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Chapter 2

LARGE-SCALE DIVERSITY PATTERNS IN SPORE COMMUNITIES OF ARBUSCULAR MYCORRHIZAL FUNGI

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ABSTRACT

Surprising little is known about the factors controlling Arbuscular Mycorrhizal (AM) fungal diversity and distribution patterns. A better understanding of these factors is necessary before mycorrhizas can be effectively managed for their benefits in ecosystem restoration and agriculture. The goal of this chapter is to examine the relationships between AM fungal diversity, plant diversity and latitude across a variety of vegetation types and disturbance regimes. We created a large database by compiling seven distinct datasets from across North America to test the hypotheses that 1) diversity of AM fungal communities should be positively related to plant diversity; 2) AM fungal diversity should be higher in low latitudes than in high latitudes; and 3) disturbance and land use should influence AM fungal diversity. The database was composed of 523 samples collected by research groups from Mexico and United States of America with eight different vegetation types and land uses. Abundance of 121 AM fungi taxa as well as data on geographic location, vegetation type, and disturbance history were included in the database. Contrary to our expectations, species richness and evenness of AM fungal spore communities were not correlated with plant richness or latitude. The influence of disturbance on AM fungal species diversity varied with climate. Our findings indicate

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that the factors controlling community diversity differ for plants and mycorrhizal fungi. Disturbance influences AM fungal spore diversity, and the outcome of these effects varies among ecosystems.

Keywords: Arbuscular mycorrhizal fungi, disturbance, diversity, land use, North America.

INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are ancient soil organisms belonging to the Phylum Glomeromycota (Schüβler et al. 2001). These fungi form obligate symbiotic relationships with plant roots in most terrestrial ecosystems (Trappe 1987, Harrison 1997, Camargo-Ricalde 2002). In this symbiosis, the fungi facilitate plant uptake of soil resources and reciprocally gain fixed carbon (Smith and Read 1997). Moreover, AM fungi can affect plants' competitive abilities (Guadarrama et al. 2004) and play a determinant role in regeneration and plant succession (Carey et al. 1992, Allsopp and Stock 1994, Kardol et al. 2006). Mycorrhizal hyphae contribute to soil aggregate formation, soil conservation and reestablishment of plants in disturbed areas (Bethlenfalvay 1992, Cuenca et al. 1998, Miller and Jastrow 2000). In this regard, AM fungi play key roles in plant community structure, and ecosystem processes.

Despite their wide distribution and importance in ecosystems, the factors that influence the geographic distribution of AM fungi in natural and managed ecosystems are still unclear, in large part because of the difficulty of studying these fungi in nature, and the complex factors that can affect their distribution. Chaudhary et al. (2008) proposed a model for Glomeromycotan biogeography that illustrates this complexity. In the early Devonian (400 million years ago), plants had endophytic associations resembling vesicular–arbuscular mycorrhizas (Brundrett 2002), and continental drift may have contributed to diversification and large scale distribution patterns of AM fungi (Allen et al. 1995, Chaudhary et al. 2008). At a more proximate timescale, abiotic forces such as climate and soil properties, combined with biotic forces such as host plant community composition and inter- and intra-specific interactions are likely to be important factors (Rillig et al. 2002, Pringle et al. 2009). Furthermore, Glomeromycotan distribution may be controlled by intrinsic properties of the fungi such as their dispersal ability (Warner et al. 1987) and speciation and extinction rates (Chaudhary et al. 2008). Finally, disturbance history is likely to be an important driver of Glomeromycotan biogeography (Egerton-Warburton et al. 2007, Alguacil et al. 2008).

Glomeromycota are obligate biotrophs, consequently, their distribution is ultimately dependent on the distribution of living plants. Despite this restriction, AM fungi are often reported to have low host specificity because in controlled experiments individual fungal taxa have been shown to colonize hundreds of different plant species (Trappe 1987, Allen et al. 1995, Sanders 2003). However, upon closer examination, AM fungi do exhibit some degree of host preference in natural systems (Bever et al. 2001, Helgason et al. 2002); certain taxa of AM fungi proliferate with certain plant species (e.g. Johnson et al. 1992, Bever et al. 1996, Helgason et al. 1998, Vandenkoornhuyse et al. 2002). Several studies show that AM fungi can influence plant diversity and productivity (van der Heijden et al. 1998, Hartnett and Wilson 1999). Moreover, it has been reported that individual species of AM fungi and different assemblages of fungal taxa have variable effects on plant productivity and community structure (Klironomos et al. 2000, Klironomos 2002). Consequently, mycorrhizal

symbioses may influence how plant species coexist and how soil resources are distributed among co-occurring plant species (van der Heijden et al. 2003). It is clear that AM fungi are an important regulator of plant community structure, but what are the reciprocal effects of plants on the community structure of AM fungi?

Wardle et al. (2004) suggest that aboveground and belowground diversity is often linked, but studies show contradictory patterns in the relationship between plant diversity and mycorrhizal fungal diversity. Arbuscular mycorrhizal fungal diversity may have positive (Burrows and Pfleger 2002, Oehl et al. 2003, Chen et al. 2004, Börstler et al. 2006), negative (Pietikäinen et al. 2007, Antoninka in preparation), no relationship (Johnson and Wedin 1997), or scale dependent relationships (Landis et al. 2004) with plant diversity.

