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REPORT

Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity

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Abstract

The potential for mycorrhizae to influence the diversity and structuring of plant communities depends on whether their affinities and effects differ across a suite of potential host species. In order to assess this potential for a tropical forest community in Panama, we conducted three reciprocal inoculation experiments using seedlings from six native tree species. Seeds were germinated in sterile soil and then exposed to arbuscular mycorrhizal fungi in current association with naturally infected roots from adults of either the same or different species growing in intact forest. The tree species represent a range of life histories, including early successional pioneers, a persistent understory species, and emergent species, typical of mature forest. Collectively, these experiments show: (i) the seedlings of small-seeded pioneer species were more dependent on mycorrhizal inocula for initial survival and growth; (ii) although mycorrhizal fungi from all inocula were able to colonize the roots of all host species, the inoculum potential (the infectivity of an inoculum of a given concentration) and root colonization varied depending on the identity of the host seedling and the source of the inoculum; and (iii) different mycorrhizal fungal inocula also produced differences in growth depending on the host species. These differences indicate that host–mycorrhizal fungal interactions in tropical forests are characterized by greater complexity than has previously been demonstrated, and suggest that tropical mycorrhizal fungal communities have the potential to differentially influence seedling recruitment among host species and thereby affect community composition.

Keywords

Anacardium, *Dipteryx*, diversity, *Ficus*, *Licania*, *Luehea*, mutualism, mycorrhizae, *Ochroma*, reciprocal inoculation, specificity, *Theobroma*, tropical forests.

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INTRODUCTION

Arbuscular mycorrhizal (AM) associations with host plants have been documented in numerous host species over an extensive range of habitats (see Brundrett 1991). Although the importance of the effects of mycorrhizae on host survival and growth is increasingly appreciated, many basic questions remain. For example, the extent to which different mycorrhizal fungi interact differently with different host species is only beginning to be explored. Such inquiries hold consequential implications for understanding the community composition of host plant species (van der Heijden *et al.* 1998). Specifically, if AM fungal species show different affinities and effects on fitness across different host species, then mycorrhizal fungal communities have the potential to influence the diversity and distribution of the associated host plants (Grime *et al.* 1987; Connell & Lowman 1989; Allen 1991; Bever 1992; Johnson *et al.* 1992; Alexander *et al.* 1992; Francis & Read 1994; Leigh & Rowell 1995; Bever *et al.* 1996; Bever *et al.* 1997; Helgason *et al.* 1998; van der Heijden *et al.* 1998).

The observation that AM fungal species are able to colonize the roots of most host plant species (Malloch *et al.* 1980; Janos 1980) appears to be consistent with the view that differential affinities and effects are unlikely. However, evidence is accumulating that AM fungal communities are composed of complex mixes of functionally distinct species, that even nearby sites can differ in mycorrhizal fungal composition, and, importantly, that individual species can have a spectrum of effects on

different host plants (van der Heijden *et al.* 1998). These effects appear to depend upon the AM fungal species, their compatibility with particular host species, and on the environmental conditions in which the plant is growing (Howeler *et al.* 1987; Francis & Read 1994, 1995; Johnson *et al.* 1997; Helgason *et al.* 1998, 1999; van der Heijden *et al.* 1998).

Unfortunately, essentially all such studies have been carried out on herbaceous species from temperate grassland communities, and information is particularly scarce for host–AM fungal interactions in the extremely diverse communities found in tropical rainforests. The potentially beneficial effect of mycorrhizae in tropical forests has been shown by the increased growth of seedlings from a range of tropical tree species when infected with mycorrhizae, compared with nonmycorrhizal controls (Janos 1980). Nonetheless, the fungi were derived from the roots of a single host species, and therefore this experiment does not address the key issue of the degree to which different components of tropical AM fungal communities have differential effects on native plant species.

In order to test for differences in affinities and effects of tropical AM fungal communities on their hosts, we used naturally infected roots of different tree species growing in intact tropical forest as the source of inocula for seedlings of either the same or different species. Using two pioneer species and four species more typical of mature tropical forest in Panama (see Leigh 1999), we conducted three greenhouse experiments to test whether host seedlings are differentially colonized when supplied with the same quantity of root inocula, and whether there are differential effects on host growth depending on the identity of the host and the source of the AM fungal inocula. We thereby assess the potential for host–AM fungal associations to affect the diversity and distribution of trees in tropical forest.

