Preferential allocation, physio-evolutionary feedbacks, and the stability and environmental patterns of mutualism between plants and their root symbionts

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Summary

- The common occurrence of mutualistic interactions between plants and root symbionts is problematic. As the delivery of benefit to hosts involves costs to symbionts, symbionts that provide reduced benefit to their host are expected to increase in frequency. Plants have been shown to allocate preferentially to the most efficient symbiont and this preferential allocation may stabilize the mutualism.
- I construct a general model of the interactive feedbacks of host preferential allocation and the dynamics of root symbiont populations to evaluate the stability of nutritional mutualisms.
- Preferential allocation can promote the evolution of mutualism even when the cost to the symbiont is very large. Moreover, the physiological plasticity of preferential allocation likely leads to coexistence of beneficial and nonbeneficial symbionts. For arbuscular mycorrhizal fungi, which facilitate plant uptake of phosphorus (P), the model predicts greater P transfer from these fungi per unit carbon invested with decreasing concentrations of soil P and with increasing concentrations of atmospheric CO_2, patterns that have been observed in laboratory and field studies.
- This framework connects physiological plasticity in plant allocation to population processes that determine mutualism stability and, as such, represents a significant step in understanding the stability and environmental patterns in mutualism.

Introduction

Mutualistic interactions are very common (Janzen, 1986), yet simple expectations from evolutionary theory predict that they should be rare. If benefit provided to a second species is delivered at a cost to the first species, selection would favor individuals of the first species that provide reduced benefit and thereby incur less cost. The evolutionary result of this selection favoring 'cheaters' would be the dissolution of the mutualism (Bever, 2002b; Porter & Simms, 2014). Several classes of mechanisms have been posited to allow the evolution of mutualism. However, none of these mechanisms prove to be generally applicable across the diverse array of mutualisms. In particular, horizontally transmitted and promiscuous interactions, such as the mutualisms between plants and soil microorganisms, remain a particular challenge to evolutionary explanation, despite being very common, having important effects on ecosystem processes and having evolved on many independent occasions (Hoeksema & Bruna, 2000; Wilkinson & Sherratt, 2001; Denison *et al.*, 2003; Kiers & van der Heijden, 2006).

Spatial structure created by limited dispersal can facilitate stability of mutualisms by increasing the frequency of contact between mutually beneficial partners (Kinzig & Harte, 1998;

Bever & Simms, 2000; Mack, 2012). Yet, for many root symbiont mutualisms, the symbionts are strictly horizontally transmitted and form dynamic and ephemeral associations with multiple hosts; as a result, the spatial structure alone does not explain the high frequency and broad taxonomic range of mutualisms between plants and soil microorganisms.

Models of partner choice find that mutualisms can be stabilized when the host can discriminate between symbionts and associate only with the mutualistic type (Bull & Rice, 1991; Weisbuch & Duchateau, 1993; Noe & Hammerstein, 1994). Partner choice requires that the hosts have prior 'knowledge' of the symbiont's benefit to the host. While this 'knowledge' has usually been thought to result from the individual experience of a cognizant organism, preferential association could also result from evolutionary adaptations through which the host evolves the ability to identify its best symbiont (Bull & Rice, 1991; Noe & Hammerstein, 1994). This mechanism, however, remains vulnerable to invasion by 'good partner' mimics (Zee & Bever, 2014) and therefore is not likely to be a general explanation for the persistence of mutualism. Plant–symbiont signaling systems in arbuscular mycorrhizal (AM) fungi and rhizobium (Harrison, 2005; Jones *et al.*, 2007), for example, operate similarly during initiation of symbioses with microbes of a wide range of potential to

promote plant growth. In practice, plants associate with a diversity of soil symbionts that vary in their growth promotion, and experimental evidence does not indicate that plants consistently differentially associate with beneficial symbionts, with many studies showing the opposite pattern (Amarger, 1981; Bever, 2002b; Bennett & Bever, 2009; Heath & Tiffin, 2009; Sachs *et al.*, 2010; Wagg *et al.*, 2011).

Several models demonstrate that plant-mediated sanctions, which increase the death rates of microbial cheaters, can reinforce mutualism of some root symbionts, including nodulating bacteria (West *et al.*, 2002) and ectomycorrhizal fungi (Hoeksema & Kummel, 2003). While there is empirical evidence of the potential for legumes to terminate ineffective nodules (Kiers *et al.*, 2003) and thereby sanction nonbeneficial bacteria, there is little evidence of plant sanctions (i.e. increased microbial death rates by host) policing ineffective symbionts within other mutualistic plant–soil microbe interactions. In arbuscular mycorrhizas (AM), for example, fungal infection of plant roots can elicit a plant defensive response in nonmycorrhizal hosts (Allen *et al.*, 1989), but there is no evidence that host defense is differentially applied based on the rate of resource transfer. Preferential allocation of resources, which increases the growth rates of the most beneficial mutualist, has recently been demonstrated and has been shown to be important to the stabilization of the AM fungal mutualism (Bever *et al.*, 2009; Kiers *et al.*, 2011) and to operate in rhizobium (Simms *et al.*, 2006; Sachs *et al.*, 2010). While phenomenologically similar to sanctions, preferential allocation does not necessarily involve termination of relationships with less beneficial microbial mutualists, and, in fact, the nonbeneficial mutualists can reproduce within the host in spite of preferential allocation toward a better symbiont (Bever *et al.*, 2009).

In this paper, I develop a general model of preferential allocation to the most beneficial microbial mutualist, and its effect of symbiont population dynamics and the stability of mutualism. Preferential allocation as a process differs in several ways from other mechanisms stabilizing mutualism. First, it requires the initial establishment of the symbiosis and initial investment by the host before evaluation of the quality of the symbiont. This initial investment makes the host particularly vulnerable to cheating symbionts, because even if the plant allocates perfectly to the best mutualist, the nonmutualist still benefits from the plant's initial investment, which is in contrast to perfect partner choice or perfect sanctions. Secondly, logically and empirically (Bever *et al.*, 2009), preferential allocation will not be perfect, again creating opportunities for the proliferation of cheaters. And thirdly, for nutritional mutualisms, the value of particular symbionts will depend upon the plant's nutritional demands, and therefore plant investment in preferential allocation is expected, and has been shown, to decline with a decline in plant resource (Zheng *et al.*, 2014) and with an increase in availability of the resource acquired from the symbiont (B. Ji & J. D. Bever, unpublished). The feedbacks between the rates of plant allocation to the mutualist and the relative abundance of soil mutualists may stabilize mixed populations of beneficial and nonbeneficial symbionts. This physio-evolutionary feedback can generate predictions for the direction of evolution of plant nutritional mutualisms as a function of environmental factors, including across anthropogenic change.

Description

Essential features of the interactions of plants and root symbionts

Plant–soil microbe mutualisms involve a phylogenetically diverse group of microorganisms, including several lineages of bacteria and fungi. These mutualisms increase plant access to many essential minerals, including water, phosphorus (P) and nitrogen (N). Microbial symbionts, particularly N-fixing bacteria and mycorrhizal fungi, are widely regarded as critical to soil fertility and ecosystem function. Soil organisms associate with plant roots in a variety of ways including intracellular (e.g. AM fungi, N-fixing bacteria and endophytic bacteria) and intercellular (e.g. ectomycorrhizal fungi) infection, as well as by growing on or near the root surface (e.g. rhizosphere bacteria, actinomycetes). For ease of discussion, I will refer to the collection of potentially beneficial root or rhizosphere microorganisms as root 'symbionts'.

