

Plant-mycorrhizal interactions mediate plant community coexistence by altering resource demand

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Abstract. As the diversity of plants increases in an ecosystem, so does resource competition for soil nutrients, a process that mycorrhizal fungi can mediate. The influence of mycorrhizal fungi on plant biodiversity likely depends on the strength of the symbiosis between the plant and fungi, the differential plant growth responses to mycorrhizal inoculation, and the transfer rate of nutrients from the fungus to plant. However, our current understanding of how nutrient-plant-mycorrhizal interactions influence plant coexistence is conceptual and thus lacks a unified quantitative framework. To quantify the conditions of plant coexistence mediated by mycorrhizal fungi, we developed a mechanistic resource competition model that explicitly included plant-mycorrhizal symbioses. We found that plant-mycorrhizal interactions shape plant coexistence patterns by creating a tradeoff in resource competition. Especially, a tradeoff in resource competition was caused by differential payback in the carbon resources that plants invested in the fungal symbiosis and/or by the stoichiometric constraints on plants that required additional, less-beneficial, resources to sustain growth. Our results suggested that resource availability and the variation in plant-mycorrhizal interactions act in concert to drive plant coexistence patterns. Applying our framework, future empirical studies should investigate plant-mycorrhizal interactions under multiple levels of resource availability.

Key words: coexistence; mycorrhizae; plant-soil feedback; R^* model; resource competition; resource ratio theory; soil.

INTRODUCTION

The diversity of plants across landscapes is staggering and results in numerous competitive interactions (Tilman 1980). However, less acknowledged in these competitive interactions are the mycorrhizal fungi in soil which, via their symbiotic relationship with plants, influence coexistence of plants in a community by increasing the nutrient acquisition of the plants they associate with (Read and Perez-Moreno 2003, Kleczewski et al. 2010, Jones et al. 2012, Pritchard et al. 2014). Classic tradeoff-based niche theories of resource competition, which ignore the presence of mycorrhizae, suggest plant coexistence depends on plant species traits related to resource uptake and the nutrient stoichiometry of plant biomass (Tilman 1980). Plant-mycorrhizal interactions likely vary across the landscape, but are strongest when soil nutrients are limiting to plant growth (Hoeksema et al. 2010, Yang et al. 2014). In fact, when nutrients become less limiting for plant growth, the plant-mycorrhizal interaction can shift from mutualistic to parasitic, putting plants that host mycorrhizae at a competitive disadvantage in the

community (Johnson et al. 1997, Klironomos 2003, Neuhauser and Fargione 2004). Thus plant-mycorrhizal associations can change from positive to negative as soil resource availability changes over time. How these nutrient-plant-mycorrhizal interactions influence plant coexistence and diversity patterns in ecosystems remains underexplored.

A growing body of work supports the hypothesis that the influence of mycorrhizal fungi on plant biodiversity depends on the strength of the symbiosis between the plant and fungi, the differential plant growth responses to mycorrhizal inoculation, and the transfer rate of nutrients from the fungus to plant (van der Heijden et al. 1998a, b, Kiers et al. 2000, Klironomos 2002, Hart et al. 2003, Scheublin et al. 2007). While mycorrhizal fungi can affect plant biodiversity, mathematical theories that explore mycorrhizal mediated plant coexistence lag behind our conceptual understanding. According to plant-soil feedback theory, positive plant-mycorrhizal feedbacks should reduce plant biodiversity, because the plant with the strongest mycorrhizal symbioses will always monopolize resource acquisition, outcompeting other plants in the community (Bever et al. 1997, Johnson et al. 2013). However, current theories ignore resource competition tradeoffs as well as the carbon investment that plants allocate away from their own growth and to

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mycorrhizal biomass production. Both of these mechanisms could reduce the competitive advantage of mycorrhizal plants in a community (Hobbie 2006).

Empirical studies that suppress the mycorrhizal symbiosis between plants and mycorrhizal fungi show contrasting outcomes on plant coexistence (Moora and Zobel 1996, Hartnett and Wilson 1999, van der Heijden et al. 2003, Collier and Bidartondo 2009, Gross et al. 2010, Zhang et al. 2010). Conceptual models that were developed based on the results from these experiments hypothesized that plant coexistence depended on the competitive ability among different plant species and the presence of mycorrhizal fungi within the plant community (Hart et al. 2003, van der Heijden 2003, Johnson et al. 2013). On one hand, fungi could promote coexistence and diversity by colonizing a less competitive plant and increasing its ability to gain resources (Moora and Zobel 1996) and plant growth rates (Kiers et al. 2000, Treseder 2013). On the other hand, mycorrhizal colonization may inhibit plant coexistence and decrease plant species diversity through positive feedbacks that result from colonizing a highly competitive dominant plant (Hetrick et al. 1994, Gross et al. 2010). However, if we take plant carbon investment in the mycorrhizal symbiosis into account, then the existing conceptual models have difficulty explaining the complex plant-mycorrhizal interactions and their influence on community dynamics.

Clearly, mycorrhizal fungi can change plant resource demand and these interactions with plants can, in turn, influence mycorrhizal fungal communities (Umbanhowar and McCann 2005, Bever et al. 2010, Kiers et al. 2011). Patterns of plant carbon allocation to mycorrhizae may affect plant coexistence by influencing the bidirectional interactions between plants and mycorrhizae. One hypothesis suggests that plants maintain a cost-benefit balance by reducing carbon allocation to fungi if they can acquire nutrients readily from soil, in turn reducing mycorrhizal abundance (Johnson et al. 2003, Treseder 2004, Corrêa et al. 2011), a process that we refer to as “plastic allocation.” Nevertheless, carbon investments made by mycorrhizal plants may not be efficient because the quantity of mineral nutrients acquired per unit of carbon invested by the plant is low (Tuomi et al. 2001), suggesting that in some cases plants allocate excess carbon to mycorrhizal fungi (Corrêa et al. 2008, 2012). In other words, the amount of carbon allocated to fungi is unrelated to the amount of nutrients transferred from fungus to plant (Grman 2012), a process that we refer to as “constant allocation”. Regardless of the controversy over patterns of plant carbon allocation to mycorrhizal fungi, it is still unknown how the patterns of plant carbon allocation to mycorrhizal fungi affect plant coexistence.

In this paper, we quantified the conditions of plant coexistence mediated by mycorrhizal fungi. We developed a mechanistic resource competition model that explicitly included plant-mycorrhizal symbioses, and explored how resource availability and plant-mycorrhizal interactions act in concert to drive plant coexistence patterns. Our

simple and intuitive framework explored the effects of mycorrhizal fungal association on plant coexistence and enabled us to ask how the addition of mycorrhizal associations with plants changed the conditions leading to coexistence among competing plants and what the potential mechanisms leading to those changes were. Our model advances our understanding of mycorrhizal mediated plant coexistence by demonstrating that tradeoffs among resource competition arise from differential plant-mycorrhizal interactions.

