Multiple Friends with Benefits: An Optimal Mutualist Management Strategy?

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abstract: Most mutualisms in nature involve interactions between multispecies mutualist guilds and multiple partner species. While mechanisms such as niche partitioning can explain part of this diversity, the presence of low-quality partners, which produce relatively low returns on investment compared with other guild members, is not well understood. Here, we consider a novel explanation for this persistence: that low-quality partners are actively maintained by their hosts as part of a growth-maximizing strategy, even in the presence of higher-quality alternatives. We use a model inspired by the interaction between host trees and ectomycorrhizal fungi to demonstrate that when the environment is variable, trees maintain low-quality fungal partners that they would not otherwise maintain in constant environments. This active investment, which emerges as a response to saturating returns on investment in higher-quality partners, could contribute to the maintenance of diversity in multi-species mutualisms.

Keywords: bioeconomic models, cheating, ectomycorrhizae, optimal control theory, tree-fungal mutualisms.

Introduction

Multimutualist systems, wherein multispecies mutualist guilds cooperatively interact with one or more partner species, are the most common form of mutualistic interactions in nature (Stanton 2003). In part, this diversity has been explained by niche partitioning, that is, that different partner species provide different mutualistic benefits. However, many multimutualist guilds include species that vary in the quality of the benefits that they provide, in addition to the type of benefits that they provide (Stanton 2003).

While traditional explanations of mutualism evolution and stability are based on coevolved, highly specific, pair-wise interactions (Schwartz and Hoeksema 1998, reviewed in Herre et al. 1999; McGill 2005; de Mazancourt and Schwartz 2010), in reality many processes work against a single-partner monopoly in nature. For example, mutation may give rise to alternate genotypes corresponding to phenotypes of varying partner quality (Golubski and Klausmeier 2010; Porter and Simms 2014). Cheating phenotypes may also arise because of the fitness advantages to cheaters (McGill 2005; Porter and Simms 2014). Because such diversification processes may destabilize the mutualism (Bronstein et al. 2003; Hoeksema and Kummel 2003; Palmer et al. 2003), these guild members are thought to be transient partners quickly eliminated through the mutualism equivalent of an evolutionary arms race as mutualists evolve greater efficiency in partner selection (Noë and Hammerstein 1994; West et al. 2002; Kiers and van der Heijden 2006).

Here, we provide a counterexample to this conventional wisdom by exploring another mechanism that maintains diversity in partner quality: the active maintenance of low-quality partners. We use optimal control theory to find growth-maximizing solutions to a biological market model describing a host that acquires resources from multiple mutualistic partners that vary in quality. Our model is inspired by mycorrhizal tree-fungal mutualisms, which are both ecologically important and highly diverse (Trappe 1962; Molina and Trappe 1982). Individual trees may simultaneously associate with dozens of mycorrhizal fungal partners (Trappe 1977), but the ecological significance of this diversity has been only partially explained by niche partitioning mechanisms (Bruns 1995). In addition, evidence of variable fungal partner quality exists in mycorrhizal systems (Kiers and Denison 2008; Bever et al. 2009; Kiers et al. 2011; Hart et al. 2012).

In particular, we consider the importance of environmental variation to partner maintenance. Given that host trees are long-lived, they experience many scales of temporal variation, from diel light cycles to annual seasonal cycles to multiyear climatic oscillations. We show that the associated fluctuations in resource availability alter a tree's

need for mutualistic partners over time, resulting in optimal investment strategies that include a more diverse suite of partners than would be maintained in constant environmental conditions. The fact that the growth-maximizing tree strategy includes investment in low-quality fungal partners indicates that active partner maintenance can potentially play an important role in maintaining partner diversity in multispecies mutualisms. These results stand in contrast to conventional wisdom that low-quality partners should be avoided through partner choice mechanisms and, as a result, eliminated from multimutualist systems.

The Model

Our model describes the interaction of a host tree with a set of mycorrhizal fungi (fig. 1). The formulation we use, in which the tree interacts with the fungi through individual root tips, is inspired particularly by ectomycorrhizal interactions, though our model is generalizable to a variety of resource exchange mutualisms. Because we are interested in temporal variation and partner quality, rather than niche partitioning, we focus on a single nutrient whose acquisition by the tree is mediated by its fungal partners. To examine the maintenance of low-quality partners, we further simplify by considering a system with only two fungal partners, one of which is relatively higher in quality (e.g., has a lower maintenance cost or lower mortality rate) than the other. To quantify the effects of environmental variation on a tree's investment in fungal partners, we consider environmental variation that affects nutrient availability in the soil, as this can impact the relative benefit of associating with mycorrhizal fungi (Neuhauser and Fargione 2004; Grman et al. 2012), for example, by directly impacting fungal performance (Hoeksema and Schwartz 2003; Heath and Tiffin 2007; Franklin et al. 2014).

Our model captures the dynamics of a tree's photosynthetic carbon biomass B at time T, which grows proportionately to the tree's nutrient content (N_T) at a photosynthetic rate p and releases carbon (due to mortality, respiration, etc.) at a rate m_B:

$$\frac{dB}{dT} = pN_T - m_B B - C(T). \quad (1)$$

Here, $C(T)$ represents additional carbon costs that the tree incurs from the growth of its root system and payments to its fungal partners. We assume that root tip production at rate G comes at a fixed carbon cost c_1 per root tip and that costs increase at a rate $c_2 G$ for additional root tips produced simultaneously. We also assume that payments to a fungal partner are proportional to the abundance of that partner on the host tree's root system (measured as root tips, F_i). We account for two forms of this payment: a baseline maintenance cost specific to each fungal partner (w_i)

and a discretionary payment (i.e., a reward) controlled by the tree that allows for differential carbon allocation to each fungal partner (H_i). Thus, $C(T)$ is

$$C(T) = G(T)(c_1 + c_2 G(T)) + \sum_i (w_i + H_i(T))F_i. \quad (2)$$

These costs include two optimizable controls that depend on time: $G(T)$, the rate of production of new root tips, and $H_i(T)$, the carbon reward allocated per fungus-occupied root tip. (A list of state variables and parameters is given in table 1.)