Symbionts vary in their ability to promote plant growth. This is known to be true in the well characterized systems, including AM fungi (Bever, 2002b; Klironomos, 2003) and rhizobia (Heath & Tiffin, 2009; Sachs *et al.*, 2010; Bever *et al.*, 2013; Porter & Simms, 2014). Assuming that there is a cost to the soil microbe for promoting plant growth, resources available for growth of the microbe will be negatively correlated with resources extended to the plant. For example, there is likely to be an energetic cost to AM fungi for acquiring, transporting, and delivering P to the host. As a result of these costs, one would expect a trade-off between symbiont growth rate per unit carbon (C) and mutualistic ability, as has been observed in AM fungi (Bever, 2002b; Bennett & Bever, 2009; Bever *et al.*, 2009) and rhizobia (Porter & Simms, 2014). Given this tradeoff, the least beneficial symbiont would have the highest rate of increase and the mutualism would be expected to evolve toward parasitism in a well-mixed system. Consistent with this expectation, communities of AM fungi were observed to change in a manner that decreased benefit to their host in the absence of spatial structure in their roots (Bever, 2002a,b; Castelli & Casper, 2003; Bever *et al.*, 2009).

Soil, however, is highly viscous, with soil organisms having limited ability for dispersal. As expected, the composition of the soil community is known to be heterogeneous over very small scales, including scales of cm and mm (Mummey & Stahl, 2003; Nicol *et al.*, 2003; Nunan *et al.*, 2003). This is also true for rhizosphere- and root-inhabiting organisms. N-fixing bacteria and ectomycorrhizal fungi, for example, associate with the plant at spatially discrete sites, the nodules and root tip, respectively. AM fungi infect the cortical cells of spatially separated short roots and have also been observed to be structured on the scale of a single plant's root system (Bever *et al.*, 1996) and finer (Wolfe *et al.*, 2007; Mummey & Rillig, 2008). Because of this spatial structure, the dynamics of root symbionts separated by a short distance may be partially independent of each other. Population dynamics in spatially structured environments have been shown

to vary from those predicted in well-mixed systems (Durrett & Levin, 1994; Molofsky & Bever, 2002) and spatial structure has been shown to increase the likelihood of the evolution of mutualism (Doebeli & Knowlton, 1998; Bever & Simms, 2000; Mack, 2012; Zee & Bever, 2014).

Individual plants, therefore, may interact with spatially discrete soil communities, and they may do so in a physiologically integrated manner. The behavior of plant roots penetrating different regions of the soil matrix are not independent. Instead, the entire root system can be responsive to the demands of whole-plant photosynthesis. The behavior of an individual root will then be a function of the physiological demand at the whole-plant level and the relative ability of the other roots of that plant to meet this demand. Within a heterogeneous soil matrix, plants can maximize their growth rate by optimizing the allocation of resources to the roots with the highest rates of acquisition of soil resources. Plants are well known to have the ability to increase allocation to nutrient-rich regions through secondary proliferation of roots (reviewed in Caldwell, 1994; Fitter, 1994) and through increased allocation of mobile C resources as evidenced by rapid and dramatic localized increases in enzymatic activity in response to exposure to nutrients (Robinson & Rorison, 1983; Burns, 1991; Jackson & Caldwell, 1991; Van Vuuren et al., 1996). Preferential allocation to the best biotic source of soil resources has been observed in AM fungi (Bever et al., 2009; Kiers et al., 2011) and rhizobia (Simms et al., 2006; Sachs et al., 2010). Given the commonality with allocation to nutrient hotspots, plants may be preadapted to preferential allocation to the best root symbionts (Frederickson, 2013); however, whether the original selective force favoring this ability was allocating to symbionts or resource hotspots cannot be differentiated, given that early plants associated with AM fungi before the origin of roots (Remy et al., 1994; Taylor et al., 1995).

Plant preferential allocation can have large impacts on the dynamics of the root symbionts through promoting the fitness of beneficial AM fungi and therefore the evolution of mutualism where multiple symbionts are associated with individual plants (Bever et al., 2009). However, preferential allocation is not a perfect mechanism as imagined in simple models. The host has to invest in the symbiont, via signaling and construction costs of symbiotic structures and via the initial investment in resource exchange, before the plant has information on symbiont quality. Also, at least some plants cannot allocate on the scale of individual infections when the symbionts are mixed within a root length, thereby allowing nonbeneficial fungi to benefit from the plant's attempt at preferential allocation (Bever et al., 2009).

Finally, because the value of particular symbionts will depend upon the host's need for its nutrients, plant allocation to the symbiosis (Olsson et al., 2010) and preferential allocation to beneficial symbionts, in particular, will be expected to decline with a reduction in its physiological demand for resource for which it is trading. As expected, preferential allocation to the most beneficial AM fungus was observed to decline with increasing soil P (B. Ji & J. D. Bever, unpublished) and with declining light (Zheng et al., 2014). However, preferential allocation of legumes to the best rhizobium did not decline with increasing soil N (Regus et al., 2014).

Results

The stabilization of mutualism between plants and their root symbionts

I developed the model in the context of the specific interaction between plants and AM fungi. While AM fungi have been credited with benefiting plant growth through several mechanisms and the benefit from AM fungi can be context-dependent (Newsham et al., 1995; Reynolds et al., 2006; Sikes et al., 2009), the major benefit of AM fungi is believed to be the facilitation of P uptake (Smith & Read, 2008).

Population growth rates of the symbionts I imagined two fungal types: a mutualistic fungus that effectively delivers P to the plant and a nonmutualistic fungus that does not. These fungi compete for two types of resources: C resources available before preferential allocation and preferentially allocated C. The C available before preferential allocation might include saprophytic growth (for ectomycorrhizal fungi) as well as C available through roots during the initiation and evaluation of the symbionts. I assume that the uptake and transfer of P to the plant is energetically costly. As a result, the mutualistic fungus has reduced fitness relative to that of the nonmutualistic fungus. I set the basal growth rate of the nonmutualistic fungus to 1, while that of the mutualistic fungus is $(1-b)$, with b representing the cost on pre-preferentially allocated C (see Table 1 for a list of parameters). The growth rate of the nonmutualistic fungus per additional unit of C preferentially allocated by the plant is set to ε, while that of the mutualistic fungus is $(1-d)\varepsilon$, with d representing the reduction in growth as a result of the cost of providing P to the plant. While there is evidence of tradeoffs between mutualistic benefit and growth rate in AM fungi (Bever, 2002b; Bennett & Bever,

Table 1 Description of model parameters

Parameters	Biological meaning
M	Proportion of mutualist symbionts
W_M	Fitness of mutualist symbionts
W_N	Fitness of nonmutualist symbionts
$\overline{W}$	Average symbiont fitness
f	Fidelity of plant allocation to mutualist symbionts
b	Cost of mutualism in basal growth rate including growth on pre-preferential allocation carbon
d	Cost of mutualism on preferentially allocated carbon
ε	Fitness of nonmutualist per unit of plant preferentially allocated carbon
C	Rate of preferential allocation of carbon to mutualist
$\hat{C}$	Rate of preferential allocation of carbon that equalizes fitness of mutualist and nonmutualist
u	Phosphorus uptake per unit of preferentially allocated carbon received by mutualist
C_M	Preferentially allocated carbon received by mutualist
P_s	Phosphorus availability in soil
C'	Minimum rate of carbon allocation to mutualist required to meet plant phosphorus need
$\hat{M}$	Equilibrium proportion of mutualists in the population

2009; Bever *et al.*, 2009), there is no evidence of a difference in this tradeoff in growth rates on these two resources, so *b* may be equal to *d*. However, in other systems, costs have been constructively broken down into analogous terms (e.g. the carriage cost and expression cost; Platt *et al.*, 2012).