MODEL DESCRIPTION

We modified Tilman’s (1980) resource competition model to explore feedbacks between plant and mycorrhizal fungi. In our modified model, multiple plant species (B_i) could use multiple resources (R_j). For simplification, in this model, we assumed that each plant species associated with a host-specific mycorrhizal fungal species (M_i) and that mycorrhizal association increased the uptake of the nutrient most limiting to plant production. In the model, B_i and M_i were plant/mycorrhizal biomass expressed as carbon per unit land area (i.e., g carbon m⁻²) and R_j was the pool of soil inorganic nutrients available for plant and fungal uptake (i.e., g nitrogen m⁻² or g phosphorus m⁻²). All variables and parameters are listed in Table 1.

$$\frac{dB_i}{dt} = r_i B_i g_i - d_i B_i - \alpha_i B_i \quad (1a)$$

$$\frac{dM_i}{dt} = \alpha_i B_i - \mu_i M_i \quad (1b)$$

$$\frac{dR_j}{dt} = c_j (S_j - R_j) - \sum_i r_i B_i g_i / q_{ij} \quad (1c)$$

In this expression, r_i represented the maximum growth rate of a plant species i , and d_i was the mortality rate of a species i . α_i was the carbon allocation rate from the plant to the mycorrhizal fungus. This model scaled plant growth by a multiplier (g_i) that followed Liebig’s law of the minimum and depended on the availability of a limiting resource.

$$g_i = \text{Min} \{g_{ij}(R_j)\}$$

where g_{ij} was a Monod function that represented the growth limitation of plant i when limited by a nutrient j . For example, plant x was limited by resource 1 (R_1) when $g_{x1} < g_{x2}$.

$$g_{ij} = \frac{R_j(1 + \beta_{ij}M_i)}{k_{ij} + R_j(1 + \beta_{ij}M_i)} \quad (2)$$

where k_{ij} was a half-saturated constant in which a low k_{ij} represented a high affinity for the nutrient. Mycorrhizal fungal association increased the uptake of nutrient j for its specific host plant i , modeled here as reducing the

TABLE 1. Description of variables, parameters, and notations.

Symbol	Description	Unit
Variable		
B_i	Biomass of plant i , with $i = x, y, \dots$	g m^{-2}
M_i	Host specific mycorrhizal associated with plant i	g m^{-2}
R_j	Resource j in the soil, with $j = 1, 2, \dots$	g m^{-2}
Parameter		
r_i	Maximum growth rate of a plant species i	yr^{-1}
d_i	Mortality rate of a plant i	yr^{-1}
μ_i	Mycorrhizal turnover rate	yr^{-1}
g_{ij}	Plant growth rate limitation coefficient by R_j	-
k_{ij}	Half-saturated constant of plant i limited by R_j	g m^{-2}
β_{ij}	Specific enhancement of R_j affinity by M_i	g^{-1}
α_i	Plant carbon allocation to mycorrhizal fungi	yr^{-1}
α_{const}	Constant plant carbon allocation	yr^{-1}
α_{max}	Maximum plant carbon allocation	yr^{-1}
c_j	Flux rate of resource j in the environment	yr^{-1}
S_j	Resource supply level	g m^{-2}
q_{ij}	Ratio of carbon to R_j in plant i	g g^{-1}
Notation		
R^*	General notation for equilibrium resource level	g m^{-2}
$[R_j]_i^*$	R^* for plant i when limited by resource j	g m^{-2}
$[R_j]_{i, m}^*$	R^* when mycorrhizae were present	g m^{-2}
$S_j^{(k), V1}$	The k th critical value of S_j when the plant allocated constant carbon to mycorrhizae, $k = 1, 2$.	g m^{-2}
$S_j^{(k), V2}$	The k th critical value of S_j when the plant carbon allocation was plastic, $k = 1, 2$, and 3.	g m^{-2}

half-saturated constant by a ratio of $(1 + \beta_{ij}M_i)$. We defined β_{ij} as the increase or enhancement of plant i 's nutrient uptake affinity of R_j due to mycorrhizal fungi i . Mycorrhizal fungal turnover was represented as a rate of μ_i .

In the absence of both plants and mycorrhizal fungi, nutrient j reached the maximal concentration in the nutrient pool S_j and a nutrient supply point consisted of different levels of each nutrient $[S_1, S_2, \dots, S_j]$ in the environment. c_j represented the rate of nutrient return to the soil nutrient pool S_j . The model assumed plants would consume nutrients in fixed ratios, so that q_{ij} was the ratio of carbon to nutrient j in plant i . Relative to plants, mycorrhizal fungi have high turnover rates and a low biomass pool (Courty et al. 2010). Thus, we assumed that mycorrhizal fungi did not consume nutrients exploitatively and nutrients concentrated in mycorrhizal biomass were recycled rapidly and not lost, although we recognize that mycorrhizal fungi have a much lower carbon-to-nutrient ratio than do plants (Courty et al. 2010).

We analyzed two versions of α_i , representing two strategies of plant carbon allocation: constant and plastic allocation. In the constant plant carbon allocation analysis, plants treated mycorrhizal fungi as part of the fine root pool, and thus allocated a constant amount of carbon per unit plant biomass ($\alpha_i = \alpha_{const}$). This plant allocation strategy was independent of resource availability. The second strategy we analyzed assumed that plant carbon allocation to mycorrhizal fungi was a plastic trait, which depended on how much benefit the plant got from associating with mycorrhizal fungi.

$$\alpha_i = \alpha_{max} \text{Max} \left\{ \left(g_{ij} - \frac{R_j}{k_{ij} + R_j} \right) / \frac{R_j}{k_{ij} + R_j} \right\} \quad (3)$$

where α_{max} was the maximum plant carbon allocation rate. For each resource, the plant benefit was calculated as the relative potential plant growth rate increment when plants were associated with mycorrhizal fungi. For simplicity, we only considered the fungal-provided resource that conferred the greatest benefit to the host plant. For example, arbuscular mycorrhizal fungi can increase phosphorus uptake as well as nitrogen uptake, but phosphorus confers a greater benefit to the plant than nitrogen does (van der Heijden 2003).

In the absence of mycorrhizal associations ($\alpha_i = 0$), Eqs. 1a and 1c reflected the classic plant resource competition model (Tilman 1980). The resource R_j would reach equilibrium at, $R_j^* = k_{ij}d_i/(r_i - d_i)$, where R_j^* denoted an equilibrium nutrient concentration at which the plant can exist. Plants could only survive when the external supply of nutrient j , $S_j > R_j^*$ was met. If there was only a single resource limiting plant growth, the plant in the community that survived on the lowest-level of the limiting resource would drive the other plants in the community to local extinction. Coexistence of multiple plant competitors required that each plant species was limited by a different resource, and that each species consumed more of the resource that limited their own growth in the community (Chase and Leibold 2003). That is, each plant species' Zero Net Growth Isoclines (ZNGIs) needed to intersect and the consumption vector must be steeper for species with higher R^* on the y -axis.