There is generally a negative relationship between diversity and latitude among many groups of macro and microorganisms (Rosenzweig 1995, Kaufman and Willig 1998, Willig et al. 2003), though exceptions exist (Hillebrand 2004, Hughes et al. 2006). Since tropical plant communities are generally much more diverse than temperate plant communities, one may expect that AM fungal diversity may also exhibit a negative relationship with latitude. Surprisingly little is known about latitudinal patterns in AM fungal distribution. Taxonomists have informally noted that AM fungal diversity appears to be greater in tropical locations, with a greater diversity of Gigasporaceae species in particular closer to the equator (Walker 1992, Herrera-Peraza et al. 2001). Formal comparisons of AM fungal diversity between tropical and temperate locations using field spore data (Chaudhary et al. in preparation) and meta-analysis (Öpik et al. 2008) have demonstrated higher diversity in the tropics (but see Stutz et al. 2000). Studies within temperate North America, have demonstrated latitudinal gradients in species distributions (Koske 1987, Allen et al. 1995), but a large-scale latitudinal gradient study of AM fungal species that spans temperate and tropical locations has never been conducted for AM fungi.

Disturbance can play a pivotal role in ecosystems from promoting species diversity (Odion and Sarr 2007) to reducing ecosystem function and diversity (Jiménez-Esquilina et al. 2007, Odion and Sarr 2007), depending on the type and severity of the disturbance. AM fungi can be sensitive to disturbances that alter soil characteristics, such as tillage, agricultural and land management practices. But, can these disturbances influence AM fungal diversity? Tillage practices can alter AM fungal community composition and reduce sporulation of certain AM species (Jansa et al. 2002, Alguacil et al. 2008). Nitrogen enrichment or fertilization can reduce or increase AM species richness and diversity depending on the amount of available phosphorus and types of available host-plants (Egerton-Warburton et al. 2007). As the amount of N-deposition increases, it can promote a shift in AM fungal species composition, favoring certain *Glomus* species and displacing 'larger' spore species (Egerton-Warburton and Allen 2000). Soil compaction has been shown to reduce or have no effect on AM fungal colonization (*reviewed in* Entry et al. 1996, Nadian et al. 1997). Management practices, such as forest fuel reduction, can reduce AM fungal propagule abundance (Korb et al. 2004), reduce AM species richness and alter community composition (Owen et al. 2009). Disturbances associated with exotic plant invasions can either inhibit or promote AM fungal growth (Pringle et al. 2009).

Disturbances associated with climate change can also influence the distribution of AM fungi. Simulated climate change, by warming can increase the hyphal length of AM fungi and root colonization (Rillig et al. 2002). CO_2 enrichment tends to increase AM fungal abundance while N deposition tends to decrease AM fungal abundance (*reviewed by* Treseder 2004).

Some AM fungi respond differently to soil disturbances, for example Hart and Reader (2004) found that species from the suborder Glomineae were much less resilient to soil disturbances than species from the suborder Gigasporineae, likely due to the traits of either colonizing plant roots mostly by hyphae or by spores.

Molecular methods are increasingly useful for identification of Glomeromycota in field collected samples (Börstler et al. 2006, Hempel et al. 2007), and these methods have been successfully applied to biogeographical studies (Oehl et al. 2003, Öpik et al. 2008). However the usefulness of molecular data to study large scale patterns of AM fungal diversity is limited because currently there are relatively few data sets available which use the same gene regions to identify AM fungi. Unlike molecular data, many data sets of AM fungal spore populations from a wide range of locations are currently available. Analysis of AM fungal spore populations in soils can provide a useful indicator of community composition and diversity (e.g. check Bever et al. 2001, check Landis et al. 2004) as long as the strengths and weaknesses of this method are recognized (Table 1). Spore community data does not provide a perfect measure of AM fungal diversity because not all AM fungi produce spores (Clapp et al. 1995). Also, there is no relationship between spore abundance and total fungal biomass in roots and soils; some taxa of AM fungi produce copious spores, while other taxa produce very few spores per unit biomass. Consequently cross-species comparison of spore abundance is not useful; however, within a single species of AM fungus, comparison of spore abundance across treatments or environmental gradients can be very informative (e.g. Johnson et al. 1991, 1992). Furthermore, large scale patterns in species richness and community composition of AM fungal spores across environmental gradients can be very useful (e.g. Egerton-Warburton et al. 2007).

This chapter reports the results of a large-scale study of the species richness, evenness and diversity of AM fungal spores across temperate and tropical latitudes and plant diversity and disturbance gradients in natural and managed lands. The goal of this chapter is to help elucidate the factors controlling the distribution and diversity of this important group of fungi by addressing three questions. First, what is the relationship between plant diversity and AM fungal diversity? Second, is AM fungal diversity greater at tropical latitudes than temperate latitudes? Finally, how does disturbance and land use influence AM fungal diversity?

