

From Lilliput to Brobdingnag: Extending Models of Mycorrhizal Function across Scales

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Mycorrhizae occur in nearly all terrestrial ecosystems. Resource exchange between host plants and mycorrhizal fungi influences community, ecosystem, and even global patterns and processes. Understanding the mechanisms and consequences of mycorrhizal symbioses across a hierarchy of scales will help predict system responses to environmental change and facilitate the management of these responses for sustainability and productivity. Conceptual and mathematical models have been developed to help understand and predict mycorrhizal functions. These models are most developed for individual- and population-scale processes, but models at community, ecosystem, and global scales are also beginning to emerge. We review seven types of mycorrhizal models that vary in their scale of resolution and dynamics, and discuss approaches for integrating these models with each other and with general models of terrestrial ecosystems.

Keywords: mycorrhizae, models, plant–microbe interactions, scale, stoichiometry

Mycorrhizae are nearly ubiquitous symbioses formed between plants and fungi. Plants provide fungi with carbon captured through photosynthesis, while fungi provide plants with soil resources. Historically, research has focused on the effects of mycorrhizae on nutrient uptake and the fitness of individual plants. More recently, there has been a growing appreciation for the importance of mycorrhizal functions at higher levels of organization, including populations, communities, and ecosystems (figure 1). Mycorrhizal fungi influence soil carbon storage, nutrient cycling, and soil stability within ecosystems. Populations of plants and mycorrhizal fungi interact to influence community structure, and

mycorrhizal fungi influence size and reproductive hierarchies in plant populations. Thus, research on the outcome of individual plant–fungus relationships must evolve to include mycorrhizal functions at higher levels of organization.

Much as Gulliver's travels through Lilliput, a land of miniatures, and Brobdingnag, a land of giants, provide insights into the human condition (Swift 1726), studies of mycorrhizal relationships across scales can provide insights into the mechanisms and consequences of their functioning. Mycorrhizal functions include the additive effects of individual mycorrhizae as well as emergent properties of the symbiosis.

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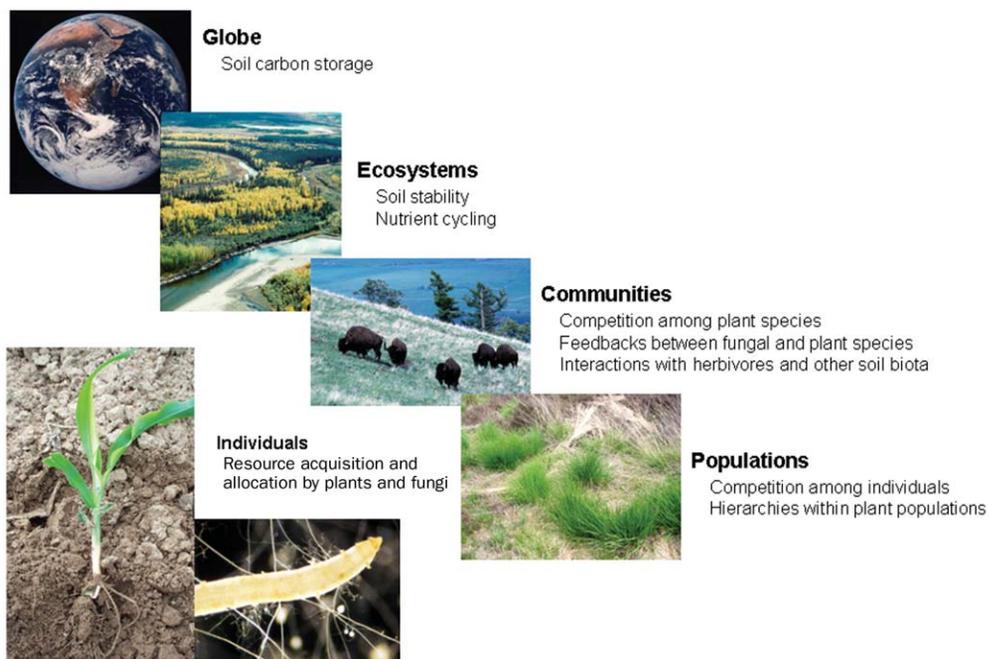


Figure 1. Mycorrhizal functions across ecological scales. Photographs used to illustrate globe, ecosystems, and communities are from the US Fish and Wildlife Service; the other photographs are from Roger Koide's personal collection.

Mycorrhizal functions may be of great practical value for horticulture, agriculture, forestry, and land restoration. The potential for mycorrhizal fungi to improve plant growth, resistance to pests, and tolerance of extreme conditions has led to their use in promoting plant growth in nurseries, gardens, plantations, and agricultural operations, and in restoring degraded lands. The use of commercial products containing mycorrhizal fungal inoculum is increasing, along with the recognition that management practices can be modified to encourage the proliferation of these fungi. However, understanding the factors that control mycorrhizal function is prerequisite to effectively managing them, and little is known about the mechanisms and consequences of mycorrhizal functioning at community and ecosystem scales. Thus the knowledge that currently guides mycorrhizal management is largely anecdotal.

We do understand that because resource exchange is critical to mycorrhizal function, any natural phenomenon or anthropogenically mediated activity that changes the availability of limiting resources has the potential to affect the dynamics of the symbiosis across multiple ecological scales. Individual plants and fungi may exhibit plasticity in biomass allocation in response to changes in resource availability. Population gene pools can change as individuals with the highest fitness in the changed environment become relatively more abundant with every generation. Community- and ecosystem-scale changes may occur as plant and fungal taxa that are best adapted to the altered environment become dominant, affecting nutrient cycles and energy flow. Missing from our calculus is a synthesis that couples our understanding of the plant–fungus symbiosis with community- and

ecosystem-level processes in a way that allows us to predict the results of mycorrhizal interactions.

Seven approaches to modeling mycorrhizal function

Models are useful tools for studying complex mycorrhizal interactions because they propose mechanisms and help explicitly formulate hypotheses and predictions. Conceptual and mathematical approaches to modeling mycorrhizal symbioses are emerging. These range from empirically based simulation models to more abstract theoretical models. This article presents several modeling approaches that help us understand mycorrhizal responses to resource variation across multiple scales (table 1). Our goal is to summarize the hypotheses being made explicit by some of these emerging approaches. Such a synthesis can catalyze theoretical progress in the concepts highlighted by these models, stimulate empirical research where there are gaps in our understanding, and encourage the incorporation of mycorrhizal processes into general models of terrestrial systems.