When plants allocated carbon to mycorrhizal fungi in exchange for nutrient acquisition ($\alpha_i > 0$), their ZNGIs changed (Fig. 1). The new coexistence criteria could depend on plant dominance in a mycorrhizal-free environment and plant growth response when mycorrhizal fungi were present. A conceptual model (van der Heijden 2003, Johnson et al. 2013) hypothesized that: (1) associating with mycorrhizal fungi may increase a host plants' competitive ability for one of the resources leading to possible coexistence with non-mycorrhizal plants; (2) if the ZNGIs of R^* already intersected between the two competing plant species, the colonization of mycorrhizal fungi of one plant could break the tradeoff leading to competitive exclusion of the non-mycorrhizal plant. We analyzed these two hypotheses separately. In the first analysis (hypothesis 1; Fig 1a), plant y excluded plant x . If host-specific mycorrhizal fungi increased the ability for plant x to acquire Resource 1, then coexistence was possible (Fig. 1b, c) as in Johnson et al. (2013). In the second analysis (hypothesis 2; Fig 1d), plants x and y coexisted

before mycorrhizal fungi colonized plants, but mycorrhizal colonization of plant x may make it a better competitor for both of the resources. Although other conceptual studies suggested mycorrhizal fungi suppress coexistence (Johnson et al. 2013), we quantified conditions where ZNGIs of plant x and plant y remain intersected, suggesting the possibility of plant coexistence (Fig. 1e, f). Mycorrhizal biomass, which determined the location of new ZNGIs of plant x , also depended on an external nutrient supply as well as carbon allocation from the plant. Thus, stable coexistence required not only the intersection of ZNGIs, but also that each species consumed more of a resource that limited intraspecific competition, and less of a resource that limited interspecific competition.

First, we analyzed plant-mycorrhizal interactions to quantify the changes of resource demand caused by mycorrhizal fungi. Next we analyzed a simplified scenario where non-mycorrhizal plants competed with mycorrhizal-associated plants for two available nutrients. Clearly, including multiple plant-mycorrhizal interactions or even

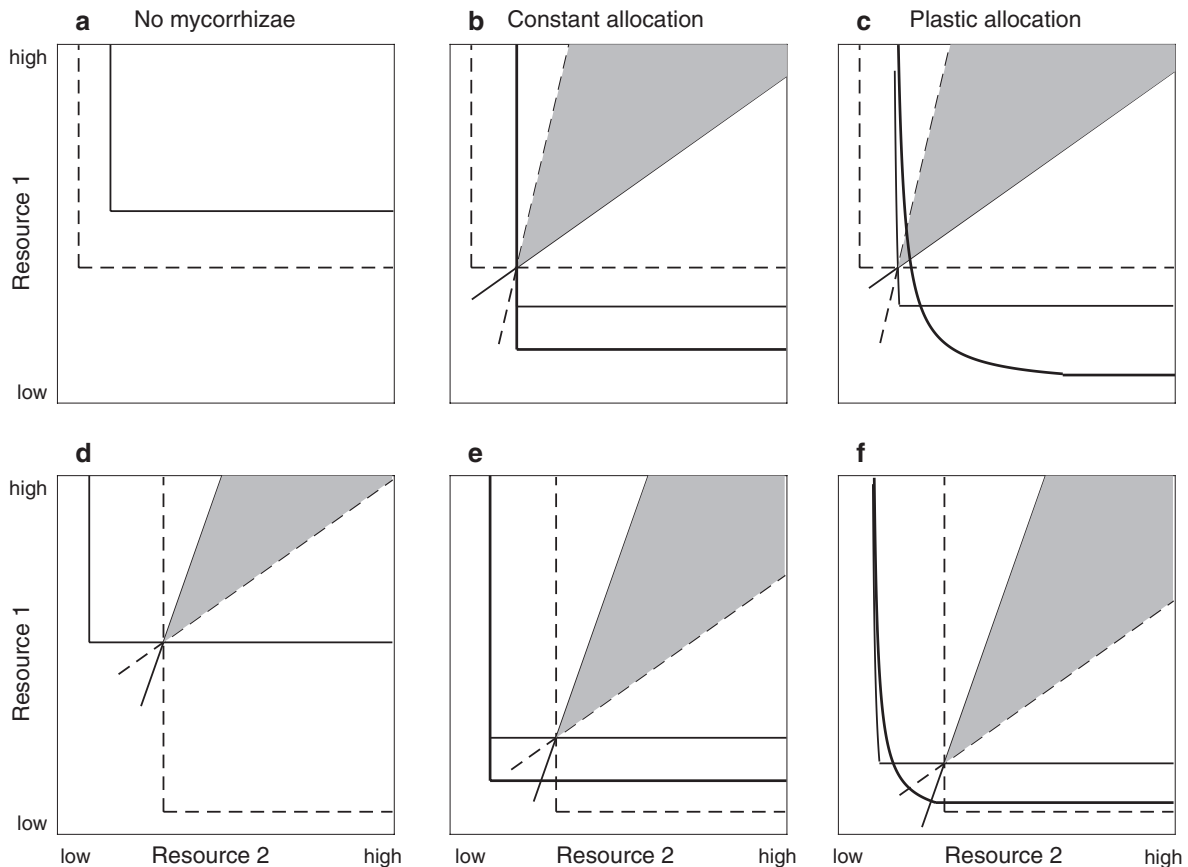


FIG. 1. Zero Net Growth Isoclines (ZNGIs) for Plant x (solid lines) and Plant y (dashed lines) when neither plant associated with mycorrhizae (a, d). Zero Net Growth Isoclines (ZNGIs) for plant x when it allocated carbon to mycorrhizae at a constant (b, e) and at a plastic rate (c, f). In top panels, Plant y excluded Plant x when they did not associate with mycorrhizae; however mycorrhizal colonization of the plant promoted coexistence. In the bottom panels, mycorrhizal colonization shifted plant coexistence patterns. The shaded areas at a given, low mycorrhizal biomass were examples of coexistence zone. Thick lines (or curves) represented ZNGIs of Plant x at a given, high mycorrhizal biomass. The diagonal lines represented consumption vectors, the ratio of changes in resource availability caused by consumption, for each plant. The slope of consumption vectors were c_2q_{x2}/c_1q_{x1} and c_2q_{y2}/c_1q_{y1} for Plant x and y , respectively (this is constant in all figures).

plants with a shared mycorrhizal network could be expanded in the model; however, including all these interactions may not be mathematically tractable. Here, we analyzed two cases where plants can and cannot coexist before mycorrhizal fungi colonized plants (Fig. 1). In each case, we analyzed the constant and a plastic plant carbon allocation strategy, separately. We derived analytical results for the constant carbon allocation strategy, but numerical simulations for the plastic carbon allocation strategy when explicit solutions were impossible. For consistency with classical R^* theory, we presented a graphical analysis on the two-dimensional space of R_1 and R_2 , and we also presented the detailed mathematical analysis in the Supporting Information.

RESULTS

How did mycorrhizal colonization affect plant resource demand?