Table 1. Strengths and weaknesses of spore analysis

Strengths Spore population data CAN	Weaknesses Spore population data CAN NOT
Elucidate occurrence of spore-forming AM fungi	Detect occurrence of AM fungi that do not sporulate
Inform ecological inferences ***within*** morpho-species of AM fungi	Inform ecological inferences ***between*** morpho-species of AM fungi
Measure reproductive allocation to spores	Measure total biomass of AM fungi
Reveal patterns in AM fungal community structure	Reveal AM fungal functioning

METHODS

We compiled seven distinct datasets to generate a large database composed of 523 samples from 8 sites in Mexico and United States of America (USA) (Figure 1). These sites included eight distinct vegetation types and land uses: tropical wet forest, tropical dry forest, temperate forest, pasture, grassland, shrubland, old field and cropland. More details of the study sites can be found in Table 2. A total of 121 AM fungal taxa were reported in the database, of which 76 were identified to species. Geographic location, disturbance history, climate and soil properties were included in the database. Although data were collected by different researchers and for different purposes, our collection techniques were similar enough to allow for useful comparisons.

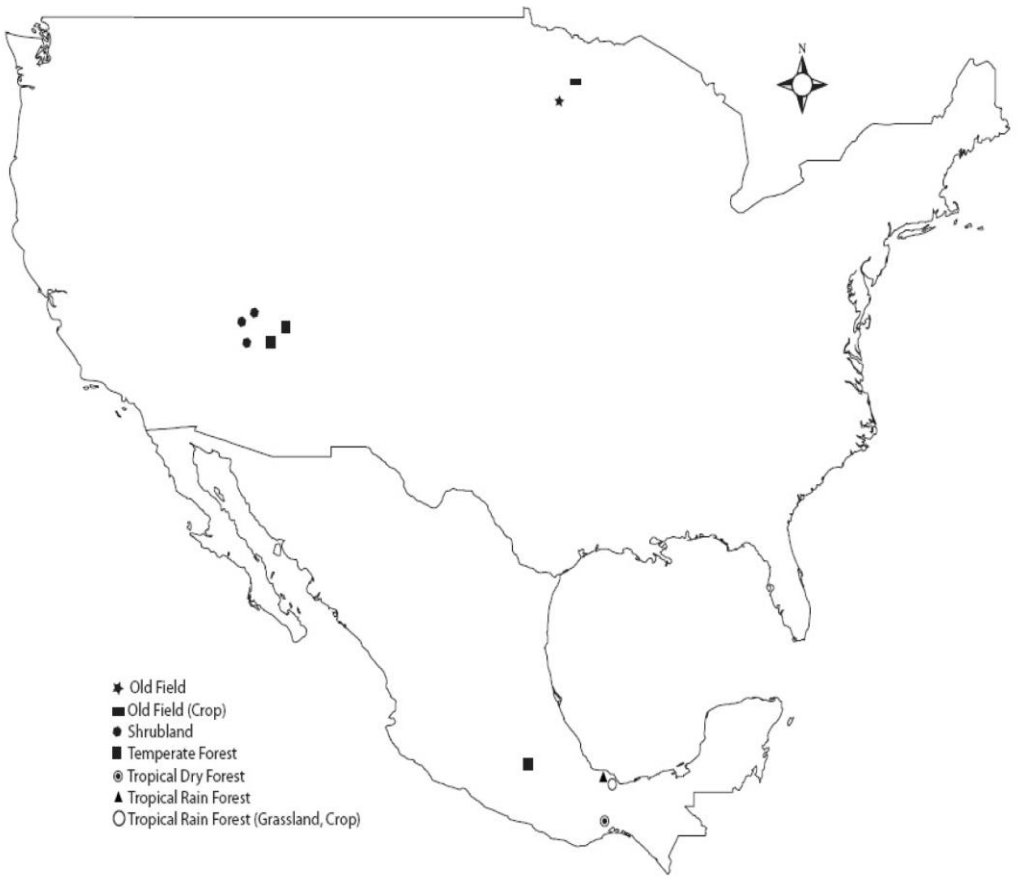

Figure 1. Map of sites location, according to vegetation type.

Sample Collection and Spore Extraction

USA sites - Soils were collected using a pipe or soil sampler ranging in size from 2.5 to 5 cm in diameter and 15 to 20 cm deep. Soils were placed in plastic bags and stored frozen until they were processed. Spores were extracted from soils using a modified wet-sieving and

density centrifugation technique (Gerdemann and Nicolson 1963, McKenney and Lindsey 1987). A 25 g to 30 g soil sample was placed in a 2 L bucket and vigorously filled with water. The soil suspension was poured through two nested sieves with 250 µm and 25 µm openings. Material collected on the 250 µm sieve was rinsed into a petri dish and spores were picked out using a fine forceps. Material collected on the 25 µm sieve was rinsed into (50 ml) centrifuge tubes and spun at 500 g for 3 minutes. The supernatant was poured away and the pellet re-suspended in 2M sucrose and spun at 500 g for 1.5 minutes. The sucrose supernatant was collected on the 25 µm sieve, and the sucrose residue was rinsed away using tap water. The rinsed material was suctioned through a gridded membrane filter and a subsample of spores on the filter were scraped off the membrane filter and mounted on microscope slides using polyvinyl-lacto-glycerol (PVLG). Spores were counted and identified morphologically using a compound microscope (200 - 1,000X). Spores were identified to species using original species descriptions (Schenck and Perez 1990) and on-line references of species descriptions (INVAM, http://invam.caf.wvu.edu and http://www.lrz-muenchen.de/~schuessler/amphylo).

