



**Influence of Phylogeny on Fungal Community
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Influence of Phylogeny on Fungal Community Assembly and Ecosystem Functioning

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Ecology seeks to explain species coexistence and its functional consequences, but experimental tests of mechanisms that simultaneously account for both processes are difficult. We used an experimental mycorrhizal plant system to test whether functional similarity among closely related species (phylogenetic conservatism) can drive community assembly and ecosystem functioning. Communities were constructed with the same number of fungal species, but after 1 year of growth, realized species richness was highest where the starting species were more distantly related to each other. Communities with high realized species richness also stimulated plant productivity more than those with low realized species richness. Our findings suggest that phylogenetic trait conservatism can promote coexistence because of reduced competition between distinct evolutionary lineages and enhance ecosystem function because of functional complementarity among those same lineages.

Although it has long been recognized that ecological communities are not random collections of species, ecologists still seek to understand the processes that shape community assembly (1–4). One hypothesis that explains nonrandom species assemblages is that competitive interactions limit the long-term coexistence of species with similar fundamental niches (2, 5–7). If closely related species share a fundamental niche (niche conservatism), competitive exclusion will cause communities to be made up of species that are phylogenetically overdispersed, or more distantly related to each other than would be expected by chance (2, 5, 8–10). This hypothesis is difficult to test directly because the spatial and temporal scales of the critical processes in plant and animal communities are typically too large for manipulation (11). Recent research indicates that the degree of phylogenetic dispersion varies across communities and depends on the level of phylogenetic relatedness within a particular community and the spatial scale of species interactions (3, 10, 12–14). However, this evidence is correlative rather than causative because most previous studies have been confined to comparative analyses of existing communities (15, 16). In addition, the strength of a phylogenetic signal in the species assemblage of communities is often obscured by stochastic processes and dispersal limitations (8).

Using a model mycorrhizal plant community, we experimentally determined whether commu-

nity assembly depends on the phylogenetic relatedness of species. The model community consisted of sympatric arbuscular mycorrhizal fungi (AMF) growing on plant roots of *Plantago lanceolata* (17) (Fig. 1). The arbuscular mycorrhizal symbiosis is ideal for testing hypotheses about community assembly for two reasons. First, the small size and short generation time of the organisms allow us to manipulate and observe ecologically meaningful interactions in tractable experimental units on a short time scale. Second, most described AMF are confined to three distinct taxonomic families (Glomeraceae, Acaulosporaceae, and Gigasporaceae) within two orders (Glomerales and Diversisporales) (18) in which functional traits associated with spatial niche requirements are phylogenetically conserved (19) (Fig. 2). For example, the majority of fungal biomass in the Gigasporaceae is found in the hyphae that are located outside the plant root (Fig. 2, A and B). In contrast, the majority of fungal biomass in the Glomeraceae is found in hyphae growing inside the root (Fig. 2, A and B). The Acaulosporaceae form a third distinct group, because species in this taxon produce low biomass inside and outside the root (Fig. 2, A and B).

Species from these major evolutionary lineages were sampled to form experimental communities. We manipulated the level of phylogenetic relatedness in the species pool by constructing communities sampled from all three AMF families (relatively overdispersed) or from two or fewer families (relatively underdispersed) (Fig. 1). We predicted that species within each family were less likely to coexist with each other because of similar spatial niche requirements. In contrast, we

expected that taxa from distinct lineages such as the Gigasporaceae and the Glomeraceae should coexist because they each specialize on different spatial components of the rhizosphere.

We found that community assembly depended on phylogenetic relatedness. Experimental communities were constructed with eight AMF species, but after 1 year of growth, realized species richness was highest in those communities that were assembled using taxa from all three families as compared to those communities assembled using taxa from two or fewer families (Fig. 2C). Realized species richness after 1 year was >80% of the initial value in communities with representatives from all three families. In contrast, communities made up largely of species from one family retained <40% of the initial species pool. We also found that realized species richness in phylogenetically overdispersed communities was similar regardless of the identity of the sampled species within each family (Fig. 2C), a result consistent with our expectation that there is trait conservatism and therefore a degree of functional redundancy within each AMF family (Fig. 2, A and B, and table S1) (19).