Functional equilibrium models. Functional equilibrium models predict that the allocation of biomass to aboveground and belowground organs within plants is controlled by the most limiting resource: Allocation to shoots is emphasized when light is most limiting, and allocation to roots is emphasized when minerals and water are scarcer than light (Brouwer 1983). It is generally assumed that mycorrhizal fungi are highly dependent on the balance between plant carbon and soil nutrient supplies. Treseder and Allen (2002) illustrate this in a conceptual model predicting that fertilization should increase mycorrhizal fungal biomass when soil

Table 1. Models of mycorrhizal function, scales at which they operate, and variables involved.

Model	Scale of responses	Variables	Reference
Functional equilibrium (biomass allocation)	Individuals and populations of plants and fungi	Resource availability	Brouwer 1983, Treseder and Allen 2002, Johnson et al. 2003
Economic (biological markets)	Individuals and populations of plants and fungi	Resource availability	Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003
Integrative, agent based	Individuals and populations of plants and fungi	Resource availability or the states of other agents	Bousquet and Le Page 2004
Community feedback	Communities of plants and fungi	Symbiotic effects on populations	Bever et al. 1997, 2002, Bever 1999
Coevolutionary mosaic	Communities of plants and fungi	Evolutionary processes	Thompson 2005
Food web (trophic)	Biotic communities and ecosystems	Exchange of matter and energy	Hunt et al. 1987, Moore et al. 2003
Pedogenesis	Ecosystems	Biotic and abiotic responses to inputs of matter and energy	Miller and Jastrow 1990, Jastrow and Miller 1998

fertility is low because carbon fixation is limited by mineral nutrients; at high soil fertility, however, neither fungus nor host plant is nutrient limited, and fertilization will cause mycorrhizal biomass to decline as host plants allocate less photosynthate belowground to roots and mycorrhizae (figure 2). Such resource-induced shifts in biomass allocation between hosts and fungi suggest that the functional equilibrium model can be extended to include allocation to mycorrhizal structures (Johnson et al. 2003).

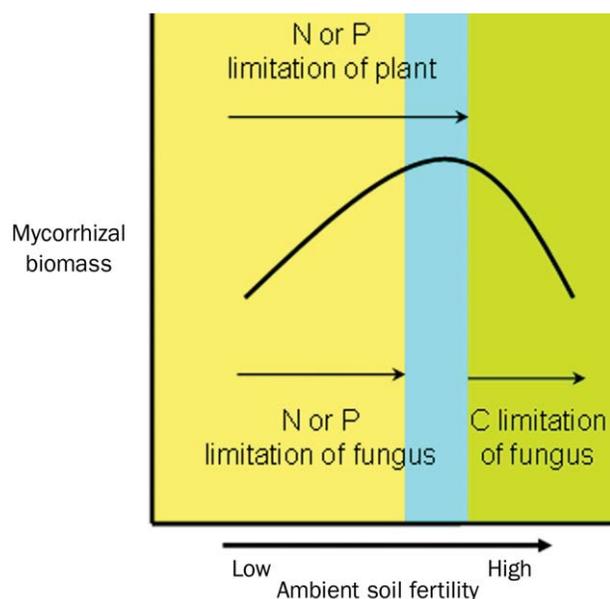


Figure 2. Treseder and Allen's (2002) model of the relationship between mycorrhizal biomass and resource availability. In very low-fertility soil (yellow zone), mycorrhizal biomass is expected to increase when soils are enriched with nitrogen (N) and phosphorus (P), because both fungi and plants are limited by these nutrients. In high-fertility soil (green zone), host plants are not nutrient limited, and fertilization is expected to reduce mycorrhizal growth because carbon (C) becomes more limited to the fungi as the host plant allocates more C above ground and less below ground.

Fungal morphology has been incorporated into the functional equilibrium model by differentiating mycorrhizal fungal structures according to the functions they serve in the symbiosis (Johnson et al. 2003). Vast networks of extraradical hyphae extend into the soil and forage for nutrients (figure 3a, 3b). Hartig nets in ectomycorrhizal (EM) fungi, and arbuscules and intraradical coils in arbuscular mycorrhizal (AM) fungi, are sites for resource exchange between fungi and host plants (figure 3c, 3d). These fungal structures acquire and exchange nutrients and water between fungi and their host plants. In contrast, reproductive structures in EM fungi and spores in AM fungi (figure 3e, 3f) only consume plant carbon and never supply nutrients or water to the host. If biomass allocation in mycorrhizal fungi were influenced by the nutrient status of the host plant, then we would predict greater allocation to supplier structures in low-fertility soil than in high-fertility environments. Empirical studies have supported these predictions, as extraradical hyphae and arbuscules are positively correlated with benefits provided to host plants (Graham et al. 1982, Johnson 1993) and the relative allocation to both AM and EM supplier structures is reduced by fertilization (Johnson et al. 2003, Nilsson and Wallander 2003). Also, we expect to see differentiation by plant hosts in terms of carbon allocation to individual fungal genotypes according to the nutrient benefits that they deliver (Hoeksema and Kummel 2003).

More studies are needed to understand the relationship between mycorrhizal functioning and allocation to structures involved with resource acquisition and transfer in natural ecosystems. This line of research should be encouraged, because linking easily measured structural characteristics with function will help define concrete goals for mycorrhizal management, particularly in systems that are traditionally fertilized. There is a growing recognition that in fertilized systems the relative proportions of nitrogen, phosphorus, and carbon (i.e., light or another surrogate for photosynthetic rate) may have as much impact on mycorrhizal allocation and functioning as the absolute availability of any one element in isolation. Economic models can be used to help understand the synergistic effects of multiple resources on mycorrhizal function.