To investigate effect of mycorrhizal colonization on plant resource demand, we analyzed a community dominated by one plant species. We assumed mycorrhizal fungi would enhance plant access to one nutrient (R_1) more than to another nutrient (R_2) with $\beta_{x1} > \beta_{x2}$. For example, arbuscular mycorrhizal fungi often confer greater plant phosphorus relative to nitrogen acquisition (Johnson et al. 2015). To simplify the scenarios for analysis, we assumed $\beta_{x2} = 0$. We calculated the R^* by setting Eq. 1a equal to zero.

$$[R_1]_{x,m}^* = \frac{k_{x1}(d_x + \alpha_x)}{(r_x - d_x - \alpha_x)(1 + \beta_{x1}M_x^*)} \quad (4a)$$

$$[R_2]_{x,m}^* = \frac{k_{x2}(d_x + \alpha_x)}{(r_x - d_x - \alpha_x)}. \quad (4b)$$

Here, $[R_j]_{i,m}^*$ was the equilibrium concentration of nutrient j in soil when plant i was colonized by mycorrhizae and limited by R_j (see Table 1 for notations). Without mycorrhizae, the Eqs. 4a and 4b would be same as classical R^* theory ($[R_j]_i^* = k_{ij}d_i/(r_i - d_i)$). Mycorrhizal presence reduced plant R_1^* by a ratio of $(1 + \beta_{x1}M_x)$, and this ratio overcame the cost of plant carbon allocation to mycorrhizae α_x (Eq. 4a). The carbon allocation also generated a tradeoff in the R^* for a second soil resource (Bever et al. 2010), and thus increased R_2^* (Eq. 4b).

When we assumed the plant-mycorrhizal system was limited by R_1 , we found several critical values for resource supply, which determined whether mycorrhizal fungi colonized the plant host and whether the plant persisted alone (Appendix S1). For example, under the constant carbon allocation strategy, the plant did not survive regardless of the presence or absence of mycorrhizal fungi if the external supply of resource 1 was less than a critical value ($S_1 < S_{1,critical}^{(1),V1}$) (Fig. 2). Here, the superscript (1) denoted the first critical value, and the V1 notation denoted constant carbon allocation, thus the first allocation strategy

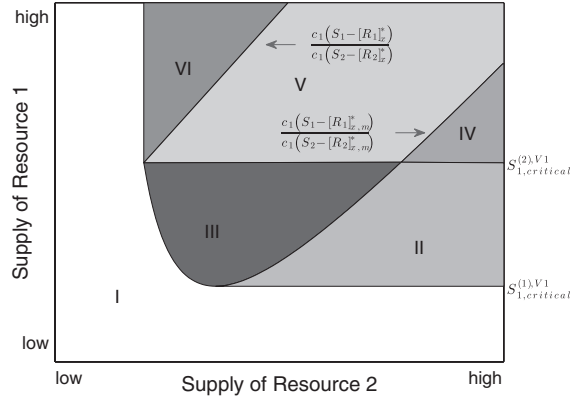


FIG. 2. Zones indicating plant growth limitation in parameter space of S_1 - S_2 . Neither the plant nor mycorrhizae could survive if nutrient supplies were located in zone I, the zone where nutrients were too low for biomass production. The plant could not persist alone but could persist and grow when associated with mycorrhizae in zones II and III. Mycorrhizae could always colonize the host plant in zone IV, V and VI. Above and to the left of the diagonal line (with slope of c_2q_{x2}/c_1q_{x1}), plant growth was limited by R_2 in the classical model without mycorrhizae (zone VI), below the line plant growth was limited by R_1 (zone IV and V). When the plant is in the presence of mycorrhizae, zone V shifts to R_2 limitation. The new R_2 plant growth limitation zone includes zone III, V, and VI above a boundary curve, below which exists a zone of R_1 limitation (zone II and IV).

was being used. When $S_{1,critical}^{(1),V1} < S_1 < S_{1,critical}^{(2),V1}$ the plant did not persist alone and required mycorrhizal colonization to survive. An Allee effect existed in this situation; the plant-mycorrhizal symbiosis did not persist unless the plant passed a biomass threshold. When $S_1 > S_{1,critical}^{(2),V1}$ mycorrhizal fungi always colonized the host plant. These critical resource supply ranges for the plastic carbon allocation strategy were similar to the constant carbon allocation strategy, except there was an additional range where alternative stable states between the isolated plant and plant-mycorrhizal symbiosis existed (Appendix S1). However, input of carbon from outside of the system (e.g., from the hyphal network) could drive the isolated plant state to a mycorrhizal-associated state. See Appendix S1 for the critical value expressions and the bifurcation analysis. Note that the second critical values were analogous to $[R_1]_{x,m}^*$ as in the classical R^* model with, $S_{1,critical}^{(2),V1} = \frac{k_{x1}(d_x + \alpha_{const})}{r_x - d_x - \alpha_{const}}$ and $S_{1,critical}^{(2),V2} = \frac{k_{x1}d_x}{r_x - d_x}$. In these analyses, we assumed the plant-mycorrhizal system was limited by one nutrient, R_1 .

Plant growth became limited by other nutrients after plant access to nutrient R_1 was increased or saturated by the developing plant-mycorrhizal symbiosis. Thus, at some point, the system switched from being limited by the first resource to being limited by a second resource, R_2 . As in classical models, external supply vectors determined which resource was limiting. If

$$\frac{c_1(S_1 - [R_1]_{x,m}^*)}{c_2(S_2 - [R_2]_{x,m}^*)} > \frac{q_{x2}}{q_{x1}} \quad (5)$$

then the system was considered to be limited by R_2 (Fig. 2), where the left side of the inequality was the slope of the supply vector. By replacing $[R_1]_{x,m}^*$ and $[R_2]_{x,m}^*$ with $[R_1]_x^*$ and $[R_2]_x^*$, respectively, we obtained the solution for the classical model when mycorrhizal fungi were absent. However, when mycorrhizal fungi were present, $[R_1]_{x,m}^*$ (Eq. 4a) depended on the amount of mycorrhizal biomass, which was also a function of external nutrient supply. Solving for the inequality (5; Appendix S1), we found,

$$S_1 > \frac{c_2 q_{x2}}{c_1 q_{x1}} (S_2 - [R_2]_{x,m}^*) + \frac{[R_1]_x^*}{1 + \frac{\alpha_x \beta_{x1}}{\mu_x (d_x + \alpha_x)} c_2 q_{x2} (S_2 - [R_2]_{x,m}^*)} \quad (5')$$

where a nonlinear curve of S_1 against S_2 separated R_1 limitation and R_2 limitation in parameter space of S_1 – S_2 (Fig. 2). Fig. 2 was the parameter space of S_1 – S_2 , rather than ZNGIs, although some lines are identical to ZNGIs. By overlapping the ZNGIs from the classical model and the S_1 – S_2 space, we showed the range of parameters for when the system shifts from R_1 limitation to R_2 limitation after mycorrhizal colonization. The resource limitation curves are similar between the constant and the plastic carbon allocation models; however, under plastic carbon allocation there was a zone where mycorrhizal fungi were excluded at low resource supply of R_2 (Appendix S3; Fig. S1).