METHODS

The experiments were carried out from October 1996 to April 1998 on Barro Colorado Island, a field station operated by the Smithsonian Tropical Research Institute in the Republic of Panama (9°10′ N, 79°51′ W), mean precipitation 2.6 m. For detailed descriptions of the vegetation and climate refer to Leigh *et al.* (1982) and Leigh (1999). Intense sampling in this forest has shown that ectomycorrhizal fungi, which often dominate the mycorrhizal flora of temperate forests, are vanishingly rare. Further, preliminary molecular analyses show that different AM fungal species are often associated with different host species in this Panamanian forest (P. Young, R. Gallery, R. Husband, and E.A. Herre, unpublished).

We chose seedlings from six host species that represent a range of life histories found in the Panamanian forest: three large seeded (>1 g), mid-to late-successional species associated with mature forest species, *Anacardium excelsum* (Bertero and Balb.) Skeels (Anacardiaceae), *Dipteryx panamensis* (Pitt.) Rec & Mell (Fabaceae/Papilonoidea), *Licania platypus* (Hemsl.) Fritsch (Chrysobalanaceae), an understory tree species, *Theobroma cacao* L. (Sterculiaceae), and two small-seeded (<0.005 g) pioneer species, *Luehea seemannii* Tr. & Planch. (Tiliaceae), and *Ochroma pyramidale* (Cav. ex Lam.) Urban (Bombacaceae). Previously examined roots from adults showed that all species have arbuscular mycorrhizal associations (Janos 1996; E. Kiers, unpublished).

In all experiments, the AM fungal inoculum consisted of chopped and homogenized root fragments obtained from at least three adult individuals of the species used in the experiments. We also included roots from *Ficus insipida* (experiment 3) and the palm, *Oenocarpus panamanus* (experiment 2), an inoculum that has been used in previous experiments (see Lovelock *et al.* 1996). Importantly, in order to insure that the AM fungi obtained from the field roots were currently symbiotic with the root segment of those species, all excess soil was removed by thoroughly washing the roots. To equalize the amount of other soil microflora in each pot we added a filtrate made from the collected roots soaked in water and filtered through a fine mesh (40 μm) to exclude AM fungal spores. In order to ensure the control plants uninoculated with a live mycorrhizal source had similar levels of organic matter in each pot, equal weights of chopped, washed roots were sterilized in an autoclave and then added to the soil of the controls.

Soil for all experiments was a well-drained Alfisol with approximately 200 mg kg^{-1} phosphorous, 1100 mg kg^{-1} nitrogen, 300 mg kg^{-1} sulphur and 3000 mg kg^{-1} carbon (Yavitt *et al.* 1993), obtained from between 30 and 100 cm below the surface. The soil was mixed with washed river sand (one part sand: one part soil) to improve drainage. Soil in experiments 1 and 3 were sterilized in an autoclave oven for 1 h at 120°C (see Howeler *et al.* 1987). Soil for the second experiment was sterilized using a one time application of 4.4 g L^{-1} 50% benomyl, which showed no apparent residual effects (see Fitter & Nichols 1988). Trial seedlings were clear of all AM fungal colonization after 3 weeks of growth in the sterilized soil.

In experiments 1 and 3, the seeds were germinated on sterile soil in nursery flats and later transplanted into individual "Tall one" (10 × 10 × 35 cm) tree pots (Hummert Int., Earth City, MO) that contained either inoculated or control soils. In experiment 2, an excess of seeds was germinated directly in the inoculated and control pots and then thinned to obtain seedlings with

similar initial sizes. In all cases, seedlings received 50% full sunlight in a uniformly lit, screened greenhouse. They were exposed to ambient levels of humidity of 80%–100% and air temperatures of 28–35°C. Leaf area was measured using an area meter (Li-3000 A, attached to a transparent belt conveyer Li-3050 A, Li-Cor, Lincoln, NE).