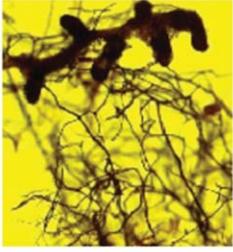
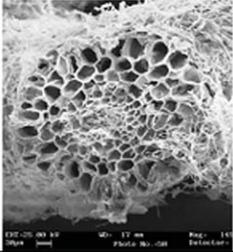
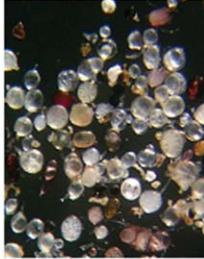
EM associations		AM associations		
a		Resource acquisition — hyphae extend beyond the plant roots into the soil to forage for resources in pore spaces too small to be accessible to the root	b	
c		Resource transfer — hyphal structures internal to the root serve as areas of exchange of carbon and mineral nutrients	d	
e		Fungal reproduction — EM fungi produce macroscopic fruiting bodies, while AM fungi produce single spores or sporocarps on soil hyphae or inside plant roots	f	

Figure 3. Resource acquisition, resource transfer, and fungal reproduction in the functional equilibrium model. The relative allocation of biomass to different fungal structures can provide insights into mycorrhizal function. The external mycelia of (a) ectomycorrhizal (EM) and (b) arbuscular mycorrhizal (AM) fungi forage for soil resources. Structures involved with transferring resources among fungi and plant hosts include (c) EM Hartig nets and (d) arbuscules. Reproductive structures that are not involved in resource transfer include (e) EM mushrooms and (f) AM spores. Photographs: R. Michael Miller (a), Julie Wolf (b, d), Randy Swaty (c), Jason D. Hoeksema (e), V. Bala Chaudhary (f).

Economic models. Models of comparative advantage in “biological markets” (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003) use economic principles to predict resource exchange among individuals. These models explicitly consider how species interactions are affected by variation among species of potential trading partners in the stoichiometry of their resource acquisition abilities and resource requirements (e.g., carbon:phosphorus ratios in the tissues and metabolisms of organisms). Variation in the concentration of elements in the tissues and metabolisms of organisms can be a powerful tool to elucidate the dynamics of interspecific relationships and ecosystem processes (Sturner and Elser 2002) and is an emerging theme in several approaches to modeling mycorrhizal symbioses.

Stoichiometry is represented explicitly in the comparative-advantage models by vectors that show optimal resource requirements and acquisition abilities, and these models

predict that potential benefits of resource exchange between species are defined by variation in this stoichiometry (box 1). One appealing aspect of these models when applied to mycorrhizae is that they predict how relationships between fungi and plants may shift for either trading partner, depending on changes in resource availability.

Departures from these predictions would suggest that one or more of the model assumptions are false. For example, the model illustrated in box 1 assumes that carbon and phosphorus are the only factors determining the net outcome of interactions between species on individual fitness (e.g., whether an interaction is mutualistic or parasitic). If one fungus was superior to another in providing plant defenses and protecting the plant from pathogens, then plant fitness would be affected accordingly in environments containing pathogens. Gauging the net benefit to the plant through combined positive effects of plant defense and negative effects of resource exchange requires a more elaborate model of the exchange of goods and services within a complex community of organisms. Another key assumption of the model—one that remains untested—is that the exchange rate of plant carbon for fungal mineral nutrients is determined by conditions analogous to a fair market.

Thus, although the model is useful in suggesting testable hypotheses and in guiding informative experimentation and data collection for simple communities, additional model development is required to capture the complexity of real ecosystems. Some of this complexity may be addressed by agent-based models.

Integrative, agent-based models. Agent-based models, sometimes referred to as “individual-based” models or “multiagent systems” (Bousquet and Le Page 2004), have their origins in computer science and complex-systems theory. These models provide a framework for exploring the spatial and temporal complexity of mycorrhizal systems by defining relatively simple transition rules that govern the response of a given agent, such as a mycorrhizal plant or fungus, to the states of other agents or environmental conditions. Nonlinear, chaotic, or “self-organizing” patterns often emerge from agents interacting

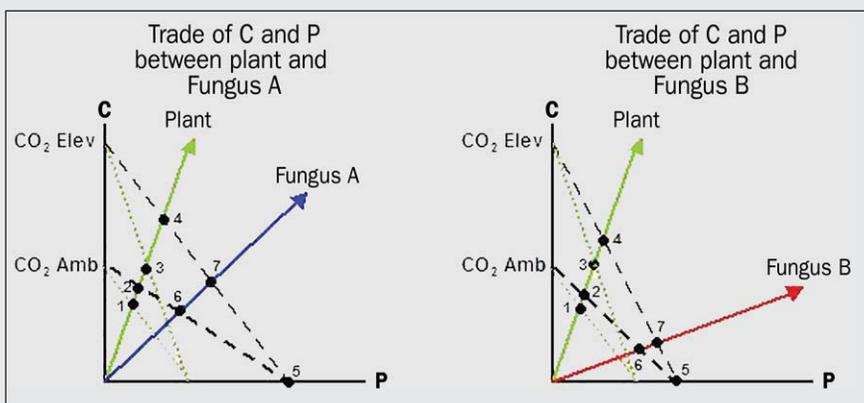
Box 1. An economic model applied to mycorrhizal function.

The figure below illustrates the fitness gain from resource exchange between a hypothetical mycorrhiza-dependent plant and two hypothetical mycorrhizal fungi under ambient and elevated concentrations of atmospheric carbon dioxide (CO_2), using concepts from the comparative-advantage biological market model (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003).

Conditions. The axes represent total carbon (C) and phosphorus (P) acquisition per unit of time. Stoichiometry of resource requirements for each species is modeled by vectors (arrows) representing the ratio of optimal consumption of the two resources. The fitness of a species is maximized by acquiring resources along its vector as far as possible from the origin. The relative slopes of the vectors (green for the plant, blue for fungus A, and red for fungus B) imply that the plant has a higher relative requirement, compared with the fungi, for carbon than for phosphorus. The slopes of the vectors also imply that fungus B has a higher relative requirement for phosphorus than fungus A. The green dotted lines represent the resource acquisition constraints for the plant, showing the maximum amounts of the two resources the plant can acquire in the absence of trade with mycorrhizal fungi. Two acquisition constraints are shown for each plant, one under ambient $[\text{CO}_2]$ (square brackets indicate molar concentrations) and one under elevated $[\text{CO}_2]$. The plant has both a higher relative ability to acquire carbon (through photosynthesis) than phosphorus, as indicated by the relative intersection points of the constraint line with the C and P axes, and an increased ability to acquire carbon under elevated $[\text{CO}_2]$. Points 1 and 3 indicate plant fitness in the absence of trade with mycorrhizal fungi, under ambient and elevated $[\text{CO}_2]$, respectively. Point 5 shows the resource acquisition stoichiometry for the fungi, and the use of a point on the P axis rather than a constraint line connecting the P axis to the C axis makes explicit the assumption that these fungi lack the ability to acquire carbon in the absence of trade with plants. The placement of the point along the P axis represents the maximum ability of the fungus to acquire phosphorus, and fungus A has a greater ability than fungus B to uptake phosphorus from the soil. Both fungi are assumed to have zero fitness in the absence of a host plant because of their inability to acquire carbon without a host.

