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Neighboring trees affect ectomycorrhizal fungal community composition in a woodland-forest ecotone

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Abstract Ectomycorrhizal fungi (EMF) are frequently species rich and functionally diverse; yet, our knowledge of the environmental factors that influence local EMF diversity and species composition remains poor. In particular, little is known about the influence of neighboring plants on EMF community structure. We tested the hypothesis that the EMF of plants with heterospecific neighbors would differ in species richness and community composition from the EMF of plants with conspecific neighbors. We conducted our study at the ecotone between pinyon (*Pinus edulis*)–juniper (*Juniperus monosperma*) woodland and ponderosa pine (*Pinus ponderosa*) forest in northern Arizona, USA where the dominant trees formed associations with either EMF (*P. edulis* and *P. ponderosa*) or arbuscular mycorrhizal fungi (AMF; *J. monosperma*). We also compared the EMF communities of pinyon and ponderosa pines where their rhizospheres overlapped. The EMF community composition, but not species richness of pinyon pines was significantly influenced by neighboring AM juniper, but not by neighboring EM ponderosa pine. Ponderosa pine EMF communities were different in species composition when growing in association with pinyon pine than when growing in association with a conspecific. The EMF communities of pinyon and ponderosa pines were similar where their rhizospheres overlapped consisting of primarily the same species in similar relative abundance. Our findings suggest that neighboring tree species identity shaped EMF community structure, but that these effects were specific to host-neighbor combinations. The overlap in community composition between pinyon pine and ponderosa pine suggests that these tree species may serve as reservoirs of EMF inoculum for one another.

Keywords Ectomycorrhizal fungi · Community dynamics · Plant neighbor · Mycorrhizal network · Species composition

Introduction

Ectomycorrhizal fungi (EMF) form symbiotic associations with the roots of many plant species, aiding in plant nutrient and water acquisition and protection from soil pathogens in exchange for photosynthate (Smith and Read 1997). Over 5,000 species of fungi are thought to form EMF associations and even small monospecific forests may have greater than 50 EMF species (Horton and Bruns 2001; Lilleskov et al. 2004). Species of EMF differ in resource utilization, colonization strategies, reproductive strategies, and response to disturbance (Taylor and Bruns 1999). This functional diversity is potentially important to host plants as species of EMF vary in their capacity to enhance plant recovery from drought stress (Parke et al. 1983), facilitate nutrient uptake (Finlay 1989), and promote plant growth (Burgess et al. 1994). EMF species richness also can contribute positively to plant performance under some environmental conditions (Baxter and Dighton 2001, 2005; Jonsson et al. 2001).

Given the variability in function of species of EMF, it is important to understand the environmental conditions that favor increased EMF richness and particular EMF species or communities. EMF communities are affected by a variety of abiotic environmental factors such as soil type, pH, temperature, precipitation, nitrogen enrichment, and CO_2 concentration (e.g., Gehring and Whitham 1994;

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Bakker et al. 2000; Lewis et al. 1994; Swaty et al. 1998, 2004; Lilleskov et al. 2002). Variation in abiotic factors may result from changes in interdependent biotic factors such as overstory plant-mediated changes in soil traits (Dickie et al. 2006). Direct biotic interactions such as those between species of fungi have been shown to alter fungal diversity through temporal or spatial niche partitioning (Dickie et al. 2002; Koide et al. 2005, 2007). Likewise, neighboring arbuscular mycorrhizal (AM) vegetation can influence EMF abundance and community structure (Haskins and Gehring 2004; McHugh and Gehring 2006).

Degree of EMF host specificity and associated relationships with neighboring ectomycorrhizal vegetation also influences EMF community structure. High levels of host preference may promote EMF diversity in mixed species forest stands. For example, Ishida et al. (2007) attributed exceptionally high EMF species richness in a conifer–broadleaf forest to large numbers of EMF host plant species with low taxonomic relatedness. In contrast, low EMF host specificity could alter EMF species richness and composition at the stand level because of significant overlap of EMF species among plant taxa. Horton and Bruns (1998) showed that EMF species infecting multiple host species were the most frequent and abundant in a mixed stand of bishop pine and Douglas-fir. Low host specificity of EMF allows neighboring trees of different species to act as EMF inoculum sources for one another (e.g., Dickie et al. 2004) and facilitates the formation of hyphal networks that connect trees belowground (Molina et al. 1992; Simard et al. 1997; Simard and Durall 2004; Nara 2006a,b).

While the above studies have provided significant insights into plant neighbor influences on EMF communities, they have focused largely on closed canopy forests where the influence of particular species of plant neighbors on EMF communities has been difficult to quantify. Isolating the effects of plant neighbors on EMF communities at a local scale could help reveal the mechanisms involved in neighbor relationships. In this study, we examined the influence of plant neighbors on the EMF community structure of pinyon pine (*Pinus edulis* Engelm.) and ponderosa pine (*Pinus ponderosa* P. and C. Lawson) at the ecotone between two adjacent ecosystems, pinyon–juniper woodland and ponderosa pine forest. We chose this study system for three reasons. First, the low stand density of the woodland-forest ecotone allowed us to compare the influence of specific plant neighbors on the EMF of focal tree species. Second, pinyon pine and ponderosa pine are often the only hosts for EMF in large tracts of their respective ecosystems (Haskins and Gehring 2005) which together occupy tens of millions of hectares in the western United States (West 1999; Abella and Covington 2006). These two tree species frequently co-occur at the ecotone of the vegetation types which they dominate, yet the influence of these hosts on each other's EMF community structure has not been explored. Third, in recent years, drought has resulted in substantial mortality of both tree species, particularly in the southwestern United States (Breshears et al. 2005; Mueller et al. 2005; Gitlin et al. 2006). Given that high tree mortality can reduce the EMF abundance and diversity of surviving trees (Swaty et al. 2004) and the inoculum potential of the soil (Haskins and Gehring 2005), surviving ectomycorrhizal host plants could become important reservoirs for EMF that facilitate the re-establishment of other tree species.

