrative examples, we present two empirical case studies which relate to the theory we develop here. First, consider the case in which fireweed aphids (*Aphis varians*) engage in intra-specific competition with conspecifics and inter-specific competition with ant-tended aphids (*Cinara sp.*) for the protection benefits provided by ant mutualists (*Formica fusca* and *Formica cinerea*) (Addicott, 1978; Cushman and Addicott, 1989; Breton and Addicott, 1992). The benefits acquired by individual fireweed aphids declined as the number of conspecifics increases (Breton and Addicott, 1992). Also, the presence of neighboring ant-tended aphids significantly reduced the number of ants tending fireweed aphid populations, resulting in increased risk of extinction (Cushman and Addicott, 1989). Second, consider the so-called "Dandelion War" in Japan (Kandori et al., 2009 and references therein), in which the invasive dandelion *Taraxacum officinale* has been competitively displacing the native dandelion *T. japonicum* across Japan over the past few decades. There is growing concern that the native species will ultimately go extinct. The invasive *T. officinale* attracts more pollinator visits than the native *T. japonicum*, likely because it produces more nectar; as a result, the native species suffers reduced seed set in the presence of the invasive species (Kandori et al., 2009). These data suggest that competition for benefits may be an important determinant of exotic species' ability to invade and displace native species. Importantly, the mathematical framework we have developed can predict the conditions under which competitive exclusion may occur; specifically, that species with a greater ability to attract mutualistic partners will have a competitive advantage and exclude its competitor. This is consistent with observations that fireweed aphids experience increased extinction risk in the presence of ant-tending aphids and that the invasive *T. officinale* attracts more pollinators and, as a result, is displacing the native *T. japonicum* in Japan.

The work presented here suggests several important future directions. First, the models we have developed are deterministic. Investigating the effects of environmental stochasticity in driving species' abundances below their extinction (Allee) thresholds, and the role of demographic stochasticity in enhancing the tendency to go extinct when rare are important future directions. Second, exploring how negative density-dependence generated by competition for benefits leads to the assembly of complex mutualistic communities is an important next step. Particularly important in this regard is to determine whether competition for benefits allows community modules to assemble in such a way that they lead to the nested structure observed in natural mutualistic communities (Bascompte et al., 2003; Bascompte and Jordano, 2007).

Our findings have potential implications for the conservation and restoration of mutualistic communities. If mutualistic partners are rare, such as in the case of pollen limitation in plants due to a scarcity of pollinators, our model predicts that plant species with greater abilities to attract pollinators (i.e., superior competitors for the attention of mutualistic partners) will be better able to persist. If such species are invaders rather than natives, then native plant species will suffer a greater extinction risk. Indeed, there is growing concern that invasive species may be competitively displacing native mutualists by attracting shared partners (e.g., McKey, 1988, Brown and Mitchell, 2001, Brown et al., 2002, Traveset and Richardson, 2006, Jakobsson et al., 2009, Kawakami et al., 2009, Kueffer et al., 2009 and Kaiser-Bunbury et al., 2010). Thus, if competition for benefits is an important mechanism for diversity maintenance in real communities, native mutualists may be at greater risk of extinction than was previously thought.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2013.03.016.

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