Experiment 1: AM inoculum potential for late-successional species

The first experiment was designed to test for differences in affinities that AM fungi derived from different sources might have for forming AM associations with seedlings of *Anacardium excelsum* and *Dipteryx panamensis*, both large-seeded, mid-to late-successional species typically found in mature forest. Chopped root fragments from either conspecific or heterospecific adults were thoroughly mixed with sterile soil in a 10-fold dilution series from 1/10 to 1/100 000 by weight, with five replicates of each host–inoculum combination per dilution and five sterile controls. The 1/10 dilution falls within the range of fine roots densities often found in tropical forest soils (i.e. 100–500 g m^{-2} for a surface layer of soil 10 cm deep, Sanford & Cuevas 1996). After 5 weeks, the entire root system of each seedling was cleared and stained using the methods of Kormanik & McGraw (1982), substituting methyl blue in 0.05% acidified glycerol for the phenol component. The presence of AM fungal colonization was based on scoring presence or absence of arbuscules, hyphae, vesicles or intraradical spores (see Carling & Brown 1982; Morton & Bentivenga 1994). These data were then used to conduct a most probable number (MPN) bioassay to compare the inoculum potential of different host-inoculum combinations (Adelman & Morton 1986) (Table 1). The presence of any nonmychorrhizal fungi was also noted.

In this experiment, survival and growth of the seedlings were also followed across the different treatments for the 5-week period. Initial measurements of the transplanted seedlings included fresh weights and height. Final measurements included fresh weight of roots, stems, and leaves, plant height, total leaf area, and dry weights of stems and leaves for each seedling. To control for the high variability in initial size of the seedlings, relative growth rates were used to measure differences in growth. For each seedling these rates were determined as $[\ln(Wt_2) - \ln(Wt_1)]/(t_2 - t_1)$, where Wt_1 and Wt_2 are the dry weights of the plants at the beginning and end of the experiment, and t is time. Because the entire root system of each seedling was used for assessing colonization with AM fungi, the final dry weights of the roots were estimated by multiplying the root fresh weight by a dry to fresh weight ratio established using plants not included in the experiment. Initial weights of seedlings were estimated from measures of plant height.

Experiment 2: Growth in seedlings of two pioneer species with three inoculum sources

The second experiment was designed to test for differences in root colonization and survival and growth in seedlings of the small-seeded pioneer species *L. seemannii* and *O. pyramidale*. The three inoculum treatments consisted of 15 g of coarsely chopped roots from either *L. seemannii*, *O. pyramidale*, or the palm, *O. panamanus*. This single dilution gave approximately the same root concentration as the 1/10 dilution for late-successional species in experiment one. There were seven replicates for each treatment, including controls. At the completion of the experiment plants were harvested. Final fresh weights for leaves, stem, and roots, as well as final leaf areas were also measured, after which each plant was dried. A randomly selected subsample of each root system was cleared and stained to determine the percentage of the root system with AM colonization. The subsamples then were quantified using a modified technique of McGonigle *et al.* (1990), examining at least 40 2–3 cm long segments scored under a light microscope.

Experiment 3: Growth in seedlings of pioneer and late-successional species with six inoculum sources

The third experiment was designed to examine growth in seedlings exposed to six different inoculum sources. We

Table 1 Summary of colonization results from experiment 1: estimates of infective propagule numbers and upper and lower 95% confidence intervals (CI) based on "most probably number" counts for particular host-inoculum combinations of *Dipteryx panamensis* and *Anacardium excelsum*, two mature forest species. Note that the inoculum from *A. excelsum* has a significantly higher affinity for colonizing the roots of conspecific seedlings. Incoculum from *D. panamensis* trends in the same direction, but not significantly.

Inoculum source	Host species	# of infective propagules	Upper 95% CI	Lower 95% CI
D. panamensis	*D. panamensis*	4922	16242	1491
D. panamensis	*A. excelsum*	2305	7606	698
A. excelsum	*A. excelsum*	23054	42084	3864
A. excelsum	*D. panamensis*	780	2574	236

used seedlings from two late-successional species (*T. cacao*, a persistent understory tree, and *Licanea platypus*, a mature forest species) and one pioneer species (*Luehea seemannii*). Similar sized seedlings were inoculated with adult roots from each of six species including the three host species, two sources used in the first experiment (*A. excelsum* and *D. panamensis*), plus *Ficus insipida* Willd. (Moraceae), a small-seeded pioneer species commonly found in secondary forest. There were seven plants per treatment, including controls. The procedures for inoculation and the determination of the percentage of root colonized were the same as those in experiment 2.