We sampled the EMF communities of pinyon and ponderosa pines growing in association with heterospecific and conspecific neighbors to test the following hypotheses: (1) pinyon and ponderosa pines neighboring heterospecific EM hosts support a different, more species-rich EMF community than pinyon and ponderosa pines neighboring conspecifics. We predicted that access to the roots of a closely related EM host neighbor would provide inoculum of additional EMF species, thus altering the EMF community composition and diversity of the focal species. (2) When their rhizospheres overlap, pinyon and ponderosa pines have similar EMF communities. We predicted that the EMF species composition of the two tree species would be similar where they co-occurred because pinyon and ponderosa pines are closely related and because they occupied similar environments in the woodland-forest ecotone, (3) pinyons neighboring AM junipers will be colonized by a different EMF community than pinyons neighboring conspecifics. We expected that interactions with the roots of junipers or their associated arbuscular mycorrhizal fungi (AMF) would affect EMF communities either directly, or through changes in rhizosphere nutrients, water or allelochemicals (Haskins and Gehring 2004).

Materials and methods

Study site

This study took place at the ecotone between pinyon–juniper woodland and ponderosa pine forest near Sunset Crater National Monument, northern Arizona, USA. The study site occurred within a narrow range of elevation (ca. 1,850 m–1,900 m) covering an area of ~35 ha. The local climate was semi-arid with mild temperatures. Annual precipitation was bimodal with heavy winter precipitation and summer monsoon rains. The mean annual precipitation and temperature near the study site from 1969–2006 were 42.5 cm and 7.67°C, respectively (http://www.wrcc.dri.edu/CLIMATEDATA.html). Sampling was conducted during two relatively normal years following 10 years of severe drought (Gitlin et al. 2006; mean annual temperature for

2005 and 2006=7.81°C and 7.58°C, respectively; mean annual precipitation for 2005 and 2006=46.5 cm and 41.5 cm, respectively). Soil at the site consisted of basaltic cinders, low in nutrients and water-storage capacity (Gehring et al. 1998) that were classified by the US Department of Agriculture as Typic Ustorthents (Hooten et al. 2001).

Three tree species occurred at the study site: (1) pinyon pine, (2) ponderosa pine, and (3) one-seed juniper (*Juniperus monosperma* (Englem.) Sarg.). Pinyon and ponderosa pine are the only known ectomycorrhiza-forming plant species at this site, with one-seed juniper and all understory vegetation forming associations with arbuscular mycorrhizal fungi (Haskins and Gehring 2005; Hubert and Gehring, personal observation). Although several tree species have experienced high mortality due to recent severe drought in northern Arizona (Mueller et al. 2005; Gitlin et al. 2006), tree mortality at this site was relatively low with EM ponderosa and pinyon pine showing higher mortality than AM juniper (Table 1). The total basal area of the three tree species was 16.4 m^2 per hectare (Table 1), a low value compared to nearby ponderosa pine forests and pinyon–juniper woodlands with basal areas of 40.1 m^2 per hectare and 50.8 m^2 per hectare, respectively (Hungate et al. 2007; Despain and Mosley 1990). Large interspaces between trees were interspersed with low densities of AM understory vegetation dominated by shrubs including Apache plume (*Fallugia paradoxa* (D. Don Endl.) ex Torr.), skunkbush sumac (*Rhus trilobata* Torr.), and ephedra (*Ephedra trifurca* Torr. ex S. Wats.). Low vegetation densities allowed us to investigate the effects of one neighboring tree species on the EMF community of a focal tree without the confounding influences of other neighboring tree species.

Root identity and sampling of EMF

Pinyon, ponderosa, and juniper roots were distinguished in the field based on root diameter, color and root tip density. To quantify the characteristics we felt adequately distinguished between pinyon and ponderosa pine roots, we measured and compared the diameter of the finest root, the length of individual EM perpendicular to their attachment to a lateral root, and EM density (number of EM with an independent attachment to a lateral root) for five randomly selected 10-cm root segments from five samples of each pine species. We could be certain of the tree species identity for these root samples because they were collected in locations where the only tree neighbors were conspecifics. Two-sample *t*-tests were performed for each variable to test for species-specific differences in root morphology.

Table 1 Stand composition of the three tree species at the study site

	Pinyon	Ponderosa	Juniper
# Live trees	218	33	42
Basal area (square meters per hectare)	6.53	6.37	3.53
% Mortality	16.48	23.26	0.00

In order to determine if the identity of a neighboring EM host tree influenced pinyon and ponderosa EMF communities, root samples were collected from the following four groups of trees: (1) 16 pinyons growing next to a conspecific neighbor (pinyon–pinyon), (2) 15 pinyons growing next to ponderosa pine (pinyon–ponderosa), (3) eight ponderosa pines growing next to a conspecific neighbor (ponderosa–ponderosa), and (4) eight ponderosa pines growing next to pinyon pine (ponderosa–pinyon). In order to determine the overlap of EMF species between pinyon and ponderosa pine, pinyon samples were also collected from group four. The first two groups were sampled in May 2005, while the latter two groups were sampled in September 2006. The differences in timing and sample sizes between the two species were the result of a loss of ponderosa samples from an initial collection in May 2005. Because of the differences in timing of sampling, pinyon pine and ponderosa pine data were analyzed separately. To measure the effect of a dominant non-EM host neighbor on pinyon EMF communities, we also compared data from root samples collected from two groups of trees in May 2005, (1) the 16 pinyons growing near conspecifics (pinyon–pinyon) described above and (2) 15 pinyons growing next to junipers (pinyon–juniper).