The black dashed lines represent maximum carbon and phosphorus acquisition by plants and fungi when trading with each other, under a scenario in which plants specialize in carbon acquisition, and trade carbon to the fungi for phosphorus. Fitness gain for the plant through trade with either fungus is indicated by the increase in distance from the origin between points 1 and 2 under ambient $[\text{CO}_2]$ and between points 3 and 4 under elevated $[\text{CO}_2]$. Fitness gain (from zero) for the fungus through trade with the plant is indicated by the distance from the origin to points 6 and 7 under ambient or elevated $[\text{CO}_2]$, respectively.

Predictions. Under these conditions, the model makes three predictions: (1) The plant will benefit more from trade with fungus A than from trade with fungus B, largely because of the assumption that fungus A has a higher rate of uptake of P from the soil; (2) this difference in benefit to the plant between fungus A and fungus B will be especially noticeable under elevated $[\text{CO}_2]$; and (3) under elevated $[\text{CO}_2]$, fungus A will benefit more from trade with the plant than will fungus B. The latter prediction is driven by two assumptions: that fungus A requires more carbon relative to phosphorus in its metabolism than fungus B, and that fungus A is better able to acquire P than fungus B. Both of these differences would result in fungus A being more C limited and less P limited than fungus B. These predictions are largely consistent with some recent experimental results for interactions among four plant species and two species of arbuscular mycorrhizal fungi under ambient and elevated concentrations of CO_2 (Johnson NC et al. 2005).



in this way. Transition rules can be quantitatively defined in terms of differences among mycorrhizal fungal taxa in their demands for carbon and in their capabilities for nutrient uptake and exchange with plants.

Box 2 illustrates an example of the output from a nonspatial agent-based model based on the ecological stoichiometry of three species of mycorrhizal fungi and a host plant. Assuming that mycorrhizal fungal taxa are likely to differ functionally, the input parameters are defined as (a) profiles describing the uptake, growth, and movement of nutrients to and from the host plant for three fungal taxa and one host plant, and (b) matrices describing soil conditions in terms of the availability of multiple soil nutrients. The simulation in box 2 is assumed to model the rhizosphere of an oak that can be

infected with both AM and EM fungi. In this case, plant biomass after one growth season is depicted as a function of the composition of its mycorrhizal fungal community and of the availability of inorganic phosphorus and nitrogen at three levels of organic nitrogen.

One consequence of this model is the emergence of quasi-economic “exchange rates” between plant and fungi, as assumed in biological market models. Furthermore, changing even one of the fungal functional types or nutrient conditions can alter the growth response of host plants in highly nonlinear ways. Nesting multiple instances of local plant–fungal interactions within individual “cells” of two- or three-dimensional simulations (i.e., cellular automata) will broaden the scope of this type of model. Simulating spatial context

(Molofsky and Bever 2004) will enable investigators to explore the ecological and evolutionary consequences of mycorrhizal networks (Southworth et al. 2005) and metacommunity structure (Leibold et al. 2004) over time. Once embedded in a spatial context, this type of integrative simulation model can also be expected to produce results consistent with community feedback models.

Community feedback models. Community-scale models have also been constructed from population growth models that incorporate terms for both host and fungal symbionts. For example, Umbanhowar and McCann (2005) and Neuhauser and Fargione (2004) used mathematical models to study the impact of nutrient exchange on mycorrhizal community dynamics. Both studies examined three species communities (two plant species interacting with one fungus and one plant interacting with two fungal species, respectively) and found that diversity of the two-species guild was dependent on the availability of resources. Umbanhowar and McCann (2005) showed that if increasing light availability affected the mycorrhizal benefits of two plant species differently, then the symbiosis could mediate a change in the order of competitive dominance of the plant species when light conditions were changed. Exploration of these potential dynamics in larger communities is hampered by the escalating complexity and corresponding increase in the number of parameters.

Insight into mycorrhizal effects on community dynamics may be gained by focusing on empirical evidence for host specificity within mycorrhizal interactions rather than on the population dynamics of all of the plants and fungi within the community. Many species of EM fungi associate with particular species of plants, and although individual species of AM fungi may associate with many different plant species and are often regarded as having low specificity of association, there is also solid evidence that species of AM fungi associate preferentially with particular plant species (Fitter 2005). Plant growth varies with species of mycorrhizal fungi (Chuchou and Grace 1985, Klironomos 2003), and fungal growth depends on the identity of the plant with which the fungi are associated (Molina and Trappe 1994, Bever 2002a, 2002b). Consequently, the composition of mycorrhizal fungal communities changes as a result of association with different plant species (Bever et al. 1996, Johnson et al. 1992a) and, similarly, the composition of plant communities changes as a result of the species of associated fungi (van der Heijden et al. 2003).

This reciprocity among species in their effects generates interdependence of plant and fungal populations and has important consequences on community and coevolutionary dynamics. Host-specific changes in populations and communities of mycorrhizal fungi could lead to increases (i.e., positive feedback) or to decreases (i.e., negative feedback) in the relative biomass of the most abundant plant species (figure 4; Bever 1999). Although the conditions leading to these two dynamics can be complicated by nonlinear responses to multiple infections (Golubski 2002), positive feedback can result

from symmetry in fitness relationships in which the fungus that promotes the growth of a given plant is also the fungus that has the highest growth rate on that plant host. As a result, an initially high frequency of one plant type will result in an increase in the abundance of its preferred fungus, which thereby increases the plant's growth rate relative to that of other plants, ultimately leading to the exclusion of the less common species. In a coevolutionary context, positive feedback can lead to greater strength of mutualism and potentially to coadaptation of mutualist partners (Bever 1999).