The access of these two fungi to the additional C preferentially invested by the plant depends upon the rate of C allocation, *C*, and the fidelity of this C to the beneficial fungus, *f*. This fidelity of investment is likely itself to be a function of the spatial structure of the symbiont community (greater spatial structure, greater fidelity), the morphological intimacy of the association (greater intimacy, greater fidelity), and the physiological precision of plant directed allocation. Here, I treat the fidelity of investment as a parameter that can vary from a high of 1, where all of the C is received by the mutualistic fungus, to a low of 0, where all of the C is dispersed and is equally accessible to nonmutualists and mutualists. As a result, the mutualist will benefit from all of the allocated C, while nonmutualists will only have access to $1-f$ of the allocated C.

The fitnesses of the nonmutualistic and mutualistic fungi, then, are

$$W_N = (1 + (1 - f)C\varepsilon) \qquad \text{Eqn 1}$$

$$W_M = (1 - b + (1 - d)C\varepsilon). \qquad \text{Eqn 2}$$

The nonmutualist has higher fitness at low concentrations of C because of the cost of mutualism (*b*). As plant allocation to the most beneficial mutualist increases, its fitness relative to that of the nonmutualist increases, provided that the fidelity of allocation (*f*) is greater than the cost of mutualism in growth with allocated C, *d* (Fig. 1). The evolution of mutualism is only possible when

$$f > d. \qquad \text{Eqn 3}$$

The fitness of the two symbionts will be equal when the rate of preferential allocation equals $\hat{C}$, where

$$\hat{C} = \frac{b}{\varepsilon(f - d)}. \qquad \text{Eqn 4}$$
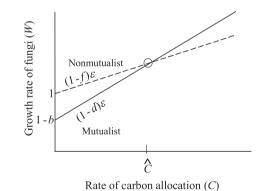
The mutualist will have greater fitness when the rate of plant preferential allocation is greater than $\hat{C}$. Provided condition 3 is met, this equilibrium value will be positive. Thus, the plant will be able to direct the evolution of mutualism in its symbionts if either the fidelity of its investment in the mutualistic fungus is high or the cost of mutualism is low.

The proportion of mutualistic fungi among all fungi (mutualistic plus nonmutualistic fungi) in the population (or community) is represented by the value *M*. The instantaneous rate of change in the frequency of the mutualist type, *M*, is then a function of its relative growth rate, W_M, and the average fitness of the population, $\overline{W} = M W_M + (1 - M) W_N$, and can be written as:

$$\frac{dM}{dt} = \frac{M(W_M - \overline{W})}{\overline{W}} = \frac{M(1 - M)((f - d)C\varepsilon - b)}{1 - bM + (1 - f + (f - d)M)C\varepsilon}. \qquad \text{Eqn 5}$$

Environmental dependence of C allocation to the mutualism The evolutionary dynamic of symbionts depends upon the rate of allocation by the plant to the mutualist. Plants allocate resources toward nutritional mutualisms in proportion to their need for the nutrient provided (Sprent, 1979; Smith & Read, 2008; Olsson *et al.*, 2010). I assume that this need-based investment is specifically applied to the preferentially allocated C, as has been demonstrated (B. Ji & J. D. Bever, unpublished; Zheng *et al.*, 2014). Total plant demand for P will be a function of its supply of other essential resources, including light, water, CO_2, N, and other soil minerals (Miller *et al.*, 2002; Johnson, 2010). The ability of a plant to meet its demand for P via direct uptake then depends on the concentration of soluble P in the soil relative to these other essential resources, as well as root morphology and physiology. When P is abundant relative to other soil resources (e.g. N), the plant might be able to meet its demand by direct P uptake and have little need of symbionts. By contrast, in a soil that is poor in P relative to other nutrients, direct P uptake might be insufficient to meet plant demand, which could lead to greater need for mycorrhizas (Smith *et al.*, 2011). With the total demand by the plant for P being scaled to 1, the quantity $(1 - P_s)$ represents the P demand unmet by direct uptake, where P_s represents the P available in the soil relative to the availability of other resources and reflects environmental conditions as well as characteristics of plant species.

I assume that plants allocate C resources, *C*, to the beneficial fungus in proportion to the P demand, that is, that plants do not

Fig. 1 Relative fitness of mutualistic and nonmutualistic symbionts. Before plant preferential allocation, the two symbionts can benefit from the investment by the plant in the initiation, construction, and initial evaluation of quality of the symbionts. The nonmutualistic symbiont has a higher relative growth rate on the initial investment because of the cost of the mutualism in the basal growth rate (*b*). The population growth rates of both the mutualist (represented by the solid line) and nonmutualist (represented by the dashed line) increase with increasing amounts of carbon preferentially allocated to the mutualist, with the growth rate of the mutualist being discounted by the cost of mutualism in symbiotic growth (*d*) and the growth rate of the symbiont being discounted by the fidelity of the plant's investment in the mutualist (*f*).

consume luxury concentrations of P (Kiers & van der Heijden, 2006) and that C not allocated to the mutualism can be productively invested in plant growth or other components of plant fitness. As a result of this assumption, C will decrease with increasing relative P availability in the soil, P_s, consistent with empirical evidence (B. Ji & J. D. Bever, unpublished). The P return for the C invested in the fungi is the product of the rate of C being received by the mutualistic fungus, C_M, and the rate of P returned per unit C from the mutualistic fungi, u. P is assumed to be exchanged at a constant rate per unit C preferentially exchanged with the beneficial symbiont (consistent with observations of B. Ji & J. D. Bever, unpublished). The rate of C being received by the mutualistic fungus is itself a function of the rate of C investment, C, and the proportion of this C that reaches the mutualistic fungus. From the definition of fidelity, a proportion f of the C goes directly to the mutualistic fungus, and $1-f$ of the C would go to the mutualistic fungus in proportion to its representation in the fungal population. This suggests that

$$C_M = C(f + (1-f)M). \qquad \text{Eqn 6}$$

However, as illustrated in Fig. 2, this relationship assumes that the plant is successful at getting C to the mutualist fungus even when the frequency of the mutualistic fungus is zero. This is not biologically plausible. As the proportion of the mutualistic fungus approaches zero, the plant would have to incur greater costs in finding the fungus. This additional cost on the part of the plant would bring the proportion of C that reaches the mutualistic fungus to zero as the proportion of mutualistic fungus approaches zero. I derive a second function that has this property (Fig. 2) by weighing the accessibility of the C to the two fungal types by the proportions of the two fungal types. This formulation reduces to

$$C_M' = C\left(\frac{M}{1-f+fM}\right). \qquad \text{Eqn 7}$$

I use Eqn 7 for the remainder of the paper because of the greater biological realism; however, I note that all of the general conclusions of the paper (including the exact condition produced in Eqn 9) hold true under the simpler Eqn 6.