We also tested whether the level of phylogenetic dispersion in an AMF community could be influenced by abiotic factors (1). If the abiotic environment acts as a habitat filter, permitting only those species with specific traits or ecological tolerances to co-occur (1, 2), then the conservatism for hyphal length and root colonization in AMF could produce communities that consist only of species that are closely related to each other, or phylogenetically underdispersed (2, 8–10). To determine whether this was the case, we sampled species richness in the old-field community from which the species pool of AMF was derived (17). We found that the community had species from all three AMF families, indicating that it was similar to our experimentally assembled species-rich communities (Fig. 2C). Thus, we conclude that the phylogenetically overdispersed experimental AMF communities we assembled were ecologically realistic.

Because of trait, and therefore niche, conservatism within the AMF (Fig. 2, A and B, and table S1) (19), our results suggest that the primary mechanism responsible for increased species richness in phylogenetically overdispersed communities is competitive exclusion preventing closely related and functionally similar species from co-occurring (2). Our results are therefore consistent with life-history and niche-based determinants of community assembly (4) as opposed to neutral models (20). Nevertheless, there is no clear consensus on the role of evolution in contemporary community assembly, in part because

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the degree of niche conservatism varies with the functional traits of interest (21) and the evolutionary and biogeographic history of a particular group (3). If niche conservatism is absent because natural selection favors ecological divergence among closely related taxa, the community and ecosystem consequences of phylogenetic relationships could be weak (2, 3). However, if niche conservatism is widespread (10, 22, 23), the patterns we report here could occur in many communities, particularly in situations where species interact on fine spatial scales (24).

Our results have implications for understanding the mechanistic basis of the relationship between species richness and ecosystem functions such as productivity, nutrient cycling and resistance to disturbance (25, 26). In particular, one mechanism that explains the positive relationship between species richness and ecosystem productivity is functional trait complementarity among co-occurring species (27). Although many experimental studies have observed support for this mechanism (25, 26), these studies are open to the criticism that measured functional consequences are an artifact of experimental designs in which communities are randomly assembled and artificially maintained over time (26, 28–31). For example, increased productivity at high species richness could be caused by the increased probability that species-rich communities will randomly contain an especially productive species (28, 29). Moreover, the trait complementarity that maintains enhanced ecosystem function in an experimentally produced species-rich community may not be representative of that found in a natural community if these traits do not also promote stable coexistence among the same species (31). Thus, tests of the mechanisms that regulate the relationship between biodiversity and ecosystem function require that community assembly in experimental units reflect realistic, nonrandom ecological processes (26, 30, 32).

Our community assembly results indicate that such a test is possible in the AMF-plant system because two functional traits that contribute to enhanced plant productivity—protection from soil pathogens and increased plant uptake of nutrients (33, 34)—appear to be conserved within an evolutionary lineage along with traits associated with spatial niche specialization. Our experiments (17) indicate that high root colonization by the Glomeraceae in comparison with other AMF families (Fig. 2A) is correlated with reduced root infection of *P. lanceolata* by two common soil pathogens (Fig. 3, A and B). In contrast, the high level of extraradical hyphal growth in the Gigasporaceae as compared with other AMF families (Fig. 2B) is correlated with enhanced P concentration in *P. lanceolata* shoots (Fig. 3C). If greater pathogen protection and enhanced P uptake are complementary, then plant productivity could be stimulated to a greater degree when both Glomeraceae and Gigasporaceae are in the same community. In contrast, the low root colonization (Fig. 2A) and short hyphal

length (Fig. 2B) of the Acaulosporaceae may allow them to coexist with either the Glomeraceae or Gigasporaceae (Fig. 2C), but the low pathogen protection and low P-uptake capacity

associated with these traits (Fig. 3, A to C) suggest that the Acaulosporaceae will not complement the function of the other two AMF families in an ecosystem.