The effects of inocula on relative growth rates, percentage root colonization and final leaf areas were analysed using analysis of variance (ANOVA) with the host plant species and inoculum as fixed effects, omitting the data from the nonmycorrhizal control plants. Leaf area data was logarithmically transformed prior to analysis to normalize the variance. The adequacy of the models was assessed by inspecting residual plots. When studentized residuals of the target variables were greater than $\pm$ 3, these outliers were removed from the analysis.

RESULTS

Dependency of host species on AM

By comparing the seedlings that either were or were not exposed to mycorrhizal fungi, the experiments permitted the assessment of the relative dependence on mycorrhizae for survival and growth in the different species. No seedlings of the late-successional species in experiment 1 died in the absence of mycorrhizal inoculum. However, in experiment 2, uninoculated (nonmycorrhizal) seedlings of both pioneer species showed significantly higher mortality compared with seedlings inoculated with any live mycorrhizal inoculum source. Over the course of the experiment, eight of 11 (73%) nonmycorrhizal *O. pyramidale* seedlings died compared with one of 31 (3%) mycorrhizal seedlings ($\chi^2 = 21.9$, $P < 0.0001$). Similarly, 14 of 17 (82%) nonmycorrhizal *L. seemannii* seedlings died compared with 12 of 25 (48%) mycorrhizal seedlings ($\chi^2 = 5.40$, $P = 0.021$). In experiment 3, there were no significant differences in the survival of the nonmycorrhizal controls (seven seedlings total for each species) or the mycorrhizal experimental treatments. However, it should be noted that in the case of the surviving seedlings of the small-seeded pioneer species, the nonmycorrhizal control plants always showed significantly decreased growth compared with those with AM fungal inocula from whatever source in both experiments 2 and 3 (Tables 2, 3). In contrast, in the large-seeded, mid-to late-successional species, the nonmycorrhizal control plants always showed similar or greater growth in both experiments 1 and 3 (Fig. 1, Tables 3, 4).

Table 2 Summary of growth results from experiment 2: the effects of inocula obtained from tree roots of con-and heterospecifics on the final leaf area of tree seedlings from two pioneer species after 9 weeks of growth. Values are the means of 3–7 plants $\pm$ standard errors. In this experiment, inoculum effects were significant; F 2,22 = 6.16, $P = 0.008$.

Tree species	Inoculum	Final leaf area (cm^2) $\pm$ SE
Luehea seemannii	Sterile	17 $\pm$ 15
	Luehea	97 $\pm$ 66
	Ochroma	79 $\pm$ 18
	Oenocarpus	190 $\pm$ 13
Ochroma pyramidale	Sterile	56 $\pm$ 54
	Luehea	177 $\pm$ 44
	Ochroma	319 $\pm$ 73
	Oenocarpus	424 $\pm$ 62

Table 3 Summary of growth results from experiment 3: the effect of inocula obtained from tree roots of a range of both con- and heterospecific species on the final leaf area of tree seedlings after 9 weeks of growth. Values are the means of 5–7 plants $\pm$ standard errors. In this experiment host species $\times$ inoculum effects were significant; F 10,100 = 2.21, $P = 0.023$. m, mature forest species; p, pioneer species; u, understory species.

Tree species	Inoculum	Final leaf area (cm^2) $\pm$ SE
Licania platypus (m)		
	Sterile	267 $\pm$ 19
	Anacardium (m)	198 $\pm$ 26
	Dipteryx (m)	268 $\pm$ 48
	Ficus (p)	275 $\pm$ 23
	Licania (m)	240 $\pm$ 35
	Luehea (p)	332 $\pm$ 25
	Theobroma (u)	207 $\pm$ 27
Luehea seemannii (p)		
	Sterile	2.4 $\pm$ 0.3
	Anacardium	24.0 $\pm$ 4.9
	Dipteryx	29.1 $\pm$ 5.7
	Ficus	30.8 $\pm$ 7.1
	Licania	47.7 $\pm$ 7.5
	Luehea	26.5 $\pm$ 6.9
	Theobroma	18.1 $\pm$ 1.7
Theobroma cacao (u)		
	Sterile	531 $\pm$ 60
	Anacardium	496 $\pm$ 46
	Dipteryx	532 $\pm$ 24
	Ficus	533 $\pm$ 27
	Licania	521 $\pm$ 61
	Luehea	446 $\pm$ 16
	Theobroma	584 $\pm$ 69

Table 4 Summary of results from the different experiments with respect to whether different host/inocula combinations show differences in colonization, growth, or dependence of seedlings on mycorrhizae for initial growth and survivorship.