We model the dynamics of the tree's root system and the associated fungi using a metacommunity of root tip patches, each of which may be colonized by one fungal species. We model changes in the number of uncolonized tips (F_0) and tips colonized by each of i fungi (F_i) over time:

$$\frac{dF_0}{dT} = -\frac{F_0}{F_T}\sum r_i(T)F_i - m_0 F_0 + G(T), \quad (3)$$

$$\frac{dF_i}{dT} = \frac{F_0}{F_T}r_i(T)F_i - m_i F_i. \quad (4)$$

Here, F_T is the total number of tips in the tree's root system.

Uncolonized root tips are produced by the tree at the rate G, and root tips die with mortality rates m_i, specific to their colonization status. The fungal species compete to colonize empty root tips. The colonization rate of fungus i is proportional to its abundance on the tree's root system (F_i), its reproductive rate (r_i), and the relative availability of uncolonized root tips (F_0/F_T). Thus, the colonization rate of fungus 1 depends on the abundance of fungus 2 and so on.

In our model, tree rewards $H_i(T)$ enhance fungal reproductive rates. Since r_i is the per–root tip reproductive rate and root tips have a finite size, we represent this with the saturating form:

$$r_i(T) = b_i\left(1 + \frac{\eta_i H_i(T)}{k_i + H_i(T)}\right), \quad (5)$$

where b_i is the basal reproductive rate supported by the maintenance cost w_i, η_i is the maximum reproductive enhancement, and k_i is the half-saturation constant. As a consequence, the marginal impact of each additional carbon reward is a declining function of H_i, so the tree's per-tip rewards do not grow without bound (though $H_i F_i$ may grow indefinitely with F_i). This is in keeping with the single–root tip intuition: instantaneous carbon flux is constrained by the physical limit of the root tip's size.

Finally, we account for the dynamics of a nutrient, N, which may be in either of two pools: the tree's tissues (N_T) or the soil pool (N_S). We assume that the tree relies
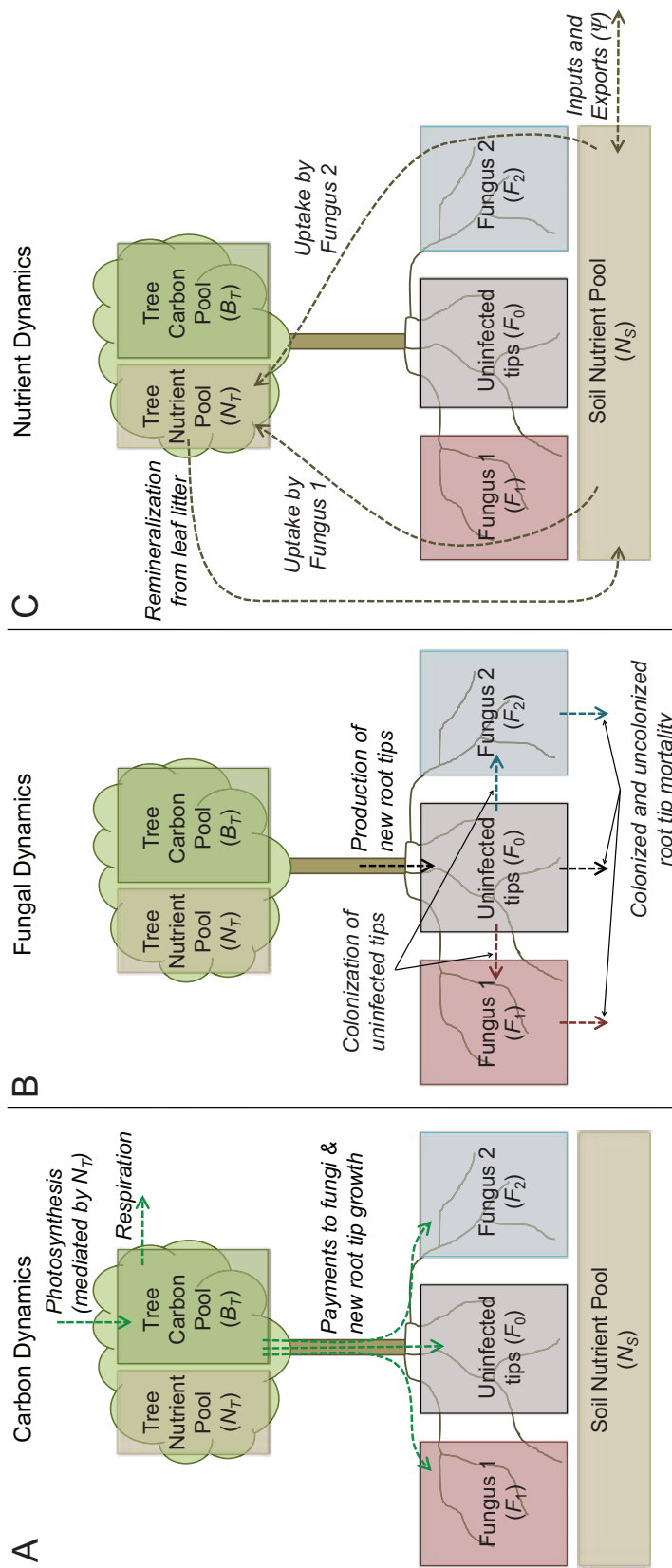
Figure 1: Conceptual diagram of the model. Boxes represent state variables. Dashed arrows represent fluxes of materials. For clarity, not all states and fluxes are shown in each panel. *A*, The tree acquires carbon through photosynthesis (dependent on its present supply of nutrients) and loses it through respiration and belowground costs. These belowground costs include the manufacture of new root tips and maintenance and reward payments to fungal partners. *B*, Fungi grow by colonizing previously uncolonized root tips that have been produced by the tree. Both colonized and uncolonized tips experience mortality. *C*, Nutrient acquisition by the tree is mediated by its fungal partners. Senescence and decay of tree materials result in remineralization to the nutrient pool. The nutrient supply may also vary with inputs to and exports from the soil pool.