Alternatively, negative feedbacks are manifested when the presence of one plant can facilitate the growth of a second plant species through changes in the composition of the mycorrhizal fungal community (Bever 1999). This dynamic results from asymmetric fitness relations, in which the fungus that promotes the growth of a given plant has the highest growth rate on a second plant species. As a result, the mycorrhizal fungal community feedbacks will contribute directly to the coexistence of competing plant species. In a coevolutionary context, negative feedback will reduce the strength of mutualism over time and lead to fluctuating polymorphisms (Bever 1999).

Terrestrial eutrophication can be expected to alter these feedbacks. According to the functional equilibrium model, soil fertilization should stimulate fast-growing and less mycotrophic plants as light limitation increases and nutrient limitation decreases. This perturbation would be expected to favor positive mycorrhizal feedbacks and reduce plant diversity if the dominant mycorrhizal fungi reinforce the dominance of eutrophilic plant species.

Detecting mycorrhizal feedbacks on plant growth through the mycorrhizal community is made difficult by the potentially confounding effects of the accumulation of host-specific pathogens and changes in rhizosphere bacteria (Bever 2002a, Bever et al. 2002). Klironomos (2002) found that the growth of dominant plant species was generally increased by endemic communities of mycorrhizal fungi (i.e., positive feedback), even though other soil microorganisms usually generated negative feedback. Alternatively, negative feedback through changes in the AM fungal community was observed in a study that eliminated pathogens (Bever 2002b). The relative frequency and spatial distribution of positive and negative mycorrhizal feedbacks within plant communities remain to be investigated. Future studies will be facilitated by recent developments in spatial ecology.

Coevolutionary mosaic model. Ecological and evolutionary dynamics of mycorrhizal symbioses in one community can be influenced by those in another, because variation in function among populations of plants and fungi may be spatially linked through dispersal. This phenomenon is a component of the geographic mosaic theory of coevolution (Thompson 2005). For example, because mycorrhizal symbioses can vary across a continuum from mutualism to parasitism, positive feedbacks between mutualistic genotypes may generate local adaptation between plant and fungal genotypes and favor

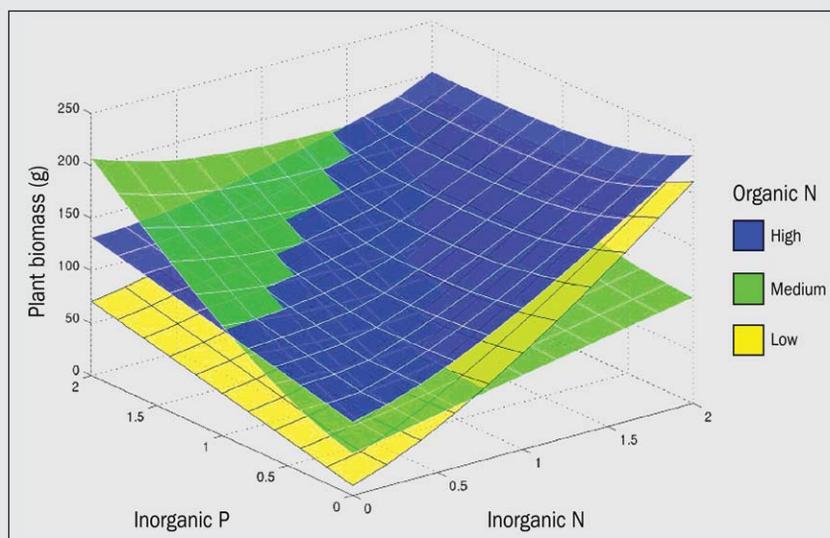
Box 2. Sample output from an agent-based simulation model built on mycorrhizal ecological stoichiometry.

In the figure below, plant growth after one hypothetical growing season is plotted against ranges of available inorganic phosphorus (P) and nitrogen (N). (Units are relative indices linearly related to grams of nutrient per gram of soil.) The three response surfaces correspond to discrete levels of available organic N. Initial conditions and transition rules for this model are entered as sets of values defining the starting biomass, the intrinsic rate of growth, the rate of nutrient uptake, and the percentage of nutrients in each organism/agent's biomass that is available for sharing with its symbiont or symbionts. Soil nutrient availability is modeled to resemble conditions in a chemostat, with specified initial availabilities, inflow and outflow rates, and saturation levels for each nutrient of interest. Each iterated cycle of the simulation comprises three phases: (1) resource uptake/fixation, (2) nutrient exchange, and (3) growth of each organism/agent. The quantitative outputs from each cycle are fed back into the simulation as the initial state of the next cycle.

In this example, the increase in plant biomass has been parameterized to simulate growth from 1 gram to 1 kilogram over the course of a growing season (2500 iterations) under ideal nutrient conditions and in the absence of mycorrhizal fungi. The simulated plant is modeled after seedlings of coast live oak in southern California, where N deposition plays a significant ecological role (Allen et al. 1998). Because these and many other oaks can form both arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) associations simultaneously, the fungal types are modeled as one AM taxon and two functionally distinct EM taxa. Although precise rates of nutrient uptake and exchange are poorly understood at present, parameter values describing relative uptake and sharing have been estimated on the basis of current understanding of mycorrhizal function.

EM fungi are assumed to exude proteolytic enzymes that enable uptake of N or P from organic compounds, while AM fungi are assumed to be more efficient at uptake of inorganic compounds. Movement of N and P across the mycorrhizal interface is assumed to be one-way from fungus to plant, and carbon is assumed to flow only from plant to fungus; however, the total quantities exchanged in the model can be thought of as *net* quantities of bidirectional movement. Micronutrients have been omitted here, but the model can be modified to include any number of nutrient parameters.

The unique attribute of this type of model lies in its capacity for revealing and predicting nonlinear dynamics in complex mycorrhizal interactions. The stoichiometry of a single community of fungi interacting with host plant functionality and differences in soil nutrient status (within the ranges defined in this set of parameters) can alter plant growth in unexpected ways: At low or high levels of available organic N, inorganic N has a stronger effect than inorganic P. In contrast, plant growth responds more strongly to inorganic P at moderate levels of organic N availability. Like most theoretical models, this integrative simulation can also point to deficiencies in existing data—a good example being the scarcity of data quantifying rates of nutrient movement through mycorrhizal systems. Experimental determination of these rates will allow more realistic parameterization and will help to move this type of model from the purely theoretical into the predictive realm.



fixation of mutualistic alleles in one community, while negative feedbacks between antagonistic genotypes may generate fluctuating polymorphisms in another nearby community of the same species. Gene flow linking the two communities could prevent fixation of mutualistic alleles in the first community, dampen the effects of negative feedbacks in the second community, or prevent local adaptation between plants and fungi.