Mexican sites - Soils were collected and stored as USA sites. We applied the wet sieving and decantation technique by Gerdemann and Nicolson (1963), modified by Brundrett et al. (1996). Spores were separated from 100 g (50 g for Tropical Dry Forest and Temperate Forest) of soil by wet sieving and decanting (Gerdemann and Nicolson 1963). Each swirling soil suspension was poured through two mesh sieves, 700 and 45 µm. The sediment was suspended (in water) and sieved again. This process was done 3 times.

Table 2. General description of the study sites

Study site	General site description	Location (lat/long)	MAP and MAT	Vegetation type/ land use (and number of samples)	Distur-bance
Cedar Creek LTER in Minnesota, USA	2200 ha Natural Reserve 50 km. The BioCON experiment is described in Reich et al. (2001)	45°24′N, 93°11′W	800 mm; 6.7ºC	(1) Old forest, abandoned agricultural fields and pristine savannah and grasslands (15) (2) Grasses *Agropyron repens*, *Bromus inermis*, *Koeleria cristata*, *Poa pratensis*, *Andropogon gerardii*, *Bouteloua gracilis*, *Schizachyrium scoparium*, *Sorghastrum nutans*; herbaceous *Achillea millefolium*, *Anemone cylindrica, Asclepias tuberosa*, *Solidago rigida*, and N-fixing legumes *Amorpha canescens*, *Lespedeza capitata*, *Lupinus perennis Petalostemum villosum* (186)	P, ES, LS
Grand Staircase-Escalante National Monument, Utah, USA	An area of 769,000 ha near the towns of Big Water, Cannonville, Escalante, and Boulder.	37°24′N, 111°41′W	296 mm; 10ºC	Shrubland with *Artemisia tridentata* and *Artemisia filifolia* (216)	ES, LS, P

Pinyon-Juniper, Colorado, USA	Semi-arid, mid-latitude Steppe	37°49′N, 108°55′W	480 mm; 8.9ºC	Shrubland with *Pinus edulis*, *Juniperus osteosperma*, *Quercus gambelii*, *Cercocarpus montanu*, *Elymus elymoide*, *Bouteloua gracilis* (70)	HD, P
Taylor Woods Ponderosa pine, Arizona, USA	Growing stock was established in 1962 and every 10 years since, study areas have been maintained at a range of growing stock levels within an even-aged management strategy	35°16′N, 111°43′W	560 mm; 6ºC	Semi-arid montane conifer forest (21)	ES, LS, P
Temperate forest, Mexico	At southern Mexico City, Central Mexico	19°14′ to 19°17′ N, 99°19′ to 99°16′W	1200; 1100 mm lower altitude; 7.1, 9.2 to12° C	Dominant species are *Pinus hartwegii* at the top, *Abies religiosa* in the middle and *Quercus rugosa* in the lower altitude (6)	LS, P
Tropical Rain forest, Veracruz, Mexico, northern site	Los Tuxtlas Biosphere Reserve, southeastern of Veracruz State	18°32’ to 18°37’ N, 95°02’ to 95°08’ W	4500 mm; 24ºC	Tropical rain forest (7)	P
Tropical rain forest, Veracruz, Mexico, southern site	At southern Los Tuxtlas.	18°15’ to 18°24’ N, 94°41’ to 94°56’ W	2900 mm; 24ºC	Tropical rain forest; four land uses were considered: mature forest, successional forest, grassland and maize crop (80)	ES, LS, P
Tropical dry forest, Oaxaca, Mexico	Southern Mexico, at Nizanda, Oaxaca.	16º 38’ to 16º 83’ N, 94º 00’ to 95º 00’ W	1000 mm; 25ºC	Parcels were grouped in three different successional stages (64)	ES, LS

MAP: Mean Annual Precipitation, MAT: Mean Annual Temperature. HD: high level disturbance; ES: medium level disturbance, early successional; LS: low level disturbance, late successional; P: pristine.

Samples were also centrifuged according to the sucrose density gradients technique by Daniels and Skipper (1982). Soil caught in the small sieve was transferred with water into 50 ml centrifuge tubes and centrifuged (Solbat C-600, 24ºC) for 4 min at 3,500 rpm. The supernatant liquid was carefully decanted; the pellet was re-suspended in a sucrose solution (440 g/L) and centrifuged at 3,500 rpm for 50 sec. The supernatant was sieved (45 µm) and washed thoroughly for at least one minute (Walker, unpublished data). A Tween solution (two drops of Tween in 100 ml of water) and 5% chlorine solution were added for one and five minutes, respectively. The solid material from the sieve was washed in a Petri dish. Spores were mounted with PVLG on permanent slides marked with a grid. Spores were counted at a compound microscope at magnification up to 10X. Spores were identified to species as USA sites.