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Table 1: State variables, parameters, and their dimensions

Symbol	Description	Units	Dimensionless version	Simulation values
Variables:				
T	Time	Year	t	
B	Tree biomass	C	b	
F_0	Uncolonized root tips	Tip	f_0	
F_i	Root tips colonized by fungus i	Tip	f_i	
F_T	Total root tip abundance	Tip		
N_T	Tree nutrients	Nutrient	n_T	
N_S	Soil nutrient pool	Nutrient	n_S	
Optimal controls:				
G	Tip growth	Tips year^{-1}	g	
H_i	Fungal carbon supplement	C tip^{-1} year^{-1}	h_i	
Parameters:				
p	Nutrient-specific photosynthetic rate	C nutrient^{-1} year^{-1}		. . .
m_B	Tree respiration rate	Year^{-1}		. . .
m_N	Tree nutrient remineralization	Year^{-1}	μ_N	.01
c_1	Tip growth cost	C tip^{-1}		. . .
c_2	Per-tip secondary costs	C year tip^{-2}	ϕ	.004
w_i	Basal fungal cost	C tip^{-1} year^{-1}	ω_i	.001
r_i	Adjusted reproduction rate of fungus i	t^{-1}	ρ_i	
η_i	Maximum reproductive enhancement factor	. . .	η_i	1
k_i	Half-saturation of reproductive enhancement	C tip^{-1} year^{-1}	κ_i	.5
b_i	Basal reproduction rate of fungus i	Year^{-1}	β_i	.01
m_0	Mortality of uncolonized root tips	Year^{-1}	μ_0	.1
m_i	Mortality of fungus i	Year^{-1}	μ_i	.05
e_i	Nutrient uptake efficiency of fungus i	Tip^{-1} year^{-1}	ϵ_i	.01
a	Amplitude of environmental variation	Nutrient year^{-1}	α	0–10
ν	Number of periods of variation within $[0, T_{end}]$	. . .	ν	0–10
∂	Discounting rate	Year^{-1}	δ	.001
T_{end}	Optimization time horizon	Year	t_{end}	100

Notes: C = carbon, tip = individual tree root tip. For ω_i, μ_i, ϵ_i, and β_i, values given are for fungus 1 (with fungus 2 values variable; see "Results").

on its fungal partners for nutrient acquisition due to specialization of the mutualist guilds on different resource acquisition strategies (Hoeksema and Schwartz 2003). Nutrients are transferred to the tree by its fungal partners, which each have a specific efficiency, e_i, and are released through the death and decay of tree tissues at a rate m_N. Nutrients enter or leave the soil according to the environmental function $\Psi(T)$:

$$\frac{dN_T}{dT} = N_S \sum_i e_i F_i - m_N N_T, \tag{6}$$

$$\frac{dN_S}{dT} = -\frac{dN_T}{dT} + \Psi(T). \tag{7}$$

We use a family of sinusoidal functions to parameterize temporal variation in a way that allows fluctuations in nutrient availability that vary in their magnitude and frequency while maintaining the same mean availability:

$$\Psi(T) = a \cos\left(\frac{2\pi}{T_{end}} \nu T\right), \tag{8}$$

where a is the amplitude and ν is the number of periods of variation experienced within the time frame evaluated ($T = 0$ to $T = T_{end}$). This permits direct comparison with closed systems (i.e., $a = 0$). We restrict the amplitude a to be small enough that the soil nutrient pool remains positive while $T \leq T_{end}$.

To reduce parameter numbers, we employ the substitutions

$$T = \frac{t}{m_B}, \quad F_0 = f_0 \frac{m_N}{e_1}, \quad F_i = f_i \frac{m_N}{e_1},$$

$$N_T = n_T \frac{c_1 m_B m_N}{p e_1}, \quad N_S = n_S \frac{c_1 m_B m_N}{p e_1}, \quad B = b \frac{c_1 m_N}{e_1}.$$

Thus, for two fungi, we have the dimensionless full model:

$$\frac{db}{dt} = n_\mathrm{T} - b - g(t)(1 + \phi g(t)) - (\omega_1 + h_1(t))f_1 \\ - (\omega_2 + h_2(t))f_2, \tag{9}$$

$$\frac{df_0}{dt} = g(t) - \frac{f_0}{f_0 + f_1 + f_2}(\rho_1(t)f_1 + \rho_2(t)f_2) - \mu_0 f_0, \tag{10}$$

$$\frac{df_1}{dt} = \frac{f_0}{f_0 + f_1 + f_2}\rho_1(t)f_1 - \mu_1 f_1, \tag{11}$$

$$\frac{df_2}{dt} = \frac{f_0}{f_0 + f_1 + f_2}\rho_2(t)f_2 - \mu_2 f_2, \tag{12}$$

$$\frac{dn_\mathrm{T}}{dt} = n_\mathrm{S}(\epsilon_1 f_1 + \epsilon_2 f_2) - \mu_\mathrm{N} n_\mathrm{T}, \tag{13}$$

$$\frac{dn_\mathrm{S}}{dt} = -\frac{dn_\mathrm{T}}{dt} + \alpha \cos\left(\frac{2\pi}{t_\mathrm{end}}\nu t\right), \tag{14}$$

where

$$\rho_i(t) = \beta_i\left(1 + \frac{\eta_i h_i(t)}{\kappa_i + h_i(t)}\right) \tag{15}$$

and

$$g(t) = \frac{e_1 G(T)}{m_\mathrm{B} m_\mathrm{N}}, \; \phi = \frac{c_2 m_\mathrm{N} m_\mathrm{B}}{c_1 e_1}, \; \omega_i = \frac{w_i}{c_1 m_\mathrm{B}}, \; h_i(t) = \frac{H_i(T)}{c_1 m_\mathrm{B}},$$

$$\rho_i = \frac{r_i}{m_\mathrm{B}}, \; \mu_0 = \frac{m_0}{m_\mathrm{B}}, \; \mu_i = \frac{m_i}{m_\mathrm{B}}, \; \epsilon_i = \frac{e_i m_\mathrm{N}}{m_\mathrm{B} e_1}, \; \mu_\mathrm{N} = \frac{m_\mathrm{N}}{m_\mathrm{B}},$$

$$\alpha = \frac{ape_1}{c_1 m_\mathrm{B}^2 m_\mathrm{N}}, \; t_\mathrm{end} = T_\mathrm{end} m_\mathrm{B}, \; \beta_i = \frac{b_i}{m_\mathrm{B}}, \; \kappa_i = \frac{k_i}{c_1 m_\mathrm{B}}.$$