Differences in:	colonization	growth	dependence
Experiment 1 (large-seeded mature forest species)	yes	yes	no
Experiment 2 (small-seeded pioneer species)	yes	yes	yes (both survival and growth)
Experiment 3 (mix of species types)	no	yes	pioneer species, yes (growth) mature and understory species, no

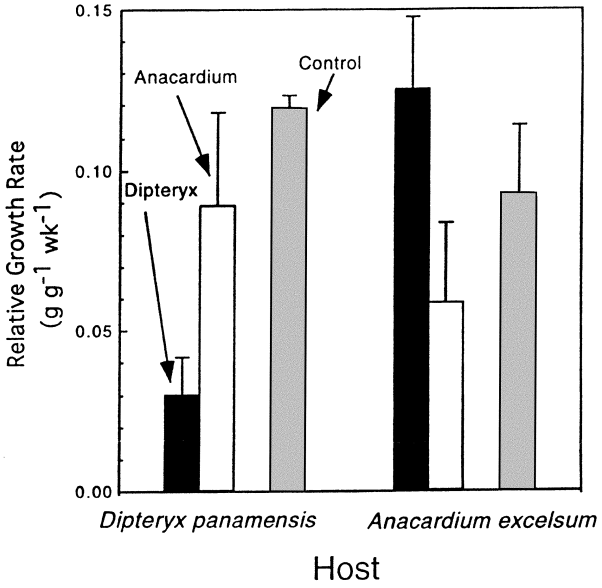

Figure 1 Relative growth rates of seedlings of the two mature forest host species used in experiment 1, *Anacardium excelsum* and *Dipteryx panamensis* (Pitt.). Host seedlings were inoculated with arbuscular mycorrhizal fungi from a 1/10 dilution (see text) of root inocula obtained from conspecific or heterospecific adults, or not inoculated (control). Values are the means of five plants ± standard errors. In this experiment, host species × inoculum effects were significant; F 1,15 = 7.57, $P = 0.015$.

Infectivity of host-inoculum combinations and root colonization

In the first experiment, using the mid-to late-successional species, the lowest concentration of root dilution (1/100 000) to produce AM fungal colonization was from a conspecific source for both mature forest species. Further, for the *Anacardium excelsum* inoculum there was a significantly higher affinity for the roots of conspecific seedlings compared with heterospecific seedlings. Results with the AM fungal inoculum obtained from *Dipteryx panamensis* showed a similar pattern that was nonsignificant (Table 1). In the second experiment using the pioneer species, seedlings of *L. seemannii* showed significantly higher AM fungal colonization when exposed to either conspecific (36.14%, SE 6.07) or the palm inocula (32.11%, SE 4.21), compared with *O. pyramidale* inoculum (25.01, SE 4.74) (host species × inoculum F 2,25 = 3.67, $P = 0.040$). In contrast, there was no significant difference in colonization of *O. pyramidale* seedlings across different inocula treatments. In experiment 3, only reciprocal crosses between *L. seemannii* and *L. platypus* were scored and no significant differences in colonization were found ($P > 0.05$; Table 4).

Growth

In all three experiments, seedlings showed significantly different growth patterns depending on the source of AM fungal inoculum (Table 4). In experiment 1, analysis of the relative growth rates of the different seedling × inoculum combinations across all dilutions showed significant inoculum effects (F 1,95 = 7.83, $P = 0.006$) and significant host species–inoculum interactions (F 1,95 = 8.83, $P = 0.0038$). The 1/10 dilution, corresponding to the concentration of root inoculum used in the other experiments, did not show a significant inoculum effect, but did show a significant host species–inoculum interaction (F 1,15 = 7.57, $P = 0.015$; Fig. 1). In experiment 2, final leaf area showed a significant inoculum effect (F 2,22 = 6.16, $P = 0.008$; Table 2). However, in this case, there was no significant host species–inoculum interaction. In experiment 3, analysis of final leaf area showed a significant host species–inoculum interaction (F 10,100 = 2.21, $P = 0.023$; Table 3).