Data Analysis

An Analysis of Variance of Multiple Regression (Zar 1999) was conducted for spore species richness, evenness, diversity (using the Shannon diversity index) and total abundance, with the predictors, plant species richness (data were natural log transformed), latitude and disturbance. We used the following disturbance categories: high disturbance, low (early successional), medium (late successional), and mature (pristine sites) (Table 2). Pristine refers to undisturbed sites and high refers to USA sites with severe soil disturbances (e.g., Pinyon-Juniper, Colorado, USA, due to long duration and high temperature fires). Because disturbance effects are different between Mexican (e.g., improved plant species responses) and USA (e.g., negative responses), we analyzed them separately.

RESULTS AND DISCUSSION

Table 3 gives the statistical results for each of the analyses discussed below.

Table 3. Results of the statistical analysis: F (P); R^2

	USA			Mexico		
	Plant species richness	Latitude	Disturbance level	Plant species richness	Latitude	Disturbance level
AM fungal spore species richness	2.02 (0.16); 0.01	0.46 (0.49); 0.001	24.54 (<0.0001); 0.19	5.02(0.03); 0.03	0.14 (0.71); 0.001	14.92 (<0.0001); 0.13
AM fungal spore species evenness	8.4 (0.004); 0.03	0.11 (0.75); 0.0003	13.76 (<0.0001); 0.11	6.15 (0.014); 0.03	0.06 (0.81); 0.0003	1.76 (0.17); 0.02
AM fungal diversity (H')	2.79 (0.10); 0.01	0.55 (0.46); 0.002	0.08 (0.97); 0.001	0.46 (0.5); 0.002	0.15 (0.70); 0.001	8.34 (0.0003); 0.08
AM fungal abundance	1.85 (0.17); 0.01	0.27 (0.60); 0.001	14.78 (<0.0001); 0.12	4.81 (0.03); 0.02		0.4 (0.67); 0.004

Relationship between AM Fungal and Plant Diversity

There was no consistent relationship between plant diversity and the diversity of Glomeromycotan spores across the full dataset. There was a weak negative relationship

between the species richness of AM fungal spores and plant species richness (Figure 2a) which was driven by lower spore species richness in the Mexican sites with high plant diversity ($R^2 = 0.03$). Species evenness of AM fungal spores had no relationship with richness of the plant communities (Figure 2b). There was no also relationship between the Shannon diversity of AM fungal spores and plant species richness (Figure 2c).

Other studies have also shown there to be very little connection between the diversity of plant hosts and their associated AM fungi. In lowland evergreen forests and pastures in Nicaragua and Costa Rica, Picone (2000) found that most of the AM fungal species produced more spores in pasture, and local AM fungal species richness did not significantly decline following conversion of forest to pasture. An extreme example of uncoupled above and belowground diversity was observed in a study showing no loss of AM fungal diversity when a diverse Costa Rican dry forests was converted to monocultures of *Hyparrhenia rufa*, an introduced C-4 grass from Africa (Johnson and Wedin 1997). Lovelock and Ewel (2005) in a study in monocultures and polycultures of cacao in Costa Rica, found that richness and the mean spores' number were similar between land uses, but in the polyculture *Acaulospora spinosa* and *A. morrowiae*, were the most and least abundant, respectively; however, according to plant species composition, the abundance was inverse in the monocultures.

Several studies do show a positive relationship with AM fungal diversity and plant diversity (Burrows and Pfleger 2002, Oehl et al. 2003, Chen et al. 2004, Börstler et al. 2006). Most of these studies were experimental, meaning that diversity had been manipulated in the field after only few years of diversity treatments. It is possible that in the longer term other factors, such as soil chemistry or soil texture play a larger role in influencing the assemblage of AM fungal spores or that these factors explain the patterns in the short term as well. For example, the Oehl et al. (2003) study demonstrates an increase in AM fungal diversity when going from a mono-crop system to natural grassland, where soil disturbances like tillage and fertilizer use have also likely shaped the AM fungal communities. More research is needed to tease out the complex interactions among biotic and abiotic factors in shaping AM fungal community structure.

Latitudinal Patterns in AM Fungal Diversity

There was no relationship between AM fungal spore richness, evenness or diversity and latitude (Figure 3). Plant diversity does show a relationship with latitude, but as AM fungal diversity is not closely related to plant diversity, perhaps this result should not be surprising. This confirms the statement of Allen et al. (1995) that diversity of mycorrhizal fungi does not follow patterns of plant diversity. These authors suggested that because AM fungi are generalists, their diversity would be determined by physiological adaptations to the environment. Recently, for phytoplankton patterns, Barton et al. (2010) discuss about two other possible explanations for changes in diversity: "hot spots" of enhanced diversity reflecting lateral dispersal, and an enabled long exclusion time scales by weak seasonality in the tropics; it is interesting that we had high AM fungal diversity in USA, and in the tropical Mexico sites. The relative availability of soil phosphorus and nitrogen may be an important determinant of the structure and function of AM fungal communities (Johnson 2010).

Influence of Disturbance on AM Fungal Diversity

Disturbance had a strong influence on species richness of AM fungal spore communities (Table 3). In the USA, species richness progressively decreased with medium and high levels of disturbance; while species richness increased under low disturbance in the Mexican sites (Figure 4a). Evenness was highest in the high disturbance plots in the USA sites but not in the Mexican sites (Figure 4b, Table 3). In the Mexican sites, diversity was greatest in sites with low levels of disturbance, but diversity was not sensitive to disturbance in the USA sites, probably because the opposite responses of species richness and evenness canceled each other (Figure 4c, Table 3).