The instantaneous rate of change in the rate of C invested in all fungi, C, is

$$\frac{dC}{dt} = 1 - P_s - C\left(\frac{M}{1-f+fM}\right)u. \qquad \text{Eqn 8}$$

Interdependent dynamics of plant allocation and evolution of mutualism Equations 5 and 8 present the codependence of the rates of investment of the plant in the mutualism with the evolutionary dynamics of the mutualism in the symbiont population. I analyze these dynamics through inspection of their zero-change isoclines. Eqn 4 is the zero change isocline for the symbiont population. When $C = \hat{C}$, the fitnesses of the mutualistic and nonmutualistic fungi are equal and their proportions will not

change. Setting Eqn 8 equal to zero, I solve for the condition in which the rate of change in C investment in the mutualism will not change.

$$M = \frac{(1-f)(1-P_s)}{Cu - f(1-P_s)}. \qquad \text{Eqn 9}$$

Therefore, the C investment zero-change isocline is an asymptotic function between M and C (Fig. 3). As this function is only biologically relevant when M is between 0 and 1, it is not relevant and must be truncated when C is less than C', where

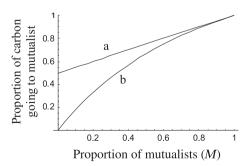$$C' = \frac{(1-P_s)}{u}. \qquad \text{Eqn 10}$$

Biologically, the value C' represents the minimum rate of plant investment in mutualists sufficient to satisfy the plants' P demand. Lower concentrations of soil P and lower efficiency of P transfer from mutualists necessitate greater minimum plant investments in mutualists. Plant investment then has to increase when the symbiont population includes nonmutualists as described by Eqn 9.

The joint dynamics of the rate of plant investment and symbiont composition depend upon whether the minimum investment by the plant in the mutualist, C', is greater or less than the switch point of relative fitness of the mutualist and nonmutualist, $\hat{C}$. When C' is greater than $\hat{C}$ (Fig. 3a), mutualists will fix in the symbiont population. Substituting in Eqns 10 and 4, I identify that this will occur when
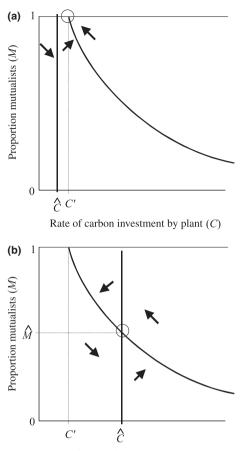
$$f \geq \frac{ub}{(1-P_s)\varepsilon} + d. \qquad \text{Eqn 11}$$

When this inequality is true, the system will equilibrate at $M = 1$ and $C = C'$ and the plant growth will be limited by P. This equilibrium is stable.

The mutualistic symbiont, however, will not fix in the population when C' is smaller than $\hat{C}$, which occurs when the inequality given in Eqn 11 is not true. In this case (Fig. 3b), C investment

Fig. 2 The relationship between the proportion of allocated carbon that reaches the mutualist is presented as a function of the proportion of mutualists in the population. Plot (a) presents the relationship derived from the definition of the fidelity (Eqn 6), while plot (b) incorporates additional costs to the plant of 'finding' the mutualists as they become rare (Eqn 7). In both plots, $f = 0.5$. The latter relationship (plot b) is used in the remainder of the article.

Fig. 3 Phase plane diagrams of the proportion of mutualists in the symbiont population and the rate of preferential allocation by the plant to the mutualist. The solid lines represent the net zero-growth isoclines and the arrows represent the direction of change over time. The rate of change of the proportion of mutualists in the population of symbionts (M) is equal to zero at $M = 0$, $M = 1$ and $C = \hat{C}$ (the solid upright line). The rate of change in investment by the plant is equal to zero along the solid curved line (Eqn 9). When Eqn 11 is true, the system will equilibrate at $M = 1$ and $C = C'$ (a). When Eqn 11 is false, the system will equilibrate at $M = \hat{M}$ and $C = \hat{C}$ (b).

will equilibrate at $C = \hat{C}$, and substituting Eqn 4 into Eqn 9, I derive the equilibrium proportion of mutualistic symbionts in the population as

$$\hat{M} = \frac{(1 - P_s)(1 - f)(f - d)\varepsilon}{ub - (1 - P_s)f(f - d)\varepsilon}.$$
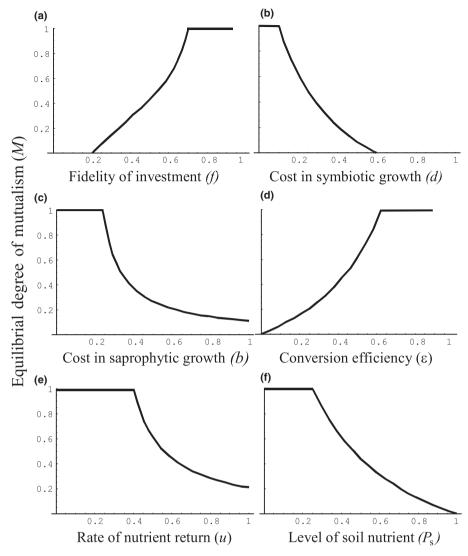
Eqn 12

This equilibrium is still stable, but the system will oscillate with declining amplitude during its approach to this equilibrium (Vandermeer, 1973). This oscillation results from an inherent time lag in the negative feedback process during which the symbiont population evolves in response to the change in the plant's investment. With this time lag, a plant in P deficit associating with a symbiont population with proportion of mutualists (M) will increase its investment in the beneficial mutualist, potentially increasing M beyond $\hat{M}$, thereby causing its investment in the mutualist, C, to decline.

This model predicts that the proportion of mutualists will increase with: increasing fidelity of investment in the symbionts (f); decreasing cost of mutualism, in terms of both the 'basal' and 'supplemental' growth rates (b and d); increasing overall dependence of the fungal growth rates on the invested C (ε); decreasing return rates of nutrients (u); and decreasing concentrations of P in the soil (P_s). However, these simple expectations will only hold for a limited region of the parameter space where the inequality in Eqn 11 is false. Once the fidelity of investment and conversion efficiency are high enough, and the costs, return rate and soil P concentration are low enough, the degree of mutualism will plateau at $M = 1$. These relationships are depicted in Fig. 4.

Once again, the rate of return of P per unit C is given by the product of the rate of C being received by the beneficial fungus, C_M, and the rate of P returned per unit C from the mutualistic fungi, u. I then examine the efficiency of the return from the symbiont at equilibrium as a function of the parameter values (Fig. 5). Note that when the inequality given in Eqn 11 is true, the efficiency reaches a maximum of u. If the inequality given in Eqn 11 is false, the efficiency is a function of $\hat{M}$. These relationships, depicted in Fig. 5, are in similar directions as identified for the equilibrium proportion of mutualists (Fig. 4), except for the nutrient return rate per unit C received by the mutualist (u). The nutrient return rate has a negative effect on the equilibrial proportion of mutualists (Fig. 3e), because the mutualistic symbiont is able to meet the plant's need with a smaller allocation of C (Eqn 5). Therefore, the symbiont population equilibrates with the mutualist at a lower frequency in the population (Fig. 4e). Even though the equilibrium proportion of mutualists is reduced with increasing rates of P return per mutualistic symbiont, the plant continues to receive P at the same rate (Fig. 5e).