	Experimental Treatments								
	1	2	3	4	5	6	7	8	9
Family Gigasporaceae									
<i>Gigaspora albida</i>		x		x	x				
<i>G. gigantea</i>		x		x	x			x	
<i>G. margarita</i>		x		x		x			
<i>G. rosea</i>		x		x		x		x	
<i>Scutellospora calospora</i>		x	x		x			x	
<i>S. dipurpurens</i>		x	x			x		x	
<i>S. heterogama</i>		x	x		x				
<i>S. pellucida</i>		x	x			x			
Family Acaulosporaceae									
<i>Acaulospora denticulata</i>					x			x	x
<i>A. laevis</i>						x			x
<i>A. morrowiae</i>					x				x
<i>A. spinosa</i>						x		x	x
Family Glomeraceae									
<i>Glomus aggregatum</i>	x			x	x				
<i>G. clarum</i>	x			x				x	
<i>G. constrictum</i>	x		x						
<i>G. etunicatum</i>	x		x		x				
<i>G. hoi</i>	x			x					
<i>G. intraradices</i>	x		x			x			
<i>G. microaggregatum</i>	x			x				x	
<i>G. mosseae</i>	x		x			x			

Fig. 1. Experimental design. Fungal taxa were assigned to each of the experimental treatments on the basis of their phylogenetically defined lineage. In treatments 1, 2, and 8, experimental units were constructed with species from one fungal family; treatments 3 and 4 with species from two fungal families; treatments 5 to 7 with species from three fungal families; and treatment 9 with no fungi.

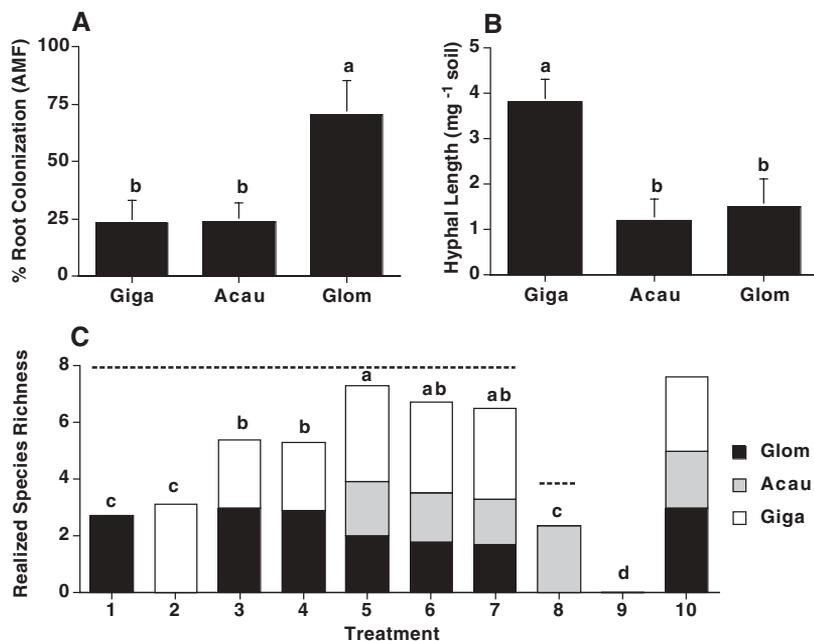


Fig. 2. Community assembly. The effect of different AMF species on (A) percent of root colonization by AMF (a measure of fungal growth inside the root) and (B) hyphal length (a measure of fungal growth outside the root). Each AMF species was grown in monoculture, but results are reported by fungal family (Giga, Gigasporaceae; Acau, Acaulosporaceae; Glom, Glomeraceae). Results by species are reported in table S1 (17). (C) The effect of phylogenetic dispersion of the fungal species pool on community assembly. Treatments are identified in Fig. 1 (number 10 represents the field study). The horizontal dashed lines represent the initial species richness. Different letters above each bar represent statistically significant differences ($P < 0.05$) after an analysis of variance (ANOVA) and a Tukey post hoc test.

We assessed one ecosystem consequence of variation in AMF species richness by measuring plant productivity (total biomass of individual *P. lanceolata*) in each community assembly treatment (Fig. 1) after 1 year of growth. *P. lanceolata* biomass was lowest in communities derived from phylogenetically underdispersed species pools. In fact, plant biomass did not differ significantly from that of nonmycorrhizal controls when grown with only a single AMF family (Fig. 3D). Plant biomass increased when the two putatively complementary AMF families (Glomeraceae and Gigasporaceae) were present in the community (Fig. 3D). In contrast, plant biomass was not stimulated by adding the third, putatively non-complementary AMF family (Acaulosporaceae) to the experimental units. Plant biomass in communities derived from native soil was similar to that in the most productive experimentally assembled fungal communities (Fig. 3D). Therefore, our results also indicate that the effect of a natural field-derived AMF community on plant productivity was ecologically similar to that found in the overdispersed AMF treatment. The complementary effect of the different AMF families on ecosystem function was also supported by a strong positive relation between realized AMF species richness and plant productivity (Fig. 3E).