It is interesting to note that low levels of disturbance did not reduce species richness in either the Mexican or the USA sites. In fact, in the Mexican dataset, species richness and diversity were significantly greater in sites with low levels of disturbance. This suggests that low levels of aboveground disturbance do not harm, and may even encourage sporulation by AM fungi. Perhaps plant carbon allocated belowground to roots and AM fungal symbioses is increased by low levels of disturbance, and this may increase solar radiation to remaining vegetation. Low levels of disturbance did not stimulate spore richness in the USA sites. Perhaps this difference among the datasets occurs because in the more northern sites the vegetation is less light limited and more limited by cold temperatures and drought. There was an extremely high disturbance treatment in the USA data set, and under this treatment spore species richness was significantly reduced while evenness was increased.

This pattern found in areas of high disturbance was mostly driven by sampling slash pile burns, which are management treatments intended to reduce forest fuels. This method of fuels reduction often creates lasting soil disturbances from long duration, high severity fires. Slashes pile burns have been shown to reduce AM fungi abundance (Korb et al. 2004, Owen et al. 2009). This result suggests that a few hardy spore species became dominate after extreme disturbance.

Management Implications

We found that species richness and evenness of Glomeromycotan spore communities were not correlated with plant richness or latitude; however, they were sensitive to disturbance (Table 3). The observation that there was no relationship between the plant diversity and Glomeromycotan diversity supports the notion that AM fungi are ancient clonal organisms that have evolved to infect relatively more ephemeral host communities which may change through successional processes. Individual plants associate with multiple AM fungal taxa and vice versa. To be successful, AM fungal taxa must be adapted to provision the local plant community with belowground resources under the ambient soil, and environmental conditions. Over long periods of time, conditions of the abiotic environment may be less variable than the biotic environment. Consequently, AM fungal communities may have adapted to be relatively resistant to change following shifts in plant community composition. This could be important to the success of traditional methods of slash-and-burn agriculture if it means that diverse AM fungal communities that are well adapted to the local environment may be present for several years after the native vegetation has been replaced with crops.