When did mycorrhizal fungal colonization promote plant coexistence?

We analyzed a case where two plants could not coexist before mycorrhizal fungi colonized plants and determined the circumstances where plant-mycorrhizal associations promoted plant coexistence. We assumed that a mycorrhizal plant x and a non-mycorrhizal plant y would compete for R_1 and R_2 . Mycorrhizal fungi colonize plant x and acquire carbon in exchange for resource R_1 . In the classical model, coexistence requires that each plant is a better competitor for one resource. If we assume that mycorrhizal fungal colonization made plant x a better competitor for R_1 and y a better competitor for R_2 , then these conditions can be expressed as,

$$[R_1]_{x,m}^* < [R_1]_y^* \quad (6a)$$

$$[R_2]_y^* < [R_2]_{x,m}^* \quad (6b)$$

$$\frac{q_{x2}}{q_{x1}} < \frac{c_1 (S_1 - [R_1]_y^*)}{c_2 (S_2 - [R_2]_{x,m}^*)} < \frac{q_{y2}}{q_{y1}} \quad (6c)$$

Under these conditions, plant x and y can coexist and reach an equilibrium state with plant x limited by R_2 , and plant y limited by R_1 (Appendix S2). Mycorrhizal plant x had a lower R_1 requirement than plant y , allowing the ZNGIs to intersect, a prerequisite for coexistence (Fig. 1b, c). If the slope of the line linking the supply point

$[S_1, S_2]$ and the point of intersection of the ZNGIs was bound by $c_2 q_{x2}/c_1 q_{x1}$ and $c_2 q_{y2}/c_1 q_{y1}$ (condition 6c), then the plants coexist. Note that without mycorrhizae, plant x would not be able to invade a system dominated by plant y .

By explicitly taking into account plant-mycorrhizal interactions, we found two mechanisms that resulted in a resource competition tradeoff between taking up limiting beneficial and less-beneficial resources, such as increasing plant uptake of R_1 and applying resource pressure on R_2 . The first mechanism arose from differential changes of R^* after mycorrhizal fungi colonized plants (Bever et al. 2010). This mechanism was represented by a change of ZNGIs; mycorrhizal colonization decreased the resource requirement of R_1 (Eq. 4a) and, due to a carbon investment by the plant, increased the resource requirement of R_2 (Eq. 4b). Therefore, the conditions 6a and 6b of the model were likely met. The other mechanisms arose from a switch in plant resource limitation following mycorrhizal fungal colonization (Fig. 2). Here, plant x switched from R_1 limitation to R_2 limitation when mycorrhizal fungi were present, because mycorrhizal fungi aided in the plant's uptake of R_1 . Plant x was R_2 limited when it was above the curve in Fig. 3, which meant an additional supply of resource R_2 was needed to maintain growth. The final coexistence zone moved away from ZNGIs to higher R_2 supply (gray area of Fig. 3) in order to maintain

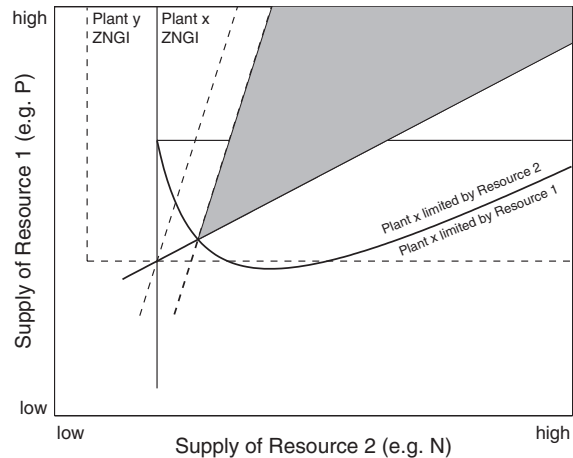


FIG. 3. Mycorrhizal fungi promoted plant coexistence under the scenario when plants could not coexist without mycorrhizae. When mycorrhizae were able to colonize Plant x , plant uptake of resource R_1 increased and the ZNGIs (solid lines) were lower. The actual position of Plant x ZNGI was not fixed; the position depended on the amount of mycorrhizal biomass that was produced, which was in turn contingent on their source supply provided to the fungi. However, coexistence in equilibrium was fixed at the intersection of the two species' ZNGIs. Plant y 's ZNGI did not change (dashed lines). The zone of coexistence (the gray area) was constrained by the consumption vector of Plant x , a line parallel to the consumption vector of Plant y , and the resource limitation boundary (solid curve). This figure represents the analysis of the constant plant carbon allocation to mycorrhizal fungi; see Appendix S3; Fig. S2 for the simulation results for the plastic plant carbon allocation to mycorrhizal fungi.

mycorrhizal fungal biomass. We derived the new criteria of external nutrient supplies for plant coexistence in Appendix S2.

$$\frac{q_{x2}}{q_{x1}} < \frac{c_1(S_1 - [R_1]_y^* - \Delta R'_1)}{c_2(S_2 - [R_2]_{x,m}^* - \Delta R'_2)} < \frac{q_{y2}}{q_{y1}} \quad (7)$$

where,

$$\Delta R'_j = \begin{cases} 0 & \text{if } [R_1]_x^* < [R_1]_y^* \\ \left(\frac{[R_1]_x^*}{[R_1]_y^*} - 1 \right) \frac{\mu(d+\alpha_x)}{\alpha_x \beta_{x1} c_j q_{xj}} & \text{if } [R_1]_x^* > [R_1]_y^* \end{cases} \text{ with } j=1,2.$$

When mycorrhizal associations were present in the model, the external supply vector (condition 6c) shifted to a correct supply vector (condition 7). For plant coexistence to be feasible, the slope of the line linking supply point $[S_1, S_2]$ and a new critical point at $[[R_1]_y^* + \Delta R'_1, [R_2]_{x,m}^* + \Delta R'_2]$ must be bound between $c_2 q_{x2} / c_1 q_{x1}$ and $c_2 q_{y2} / c_1 q_{y1}$. Although the external supply vector did not change, the corrected supply vector took into account the resource pressure needed to maintain the critical mycorrhizal biomass level for plant coexistence.

Condition (7) was contingent on the plant carbon allocation strategy, the parameter α_x . Although it was a straightforward equation under the constant carbon allocation strategy, where $\alpha_x = \alpha_{const}$, it was impossible to solve explicitly under the plastic carbon allocation strategy because plant carbon allocation was a function of soil nutrient level as well as mycorrhizal biomass. Our numerical simulations showed that the plant carbon allocation patterns in this situation did not qualitatively change the outcome of plant coexistence (Appendix S3: Fig. S2).

When did mycorrhizal colonization shift zones of plant coexistence?