Since fungal trait parameters are constant in time, we define fungus 1 as a higher-quality partner than fungus 2 when (1) $\omega_1 < \omega_2$, so that the costs of maintaining fungus 1 are lower than those for fungus 2; (2) $\mu_1 < \mu_2$, so that root tips colonized by fungus 1 experience reduced mortality compared to those colonized by fungus 2; (3) $\epsilon_1 > \epsilon_2$, so that the per–root tip nutrient supply from fungus 1 is greater than that of fungus 2; (4) $\beta_1 > \beta_2$, so that fungus 1's baseline reproductive rate is greater than that of fungus 2; or (5) $\eta_1 > \eta_2$ and/or $\kappa_1 < \kappa_2$, so that fungus 1's reproductive rate is more enhanced by a given tree carbon supply h than fungus 2's reproductive rate. In the model, these parameters are intrinsic properties of the fungus that are not sensitive to environmental conditions. Therefore, a low-quality fungus is a low-quality partner in all environmental conditions. Because the qualitative effects of all five options are similar,

we focus on a subset of these traits: ω, the maintenance cost; β, the baseline reproductive rate; ϵ, the nutrient acquisition efficiency; and μ, the mortality rate.

To link our optimal control approach to evolutionary fitness, we hypothesize that a tree seeks to maximize its available photosynthetic biomass (b) because this carbon stock both increases the tree's growth rate and fuels the tree's reproduction (Zamski 1995; LaDeau and Clark 2001). We incorporate a discounting rate δ because the future environment (and the tree's life span) is uncertain. Therefore, it is better for a tree to accumulate biomass sooner rather than later because the tree may not survive indefinitely. Thus, our objective function is

$$\max_{g, h_i \geq 0} \int_0^{t_\mathrm{end}} b(t) e^{-\delta t} dt. \tag{16}$$

We choose a time horizon ($t_\mathrm{end} = 100$) and discounting rate ($\delta = 0.001$) such that at the end of the optimization, a unit of tree biomass has approximately 90% of the value it did at the beginning. Thus, our analysis is intended to span a relatively short period in an adult tree's life history, with fluctuations representing decadal to seasonal oscillations in nutrient availability.

Several key properties make this model both interesting and biologically realistic. First, the tree faces an interesting investment problem: it seeks to maximize its carbon stock but must also expend carbon to acquire nutrients to further grow this carbon stock. Second, we have formulated the model such that the tree cannot discriminate between partners before fungal colonization. Although precolonization partner recognition systems are present in some mycorrhizal symbioses (Giovannetti et al. 1994; Martin et al. 2001), these mechanisms may be less useful when partners are genotypically similar or when partner quality depends on environmental context (Denison et al. 2003; Kiers and Denison 2008). However, we do allow the tree to fully discriminate between fungal partners when allocating reproduction-enhancing carbon rewards after colonization, when the host tree is more likely to be able to distinguish partner quality (Denison et al. 2003; Kiers and Denison 2008). Third, the tree's inability to differentiate among fungi before colonization, the rate at which the tree can produce new root tips, and the rate at which the fungi can grow to colonize these root tips result in a time lag for fungal growth: the tree cannot instantaneously increase or replace its complement of mycorrhizal fungi in response to shifts in environmental nutrient availability.

To study the tree's response to these constraints, we use optimal control theory (see app. A; apps. A and B available online) to solve for the tree's optimal investment strategy: the timing and amount of carbon it invests in root growth

and fungal rewards. This strategy depends on the environmental conditions and the traits of its available fungal partners. We use two metrics that allow us to compare tree strategies across conditions. First, we compare the total carbon the tree allocates belowground (i.e., to both root growth and fungal partners) with its net photosynthetic yield to determine I_B, the relative belowground investment:

$$I_B = \frac{\int_0^{t_{end}} \left[g(t)(1 + \omega_2 g(t)) + \sum_i (\omega_i + h_i(t)) f_i \right] dt}{\int_0^{t_{end}} (n_T - b) dt}. \quad (17)$$

Second, we compare the carbon rewards that the tree allocates to its lower-quality partner to the total carbon rewards the tree allocates to both fungal partners to determine I_L, the fraction invested in the lower-quality partner:

$$I_L = \frac{\int_0^{t_{end}} h_2(t) f_2(t) dt}{\int_0^{t_{end}} [h_1(t) f_1(t) + h_2(t) f_2(t)] dt}. \quad (18)$$

In addition, we compute the carbon to nutrient (C : nutrient) exchange rate between the tree and each of its fungal partners. For fungus i at time t, this is equivalent to

$$E_i = \frac{(\omega_i + h_i(t)) f_i}{\epsilon_i f_i}. \quad (19)$$

Finally, to determine the effects of carbon rewards on fungal persistence, we repeated our analysis with the condition that $h_2(t) = 0$ for all t (i.e., fungus 2 receives no carbon rewards from the host tree). We then computed the half-life of fungus 2 (i.e., the time until its abundance declines to half its starting condition) with and without tree rewards and calculated the relative increase in its persistence as the ratio of those two terms.

Results

We first consider the investment strategy of a tree in constant environmental conditions (i.e., $\alpha = 0$), corresponding to a closed system in which changes to the soil nutrient pool represent the balance between tree uptake (via fungal partners) and remineralization (via senescence of tree biomass, e.g., leaves). To sustain an active mycorrhizal community (fig. 2A), the tree initially makes an early large investment in root tip growth, followed by sustained rewards to its fungal partners (fig. 2B). Due to both the discounting rate and the finite time horizon of the optimization, tree biomass, tree nutrients, tree belowground investments, and fungal population size decline as time approaches t_{end}. As a consequence of temporal variability in investments and the size of the soil nutrient pool, the C : nutrient exchange rate between trees and fungi varies over time (fig. 2C).