Focal trees for sampling of EMF were reproductively mature with a trunk diameter between 25 and 30 cm at 10 cm above ground level and had only one species of neighbor tree within their putative rooting zone (no trees other than the target and neighbor within 5 m of sampling location). The rhizospheres of the target and neighbor tree were considered to overlap if the edges of the tree crowns were 2 m or less from one another. This definition of rhizosphere overlap was confirmed by the presence of target tree roots and roots of the neighbor in each sample. The density and species composition of understory vegetation was similar among all trees sampled. EMF samples consisted of a minimum of 100 EM root tips collected by digging to a depth of 20–35 cm at the edge of the crown of the target tree nearest to the target neighbor. Root samples were kept frozen in the lab at −20°C until further analysis.

In the lab, root segments were randomly selected from each sample and live EM root tips were sorted by morphological characteristics, including color, texture, architecture, and characteristics of emanating hyphae, using a dissecting scope at 15×–60× magnification (Horton and Bruns 1998). Approximately 7,000 root tips were morphotyped in this way. A minimum of two root tips per morphotype per tree were analyzed using the molecular methods of Gehring et al. (1998) as described below.

Molecular analysis of ectomycorrhizal fungi

EM root tip tissue was lysed using a geno-grinder (Allender et al. 2004) and DNA was extracted using DNEasy Kits (Qiagen, Valencia, CA, USA) according to the manufacturer's instructions. The fungal internal transcribed spacer region (ITS), between the 18S and 28S rDNA, was amplified by PCR using the primers ITS1F and ITS4 (Gardes and Bruns 1993). Amplification success was approximately 92%. The DNA from additional root tips of the same morphotype and tree was extracted and amplified when PCR failed for the first two root tips. Root tips from one very rare morphotype were never successfully amplified and were not included in subsequent analyses. DNA was successfully extracted and amplified for over 600 root tips. Successful PCR amplicons were subjected to two separate restriction digests using the enzymes *Hinf*I and *Mbo*I, which usually has been sufficient for EMF taxonomic resolution at the species level (Gardes and Bruns 1996; Dahlberg et al. 1997) and has been successfully employed in previous studies with the EMF of *Pinus* (Gehring et al. 1998; Kennedy 2005).

Restriction fragment length polymorphism (RFLP) results were visualized with agarose gel electrophoresis and digital images were analyzed using a Kodak EDAS 290 gel documentation system and accompanying software (Eastman Kodak Company, Rochester, New York, USA). RFLP patterns were compared to those obtained from previous studies of locally collected sporocarps, and *P. edulis* and *P. ponderosa* EM root tips (Gehring et al. 1998; Haskins and Gehring 2004; Swaty et al. 2004; Mueller and Gehring 2006; Kennedy 2005). The ITS regions of two DNA samples from each RFLP-type were subject to forward and reverse sequencing at the University of Arizona sequencing facility. Sequences were aligned and edited using BioEdit version 7.0.9 (Hall 2007) and identified using BLAST analysis at the UNITE web page (http://unite.ut.ee/analysis.php).

Data analysis

t-tests were used to determine if there were differences in EMF species richness on trees with heterospecific versus conspecific neighbors using SPSS version 10.0. To determine how well our sampling described EMF species richness at the study site, the Chao2 richness estimator (Chao 1987) was used to calculate the estimated species richness of pinyon pine EMF and ponderosa pine EMF regardless of neighbor association. EMF community composition of trees with conspecific versus heterospecific neighbors were visualized using non-metric multidimensional scaling (NMDS) ordinations from relative abundance data and occurrence data in PC-ORD version 4.02 (McCune and Mefford 1999). Here, the relative abundance of an EMF species is defined as the proportion of EM root tips per tree colonized by that species. Ordinations were also visualized using only species occurrence data because of the possibility that members of the same species on neighboring trees were also the same genetic individual (genet) and thus not independent of one another. Multi-response permutation procedures (MRPP) were used to test for statistical differences between EMF communities using both relative abundance and species occurrence data in PC-ORD (Faith et al. 1987). MRPP is a non-parametric test for multivariate differences between *a priori* groups. The resulting *A-value* is a test-statistic that describes the magnitude of homogeneity within groups. We chose to use the Bray–Curtis dissimilarity coefficient for both NMDS and MRPP analyses because it is useful for revealing ecological gradients and generally provides results that can be interpreted ecologically (Faith et al. 1987). When groups differed based on the results of MRPP analysis, indicator species analysis with Monte Carlo randomization was performed using PC-ORD.

In order to estimate EMF community overlap between pinyon and ponderosa pines, the abundance of shared EMF was calculated in two ways. First, EMF were considered "shared" only if they were found on both hosts within a given mixed root sample. This conservative approach identified community overlap at a local scale (i.e., between neighbors). We also estimated the number of EMF species shared by pinyon and ponderosa pine at a larger spatial scale by examining the overlap of EMF species in the 2006 portion of the study when both tree species were sampled.

To determine if linear distance between sampled trees was a significant predictor of EMF community structure, community similarity and spatial proximity were compared using a Mantel test in PC-ORD. Each sampled tree was measured for latitude and longitude using a Trimble GPS unit (model GeoExplorer 3). If the Mantel test was statistically significant ($p<0.05$) then distance between trees was an important determinant of EMF community structure.

Results

Root identity

The morphological characteristics used to distinguish between ponderosa and pinyon in the field at the time of sample collection exhibited highly significant species-specific differences when compared quantitatively in the laboratory. Mean pinyon and ponderosa fine root diameter (mean fine root diameter±1 SE=1.02±0.03 for pinyon and 0.64±0.03 mm for ponderosa; $p<0.001$), EM root tip size (mean EM root tip size±1 SE=4.49±0.32 for pinyon and 2.44±0.27 mm for ponderosa; $p<0.001$), and EM density per 10 cm root segment (mean EM density per 10-cm root segment±1 SE=18.3±1.5 for pinyon and 32.5±3.5 for ponderosa; $p<0.001$) all differed approximately two-fold, with negligible overlap between one species and the other.