With the advent of changing climates, terrestrial eutrophication, and exotic plant invasions, resource managers should consider patterns of gene flow among, and local adaptation within, populations of plants and mycorrhizal fungi in order to match plant and fungal genotypes more effectively with each other and with the environment. However, we should not assume that plant performance will be higher in

local combinations of plant and fungal genotypes. At least two theoretical results indicate that plant performance is not always higher in sympatric plant–fungus pairings. First, the geographic mosaic theory of coevolution (Thompson 2005) predicts that inherent variation in coevolutionary dynamics among populations, combined with trait remixing among communities as a result of gene flow and genetic drift, will occasionally produce maladaptation in interspecific interactions (Thompson et al. 2002). Second, if generation times or gene flow rates differ significantly between host and symbionts, or if selection is asymmetric, then local adaptation or the benefits derived from the symbiosis may also be asymmetric (Gandon and Michalakis 2002). For mycorrhizal symbioses, this could mean that fungi are well adapted to local host plant genotypes, while plants are not well adapted to local

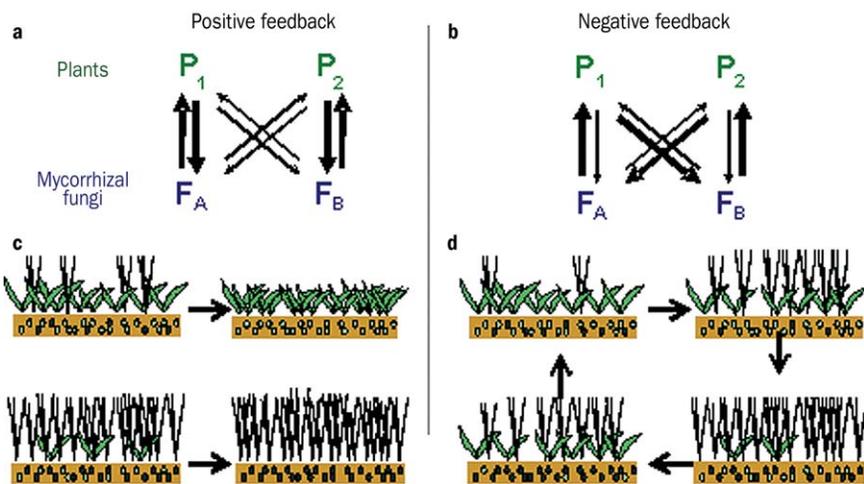


Figure 4. Community dynamics due to feedback between plant and mycorrhizal fungal communities. Two distinct dynamics result from the mutual interdependence of plant and fungal relative growth rates (Bever 1999). The direction of benefit delivered between two plant species, P_1 and P_2 , and their arbuscular mycorrhizal (AM) fungal mutualists, F_A and F_B , are indicated by the arrows, with the thickness of the arrows indicating the magnitude of benefit. When the delivery of benefit is symmetric between plants and fungi (a), a positive feedback dynamic results (c). Under positive feedback, the AM fungal community changes in a way that facilitates the success of the plant species that is initially numerically dominant. A different dynamic results when the delivery of benefit between the plant and fungus is strongly asymmetric (b). In this case, an initial abundance of one plant species causes the soil community to change in a way that facilitates the growth of the competing plant species (d). This negative feedback on plant biomass through changes in the composition of the AM fungal community can contribute directly to plant species coexistence. Panels a and b are modified from Bever et al. 1997, and panels c and d are modified from Bever et al. 2002.

fungus genotypes. Fungi that are well adapted to their host plants can cause poor performance of host plants if they place a higher carbon demand on the plant or allow the plant less control over the symbiosis, or both. This phenomenon could account for the declining yields that are often observed when crops are continuously grown on the same sites. For example, empirical studies suggest that crop monocultures can select for parasitic AM fungi in highly fertilized agricultural and natural systems (Johnson et al. 1992b, Johnson 1993).

More data are needed to describe the specific patterns and scales for which the geographic mosaic model might be appropriate for describing mycorrhizal interactions. Specifically, researchers need to better understand the situations in which mycorrhizal interactions may generate diverse co-evolutionary dynamics among populations that can be linked by gene flow and metapopulation dynamics.

Food web (trophic) models. All of the models considered so far have focused on interactions among mycorrhizal fungi and plants (table 1). Food web, or trophic, models can link the feeding and nutrient interactions among plants and mycorrhizal fungi with interactions among other organisms.

For example, these models show that aboveground herbivory can initiate plant growth responses that change allocation of carbon from roots to shoots, thereby indirectly affecting mycorrhizal interactions. Likewise, soil invertebrates that eat mycorrhizal fungi will directly affect the plant–fungus interaction (Moore et al. 1985, Klironomos and Moutoglou 1999, Johnson D et al. 2005). Early formulations of food web models that included mycorrhizae and other symbioses were largely descriptive, with the impacts of the symbiosis on community dynamics implied from the positioning and magnitudes of the interaction coefficients within the community matrices (Cohen 1978).

Hunt and colleagues (1987) include mycorrhizae in their description of the soil food webs of the North American short-grass steppe. This model is based on simple trophic dynamics and mass balance, allowing for bidirectional flow of carbon and nitrogen, currencies that are linked to mycorrhizal biomass and function. Flow of carbon from plant roots to mycorrhizal fungi is assumed to be at a steady state in which plant carbon is consumed by the fungus at a rate needed to offset fungal metabolism, the annual death rate of the fungus, and losses due to consumption by arthropods and nematodes. Flow of nitrogen to plants is governed by the carbon:nitrogen ratio of the fungus and by rates of mineralization.