When the two fungal partners are identical in their traits, the tree treats them identically, awarding 50% of carbon rewards to each partner (figs. 2B, 3, upper right corner). In contrast, when the partners are not identical, the tree always awards less carbon to the low-quality partner (fig. 3). The lower the quality of the partner, the fewer carbon rewards it receives from the host tree. These carbon rewards play an important role in fungal persistence, increasing fungal half-life by up to 12% (fig. B1; figs. B1–B7 available online). The greater the cumulative rewards provided by the tree to its fungal partner, the longer that partner persists on its root system.

Next, we consider environmental variation that is constant in amplitude but varies in frequency. While the tree's investment in root growth is qualitatively similar to its investment in constant environments (cf. fig. 2B, 2E), its optimal rewards are more temporally variable, with anticipatory peaks in fungal rewards occurring just before peaks in nutrient availability (fig. 2D, 2E). Overall, the tree's relative investment belowground (I_B) is slightly lower for environments with low-frequency variation ($\nu < 4$) than for constant or highly variable environments (fig. 4A), as a consequence of relatively lower total investments in fungal partner rewards (figs. B2–B6).

Again, when the two fungal partners are identical (fig. 4B, ticked line), the tree treats them identically, awarding 50% of its carbon rewards to each partner regardless of environmental heterogeneity. However, compared to constant environmental conditions (fig. 4B, leftmost panel), the tree's level of investment in a lower-quality partner (e.g., a partner with higher maintenance costs, lower uptake efficiency, reduced growth rate, or increased mortality, indicated by black stars in fig. 3) may change when nutrient availability varies. In particular, when the frequency of environmental variation is low (i.e., one period), the tree invests more in fungus 2 than it would in constant environmental conditions. Because the tree's total investment in fungus 2 is lower (because of reduced rewards in response to fungus 2's lower quality), fungus 2's exchange rate is typically "better" (i.e., lower C cost per unit nutrient delivered) than fungus 1's (figs. B2–B6).

The tree's differential reward pattern is intensified when fungus 2 is so low in quality that the tree gives it no carbon rewards under constant environmental conditions (e.g., extremely high maintenance costs, indicated by gray stars in fig. 3). Despite this low quality, when environmental variation is introduced, the tree provides up to 35% of its carbon rewards to the low-quality partner (fig. 5A). That is, the tree transitions from an optimal investment strategy that maintains only one highest-quality partner to one in which the tree invests in two partners, although one is relatively lower in quality. The magnitude and persistence of this investment depend on the frequency and amplitude
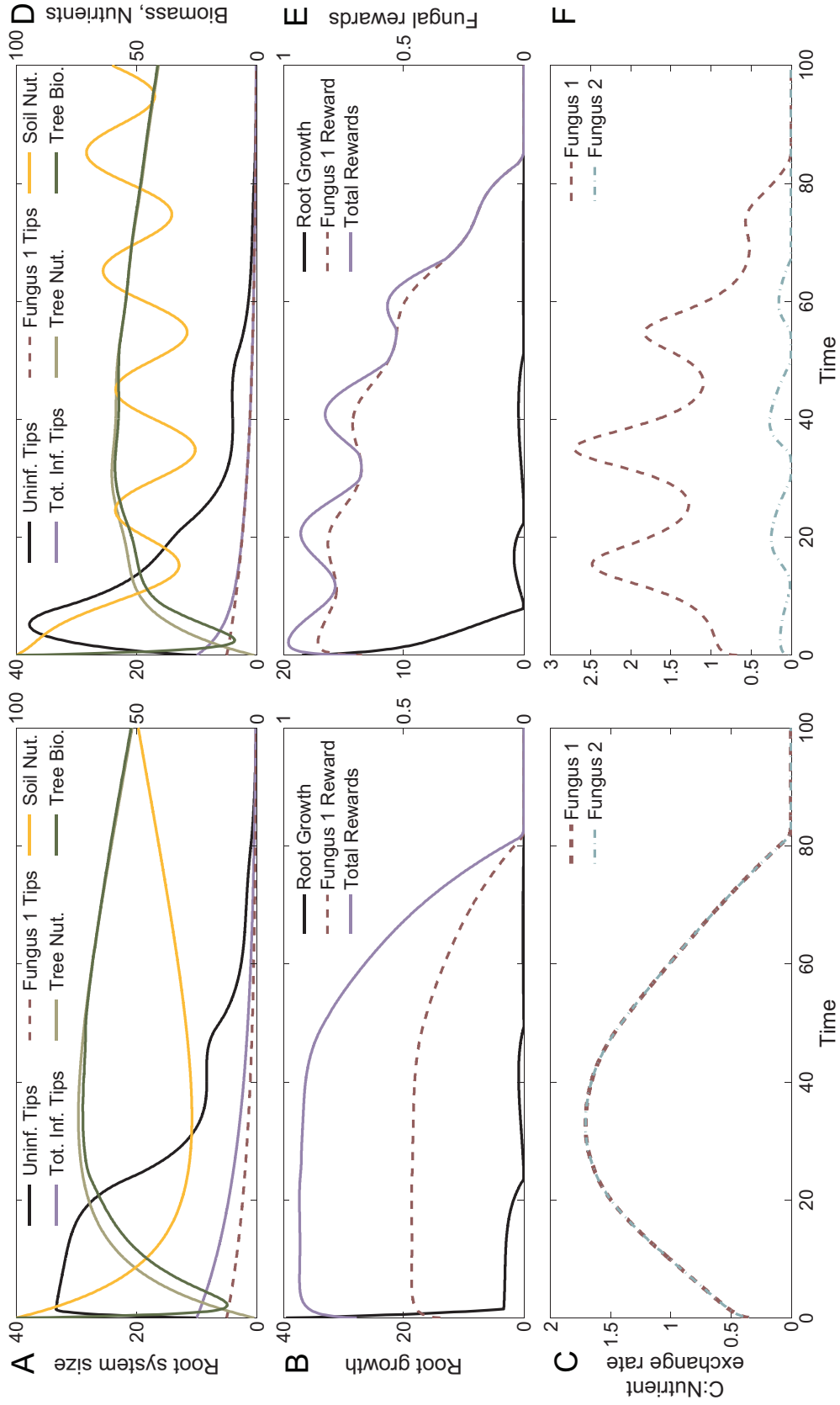
Figure 2: Time series of state variables (*A, D*), optimal controls (*B, E*), and carbon : nutrient exchange rates (*C, F*). For *A–C*, $\alpha = 0$ (i.e., no environmental fluctuations), and fungus 1 and fungus 2 are identical. For *D–F*, $\alpha = \nu = 5$, and fungus 2 is identical to fungus 1 in all parameters except mortality ($\mu_2 = 0.25$). Note that blue lines in *A, B, D*, and *E* represent total values ($f_1 + f_2$ and $h_1 + h_2$), pooled across both fungi, and that in *C*, because fungus 1 and fungus 2 are identical, their exchange rates are identical and overlapping.
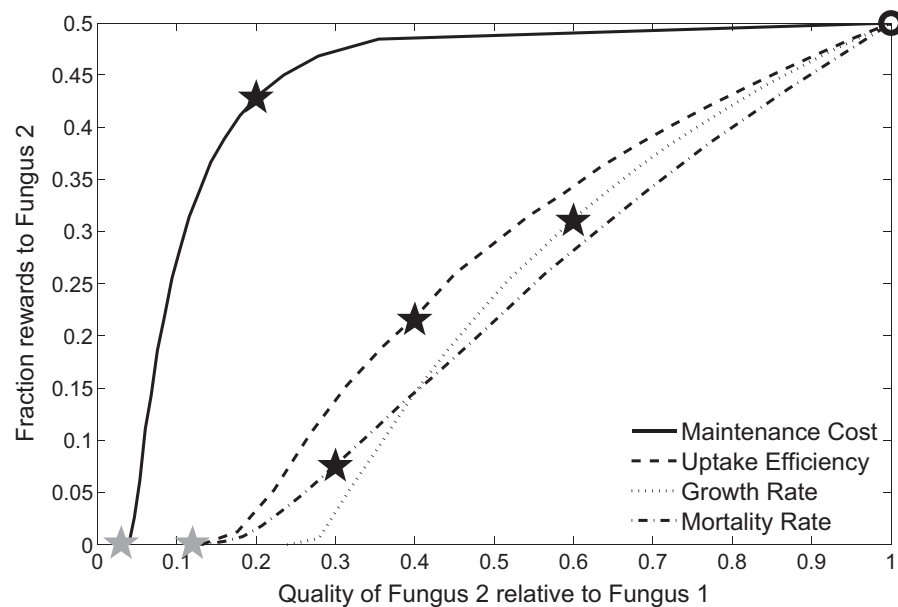
Figure 3: Relative investment in lower-quality partner (here, fungus 2) in constant environmental conditions ($\alpha = 0$). Each line represents one of four ways in which, all else being equal, the two fungal partners may differ. First, fungus 2 may have greater maintenance costs than fungus 1 ($\omega_2 > \omega_1$; solid line) but is otherwise identical to fungus 1, making partnership with it relatively more costly for the host tree. As fungus 2's quality ($1 - \log(\omega_2/\omega_1)/4$) increases, so does the tree's investment (I_L) until both partners are equivalent (circle). Second, fungus 2 may have a reduced nutrient uptake efficiency ($\epsilon_2 < \epsilon_1$; dashed line) or reduced growth rate ($\beta_2 < \beta_1$; ticked line) compared to fungus 1. As fungus 2's quality (ϵ_2/ϵ_1 or β_2/β_1) increases, so does the host tree's relative investment. Finally, fungus 2 may have a greater mortality rate than fungus 1 ($\mu_2 > \mu_1$; dot-dashed line). Here, fungus 2's quality is measured as $1 - \log(\mu_2/\mu_1)$. Four black stars indicate parameter choices ($\omega_2 = 1.53$, $\epsilon_2 = 0.004$, $\beta_2 = 0.006$, or $\mu_2 = 0.25$) used in figure 4 simulations, and two gray stars indicate the parameter choices ($\omega_2 = 7.26$ or $\mu_2 = 0.38$) used in figure 5 simulations.