Summary of EMF communities

When samples from all 70 trees (54 pinyon pines and 16 ponderosa pines) were combined, we observed 21 EMF species, 20 on pinyon pine and nine on ponderosa pine. Similar species richness values resulted from the Chao2 species richness estimator, 22 for pinyon pine and 9.5 for ponderosa pine, suggesting that our sampling captured most of the EMF species richness at the site. We were able to assign some taxonomic identification to 18 species (Table 2). Two EMF sequences yielded only "unknown EMF" when subjected to BLAST analysis (unknown EMF A and B); one EMF sequence was a poor match to a catalogued *Inocybe* sp. (unknown EMF C), and one EMF species yielded poor sequence data. One EMF species was identified as *Tricholoma terreum* because it matched a previously analyzed RFLP-type. Only one species was found only in association with ponderosa pine (unknown EMF C). Many of the species we observed could be identified only to the order Pezizales, a common occurrence at nearby study sites as well (Haskins and Gehring 2004; McHugh and Gehring 2006). As a result, the DNA sequences obtained here have not yet been submitted to GenBank because we are performing additional sequencing of the ITS and LSU regions of the rDNA as part of another study in an effort to further refine our identifications. The standardized Mantel statistic for EMF communities sampled in 2005 was $r=0.03$, $p=0.67$, indicating linear spatial proximity was not a significant driver of EMF community composition.

The influence of conspecific vs. heterospecific EMF host neighbors

Our results did not support the prediction that EMF species richness would be greater and that EMF community composition would be different for pinyons neighboring a heterospecific EMF host (e.g. ponderosa) than for pinyons neighboring conspecifics. Pinyon pines neighboring conspecifics did not differ significantly in mean EMF species richness from pinyon pines neighboring ponderosa pines (mean richness±1 SE=3.6±0.4 for pinyon–pinyon and 3.6±0.3 for pinyon–ponderosa, $t=0.05$, $p=0.48$). The EMF community composition of pinyons neighboring pinyons also was not significantly different from that of

Table 2 RFLP identification of EMF observed in this study based on ITS sequences

RFLP ID	best BLAST match	Accession #	%[a]	Bit score[b]
Hebeloma sp.	*Hebeloma* cf.	DQ974696	98	920
Pezizales A	Unknown Pezizales	AY634112	90	785
Pezizales B	Unknown Pezizales	AF266709	98	1126
Pezizales C	Unknown Pezizales	AF266709	95	708
Pezizales D	Unknown Pezizales	AY634112	91	815
Pezizales E	Unknown Pezizales	AY634112	90	747
Pezizales F	Unknown Pezizales	AY634112	89	698
Rhizopogon sp.	*Rhizopogon* sp.	AF351873	98	1348
Rhizopogon vulgaris	*Rhizopogon vulgaris*	DQ822823	98	1249
Russula A	*Russula fragilis*	DQ367914	90	854
Russula B	*Russula laricina*	AY061685	93	1009
Suillus sp.	*Suillus luteus*	UDB000171	96	1158
Thelephoraceae A	Unknown Thelephoraceae	AM181387	97	1035
Thelephoraceae B	Unknown Thelephoraceae	U83466	94	1035
Tomentella sp.	Unknown Tomentella	AY748876	97	1174
Tricholoma sp.	*Tricholoma moseri*	AF377211	96	1164
Tricholomataceae sp.	Unknown Tricholomataceae	AM181413	98	1055
Unknown EMF A	Unknown EMF	EU018570	97	1029
Unknown EMF B	Unknown EMF	DQ822805	93	821
Unknown EMF C	Unknown Inocybe	AJ893278	93	464

[a] Percent similarity of query and reference sequences.

[b] Bit score is an evaluation of sequence alignment that takes into account the number of gaps and substitutions as well as the length of the query and reference sequences. Because bit scores are normalized, they allow for comparison among searches. The sequence listed as the best identification was selected based on similarity of query and reference sequences, bit score and comparison of other very close matches.