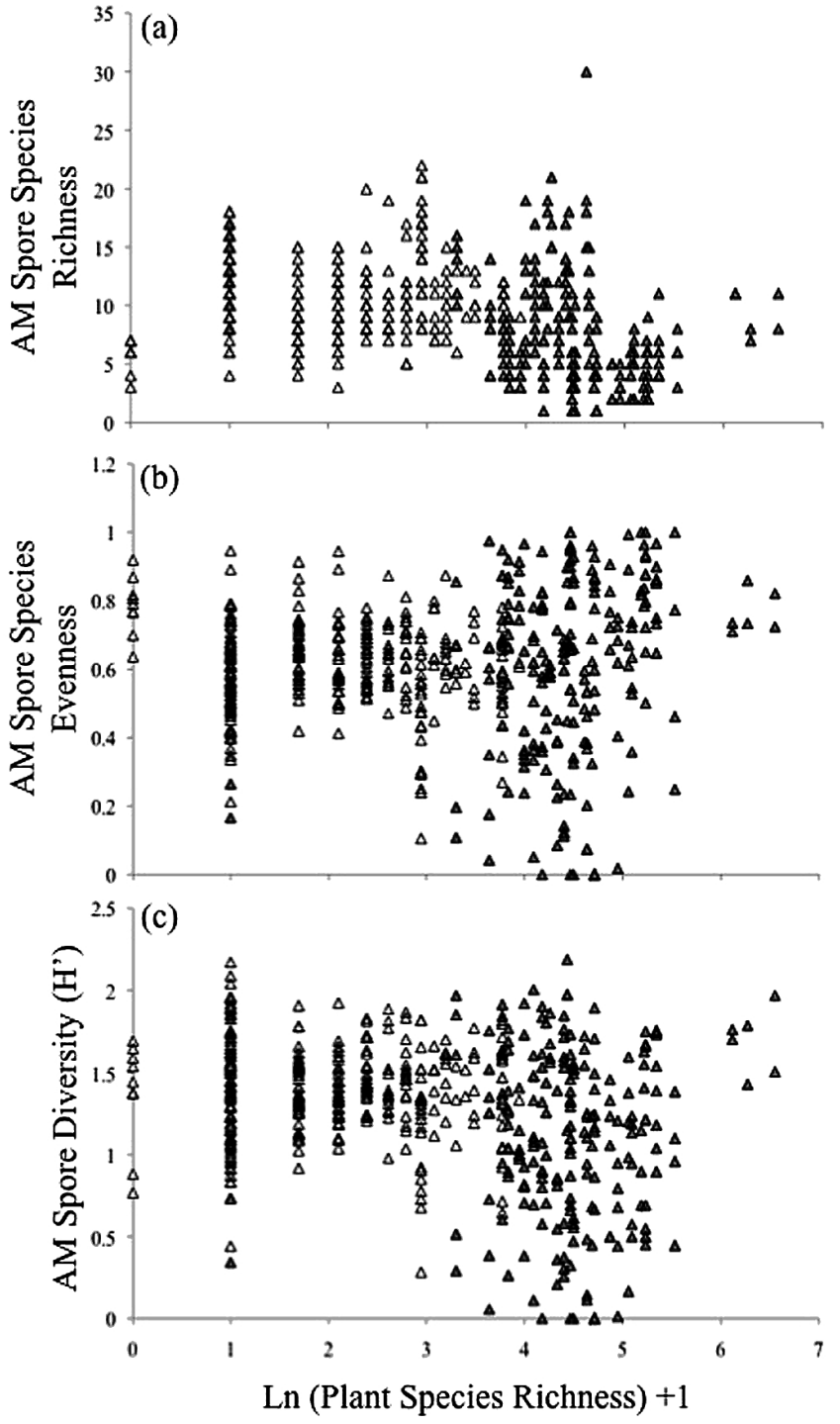

Figure 2. Relationships between plant species richness and (a) AM fungal spore species richness, (b) AM fungal spore species evenness and (c) AM fungal spore diversity. Mexican sites are indicated as gray triangles, and USA sites as open triangles.

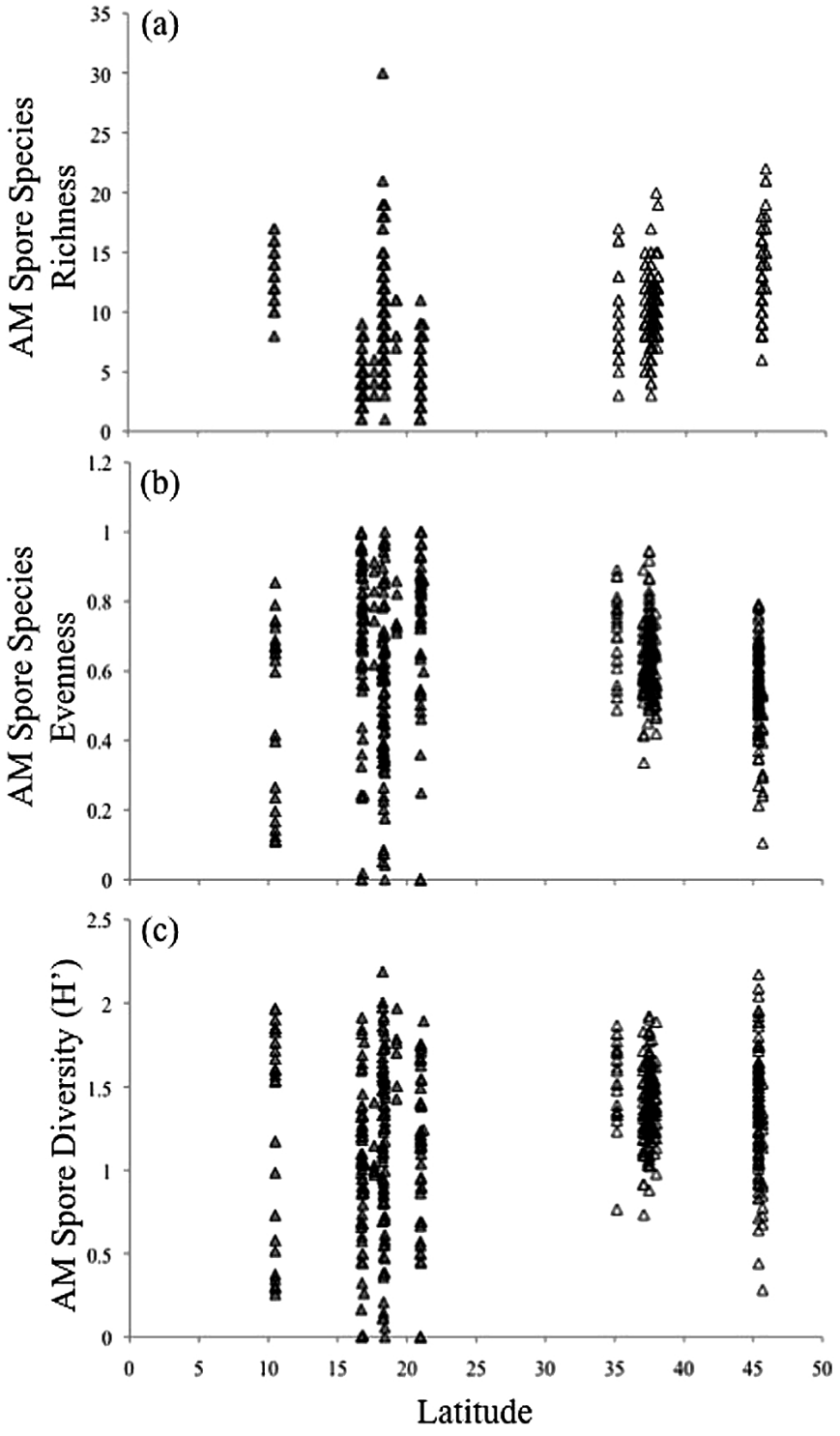

Figure 3. Relationships between latitude and (a) AM fungal spore species richness, (b) AM fungal spore species evenness and (c) AM fungal spore diversity. Mexican sites are indicated as gray triangles, and USA sites as open triangles.