of environmental variation and the trait by which the two fungi differ (fig. 5).

Discussion

Our model, a simple representation of a host tree interacting with two fungal partners to maximize its carbon biomass, gives a counterintuitive result: substantial investment in low-quality fungal partners may be optimal when the environment is variable, even when those partners would not be maintained under constant environmental conditions. Relative investment in the low-quality partner is highest when fluctuations in nutrient availability are large and when these fluctuations occur relatively slowly (i.e., frequency is low and there are relatively few complete periods within the optimization time horizon). This suggests a mechanism that depends on the tree's opportunity to harvest nutrients during peaks in availability. When these peaks are large, it is optimal for the tree to invest more in its fungal partners to increase its ability to take up available nutrients. When these partners differ in quality, the tree invests primarily in the high-quality partner. However, because growth rate saturates, marginal investments become less effectual

than investment in the low-quality partner. Thus, the tree alters its strategy to include investment in the low-quality partner. However, when the environment fluctuates rapidly, the tree's strategy reverts to the constant environment optimum. Similar results, that organisms exposed to rapid environmental fluctuations respond by using the strategy appropriate for average conditions, have been found in microbial systems (Beaumont et al. 2009; Rainey et al. 2011).

Our results suggest that over short timescales, low-quality partners may persist in mutualisms because they can provide short-term benefits in fluctuating environments. Indeed, while experiments have shown preferential carbon allocation to mycorrhizae by plant hosts (Bever et al. 2009; Kiers et al. 2011), the lower-quality partner is typically not entirely eliminated from the experimental system. Over longer, evolutionary timescales, such processes are unlikely to prevent the elimination of low-quality partners; however, our results show that optimal investment by individual host trees may allow low-quality partners to persist relatively longer than otherwise expected, contributing to diversity maintenance in mycorrhizal systems.