Moreover, in six out of seven cases, the greatest seedling growth was *not* observed with inoculum derived from conspecific adults (Fig. 1, Tables 2, 3). One explanation for the relatively reduced growth observed in these treatments is the potential effects of species-specific pathogens present in the conspecific inoculum source. However, there was no evidence of pathogen-related symptoms (necrosis, etc.) in any seedlings, nonmycorrhizal fungi were observed in only five root samples, and these cases showed no relationship to type of inoculum. Nonetheless, in order to test whether the

interactions between host growth and inocula were driven by the effects of the conspecific inocula, we analysed the results of experiments 2 and 3 for each species excluding the conspecific cases. Where it was possible to conduct these analyses (the two experiments in which the number of inocula exceeded the number of hosts), there were still significant differences in growth depending on the host-inoculum combination (in all cases the effect of inocula was significant, $P < 0.05$).

DISCUSSION

Factors that increase the heterogeneity of environments for seedling recruitment have the potential to enhance tree species diversity (Grime *et al.* 1987; Tilman & Pacala 1993). In order for AM fungal communities to provide such diversity enhancing heterogeneity, two criteria must be fulfilled. First, different AM fungal species must differentially influence survival and growth of different host plant species. Second, those different AM fungal species must be differentially distributed within the community and/or exhibit differential affinities for different hosts. Recent work using pure cultures of different AM fungal species isolated from temperate grassland communities suggests that different components of AM fungal communities differentially affect host species, and that the complexity of the AM fungal community can influence host diversity (van der Heijden *et al.* 1998). Moreover, there is accumulating evidence that AM fungal species distributions are likely to vary according to plant species composition in a particular site (Johnson *et al.* 1992; Dahlberg & Stenlid 1994; Bever *et al.* 1996, 1997; Wilkinson 1997; Helgason *et al.* 1998, 1999).

Here, we have established that six host species from a Panamanian forest differ in the dependence of their seedlings on AM for initial survival and growth, and that root colonization levels and seedling growth differ depending on the identity of the host species and the source of the AM fungal inoculum. These results are ecologically relevant for several reasons. Firstly, the duration of our experiments corresponds to the initial stages of seedling establishment, during which natural mortality is highest (Janzen 1970; Kitajima 1996). Secondly, the AM fungal species were in current, active association with trees whose extensive root systems dominate substantial portions of forest floor over which the seeds are dispersed (see Wilson 1993; Hughes *et al.* 1994; Wilkinson 1997; Dalling *et al.* 1998; Helgason *et al.* 1999). Finally, the target species represent ecologically distinctive forest trees that range from early to late-successional species. Together, these results strongly suggest that tropical AM fungal communities have the potential to affect patterns of seedling recruitment, and thereby influence community-wide patterns of host densities and distributions.

Within the overall pattern of differential effects of different incoulum sources on different host plants are a series of suggestive patterns. Specifically, the seedlings of small-seeded pioneer species show dramatically greater initial dependence on AM for survival and growth. This is likely to reflect the initial differences in resources available to developing seedlings. Further, where differences were found, the inocula showing the highest affinities for seedlings generally was derived from conspecific adults. This suggests that at least the details of the formation of host symbiont associations vary among different combinations of species. Finally, if the reduced growth exhibited by seedlings inoculated by conspecific adults is a general phenomenon, then our results suggest that what is adequate for the adults growing with their emerged canopies may not be best suited for the needs of the juveniles growing in a shaded understory, and that seeds dispersed farther from their parent are more likely to encounter AM fungi that are favourable to initial growth. It is possible that differential effects of mycorrhizae on adults and juveniles may play a role in the frequently observed phenomenon of negative density dependence.

Although preliminary, these results suggest that the complexity of interactions in natural tropical settings is greater than has been previously appreciated (Janos 1980; Connell & Lowman 1989; Leigh & Rowell 1995; Bever *et al.* 1997). If different combinations between hosts and communities of AM fungal species affect seedling performance in the field, as we have shown in the greenhouse, then AM fungi could be a factor that promotes species diversity in tropical forests through promoting habitat diversity.

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BIOSKETCH

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