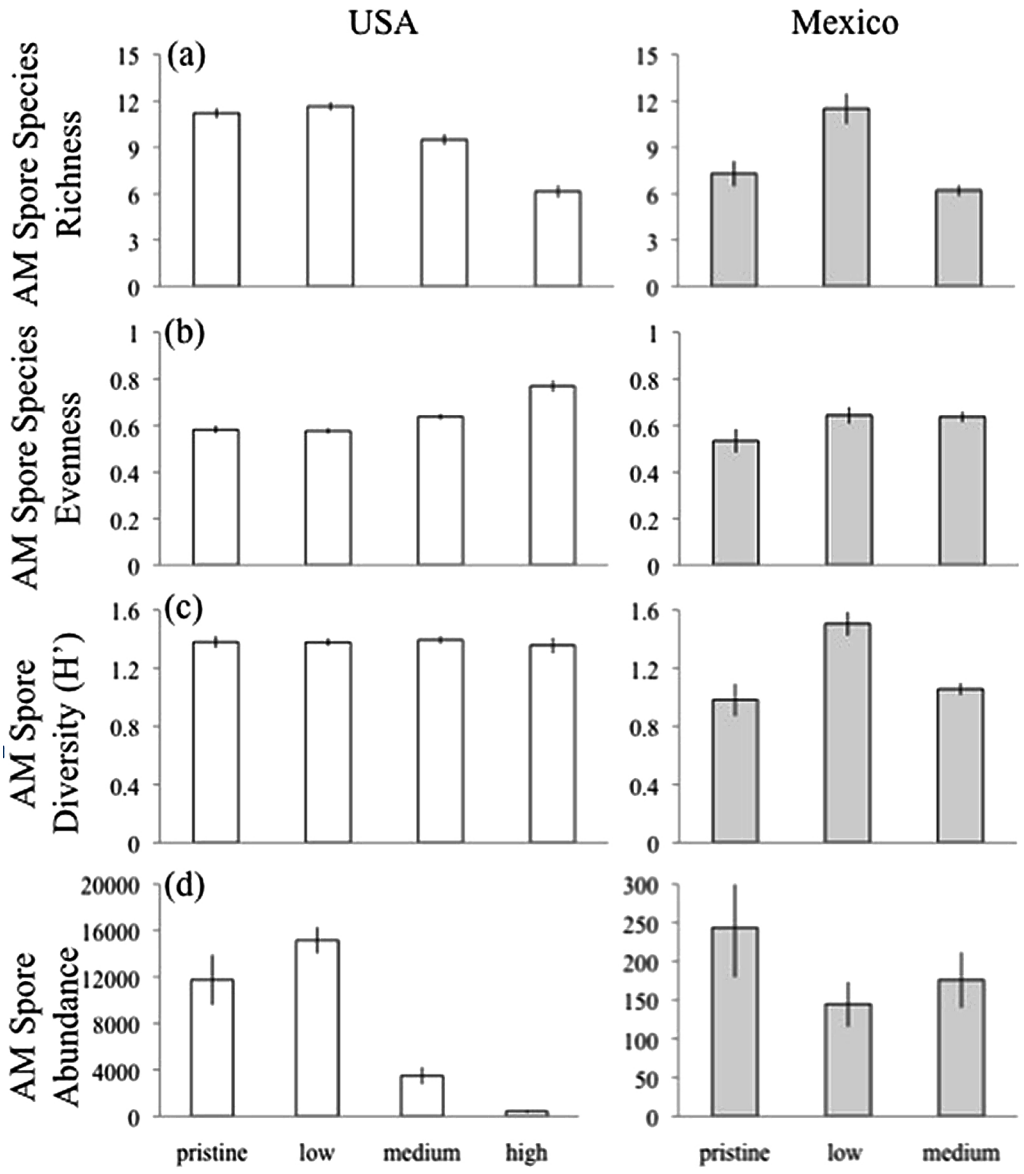

Figure 4. (a) AM fungal species richness, (b) evenness, and (c) diversity by disturbance ranking for sites in USA and Mexico. Error bars represent one standard error of the mean. Different letters above the bars indicate that the means are significantly different ($P \leq 0.05$) according to Tukey's test.

Resistance to disturbance and ability to recover following disturbance (i.e. resilience) may vary considerably among AM fungal taxa, and this may help explain why Glomeromycotan diversity was more sensitive to disturbance than to a loss of plant diversity. This indicates that tillage and other forms of disturbance such as fire and fertilization may be a strong force in structuring AM fungal communities. We are currently exploring effect of the environmental and resources gradients and the history of the land use on the community

composition of AM fungal spores. A better understanding of the factors that control the species composition of Glomeromycotan communities is a first step in effectively managing for their benefits in ecosystem restoration and agriculture.

CONCLUSION

Our findings indicate that the factors controlling community diversity differ for plants and mycorrhizal fungi. Disturbance influences AM fungal spore community diversity, and the outcome of these effects varies among ecosystems. Future studies are needed to further elucidate all the factors that structure AM fungal communities. This information will help guide the management of these important symbioses as part of integrated conservation and land management plans.

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