Discussion

Recent empirical work has demonstrated that plants can preferentially allocate their resources to the most beneficial mutualists (Simms *et al.*, 2006; Bever *et al.*, 2009; Sachs *et al.*, 2010; Kiers *et al.*, 2011), much as has been previously demonstrated with plant allocation to nutrient hotspots (Caldwell, 1994). This model demonstrates that such preferential allocation can influence the direction of evolution of their root symbionts. Through preferential allocation, an individual plant can alter the relative growth rates of its various root symbionts, thereby increasing the benefit it receives from the symbiont population or community. At the same time, this mechanism will maintain mutualistic traits in the symbiont population or community, even when the symbiont endures a significant cost of mutualism.

One notable result of this model is that the beneficial and nonbeneficial symbionts are highly likely to coexist over a large range of environmental conditions. This result stands in contrast to other models of mutualism that assume a single dimension of cost and benefit and do not represent the physiological plasticity of host–symbiont nutritional mutualisms (West *et al.*, 2002; Foster & Wenseleers, 2006). Here I identify that the host has to invest in all symbionts before identifying which symbiont provides the best reward. Nonmutualists, by avoiding the costs of
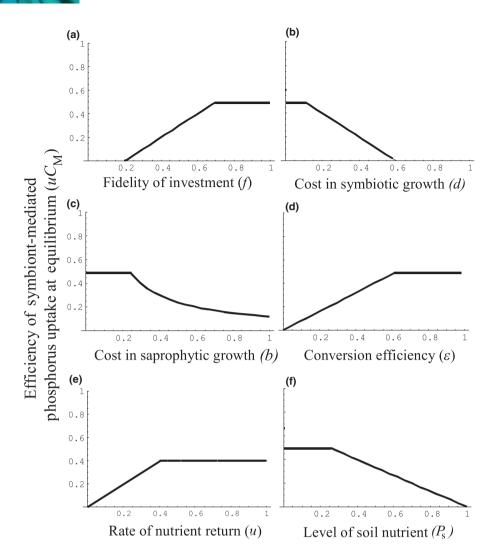
Fig. 4 Equilibrium proportion of mutualist as a function of model parameter values. (a–f) The proportion of mutualist in the symbiont population at equilibrium as a function of the fidelity of investment (a), the cost of mutualism in symbiotic growth (b), the cost of mutualism in saprophytic growth (c), the conversion efficiency of symbiotic carbon to fungal population growth (d), the rate of nutrient return per unit carbon from the mutualist (e), and the amount of soil nutrient (f). In all cases, the unvaried parameter values are $f = 0.6$, $d = 0.2$, $b = 0.3$, $\varepsilon = 0.5$, $u = 0.5$ and $P_s = 0.4$.

resource acquisition and delivery, may enjoy a competitive advantage on this initial investment. In fact, one might expect 'cheaters' to evolve which specialize in rapid colonization of new roots to best capture plant investment in symbiosis initiation. Plant preferential allocation will increase the abundance of mutualists, but ironically, a high proportion of mutualists may generate a surplus of P, thereby reducing the rate of plant allocation. This generates a negative physio-evolutionary feedback which can stabilize a diverse population of beneficial and nonbeneficial symbionts. In fact, heterogeneous populations of symbionts that differ in their growth promotion commonly occur in nature (Bever, 2002b; Bever *et al.*, 2009, 2013; Heath & Tiffin, 2009; Porter & Simms, 2014). The physio-evolutionary negative feedback in this model is analogous to the negative community feedback generated by an interspecific tradeoff because of the cost of preferential allocation (Steidinger & Bever, 2014). In the present framework, the maintenance of variation in symbiont growth promotion is an expected result of physio-evolutionary feedbacks between the rates of plant allocation and the relative abundance of mutualists in the symbiont population, not an evolutionary paradox (Heath & Stinchcombe, 2014).

The accuracy of plant allocation to the most beneficial symbiont depends upon many factors, including the physiology of plant roots and the spatial distribution of the symbionts. Plants' ability to influence the evolution of mutualistic traits in their symbionts will increase with increasing spatially clumped distributions of beneficial symbionts within the root system of an individual host plant (Bever *et al.*, 2009). The greater the precision of plant root physiology in targeting the source of the nutrients, the lower the need for spatial structure of the symbiont within the root system. One might expect high fidelity within intimate associations, such as those with N-fixing bacteria and mycorrhizal fungi. However, nonbeneficial AM fungi enjoyed a competitive advantage when mixed with beneficial fungi, but not when spatially separated (Bever, 2002b; Bever *et al.*, 2009). These findings indicate that the host cannot effectively preferentially allocate at the scale of an individual arbuscule. Similarly, legumes may not be able to differentially allocate to genetically different bacteroids within mixed nodules. In fact, this model predicts that the fidelity of plant investment in mutualists would have to be very high to explain the evolution of N-fixing symbioses, which entails a very high energetic cost (Sprent, 1979; Sprent *et al.*, 1987).

Fig. 5 The efficiency of mutualism at equilibrium. (a–f) The dependence of the efficiency of phosphorus uptake (uC_M) at equilibrium as a function of fidelity of investment (a), the cost of mutualism in symbiotic growth (b), the cost of mutualism in saprophytic growth (c), the conversion efficiency of symbiotic carbon to fungal population growth (d), the rate of nutrient return per unit carbon from the mutualist (e), and the amount of soil nutrient (f). In all cases, the unvaried parameter values are $f = 0.6$, $d = 0.2$, $b = 0.3$, $\varepsilon = 0.5$, $u = 0.5$ and $P_s = 0.4$.

Specialized structures within roots, including nodules of N-fixing bacteria and ectomycorrhizal root tips, may represent adaptations by the plant for increasing the spatial structure of the symbionts, thereby increasing the accuracy of their investments and their influence over symbiont dynamics. An improvement in our understanding of fine-scale plant root physiology will also improve our understanding of the spatial precision to which plants can allocate their resources.

The present model provides a heuristic demonstration of the ability of preferential allocation by individual plants to overcome the costs of mutualism in their root symbionts. In constructing the model, the complexity within symbionts is reduced to two types: one that does not benefit its host and a second that delivers benefit at a maximal rate. I also assumed two simple costs of this delivery rate. Of course, individual plants in nature interact with populations and communities of symbionts that are more variable than assumed within this model (and that vary in more than three dimensions). Inclusion of this additional complexity would likely alter the precise predictions of the model. A strength of the present model, however, is in providing an illustration of the consequences of simple assumptions and in providing qualitative predictions for the directions of effects.

It is interesting in this context to note that the model predicts that the evolution of mutualism is more sensitive to costs in growth with allocated C (d) (Fig. 4b) than to costs in basal growth rate (b) (Fig. 4c). In particular, the fidelity of plant allocation must necessarily be greater than the cost in symbiotic growth (Eqn 3), setting real limits on the costs of symbiotic resource acquisition and delivery. By contrast, the model predicts that a mutualism can persist even if the cost of mutualism in basal growth is complete (Fig. 4c). As costs in basal growth include saprophytic growth, it is relevant to the observation that AM fungi cannot grow in the absence of their hosts.

Relationship of preferential allocation to other hypotheses for the maintenance of mutualism

The preferential allocation mechanism developed here is distinct from other mechanisms through which hosts may influence the evolution of mutualisms such as partner choice and sanctions. Partner choice (Bull & Rice, 1991; Weisbuch & Duchateau, 1993; Noe & Hammerstein, 1994) assumes that one species associates with a second species based on an evolutionary (or personal) history of successful associations. The hypothesis requires

specificity of association, for which there is limited evidence for many root symbionts (Bever, 2002b; Bennett & Bever, 2009; Wagg *et al.*, 2011; Bever *et al.*, 2013). The preferential allocation mechanism does not require recognition of the symbiont, and instead the plant is required to allocate to the best source of its limiting resource.