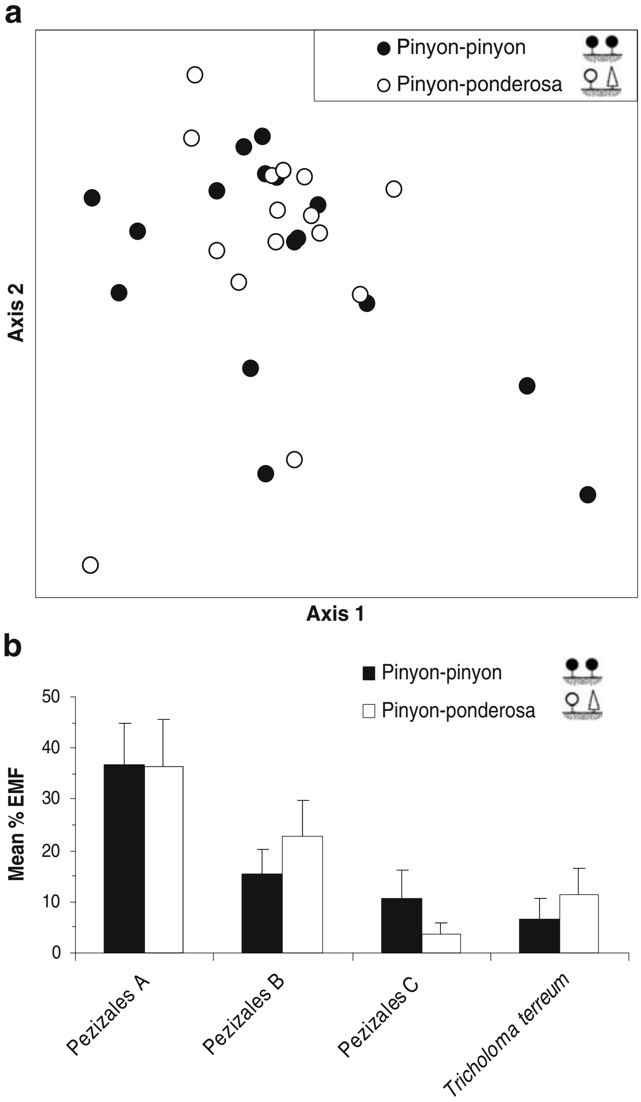

Fig. 1 Pinyon pines neighboring conspecifics and pinyon pines neighboring ponderosa pines had similar EMF communities. **a** Non-metric multidimensional scaling (NMDS) ordination showing that the EMF communities of pinyons neighboring conspecifics (pinyon–pinyon; *filled circles*) and pinyons neighboring ponderosas (pinyon–ponderosa; *open circles*) were similar, a result confirmed by MRPP analysis ($p>0.05$). **b** Histogram representing the mean (±1 SE) relative abundance of dominant EMF species found colonizing pinyons neighboring conspecifics (pinyon–pinyon; *filled bars*) and pinyons neighboring ponderosas (pinyon–ponderosa; *open bars*). Only EMF species that comprise at least 10% of all EM root tips collected from at least one group (i.e., pinyon–pinyon or pinyon–ponderosa) are shown. EMF species are represented in descending order according to conspecific relative abundance

pinyons neighboring ponderosa pine using either relative abundance ($A=-0.006$, $p=0.63$; Fig. 1a) or species occurrence data ($A=0.00016$, $p=0.42$). Pinyon–pinyon and pinyon–ponderosa samples had ten EMF species in common in roughly similar average proportions (Fig. 1b).

In contrast, ponderosa pines with conspecific neighbors differed from ponderosa pines with pinyon neighbors in EMF community composition using both relative abundance ($A=0.08$, $p=0.008$; Fig. 2a) and species occurrence data ($A=0.1172$, $p=0.002$). However, species richness was similar for both groups (mean richness±1 SE=3.0±0.4 for ponderosa–ponderosa and 2.6±0.3 for ponderosa–pinyon, $t=1.76$, $p=0.24$). No significant indicator species was

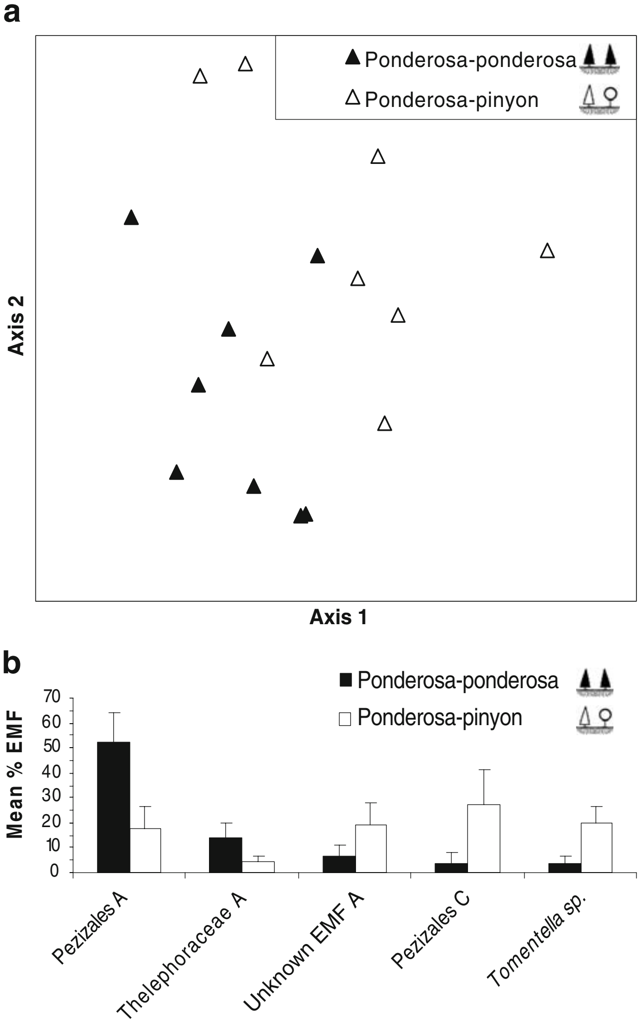

Fig. 2 Ponderosa pines neighboring conspecifics had different EMF communities than ponderosa pines neighboring pinyon pines. **a** Non-metric multidimensional scaling (NMDS) ordination showing that the EMF communities of ponderosas neighboring conspecifics (ponderosa–ponderosa; *filled triangles*) were different from ponderosas neighboring pinyons (ponderosa–pinyon; *open triangles*), a result confirmed by MRPP analysis ($p<0.05$). **b** Histogram representing the mean (±1 SE) relative abundance of dominant EMF species found colonizing ponderosas neighboring conspecifics (ponderosa–ponderosa; *filled bars*) and ponderosas neighboring pinyons (ponderosa–pinyon; *open bars*). Only EMF species that comprised at least 10% of all EM root tips collected from at least one group (i.e., ponderosa–ponderosa or ponderosa–pinyon) are represented. EMF species are presented in descending order according to conspecific relative abundance

associated with the composition difference, but all ponderosa EMF species varied in relative abundance depending on plant neighbor (Fig. 2b).