Conceptually, mycorrhizal fungi could increase a plant's ability to monopolize resource acquisition and therefore inhibit plant coexistence. However, we found that mycorrhizal colonization switched coexistence zones to be lower in R_1 and higher in R_2 . We analyzed a case where two plants coexisted prior to mycorrhizal fungal colonization of plants and investigated the circumstances under which mycorrhizal presence changed plant coexistence zones (see the bottom panels in Fig. 1). We assumed that the mycorrhizal plant x was a better competitor for R_2 , and non-mycorrhizal plant y was a better competitor for R_1 . Mycorrhizal fungi colonized plant x and conferred uptake of resource R_1 . Under this scenario, mycorrhizal plant x would become the better competitor for both of the resources, thus suppressing coexistence. As long as the following conditions hold, plant coexistence was feasible,

$$[R_1]_y^* < [R_1]_{x,m}^* \quad (8a)$$

$$[R_2]_{x,m}^* < [R_2]_y^* \quad (8b)$$

$$\frac{q_{y2}}{q_{y1}} < \frac{c_1(S_1 - [R_1]_{x,m}^*)}{c_2(S_2 - [R_2]_y^*)} < \frac{q_{x2}}{q_{x1}} \quad (8c)$$

The plant coexistence criteria required that plant x was limited by R_1 despite heightened uptake of R_1 in the presence of mycorrhizae, and plant y must be limited by R_2 , and plant x and y ZNGIs must still intersect (Fig. 1e,f).

We observed that mycorrhizal colonization could cause competitive plant exclusion at high R_1 and low R_2 , a finding that supports the conceptual models (Hart et al. 2003, van der Heijden 2003, Johnson et al. 2013). However, unlike the proposed conceptual models, we found that mycorrhizal fungi promoted plant coexistence at low R_1 and high R_2 , which suggested a shift in the coexistence zone for resource requirements (Appendix S2). The new coexistence zone depended on the stoichiometry of plant y ; a pattern reflected by two parallel lines that bind the resource supply level with a slope equal to $c_2 q_{y2} / c_1 q_{y1}$ and a resource limitation curve to the left (Fig. 4). The curve guaranteed that plant x was limited by R_1 . The lower line in Fig. 4, tangential to the curve, maintained that mycorrhizal fungal biomass was at positive equilibrium at a steady state. The upper line in Fig. 4 constrained the coexistence zone where mycorrhizal fungal biomass was relatively low, and thus prevented plant x from becoming a "super competitor" (Fig. 4). These criteria also generated a tradeoff in resource competition between the plants. The new coexistence zone moved away from ZNGIs to lower a supply of R_1 and a higher supply of R_2 .

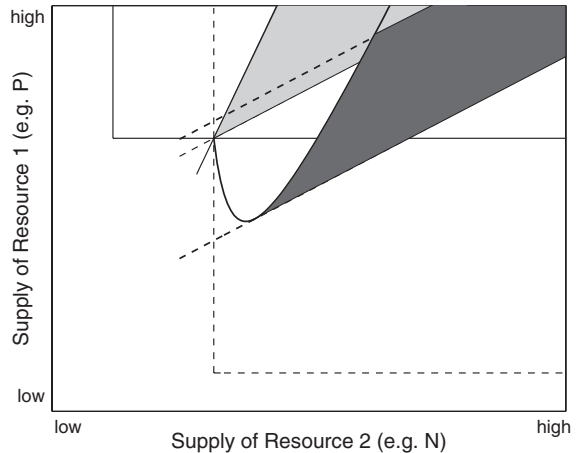


FIG. 4. Mycorrhizal associations shifted plant coexistence patterns when plants could coexist in the absence of mycorrhizae (light gray area). After mycorrhizae colonized Plant x , plant uptake of resource R_1 was greater. The two lines parallel to the consumption vector of Plant y and the resource limitation boundary (solid curve) constrained the resource requirements for plant coexistence (dark gray area). This figure represents the analysis of the constant plant carbon allocation to mycorrhizal fungi; see Appendix S3: Fig. S3 for simulation of the plastic carbon allocation to mycorrhizal fungi.

Similarly, it was again impossible to get an explicit solution for the plastic carbon allocation model in this situation. However, our numerical simulation demonstrated that the allocation strategy of plants did not change the outcome of coexistence qualitatively when a mycorrhizal-associated plant x was limited by R_1 and plant y was limited by R_2 (Appendix S3: Fig. S3).

DISCUSSION

To date, much of the theoretical work exploring how plant-mycorrhizal interactions shape plant coexistence has been conceptual (Hart et al. 2003, van der Heijden 2003, Johnson et al. 2013). We modified existing plant coexistence theoretical work (R^* , Tilman 1980) to include mycorrhizal fungal interactions with plants, because these important, often symbiotic, relationships influence plant co-existence (Hart et al. 2003, van der Heijden et al. 2003). We explored how the addition of mycorrhizal associations with plants changed the conditions leading to coexistence among competing plants, as well as what the potential mechanisms for those changes might be. Our model showed that plant-mycorrhizal interactions could create a tradeoff in community-level resource competition by (1) increasing the uptake of resources that limit individual plant growth, and by (2) applying resource pressure on other less limiting resources.

By increasing the uptake of resources that limit plant growth, mycorrhizal fungi could alter plant coexistence in a community. We found that shifts in plant resource requirements, which scaled with plant carbon allocation as well as with the plant growth response to mycorrhizal association, made plant coexistence possible. In other studies mycorrhizal colonization of plant roots increased plant coexistence, in part, because associations with mycorrhizal fungi ameliorated plant resource demand (van der Heijden et al. 2003). Using mathematical theory, the transfer of phosphorus was greater where soil phosphorus availability was low and plant carbon allocation to mycorrhizal fungi was plastic and preferential, meaning that plant carbon allocation to mycorrhizal fungi changed depending on nutrient limitation (Bever 2015). Clearly, mycorrhizal fungi allocate resources to plants that, without the symbiosis, are poor competitors. Thus, mycorrhizal symbioses can increase plant coexistence.

Our results complement plant-soil feedback theory that suggests mycorrhizal colonization of dominant plants would hinder coexistence as mycorrhizal fungi confer higher plant resource acquisition and thus biomass production of a single dominant plant species (Bever et al. 1997). We found that mycorrhizal colonization could hinder plant coexistence at some resource levels, but promote coexistence at other resource levels. To fully understand the impact of plant-mycorrhizal interactions on plant coexistence, we suggest experimental studies investigate parameter spaces that reflect the availability of both beneficial and less-beneficial nutrients (i.e., R_1

and R_2) in a plant community context. For example, plant communities have lower species richness when colonized by mycorrhizal fungi than those without mycorrhizal fungi (Klironomos et al. 2000, Klironomos 2002, Gross et al. 2010, Zhang et al. 2010) as indicated by the light gray area in Fig. 4. Although a few studies have explored the impact of mycorrhizal fungi on plant diversity at multiple levels of a single nutrient, tradeoffs among multiple nutrients are less studied (Collins and Foster 2009, Yang et al. 2014). Arbuscular mycorrhizal fungi increased species richness of nitrogen-fixing forbs (Yang et al. 2014) a pattern that might be an evolutionary consequence of tipping coexistence patterns to higher demand of a less-beneficial nutrient (nitrogen) in an ecosystem. Nitrogen fertilization was surprisingly more important than phosphorus fertilization in predicting plant responses to mycorrhizal inoculation from a meta-analysis (Hoeksema et al. 2010). This pattern was likely due to a switch in resource limitation from phosphorus to nitrogen, a pattern predicted by our model.