Sanctions have been proposed to operate within N-fixing rhizobia (Denison, 2000; West *et al.*, 2002) and in ectomycorrhizal fungi (Hoeksema & Kummel, 2003) and share important similarities to preferential allocation. Under the sanctions hypothesis, ineffective nodules or root tips senesce earlier than effective ones, because the host actively sabotages the nonmutualistic symbiont (Kiers *et al.*, 2003). Conceptually, sanctions that increase less beneficial symbiont death rates and preferential allocation, which increases beneficial symbiont birth rates, share the important commonalities of host control of microbial relative fitness and both processes could simultaneously. The preferential allocation mechanism has been shown to operate in legume nodules (Simms *et al.*, 2006; Sachs *et al.*, 2010). And preferential allocation is more likely to operate across the wide range of plant–soil microbe mutualisms, because resource allocation toward nutrient hotspots is a well-established property of plant root systems (Caldwell, 1994) and because some mutualists, including rhizosphere bacteria, which occur on the surface of roots, and AM fungi, which occur internal to roots, are not easily subject to sanctions (Denison *et al.*, 2003), but might still be responsive to preferential resource allocation. Moreover, the preferential allocation framework lends itself to incorporation into a model of whole-plant physiology, as has been done in the present paper.

Hoeksema and Kummel's model of patch dynamics in ectomycorrhizal root tips shares similarities with the present model in that both spatial structure of the symbionts and host manipulation are assumed to be important. The models differ in that Hoeksema & Kummel (2003) more explicitly assume spatial structure of the symbionts, while plant manipulation of patch life span is implicitly assumed within manipulations of model parameters. In the present model, the spatial structure of the symbiont population is an implicit factor within the fidelity parameter, while preferential allocation is explicitly assumed. Explicit incorporation of spatial dynamics and preferential allocation would be a logical next step to modeling dynamics between plants and roots symbionts.

Prediction of environmental dependence of mutualistic benefit

The present model is the first mechanistic model of the evolution of mutualism that investigates the environmental dependence of host allocation to the symbionts. Previous models have used an economic market model to describe the environmental conditions in which the mycorrhizal mutualism would benefit both partners (Schwartz & Hoeksema, 1998; Hoeksema & Schwartz, 2003; Kummel & Salant, 2006; Grman *et al.*, 2012; Wyatt *et al.*, 2014). While the economic market model identifies environmental conditions for the evolution of mutualism, it does not explain the maintenance of mutualism in the face of cheaters. Similarly

models of partner negotiation predict the environmental dependence of mutualism, but do not simultaneously explain cheater control (Akçay & Simms, 2011). Our model shares similarities with predictions of environmental dependence of mutualism and cheater coexistence from a community model of mutualism that includes a cost of preferential allocation (Steidinger & Bever, 2014). The present model builds from host physiological plasticity to the simultaneous stabilization of mutualism in the face of nonbeneficial cheating symbionts and predicts the direction of evolution of the mutualism as a function of the environmental gradients.

Plant preferential allocation to the best mutualist has been shown to increase in proportion to soil nutrient need in AM fungi (Zheng *et al.*, 2014; B. Ji & J. D. Bever, unpublished). More empirical work is needed to evaluate the generality of this result, as preferential allocation in legume–N-fixing bacteria system did not decline with increasing soil N (Regus *et al.*, 2014). The present model demonstrates that plasticity in the rates of allocation can regulate the efficiency of mutualism. As a result of this physio-evolutionary integration, the present model predicts that the equilibrium degree of mutualism should increase as soil resources become more limiting (Figs 4f, 5f). Conversely, with fertilization, the level of symbionts should evolve toward reduced mutualism. This clear prediction is strongly supported in the literature. For example, mycorrhizal fungi derived from soils with high concentrations of P have reduced P uptake compared with fungi derived from soils with low concentrations of P (Louis & Lim, 1988; Boerner, 1990). Similarly, where water is limiting, mycorrhizal fungal genotypes derived from drier sites were more efficient at water uptake (Stahl & Smith, 1984). Note that if regions differ in limiting soil resource, this model predicts that the symbionts in each region would be best able to improve plant growth in their native soils. This expectation of 'local adaptation' of microbes has been supported in a broad-scale survey of plant response to soils and microbial communities (Lambert *et al.*, 1980; Johnson *et al.*, 2010).

The prediction of reduced benefit as a result of fertilization is also supported. In experimental manipulation of N concentrations in an N-poor soil, AM fungal community composition was found to have changed in a manner that reduced the benefit to their hosts (Johnson, 1993; Corkidi *et al.*, 2002). Similarly, fertilization of soils, as in agriculture, has been repeatedly shown to result in reduced efficiency of mutualistic mycorrhizal fungi and N-fixing bacteria (Caldwell & Vest, 1970; Ham, 1980; Johnson *et al.*, 1997; Douds & Millner, 1999). Other sources of soil fertilization, such as that caused by atmospheric N deposition, would also be expected to result in reduced benefit from root symbionts. It is interesting to note in this context that a consistent shift in the composition of the mycorrhizal fungal community has been observed in response to N deposition in southern California (Egerton-Warburton & Allen, 2000); the present model predicts that the direction of this effect is toward fungi that are less effective at facilitating N uptake.

Alternatively, anthropogenic increase of nonsoil resources such as atmospheric CO_2, would cause soil resources to be more limiting (decreasing P_s), thus causing plants to increase allocation to

root symbionts and thereby increasing the degree of mutualism. Consistent with this expectation, Zheng *et al.* (2014) observed increased preferential allocation to beneficial symbionts with increasing light intensities. Experimental manipulations of atmospheric CO_2 have resulted in changes in the composition of the mycorrhizal fungal community (Klironomos *et al.*, 1998; Wolf *et al.*, 2003) and rhizobium populations (Montealegre *et al.*, 2000), and microbial changes have increased the benefit to host plants (Klironomos *et al.*, 2005), consistent with predictions of the model. Moreover, the model identifies a propensity to overshoot the equilibrium degree of mutualism in response to abrupt change, owing to the time lag in symbiont population dynamics (Fig. 3b). Such an overshoot in plant benefit was observed in an experimental manipulation (Klironomos *et al.*, 2005). The magnitudes of these oscillations, however, decrease over time, and the system equilibrates at a single level of allocation and level of mutualism. The improved efficiency of root symbionts in response to increased atmospheric CO_2 could contribute to the sustained direct fertilization effects on plant growth observed in long-term atmospheric CO_2 fertilization studies (Drake *et al.*, 2011).

In this work, I incorporated general features of the interactions between plants and soil microorganisms into a model of the evolution of mutualism in the root symbionts of plants. This model can account for maintenance of the many mutualisms between plants and soil microorganisms, even in the face of considerable costs. The model also successfully predicts qualitative patterns that have been observed in the distribution of mutualistic symbionts along gradients of soil fertility. Moreover, this model integrates physiological plasticity of plants with the evolutionary response of root symbionts into a framework that predicts responses of nutritional mutualisms to anthropogenic perturbations and provides a basis for further investigations of these systems. Further empirical work is required to test the basic assumptions and predictions of the model, including the environmental patterns in efficiency of mutualism.