Most experimental tests of the effects of species richness on ecosystem functioning rely on randomly assembling communities and then maintaining the composition of that community over time (26, 30, 31). Because we allowed AMF com-

munities to develop through a realistic ecological process based on niche conservatism, we could eliminate the role of artificially maintaining a high-diversity treatment (31) in a test for a positive relation between biodiversity and ecosystem functioning. Communities with high realized species richness only occurred when at least two lineages of AMF were present in the starting species pool (Fig. 2C). In addition, these communities contained the highest diversity of hyphal foraging capacity and pathogen protection, suggesting that enhanced plant productivity was caused by niche complementarity (35, 36). Therefore, our explicit consideration of phylogenetic trait conservatism strengthens empirical support for the hypothesis that a positive relationship between diversity and ecosystem function is caused by increased functional trait richness (25–27, 30, 31, 35).

Our results also suggest that phylogenetic relatedness can be a tool for predicting which species losses are most likely to negatively affect ecosystem functioning. For example, when species from multiple evolutionary lineages were replaced with an equal number of species from a single evolutionary lineage in experimental AMF communities, realized species richness and productivity declined. As a result, the functioning of this AMF/plant community is unlikely to be sensitive to species losses from within individual evolutionary lineages. However, the loss of an entire lineage could have strong negative ecological consequences. Our work therefore highlights the utility of information on phylogenetic relation-

ships within communities to prioritize species conservation efforts aimed at maintaining important ecosystem functions and services (37).

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Supporting Online Material

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Materials and Methods

Table S1
References

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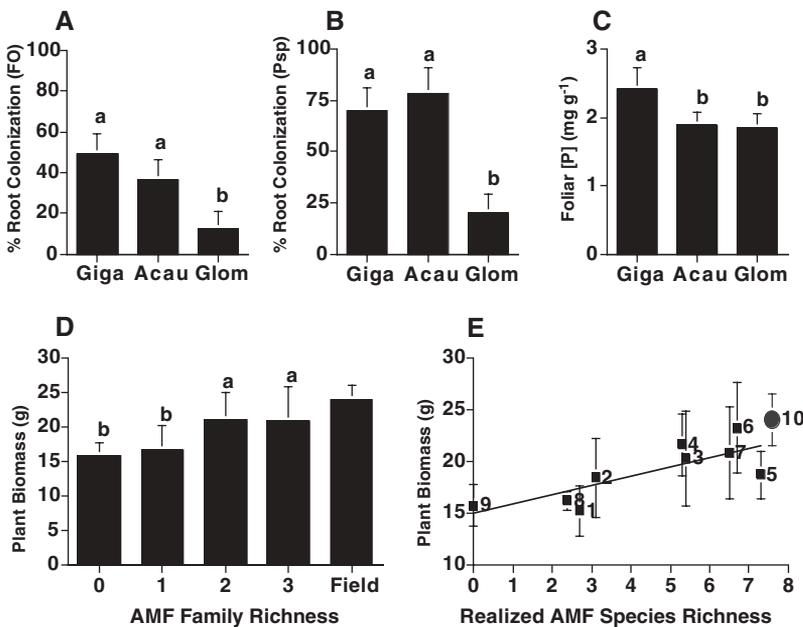


Fig. 3. Ecosystem functioning. The effect of different AMF species on (A) percent of root colonization by *Fusarium oxysporum* (FO) (root pathogen 1), (B) percent of root colonization by *Pythium* sp. (Psp) (root pathogen 2), and (C) foliar P concentration. Each AMF species was grown in monoculture, but results are reported by AMF family. Results by species are reported in table S1 (17). (D) The effect of phylogenetic dispersion (AMF family richness) and (E) realized AMF species richness on plant biomass ($y = 0.91x + 14.92$; $r^2 = 0.24$; $P = 0.001$). The numbers next to the boxes represent the experimental treatments in Fig. 1. The circle identified with number 10 represents the field study. Different letters above each bar in (A) to (D) represent statistically significant differences ($P < 0.05$) after an ANOVA and a Tukey post hoc test.