Moore and colleagues (2003) use trophic dynamic models to explore mycorrhizal mediation of plant, herbivore, and predator responses to nutrient enrichment. The plants, herbivores, and predators are modeled as a linear food chain, with each consumer–resource interaction governed by a Holling type II functional response (i.e., feeding rates are highest at low resource levels, are lower at intermediate resource levels, and level off at high resource levels; Holling 1959), using the parameterization presented by Hastings and Powell (1991). The mycorrhizal interaction is modeled implicitly as an extension of the plant root. The mycorrhizal root consumes nitrogen from a separate inorganic nitrogen pool, with the uptake rate governed by a type II functional response. Varying the half-saturation constant of the type II functional response to alter the effectiveness of mycorrhizal interactions, and thus changing the availability of nutrients, has the same effect as changing the uptake rate via other mechanisms. Not surprisingly, altering the uptake of nitrogen affected the dynamics of plants, herbivores, and predators above ground. Specifically, the plant, herbivore, and predator biomasses settled into a stable equilibrium when modeled at low levels

of nitrogen availability and uptake by the plant. As nitrogen availability and uptake increased, the aboveground component transitioned into what appeared to be a stable limit cycle and then into chaos.

Incorporating food web dynamics into population- and community-level models can improve researchers' and managers' ability to predict the outcomes of species interactions across a range of soil nutrient levels and soil biotic communities. This is important for the use of mycorrhizae in restoration scenarios, because many types of disturbance affect nutrient availability and soil community structure.

Pedogenesis models. Fungal hyphae contribute to soil formation through the creation and stabilization of soil aggregates. Yet there is no theoretical framework that explicitly links the plant–fungal symbiosis to the soil-forming processes that are central to models of pedogenesis. Mycorrhizal fungi directly change the physical and chemical environment surrounding their hosts' root systems by creating conditions conducive to the formation and stabilization of soil aggregates. Mycorrhizal hyphae mediate organic matter accrual, increase soil stabilization, and reduce erosion. From a mechanistic point of view, hyphae and roots can be viewed as a “sticky-string bag” (Miller and Jastrow 2000). Both AM and EM hyphae and associated roots contribute to the entanglement and enmeshment of soil particles to form macroaggregates (figure 5). AM fungi produce glomalin in their hyphal walls, and EM fungi produce extracellular polymeric compounds that bind soil particles and organic material together (Rillig and Mummey 2006). Also, the recalcitrant nature of hyphae allows them to become carbon and nitrogen reservoirs and to play a critical role in organic matter accrual in soils (Zhu and Miller 2003).

A framework that considers the contributions of mycorrhizal fungi to pedogenic processes needs to recognize the role of soil food webs and the differences in fungal life forms (Coleman et al. 1983). Fungi vary considerably in the sources of carbon that they consume. AM fungi are assumed to be obligate biotrophs and will cease growth in the absence of a living root system; EM fungi exhibit a range of biotrophic and saprotrophic abilities (Hobbie et al. 2001); and many non-mycorrhizal fungi are obligate saprotrophs. Hence, the contribution of fungal hyphae to aggregation

varies depending on the species composition of the fungal community and on whether carbon inputs come from an actively growing host or from the turnover of plant materials during decomposition processes. Changes in the allocation of carbon to roots and mycorrhizal fungi may shift the fungal community from one dominated by mycorrhizae to one dominated by saprotrophic forms. This shift could cascade through the food web, affecting populations of fungivores and bacteria that decompose fungal products, and thereby changing soil aggregate formation (figure 6; Moore et al. 1988, 2004).

During the coming decade, the associations among macroaggregation, organic matter accumulation, and carbon sequestration in soils will be an important area of research. The contributions of mycorrhizae within soil food webs will no doubt be an important factor in this research. The challenge for researchers is both conceptual and methodological, requiring us to better elucidate and measure the contributions of mycorrhizal fungi to the formation and stabilization of soil structure over a wide range of ecosystems, evaluated at relevant temporal and spatial scales. The linkage we envision would incorporate estimates of fungal biomass from dynamic trophic models into a dynamic version of pedogenesis

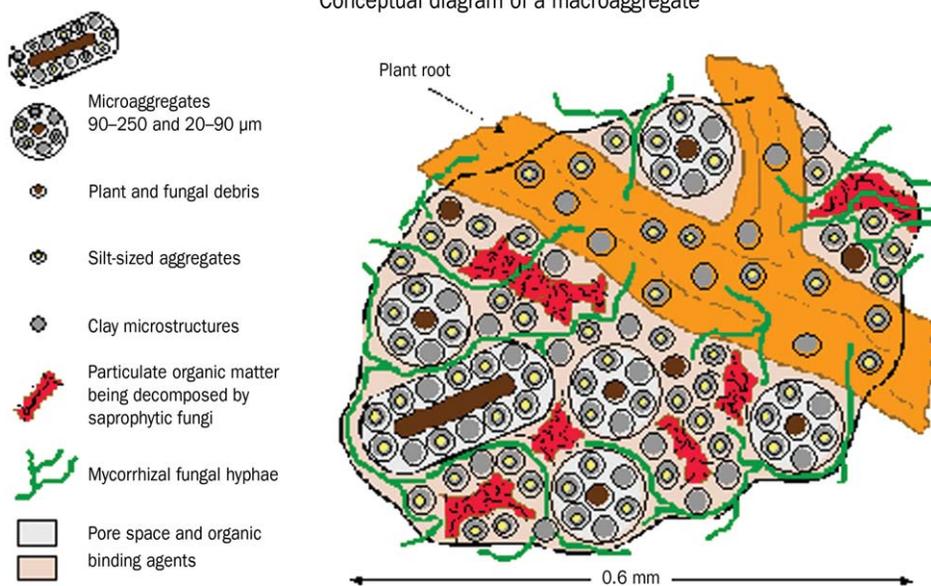


Figure 5. Conceptual diagram of a macroaggregate. The work of Jastrow and Miller (1998) in grassland ecosystems shows that roots and arbuscular mycorrhizal (AM) hyphae create the structural and physical milieu that enables microaggregates to form, enmesh, and bind together into larger macroaggregates. AM hyphae physically entangle primary particles of soil, and glomalin (a glycoprotein produced by AM fungi) serves as a binding agent at the microaggregate scale, with macroaggregate-scale outcomes. The macroaggregate shown here was formed and is transformed by a series of biotic interactions occurring over different spatial and temporal scales. Models of pedogenesis and soil organic matter dynamics capture these dynamics, but these models traditionally focus on the physical and chemical components, without implicit references to biota (Six et al. 2000). Modified from Jastrow and Miller (1998).

models. The hybrid model (figure 6) would require us to estimate the population densities of the soil biota and the production of fungal by-products, such as glomalin, that are important to the formation of soil aggregates.