While our model assumes that the host tree has full knowledge of future environmental conditions, in reality,
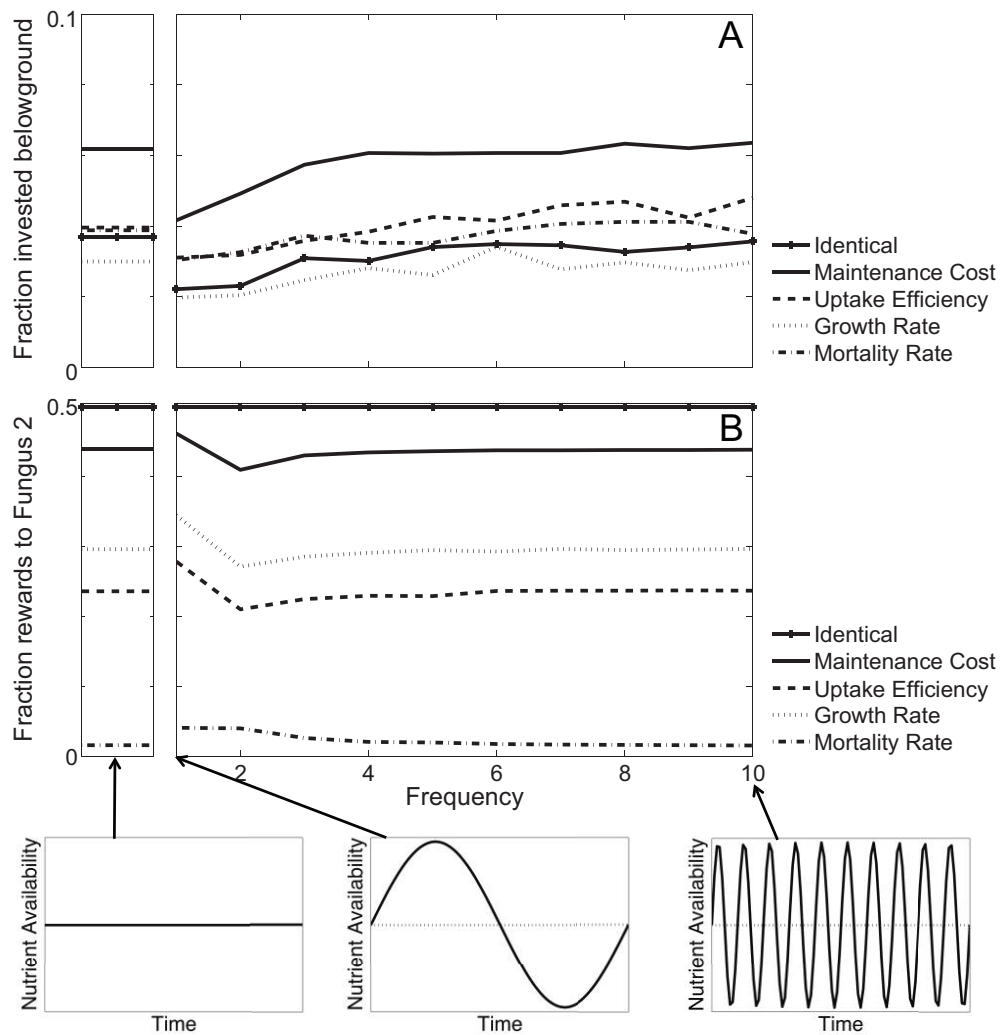
Figure 4: Relative investment belowground (I_B; *A*) and fraction of total rewards allocated to fungus 2 (I_L; *B*), when fungus 2 is either identical (ticked line) or lower in quality (four other lines) compared to fungus 1 and the available nutrient supply varies. The leftmost panels show relative investment in constant environmental conditions (constant nutrient availability, as indicated by the inset), corresponding to the black stars in figure 3. The rightmost panel shows how this relative investment first changes and then stabilizes at levels that approximate investment in the constant environment, as the frequency of environmental fluctuation increases from 1 to 10 cycles in *t*, the time period of interest over which the model optimizes. For leftmost panels, $\alpha = 0$; for rightmost larger panels, $\alpha = 5$.

nutrient availability does not fluctuate so predictably. In addition, although our model did not address niche partitioning among fungi, a tree's resource needs may change over its lifetime, such that today's best partners may not be ideal in the long term. Furthermore, trees experience a high-mortality seedling establishment phase, during which formation of ectomycorrhizal partnerships can be critical for growth and survival (Chakravarty and Unestam 1987; Perry et al. 1987; Onguene and Kuyper 2014). High levels of partner specificity at the establishment stage may be counterproductive in cases where partner availability is spatially heterogeneous and the seedling may not be able

to locate a specific fungal species. Because trees, fungi, and their partnerships are long-lived, trees also cannot instantaneously switch their complement of belowground partners. As a result, a tree with a more general fungal investment strategy may have greater fitness, on average, than one with a highly specific reward system that forms associations with or maintains only the best fungi under current environmental conditions.