Our work expanded upon Tilman's R^* rule by quantitatively demonstrating that mycorrhizal-plant interactions influenced plant coexistence in a community by shifting limiting resource availability and thus applying resource pressure on other less limiting resources. In the original R^* model, plants would not coexist if they required similar levels of nutrients (Tilman 1980); however, mycorrhizal colonization could shift plant nutrient limitation and thus makes this assumption less valid. Mycorrhizal colonization comes at a carbon cost to plants (Read and Perez-Moreno 2003, Hobbie 2006). Since the process of assimilating sugars to trade with fungal partners requires several nutrients, plant investment in a symbiont results in a greater demand for other soil nutrients (Bever et al. 2010). In other words, plant demand for a resource was lower when mycorrhizal fungi aided in the uptake of that resource; but in order for the plant to maintain the mycorrhizal symbiosis, demand for other resources increased. Our work demonstrated that variation in the resource limitation of plants, combined with plant carbon and nutrient investment in symbionts, shifted coexistence zones to be lower for one resource and higher for the other resource.

Plant-mycorrhizal interactions, as well as the variation in the strength of those interactions, may influence plant coexistence (Friesen et al. 2011). We found that the zone of plant co-existence shifted when mycorrhizal fungi were introduced to a simple two-member community where one plant was not mycorrhizal. While this was a simplified community, our conclusions should hold in more complex mycorrhizal-plant communities. For example, in communities that have more than one mycorrhizal plant, the plant-fungi interactions are highly variable in their colonization rate, their degree of mutualism, or their rates of nutrient acquisition (Kiers et al. 2000, Corr ea et al. 2008, Grman 2012). Additionally, roots are typically colonized by more than one fungal species. Even with a complex fungal community, our results will still

hold given that plants allocate C to the most beneficial fungal species (Bever et al. 2009, Kiers et al. 2011) and fungal species have distinct traits governing soil nutrient uptake and transfer rates (Pringle and Bever 2002). We recognize that communities are complex and include multiple interacting organisms such as herbivores, plants, and mycorrhizae. While our model has not been set up to test this, empirical data show that mycorrhizal presence can alter a plant's susceptibility to herbivory (Gehring and Bennett 2009) thus mycorrhizae are still influencing plant coexistence zones. Thus, increasing trait variation and diversity in plant and mycorrhizal communities could lead to increases in plant coexistence zones.

Variation in plant-mycorrhizal interactions should increase the coexistence space among plants by generating more dissimilar ZNGIs, even if all plants originally have the same nutrient limitations (ZNGI) (Bever et al. 2010). Additionally, variation in plant-mycorrhizal interactions can shift the coexistence zone of plants to a higher or to a lower resource level. This shift in coexistence zone is contingent on the stoichiometry of both plants as well as the relative benefit of each resource acquired by that plant (van der Heijden et al. 1998a, Kiers et al. 2000, Janos 2007) – which then affects the plant growth response to mycorrhizal colonization. Similarly, the effect of mycorrhizal fungi on plant resource demands and shifts in their ZNGI can vary among mycorrhizal species (van der Heijden et al. 2003). Differences in plant growth responses to mycorrhizal fungal composition as well as the plants' ability to host mycorrhizal fungi could inherently create a tradeoff in resource competition, even if all other plant functional traits remain the same. If all the plant species fall on the same interspecific resource tradeoff surface, then coexistence of multiple plant species would be possible (Tilman 2011).

Clearly, plant coexistence is due, in part, to an energy tradeoff between plant investment into competitive traits or the mycorrhizal symbiosis. We found that the resource competition tradeoff was due to two mechanisms: (1) a differential payback in resources where the plant invested more carbon in fungi where resources were limiting, giving the plant a competitive advantage and/or (2) by plant stoichiometric constraints on growth that lead to additional, less-beneficial resource stress limiting plant growth. These proposed mechanisms are supported by other findings in the literature. For example, in a recent study exploring the role of soil nutrients in controlling the costs and benefits of mycorrhizal fungi, Johnson et al. (2015) found that mutualism was common in phosphorus-limited ecosystems, whereas parasitism or commensalism was more likely in nitrogen-limited ecosystems – patterns that are comparable to R_1 and R_2 in our model. When ecosystems were phosphorus limited, mycorrhizal fungi obtained and transferred the most limiting nutrient (phosphorus) to their host and thus increased both plant and fungal biomass, also represented in Fig. 3. However, if the ecosystem was phosphorus rich, the relationship between plants and mycorrhizal fungi became parasitic

and mycorrhizal plants produced less biomass than non-mycorrhizal plants (Johnson et al. 2015).

Overall we found that resource availability and the variation in plant-mycorrhizal interactions act in concert to drive plant coexistence patterns. This finding improves on previous conceptual models because we explicitly and quantitatively accounted for the carbon costs and nutrient benefits of mycorrhizal association. Specifically, two hypotheses, that build on earlier conceptual models, emerged from our work: (1) plant-mycorrhizal interactions influence plant coexistence by increasing the acquisition of limiting resources and also by generating higher demand for less limiting resources, and (2) shifts in resources required by plants are sensitive to plant carbon allocation and growth response to mycorrhizal fungal colonization. Our work highlights that exploring how nutrient-plant-mycorrhizal interactions influence plant coexistence and diversity patterns in ecosystems will require combining theory with detailed experiments. Specifically, future empirical studies should investigate plant-mycorrhizal interactions under multiple levels of varying resource availability.

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LITERATURE CITED

- Bever, J. D. 2015. Preferential allocation, physio-evolutionary feedbacks, and the stability and environmental patterns of mutualism between plants and their root symbionts. *New Phytologist* 205:1503–1514.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* 85:561–573.
- Bever, J. D., S. C. Richardson, B. M. Lawrence, J. Holmes, and M. Watson. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* 12:13–21.
- Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D. Stock, M. Tibbett, and M. Zobel. 2010. Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology and Evolution* 25:468–478.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Collier, F. A., and M. I. Bidartondo. 2009. Waiting for fungi: the ectomycorrhizal invasion of lowland heathlands. *Journal of Ecology* 97:950–963.