Linking models to mycorrhizal management

Gulliver's experiences in Lilliput and Brobdingnag highlight our bias for the spatial scale in which we live, and they also illustrate an important distinction about the concept of scale. Geometric scale relates to size hierarchies, and ecological scale relates to organizational hierarchies. Although residents of Lilliput were 6 inches tall and those of Brobdingnag were 60 feet tall, their organizational hierarchies (i.e., communities and social systems) were similar. This insight underscores the importance of complex interactions and emergent properties in generating organizational hierarchies, concepts that are critical for understanding how individual microscopic soil organisms are linked to global scale biogeochemical processes. It also provides a starting place for linking models of mycorrhizal function to guide the management of plant–soil systems.

Future models that integrate mycorrhizal functions across scales will make it possible to (a) run “experiments” on a much more rapid timescale and with greater control of parameters than is possible with experimental systems in the laboratory or field, (b) characterize and predict patterns in nonlinear trajectories of mycorrhizal communities responding to variation in biotic and abiotic context, (c) use the principles of ecological stoichiometry to describe the mechanisms and consequences of taxonomic variation in resource exchange, and (d) construct a conceptual synthesis of the predictions of disparate theories of mycorrhizal function. Community composition within particular habitats may be drastically altered by small changes in nutrient availability and additions or subtractions of community members. The inherent sensitivity of complex systems even to slight perturbations means that predictions inferred from measurements taken at isolated moments or locations may be prone to fundamental errors. As Anand and Desrochers (2004) point out for plant communities, effective management for conservation, restoration, or productivity requires the kind of awareness that integrative models can provide with respect to the functional dynamics inherent in complex mycorrhizal communities.

Terrestrial ecosystem models predicting community productivity, structure, and succession are usually based on simple resource availability and allometric relationships involving plant biomass. Many of the forest models prioritize light availability as the resource most limiting to community development (Coates et al. 2003), with no coupling between above- and belowground processes. Some of the models include the effects of nutrient availability or water availability, or both (Messier et al. 2003), but treat microbial mediation of resource availability as a black box. Mycorrhizal effects on resource availability and biomass allocation patterns have not been included in these models, partly because of

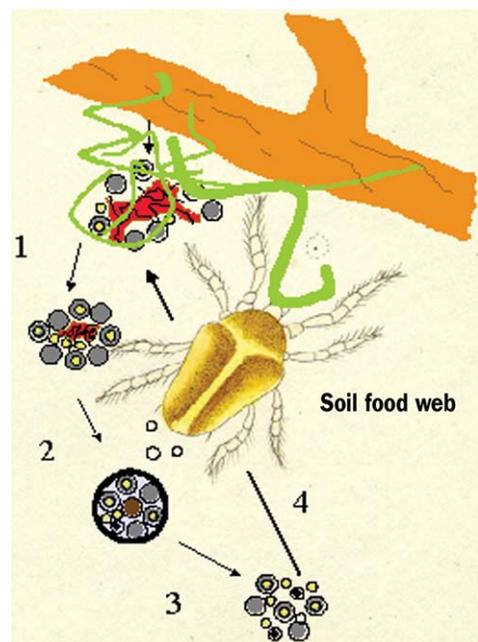


Figure 6. Mycorrhizal interactions and pedogenesis. To connect models designed to study trophic dynamics and soil formation, researchers need to understand the physical and chemical properties of soils, the contributions of mycorrhizal fungi and plant roots to soils, and the rates at which the constituent products are formed. A new generation of pedogenesis models of aggregate turnover should include biota and capture the four processes shown in this diagram: (1) Microaggregates form as decomposing roots, fungal hyphae, glomalin, fecal material, and other forms of detritus become encrusted with mineral particles. (2) Decomposition continues through the action of the soil food web, but at a slower rate due to physical protection; consequently, the aggregate is stabilized. (3) Slowed decomposition and intimate contact with soil minerals in stable aggregate enable organic matter to be humified or chemically protected by association with the mineral fraction. (4) Eventually, organic binding agents decompose sufficiently for the aggregate to be destabilized, and the mineral fraction becomes enriched with new organic matter. Each step of this cycle involves trophic exchanges within the soil food web (Hunt et al. 1987, Moore et al. 2003).

insufficient information but also because of scaling differences. Computing advances now present an opportunity for finer-scale mycorrhizal models that predict carbon:nitrogen ratios or biomass allocation relationships to inform larger-scale ecosystem models in a metamodel environment. For example, multiple models and data sets can be linked in an integrated workflow using Kepler (<http://kepler-project.org>), an open-source tool that is being developed collaboratively and is based on the Ptolemy II system for heterogeneous, concurrent modeling and design (<http://ptolemy.eecs.berkeley.edu/ptolemyII/>).

Similarly, mycorrhizal function models can be used to inform global carbon cycle models for improved predictions of atmospheric carbon dioxide (CO₂) change, and to evaluate the role of mycorrhizae for sequestering CO₂ and thereby slowing the rate of the increase in atmospheric CO₂ (Li et al. 2003). Predictions of plant community shifts and effects on productivity as a result of global environmental change can be made more accurate with the combined application of biological market models and community feedback models. The first type of model predicts how changing resource availability will shift the function of mycorrhizae, while the latter is important for estimating community shifts. In fact, Kummel and Salant (2006) recently showed how market principles could be used to construct a model that explicitly predicts shifts in plant and mycorrhizal fungus communities in response to changes in resource availability. Using the models highlighted here to more accurately parameterize other models in a hierarchical relationship may be a fruitful approach to understanding community and ecosystem responses to global environmental change.

Enormous variation in mycorrhizal functioning exists among different combinations of plant and fungal genotypes or species. Most of the mycorrhizal models that are currently available focus on the implications of variation in resource uptake and exchange. Although mycorrhizal effects on soil properties, disease resistance, and trophic cascades are not emphasized to the same extent in current models, these functions are potentially important for understanding how mycorrhizae contribute to ecosystems. We encourage future efforts to develop methods for measuring mycorrhizal structure and function at relevant spatial and organizational scales, and hope that researchers will apply this knowledge to bring about a new generation of descriptive and predictive models to guide management decisions.

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