Pinyon and ponderosa pine EMF community overlap

Our results indicated that pinyon and ponderosa pines occupying overlapping rhizospheres had similar EMF communities. The EMF communities of both hosts were comprised of seven species, with all but one rare species occurring on both tree species (Fig. 3). Mean EMF richness per tree for ponderosa pine and pinyon pine were similar (mean richness±1 SE=3.0±0.4 species for ponderosa and 2.8±0.4 for pinyon pine, $t=1.76$, $p=0.33$). There was no significant difference between the EMF community composition of pinyon and ponderosa pines ($A=-0.015$, $p=0.67$). The relative abundance of root tips that belonged to an EMF species occurring on both host species within a sample was 47.4%; indicating that the chance of a randomly chosen EM root belonging to an EMF species colonizing both the neighboring pinyon and ponderosa within a given sample was nearly 50%. However, the mean percentage of EMF species shared by neighboring pinyon and ponderosa pines was only 28.3%.

Looking at a larger spatial scale, six of the nine EMF species observed in the 2006 study were found on both tree species. The three EMF species not observed on both tree species were observed only in association with ponderosa pine. Two of these species were found only on ponderosa pines that neighbored conspecifics (unknown EMF B and unknown EMF C). There were no species of EMF restricted to pinyon pine in this sampling effort.

The effect of a neighboring AM juniper on pinyon EMF communities

Our prediction that pinyon pines growing near AM junipers would have lower EMF species richness and different EMF communities than pinyons neighboring conspecifics was not supported for species richness (mean±1 SE species richness=3.7±0.5 for pinyon–juniper and 3.6±0.4 for pinyon–pinyon, $t=-0.18$, $p=0.43$). However, the community composition of pinyons neighboring junipers differed from that of pinyons neighboring conspecifics using both relative abundance ($A=0.095$, $p<0.001$; Fig. 4a) and species occurrence data ($A=0.1482$, $p<0.0001$). Six indicator species differentiated pinyon–pinyon and pinyon–juniper EMF communities: Pezizales A, Pezizales C, *Suillus* sp., *Tricholoma terreum*, Pezizales D, and *Russula* A (Fig. 4b).

Discussion

EM host neighbor and EMF community structure

Our hypothesis that EMF species richness would be higher on trees neighboring heterospecific EM hosts than on EM hosts neighboring conspecifics was not supported. Our findings contrast with other studies that have shown a positive relationship between EMF diversity and host diversity at the stand level (e.g., Ishida et al. 2007; Nantel and Neumann 1992; Kernaghan et al. 2003). Mechanisms thought to contribute to the positive host–EMF diversity relationship include increased habitat heterogeneity due to host-specific differences in plant resource acquisition and rhizodeposition (Bruns 1995), and EMF host specificity (Molina et al. 1992; Horton and Bruns 1998; Newton and Haigh 1998; Massicotte et al. 1999; Kennedy et al. 2003; Richard et al. 2005; Nara 2006a,b). Although further study is needed, our results suggest that patterns of higher EMF species richness with higher plant species richness observed at the stand level may not be observed at the local neighbor scale. In the case of pinyon and ponderosa pines, host specificity may be unlikely because these hosts are congeners, similar to those shown by Molina et al. (1992) to share EMF taxa. In addition, habitat heterogeneity may have been too small to influence EMF richness at the local neighbor scale.

While ponderosa pine EMF community structure was affected by neighboring pinyon pines as hypothesized, pinyon pine EMF communities were insensitive to the presence of ponderosa pine neighbors. One explanation for this difference is that some species of EMF associated with ponderosa pine at the center of its range may not be able to survive at the ponderosa pine/pinyon–juniper woodland

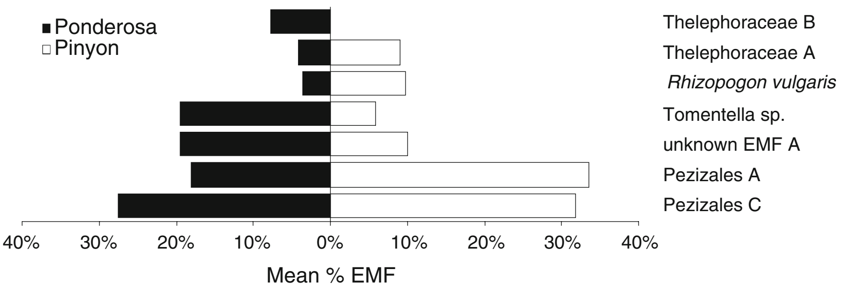

Fig. 3 The mean relative abundance of EMF species found on ponderosa (*closed bars*) and pinyon (*open bars*) when sampled in a location where their rhizospheres overlapped. All EMF species found in this sampling effort are represented