Acknowledgements

References

Akçay E, Simms EL. 2011. Negotiation, sanctions, and context dependency in the legume–Rhizobium mutualism. *The American Naturalist* **178**: 1–14.

Allen MF, Allen EB, Friese CF. 1989. Responses of the non-mycotrophic plant *Salsola kali* to invasion by vesicular arbuscular mycorrhizal fungi. *New Phytologist* **111**: 45–49.

Amarger N. 1981. Competition for nodule formation between effective and ineffective strains of rhizobium meliloti. *Soil Biology & Biochemistry* **13**: 475–480.

Bennett A, Bever JD. 2009. Trade-offs between AM fungal competitive ability and host growth promotion in *Plantago lanceolata. Oecologia* **160**: 807–816.

Bever JD. 2002a. Host-specificity of AM fungal population growth rates can generate feedback on plant growth. *Plant and Soil* **244**: 281–290.

Bever JD. 2002b. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. *Proceedings of the Royal Society of London, B* **269**: 2595–2601.

Bever JD, Broadhurst LM, Thrall PH. 2013. Microbial phylotype composition and diversity predicts plant productivity and plant–soil feedbacks. *Ecology Letters* **16**: 167–174.

Bever JD, Morton JB, Antonovics J, Schultz PA. 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *Journal of Ecology* **84**: 71–82.

Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* **12**: 13–21.

Bever JD, Simms EL. 2000. Evolution of nitrogen fixation in spatially structured populations of *Rhizobium. Heredity* **85**: 366–372.

Boerner REJ. 1990. Role of mycorrhizal fungus origin in growth and nutrient uptake by *Geranium robertianum. American Journal of Botany* **77**: 483–489.

Bull JJ, Rice WR. 1991. Distinguishing mechanisms for the evolution of cooperation. *Journal of Theoretical Biology* **149**: 63–74.

Burns IG. 1991. Short- and long-term effects of a chane in the spatial distribution of nitrate in the root zone on N uptake, growth and root development of young lettuce plants. *Plant, Cell & Environment* **14**: 21–33.

Caldwell BE, Vest G. 1970. Effect of *Rhizobium japonicum* strains on soybean yields. *Crop Science* **10**: 19–21.

Caldwell MM. 1994. Exploiting nutrients in fertile soil microsites. In: Caldwell MM, Pearcy RW, eds. *Physiological ecology: exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground.* San Diego, CA, USA: Academic Press, 325–347.

Castelli JP, Casper BB. 2003. Intraspecific AM fungal variation contributes to plant-fungal feedback in a serpentine grassland. *Ecology* **84**: 323–336.

Corkidi L, Rowland DL, Johnson NC, Allen EB. 2002. Nitrogen fertilization alters the functioning of arbuscular mycorrhizae at two semiarid grasslands. *Plant and Soil* **240**: 299–310.

Denison RF. 2000. Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *The American Naturalist* **156**: 567–576.

Denison RF, Bledsoe C, Kahn M, O'gara F, Simms EL, Thomashow LS. 2003. Cooperation in the rhizosphere and the "free rider" problem. *Ecology* **84**: 838–845.

Doebeli M, Knowlton N. 1998. The evolution of interspecific mutualisms. *Proceedings of the National Academy of Sciences, USA* **95**: 8676–8680.

Douds DD, Millner PD. 1999. Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. *Agriculture, Ecosystems and Environment* **74**: 77–93.

Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML et al. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. *Ecology Letters* **14**: 349–357.

Durrett R, Levin S. 1994. The importance of being discrete (and spatial). *Theoretical Population Biology* **46**: 363–394.

Egerton-Warburton LM, Allen EB. 2000. Shifts in arbuscular mycorrihizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* **10**: 484–496.

Fitter AH. 1994. Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell MM, Pearcy RW, eds. *Exploitation of environmental heterogeneity by plants.* New York, NY, USA: Academic Press, 305–323.

Foster KR, Wenseleers T. 2006. A general model for the evolution of mutualisms. *Journal of Evolutionary Biology* **19**: 1283–1293.

Frederickson ME. 2013. Rethinking mutualism dtability: cheaters and the evolution of sanctions. *The Quarterly Review of Biology* **88**: 269–295.

Grman E, Robinson TMP, Klausmeier CA. 2012. Ecological specialization and trade affect the outcome of negotiations in mutualism. *The American Naturalist* **179**: 567–581.

Ham GE. 1980. Interaction of *Glycine max* and *Rhizobium japonicum.* In: Summerfield RJ, Bunting AH, eds. *Advances in legume science.* Kew, UK: Royal Botanical Garden, 298–306.

Harrison MJ. 2005. Signaling in the arbuscular mycorrhizal symbiosis. *Annual Review of Microbiology* 59: 19–42.

Heath KD, Stinchcombe JR. 2014. Explaining mutualism variation: a new evolutionary paradox? *Evolution* 68: 309–317.

Heath KD, Tiffin P. 2009. Stabilizing mechanisms in a legure-rhizobium mutualism. *Evolution* 63: 652–662.

Hoeksema JD, Bruna EM. 2000. Pursuing the big questions about interspecific mutualism: a review of theoretical approaches. *Oecologia* 125: 321–330.

Hoeksema JD, Kummel M. 2003. Ecological persistence of the plant-mycorrhizal mutualism: a hypothesis from species coexistence theory. *The American Naturalist* 162: S40–S50.

Hoeksema JD, Schwartz MW. 2003. Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 913–919.

Jackson RB, Caldwell MM. 1991. Kinetic responses of *Pseudoroegneria* roots to localized soil enrichment. *Plant and Soil* 138: 231–238.

Janzen DH. 1986. The natural history of mutualisms. In: Boucher D, ed. *The biology of mutualism.* London, UK: Croom Helm, 40–99.

Johnson NC. 1993. Can fertilization of soil select for less mutualistic mycorrhizae? *Ecological Applications* 3: 749–757.

Johnson NC. 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist* 185: 631–647.

Johnson NC, Graham JH, Smith FA. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist* 135: 575–585.

Johnson NC, Wilson GWT, Bowker MA, Wilson JA, Miller RM. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences, USA* 107: 2093–2098.

Jones KM, Kobayashi H, Davies BW, Taga ME, Walker GC. 2007. How rhizobial symbionts invade plants: the Sinorhizobium-Medicago model. *Nature Reviews. Microbiology* 5: 619–633.

Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A *et al.* 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333: 880–882.

Kiers ET, Rosseau RA, West SA, Denison RF. 2003. Host sanctions and the legume–rhizobium mutualism. *Nature* 425: 78–81.

Kiers ET, van der Heijden MGA. 2006. Mutualistic stability in the arbuscular mycorrhizal symbiosis: exploring hypotheses of evolutionary cooperation. *Ecology* 87: 1627–1636.

Kinzig AP, Harte J. 1998. Selection of micro-organisms in a spatially explicit environment and implications for plant access to nitrogen. *Journal of Ecology* 86: 841–853.

Klironomos JN. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84: 2292–2301.

Klironomos JN, Allen MF, Rillig MC, Piotrowski J, Makvandi-Nejad S, Wolfe BE, Powell JR. 2005. Abrupt rise in atmospheric CO_2 overestimates community response in a model plant-soil system. *Nature* 433: 621–624.

Klironomos JN, Ursic M, Rillig M, Allen M. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO_2. *New Phytologist* 138: 599–605.