In our model, low-quality partners may be deliberately maintained concurrently with higher-quality partners because they provide a net benefit during resource surpluses. However, low-quality partners may benefit their hosts in
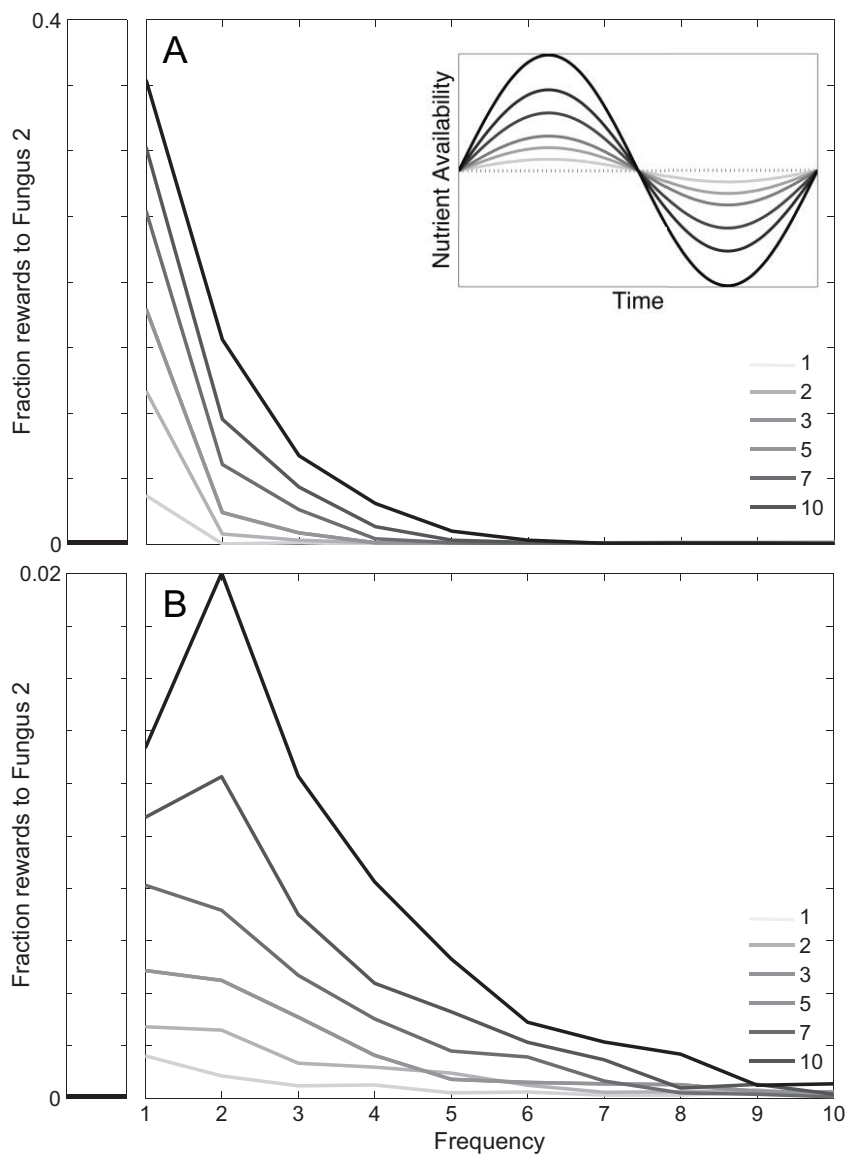
Figure 5: Relative investment in fungus 2 (I_L) for different environmental variation scenarios. For *A*, fungus 2 has a sufficiently greater maintenance cost than fungus 1 ($\omega_2 = 1.53$) that it receives no investment ($I_L = 0$) in constant environmental conditions (leftmost panel). However, when nutrient availability fluctuates at low frequency, the tree's optimal strategy changes and includes investment in fungus 2. For *B*, fungus 2 has a greater mortality rate than fungus 1 ($\mu_2 = 0.25$). Relative investment increases as the magnitude of fluctuations in nutrient availability increases (see inset for $\nu = 1$) but eventually decreases to 0 as the frequency of fluctuations increases.

other ways. For example, in an ant-acacia system, Palmer et al. (2010) show that temporary associations with "freeloader" parasitic ant species can actually increase host tree lifetime fitness by, for example, temporarily sterilizing the plant but enhancing its survival during early life stages. In a seed dispersal mutualism, Fedriani et al. (2012) demonstrate that mammalian pulp-feeding "cheaters" may actually improve seed germination and survival. More nuanced

studies of mutualisms will likely continue to exonerate presupposed cheaters and low-quality partners.

Our model assumes that fungal traits—that is, maintenance costs and basic vital rates—are constant over time. However, Näsholm et al. (2013) found that fungal partner quality, when measured as the exchange rate of nutrients for carbon, may vary as a function of environmental conditions. By applying game theory to a biological market

model, Franklin et al. (2014) show that this variation may arise from market dynamics and has important consequences for plant growth and the stability of the mycorrhizal mutualism. Our model does not explicitly parameterize an analogous carbon-to-nutrient exchange rate. However, both the tree's per-tip rewards and each fungus's nutrient return to the tree (which depends on soil nutrient availability) vary over time; thus, our model allows for temporal, condition-dependent variation in carbon and nutrient exchange even as fungal traits are held constant.

The exchange rates that emerge from our analysis highlight ambiguities in the concept of "partner quality." Here, we have defined partner quality based on differences in traits. For example, if fungus 2 is identical to fungus 1 except that it has a higher mortality rate, fungus 2 is by definition a lower-quality partner than fungus 1. However, we also find that from the tree's perspective fungus 2 has a "better" exchange rate (i.e., provides more nutrients per unit of carbon) than fungus 1 (figs. 2*F*, B6). Why, then, does the tree not invest more in fungus 2? The answer lies in the optimization criteria (see app. A). Unlike a biological market model in which exchanges are negotiated based on current exchange rates (Franklin et al. 2014), in our optimization problem the tree's investments also depend on future needs. Thus, tree rewards to fungus 2 depend not simply on its exchange rate compared to that of fungus 1 but rather on its future value compared to the future value of uncolonized root tips (both of which are affected by, e.g., the abundance of fungus 1, future environmental conditions, tree carbon availability, etc.).

While our model incorporates competition for root tip occupancy, it neglects the many additional mechanisms through which ectomycorrhizal fungi may interact. For example, ectomycorrhizal fungi may compete for soil resources, defend territories that segment the tree's root system or adjacent space, or exhibit mycoparasitism (Bruns 1995; Kennedy 2010). Inclusion of these interactions could alter the tree's optimal investment strategy. For example, if an already low-quality partner was also a poor competitor in other ways, the tree's relative investment might be further reduced. In contrast, a low-quality partner able to nonetheless monopolize a large fraction of the soil nutrient pool might garner additional rewards.

Ultimately, the fitness consequences to the host tree depend on the relative magnitude of carbon allocation to symbiotic fungi, compared to other carbon costs in its life history. In our model, the host tree allocates roughly 5% of its carbon belowground over the course of the analyzed time period, which is in line with prior estimates of 0%–22% of tree net primary production in field and laboratory studies (Hobbie 2006). However, Corrêa et al. (2011) argue that carbon allocation to fungi comes from surplus carbon pools and therefore should not have substantial fitness impacts. If this is true, natural selection may not operate on tree allocation strategies, and fungal diversity may be maintained by leaky host root systems (e.g., Jones et al. 2009) and fungal interspecific dynamics. Indeed, the strategy of supplying ample resources to potential fungal partners may act as a screening mechanism that facilitates competition among fungal partners and indirectly selects for the most efficient partner (Archetti et al. 2011). Our results demonstrate the potential value of low-quality partners and support the idea that nonspecific investment mechanisms, which can inadvertently maintain diverse fungal communities, may actually be the product of natural selection.

Acknowledgments

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