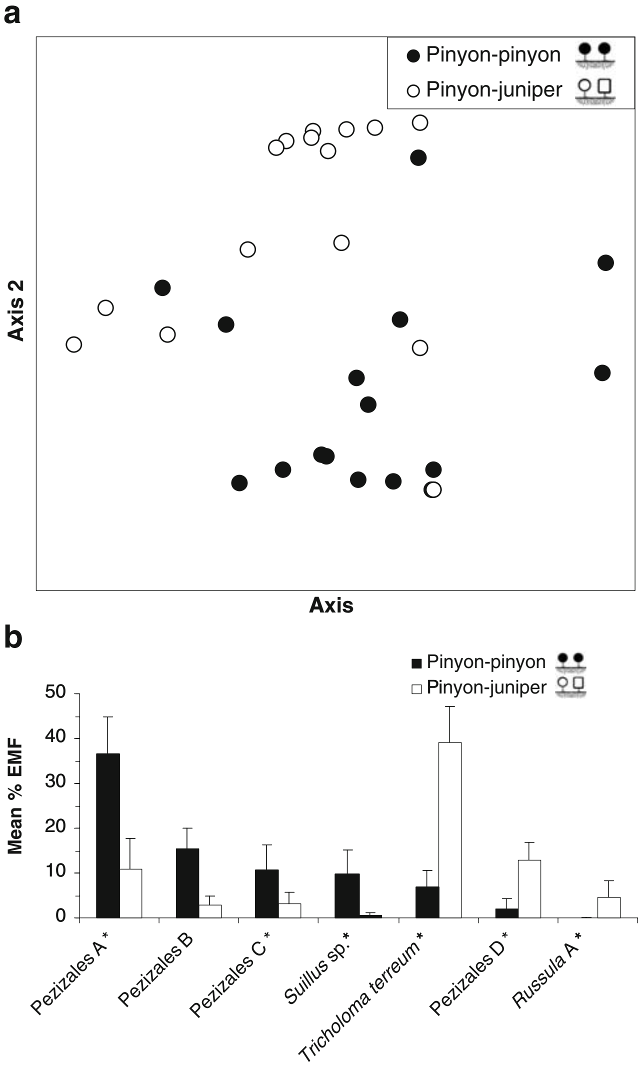

Fig. 4 Pinyon pines neighboring conspecifics had a different EMF community than pinyon pines neighboring one-seed juniper. **a** Non-metric multidimensional scaling (NMDS) showing that the EMF communities of pinyons neighboring conspecifics (pinyon–pinyon; *filled circles*) were different from pinyons neighboring junipers (pinyon–juniper; *open circles*), a result confirmed by MRPP analysis ($p<0.05$) **b** Histogram representing the mean (±1 SE) relative abundance of dominant EMF species found colonizing pinyons neighboring conspecifics (pinyon–pinyon; *filled bars*) and pinyons neighboring junipers (pinyon–juniper; *open bars*). Only EMF species that were indicator species or comprise at least 10% of all EM root tips collected from at least one group (i.e., pinyon–pinyon or pinyon–juniper) are represented in this histogram. Significant indicator species are indicated by an *asterisk*. EMF species are presented in descending order according to conspecific relative abundance

ecotone, where conditions are warmer and drier. In an analysis of sporocarps, Nantel and Neumann (1992) observed that EMF species did not occupy the entire range of their associated host due to abiotic factors. In study sites near ours but at higher elevation where ponderosa pine dominated, Kennedy (2005) observed higher species diversity and a different community of EMF than we did. Several studies have shown that the EMF community of pinyon pines on cinder soils is composed largely of ascomycete fungi that were thought to tolerate stressful abiotic conditions (Gehring et al. 1998; Swaty et al. 2004; Haskins and Gehring 2004), much as we observed in the present study. Although EMF community structure was not measured in this study, Dickie et al. (2006) found that EMF colonization of seedlings was influenced more by changes in soil properties associated with different overstory tree species than by taxonomic relatedness between the seedlings and trees. These findings support the hypothesis that established vegetation strongly influences abiotic and biotic soil traits, which in turn, influence EMF community structure.

The low density of ponderosa pine hosts at our study site also may have contributed to the lack of influence of ponderosa pine on the EMF communities of pinyon pine. Low sporocarp production in these semi-arid environments (Gehring et al. 1998) combined with large distances between trees may alter the propagule abundance of EMF species associated with upper elevation ponderosa pine. Low propagule abundance could limit colonization by some species of EMF even if they are able to survive in the warmer, drier lower elevation ecotone. Moreover, the inoculum potential of EMF has been shown to decrease rapidly with distance from established EM host plants (15–20 m; Dickie and Reich 2005). Hasselquist et al. (2005) found that *Picea* seedlings at an alpine-treeline ecotone had four-fold higher levels of root colonization by the EM fungus, *Cenococcum geophilum*, when adjacent to established trees compared to 7 m distant. If subordinate host species generally occur in somewhat isolated patches as we observed, we predict that the EMF community of rarer host species frequently will be affected by more common hosts, but not vice versa.

Overall EMF richness of ponderosa pine was relatively low at this site compared to studies at nearby sites (Kennedy 2005). We found only nine EMF species colonizing 16 ponderosa pines within a 35-ha area while a few miles from the present study at slightly higher elevation, Kennedy (2005) found 27 RFLP types on 60 mature ponderosa pine trees. In Oregon, Smith et al. (2004) found 140 EMF RFLP types colonizing ponderosa pine roots from 144 cores across 2 years and two sites separated by a distance of 14.5 km. Many factors may contribute to the lower richness in the present study, including lower sampling intensity, a more restricted area of sampling, and shorter duration of our study. However, the species accumulation curve for ponderosa pine EMF (not shown) and the Chao2 species richness estimate indicated that we had sampled sufficiently and suggests that low EMF species richness may be characteristic of the study site. The species richness of pinyon EMF in our study is also lower than previous studies at nearby lower elevation sites

(Gehring et al. 1998; Haskins and Gehring 2004), particularly those conducted prior to the recent drought (Gehring et al. 1998).