- Collins, C. D., and B. L. Foster. 2009. Community-level consequences of mycorrhizae depend on phosphorus availability. *Ecology* 90:2567–2576.
- Corrêa, A., R. Strasser, and M. Martins-Loução. 2008. Response of plants to ectomycorrhizae in N-limited conditions: which factors determine its variation? *Mycorrhiza* 18:413–427.
- Corrêa, A., R. Hampp, E. Magel, and M.-A. Martins-Loução. 2011. Carbon allocation in ectomycorrhizal plants at limited and optimal N supply: an attempt at unraveling conflicting theories. *Mycorrhiza* 21:35–51.
- Corrêa, A., J. Gurevitch, M. Martins-Loução, and C. Cruz. 2012. C allocation to the fungus is not a cost to the plant in ectomycorrhizae. *Oikos* 121:449–463.
- Courty, P.-E., M. Buée, A. G. Diedhiou, P. Frey-Klett, F. Le Tacon, F. Rineau, M.-P. Turpault, S. Uroz, and J. Garbaye. 2010. The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. *Soil Biology and Biochemistry* 42:679–698.
- Friesen, M. L., S. S. Porter, S. C. Stark, E. J. von Wettberg, J. L. Sachs, and E. Martinez-Romero. 2011. Microbially mediated plant functional traits. *Annual Review of Ecology, Evolution, and Systematics* 42:23–46.
- Gehring, C., and A. Bennett. 2009. Mycorrhizal fungal–plant–insect interactions: the importance of a community approach. *Environmental Entomology* 38:93–102.
- Grman, E. 2012. Plant species differ in their ability to reduce allocation to non-beneficial arbuscular mycorrhizal fungi. *Ecology* 93:711–718.
- Gross, N., L. Bagousse-Pinguet, P. Liancourt, C. Urceley, R. Catherine, and S. Lavorel. 2010. Trait-mediated effect of arbuscular mycorrhiza on the competitive effect and response of a monopolistic species. *Functional Ecology* 24:1122–1132.
- Hart, M. M., R. J. Reader, and J. N. Klironomos. 2003. Plant coexistence mediated by arbuscular mycorrhizal fungi. *Trends in Ecology and Evolution* 18:418–423.
- Hartnett, D. C., and G. W. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80:1187–1195.
- Hetrick, B., D. Hartnett, G. Wilson, and D. Gibson. 1994. Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. *Canadian Journal of Botany* 72:168–176.
- Hobbie, E. A. 2006. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. *Ecology* 87:563–569.
- Hoeksema, J. D., V. B. Chaudhary, C. A. Gehring, N. C. Johnson, J. Karst, R. T. Koide, A. Pringle, C. Zabinski, J. D. Bever, and J. C. Moore. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* 13:394–407.
- Janos, D. P. 2007. Plant responsiveness to mycorrhizas differs from dependence upon mycorrhizas. *Mycorrhiza* 17:75–91.
- Johnson, N., J. H. Graham, and F. Smith. 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist* 135:575–585.
- Johnson, N. C., D. L. Rowland, L. Corkidi, L. M. Egerton-Warburton, and E. B. Allen. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. *Ecology* 84:1895–1908.
- Johnson, N. C., C. Angelard, I. R. Sanders, and E. T. Kiers. 2013. Predicting community and ecosystem outcomes of mycorrhizal responses to global change. *Ecology Letters* 16:140–153.
- Johnson, N. C., G. W. T. Wilson, J. A. Wilson, R. M. Miller, and M. A. Bowker. 2015. Mycorrhizal phenotypes and the law of the minimum. *New Phytologist* 205:1473–1484.
- Jones, M. D., L. A. Phillips, R. Treu, V. Ward, and S. M. Berch. 2012. Functional responses of ectomycorrhizal fungal communities to long-term fertilization of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands in central British Columbia. *Applied Soil Ecology* 60:29–40.
- Kiers, E. T., C. E. Lovelock, E. L. Krueger, and E. A. Herre. 2000. Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. *Ecology Letters* 3:106–113.
- Kiers, E. T., M. Duhamel, Y. Beesetty, J. A. Mensah, O. Franken, E. Verbruggen, C. R. Fellbaum, G. A. Kowalchuk, M. M. Hart, and A. Bago. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333:880–882.
- Kleczewski, N. M., D. A. Herms, and P. Bonello. 2010. Effects of soil type, fertilization and drought on carbon allocation to root growth and partitioning between secondary metabolism and ectomycorrhizae of *Betula papyrifera*. *Tree Physiology* 30:807–817.
- Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70.
- Klironomos, J. N. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84:2292–2301.
- Klironomos, J. N., J. McCune, M. Hart, and J. Neville. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecology Letters* 3:137–141.
- Moora, M., and M. Zobel. 1996. Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. *Oecologia* 108:79–84.
- Neuhauser, C., and J. E. Fargione. 2004. A mutualism–parasitism continuum model and its application to plant–mycorrhizae interactions. *Ecological Modelling* 177:337–352.
- Pringle, A., and J. D. Bever. 2002. Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. *American Journal of Botany* 89:1439–1446.
- Pritchard, S. G., B. N. Taylor, E. R. Cooper, K. V. Beidler, A. E. Strand, M. L. McCormack, and S. Zhang. 2014. Long-term dynamics of mycorrhizal root tips in a loblolly pine forest grown with free-air CO₂ enrichment and soil N fertilization for 6 yr. *Global Change Biology* 20:1313–1326.
- Read, D., and J. Perez-Moreno. 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? *New Phytologist* 157:475–492.
- Scheublin, T. R., R. S. Van Logtestijn, and M. G. Van Der Heijden. 2007. Presence and identity of arbuscular mycorrhizal fungi influence competitive interactions between plant species. *Journal of Ecology* 95:631–638.
- Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. *The American Naturalist* 116:362–393.
- Tilman, D. 2011. Diversification, biotic interchange, and the universal trade-off hypothesis. *The American Naturalist* 178:355–371.
- Treseder, K. K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164:347–355.
- Treseder, K. K. 2013. The extent of mycorrhizal colonization of roots and its influence on plant growth and phosphorus content. *Plant and Soil* 371:1–13.
- Tuomi, J., M. M. Kytöviita, and R. Härdling. 2001. Cost efficiency of nutrient acquisition and the advantage of mycorrhizal symbiosis for the host plant. *Oikos* 92:62–70.

- Umbanhowar, J., and K. McCann. 2005. Simple rules for the coexistence and competitive dominance of plants mediated by mycorrhizal fungi. *Ecology Letters* 8:247–252.
- van der Heijden, M. G. 2003. Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search of underlying mechanisms and general principles. Pages 243–265. *Mycorrhizal ecology*. M. G. A. van der Heijden and I. R. Sanders, editors. Springer, Berlin Heidelberg, Berlin, Germany.
- van der Heijden, M. G., T. Boller, A. Wiemken, and I. R. Sanders. 1998a. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79:2082–2091.
- van der Heijden, M. G., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998b. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396:69–72.
- van der Heijden, M. G., A. Wiemken, and I. R. Sanders. 2003. Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. *New Phytologist* 157:569–578.
- Yang, G., N. Liu, W. Lu, S. Wang, H. Kan, Y. Zhang, L. Xu, and Y. Chen. 2014. The interaction between arbuscular mycorrhizal fungi and soil phosphorus availability influences plant community productivity and ecosystem stability. *Journal of Ecology* 102:1072–1082.
- Zhang, Q., R. Yang, J. Tang, H. Yang, S. Hu, and X. Chen. 2010. Positive feedback between mycorrhizal fungi and plants influences plant invasion success and resistance to invasion. *PLoS ONE* 5:e12380.

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