Kummel M, Salant SW. 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. *Ecology* 87: 892–902.

Lambert DH, Cole H, Baker DE. 1980. Adaptation of vesicular-arbuscular mycorrhizae to edaphic factors. *New Phytologist* 85: 513–520.

Louis I, Lim G. 1988. Differential response in growth and mycorrhizal colonization of soybean to inoculaton with two isolates of *Glomus clarum* in soils of different P availability. *Plant and Soil* 112: 37–43.

Mack KML. 2012. Selective feedback between dispersal distance and the stability of mutualism. *Oikos* 121: 442–448.

Miller RM, Miller SP, Jastrow JD, Rivetta CV. 2002. Mycorrhizal mediated feedbacks influence net carbon gain and nutrient uptake in *Andropogon gerardii.* *New Phytologist* 155: 149–162.

Molofsky J, Bever JD. 2002. A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. *Proceedings of the Royal Society of London, B* 269: 2389–2393.

Montealegre CM, Van Kessel C, Blumenthal JM, Hur H, Hartwig UA, Sadowsky MJ. 2000. Elevated atmospheric CO_2 alters microbial population structure in a pasture ecosystem. *Global Change Biology* 6: 475–482.

Mummey DL, Rillig MC. 2008. Spatial characterization of arbuscular mycorrhizal fungal molecular diversity at the submetre scale in a temperate grassland. *FEMS Microbiology Ecology* 64: 260–270.

Mummey DL, Stahl PD. 2003. Spatial and temporal variability of bacterial 16S rDNA-based T-RFLP patterns derived from soil of two Wyoming grassland ecosystems. *FEMS Microbiology Ecology* 46: 113–120.

Newsham KK, Fitter AH, Watkinson AR. 1995. Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *Journal of Ecology* 83: 991–1000.

Nicol GW, Glover LA, Prosser JI. 2003. Spatial analysis of archaeal community structure in grassland soil. *Applied and Environmental Microbiology* 69: 7420–7429.

Noe R, Hammerstein P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology* 35: 1–11.

Nunan N, Wu KJ, Young IM, Crawford JW, Ritz K. 2003. Spatial distribution of bacterial communities and their relationships with the micro-architecture of soil. *Fems Microbiology Ecology* 44: 203–215.

Olsson PA, Rahm J, Aliasgharzad N. 2010. Carbon dynamics in mycorrhizal symbioses is linked to carbon costs and phosphorus benefits. *Fems Microbiology Ecology* 72: 123–131.

Platt TG, Bever JD, Fuqua C. 2012. A cooperative virulence plasmid imposes a high fitness cost under conditions that induce pathogenesis. *Proceedings of the Royal Society B – Biological Sciences* 279: 1691–1699.

Porter SS, Simms EL. 2014. Selection for cheating across disparate environments in the legume–rhizobium mutualism. *Ecology Letters* 17: 1121–1129.

Regus JU, Gano KA, Hollowell AC, Sachs JL. 2014. Efficiency of partner choice and sanctions in *Lotus* is not altered by nitrogen fertilization. *Proceedings of the Royal Society B – Biological Sciences.* 281: 20132587.

Remy W, Taylor TN, Hass H, Kerp H. 1994. 4 hundred million year old vesicular–arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences, USA* 91: 11841–11843.

Reynolds HL, Vogelsang KM, Hartley AE, Bever JD, Schultz PA. 2006. Variable responses of old-field perennials to arbuscular mycorrhizal fungi and phosphorus source. *Oecologia* 147: 348–358.

Robinson D, Rorison IH. 1983. A comparison of the responses of *Lolium perenne* L., *Holcus lanatus* L. and *Deschampsia flexuosa* (L.) Trin. to a localized supply of nitrogen. *New Phytologist* 94: 263–273.

Sachs JL, Russell JE, Lii YE, Black KC, Lopez G, Patil AS. 2010. Host control over infection and proliferation of a cheater symbiont. *Journal of Evolutionary Biology* 23: 1919–1927.

Schwartz MW, Hoeksema JD. 1998. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology* 79: 1029–1038.

Sikes BA, Cottenie K, Klironomos JN. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *Journal of Ecology* 97: 1274–1280.

Simms EL, Taylor DL, Povich J, Shefferson RP, Sachs JL, Urbina M, Tausczik Y. 2006. An empirical test of partner choice mechanisms in a wild legume–rhizobium interaction. *Proceedings of the Royal Society of London* 273: 77–81.

Smith SE, Jakobsen I, Gronlund M, Smith FA. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between rathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiology* 156: 1050–1057.

Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis.* Amsterdam, the Netherlands: Academic Press.

Sprent JI. 1979. *The biology of nitrogen-fixing organisms.* London, UK: McGraw-Hill.

Sprent JI, Sutherland JM, de Faria SM. 1987. Some aspects of the biology of nitrogen-fixing organisms. *Philosophical Transactions of the Royal Society of London B* 317: 111–129.

Stahl PD, Smith WK. 1984. Effects of different geographic isolates of *Glomus* on the water relations of *Agropyron smithii.* *Mycologia* 76: 261–267.

Steidinger BS, Bever JD. 2014. The coexistence of hosts with different abilities to discriminate against cheater partners: an evolutionary game-theory approach. *The American Naturalist* 183: 762–770.

Taylor TN, Remy W, Hass H, Kerp H. 1995. Fossil arbuscular mycorrhizae from the early Devonian. *Mycologia* 87: 560–573.

Van Vuuren MMI, Robinson D, Griffiths BS. 1996. Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. *Plant and Soil* 178: 185–192.

Vandermeer JH. 1973. Generalized models of two species interactions: a graphical analysis. *Ecology* 54: 809–818.

Wagg C, Jansa J, Schmid B, van der Heijden MGA. 2011. Belowground biodiversity effects of plant symbionts support aboveground productivity. *Ecology Letters* 14: 1001–1009.

Weisbuch G, Duchateau G. 1993. Emergence of mutualism: application of a differential model to endosymbiosis. *Bulletin of Mathematical Biology* 55: 1063–1090.

West SA, Kiers ET, Simms EL, Denison RF. 2002. Sanctions and mutualism stability: why do rhizobia fix nitrogen. *Proceedings of the Royal Society of London* 269: 685–694.

Wilkinson DM, Sherratt TN. 2001. Horizontally acquired mutualisms, an unsolved problem in ecology? *Oikos* 92: 377–384.

Wolf J, Johnson NC, Rowland DL, Reich PB. 2003. Elevated CO_2 and plant species richness impact arbuscular mycorrhizal spore communities. *New Phytologist* 157: 579–588.

Wolfe BE, Mummey DL, Rillig MC, Klironomos JN. 2007. Small-scale spatial heterogeneity of arbuscular mycorrhizal fungal abundance and community composition in a wetland plant community. *Mycorrhiza* 17: 175–183.

Wyatt GAK, Kiers ET, Gardner A, West SA. 2014. A biological market analysis of the plant-mycorrhizal symbiosis. *Evolution* 68: 2603–2618.

Zee PC, Bever JD. 2014. Joint evolution of kin recognition and cooperation in spatially structured Rhizobium populations. *PLoS ONE* 9: e95141.

Zheng C, Ji B, Zhang J, Zhang F, Bever JD. 2014. Shading decreases plant carbon preferential allocation towards the most beneficial mycorrhizal mutualist. *New Phytologist* 205: 361–368.

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