Pinyon and ponderosa pine EMF community overlap

In agreement with our hypothesis, we found high similarity between the EMF communities colonizing pinyon and ponderosa pines in locations where the rhizospheres of the two host species overlapped (Fig. 3). Co-occurring plants forming the same type of mycorrhizal association often overlap in fungal community composition (Kennedy et al. 2003; Dickie et al. 2004). Pinyon and ponderosa pines had six of seven EMF species in common with only one comparatively rare species occurring on only one of the two host species. Nearly half of all EM root tips collected in this portion of the study belonged to an EMF species that was found on both pinyon and ponderosa within samples, while only ~28% of within-sample species richness was shared. This result suggests that the relatively small proportion of EMF species that were shared when rhizospheres overlapped were over-represented in terms of EMF root tips. The high extent of EMF community overlap between neighboring heterospecific hosts that we observed is not surprising in a two-host-species ecosystem and is comparable to that documented in other ecosystems with few EM hosts. In a mixed stand of Douglas-fir (*Pseudotsuga menziesii* D. Don) and bishop pine (*Pinus muricata* D. Don) along the coast of California, 75% of EMF species observed were shared by both host plant species (Horton and Bruns 1998). While similarly high overlap in EMF species was not observed between Douglas-fir (*Pseudotsuga*) and an understory tree species (*Lithocarpus densiflora*) where only 30% of taxa overlapped, most of the samples contained species common to both hosts (Kennedy et al. 2003).

High overlap of EMF species among hosts, as between pinyon and ponderosa pines in this study, may increase the likelihood of the formation of mycorrhizal networks (MNs) that connect trees belowground. In addition, there is significant potential for MN formation if the EMF species that are shared among plants are found in high abundance. For example, Richard et al. (2005) found 12.9% of EMF RFLP types on both of the only two hosts in their study system *Quercus ilex* and *Arbutus unedo*; however, this small diversity accounted for 69.4% of EMF abundance. In our system, species overlap and the relative abundance of overlapping species were both high, suggesting that pinyon and ponderosa pine have abundant opportunities for MN formation.

Mycorrhizal networks could be important for exchange of resources and for provision of inoculum. For example, Simard et al. (1997) found significant transfer of nutrients and carbon between different plant taxa via mycorrhizal networks. Nara (2006b) found improved nutrient acquisition and growth of seedlings when they were connected to a mycorrhizal network. At the pinyon–ponderosa ecotone, the distribution limitations of ponderosa pine resulting from dry environmental conditions may be buffered if resources move through a mycorrhizal network from more stress tolerant pinyons. Further research is necessary to determine if mycorrhizal networks form between pinyon and ponderosa pines and if net resource movement is observed.

The high overlap in EMF community composition between pinyon and ponderosa pine also suggests the possibility that pinyon and ponderosa pines can provide EMF inoculum for one another. EMF inoculum is potentially limited at this study site due to a low number of EM host species and poor sporocarp production due to dry conditions (Gehring et al. 1998). The facilitation of EMF colonization by neighboring vegetation can be important for the successful establishment and subsequent performance of EM vegetation, especially in woodlands characterized by large interspaces and/or AMF-dominated soil matrices (Dickie et al. 2002, 2006; Dickie and Reich 2005).

Pinyon pine EMF community structure is affected by an AM neighbor

Juniper neighbors influenced EMF community composition, but not the EMF species richness of pinyon pine. Other studies have documented that neighboring plants influenced EMF, though few have examined consequences for EMF community structure (Nilsson et al. 1993; Michelsen et al. 1995; Urcelay et al. 2003; Haskins and Gehring 2004; McHugh and Gehring 2006). At a site a few kilometers from the present study, EMF colonization and growth of pinyon pine was negatively correlated with the abundance of AM shrubs (McHugh and Gehring 2006). Shrub removal resulted in increased colonization by EMF, but no change in community composition. In agreement with Haskins and Gehring (2004), who looked at the EMF communities colonizing pinyon pines that had been experimentally trenched to exclude juniper roots, we observed changes in the EMF community but no changes in EMF species richness. However, we observed an increase in *Tricholoma terreum*, a basidiomycete, with proximity to juniper while Haskins and Gehring (2004) found that non-trenched pinyon pines were dominated by ascomycete fungi. This difference between studies may be due to site variation in EMF species composition and abundance.

It has been proposed that neighboring non-EM vegetation may be detrimental to EMF and their host plants, but the mechanism of these effects remains poorly understood.

Some AM plants produce allelochemicals that could negatively affect EMF as seen with the arboreal dwarf shrub *Empetrum hermaphroditum* that retarded EM formation and reduced the ability of EMF to transfer nutrients to Scots pine (*Pinus sylvestris*; Nilsson et al. 1993). Competition between plants for resources could also affect EMF species indirectly (Urcelay et al. 2003). Species of EMF are known to interact with one another in the soil (Kennedy et al. 2007). Kennedy et al. (2007) found competitive exclusion occurred 75% of the time between two *Rhizopogon* species and work by Koide et al. (2005) suggests that these interactions could influence EMF community composition. The potential interactions of AMF and EMF have not been explored in detail and deserve further study.

Implications of EMF–neighbor interactions with climate change

Our finding that the EMF communities of pinyon and ponderosa pines overlapped extensively is potentially significant because both of these tree species have been experiencing high rates of mortality in the southwestern United States due to drought and associated insect outbreaks (Breshears et al. 2005; Mueller et al. 2005; Gitlin et al. 2006). A synthesis of projections from 19 climate models predicted drying conditions for the southwest through the remainder of this century (Seager et al. 2007). Our results indicate that at least in some habitats, ponderosa pine could provide EMF inoculum for pinyons moving up in elevation as the climate dries. During wetter times, pinyon pine could provide suitable inoculum for ponderosa pine extending their range downward in elevation. These reservoirs of EMF inoculum could be particularly important because pinyon and ponderosa pine are the only EM hosts in parts of their geographic range (Haskins and Gehring 2005; Hubert personal observation). Whole soil or pure culture inoculum developed from adjacent ponderosa pine forests could potentially be used to restore pinyon–juniper woodland habitats that have been lost to drought or fire. Host overlap could also be important to maintain populations of EMF, particularly in locations such as our study site, where many of the taxa cannot be identified to species using existing sequence data bases and, thus, may be undescribed. Species of fungi occupying stressful locations, like Sunset Crater, could be important to conserve because of their ability to survive in the increasingly arid southwestern US.

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