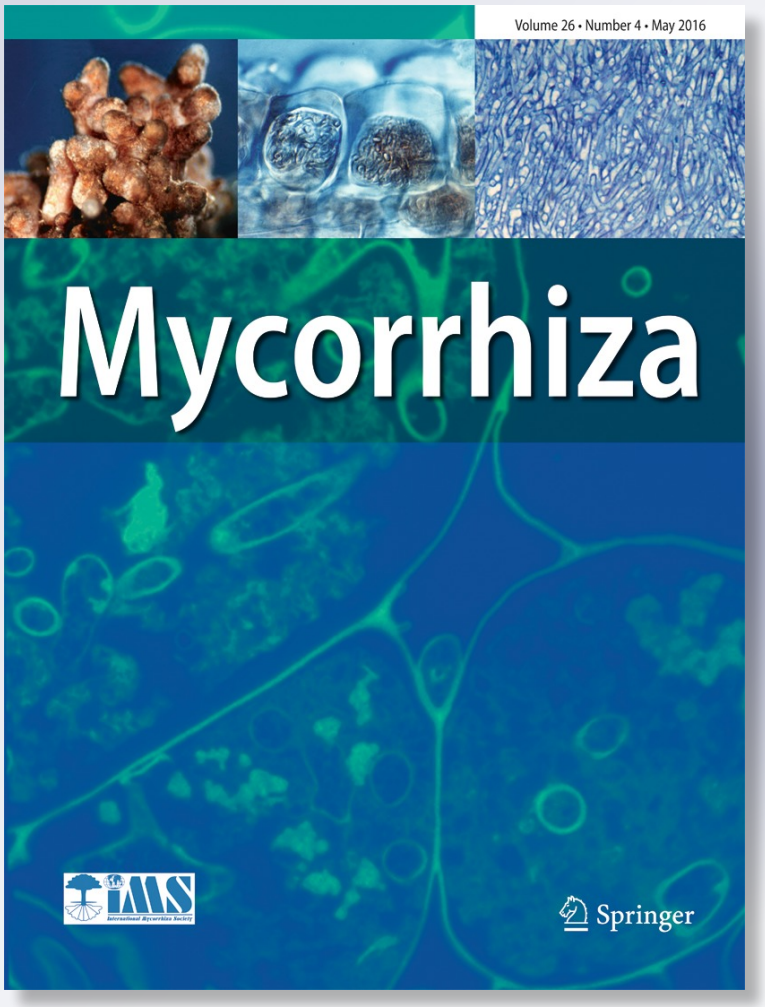
Ectomycorrhizal communities of ponderosa pine and lodgepole pine in the south-central Oregon pumice zone

Maria O. Garcia, Jane E. Smith, Daniel L. Luoma & Melanie D. Jones

Mycorrhiza

ISSN 0940-6360
Volume 26
Number 4

Mycorrhiza (2016) 26:275-286
DOI 10.1007/s00572-015-0668-x



Springer

Mycorrhiza (2016) 26:275–286
DOI 10.1007/s00572-015-0668-x

ORIGINAL ARTICLE

Ectomycorrhizal communities of ponderosa pine and lodgepole pine in the south-central Oregon pumice zone

Maria O. Garcia [1,2] · **Jane E. Smith** [3] · **Daniel L. Luoma** [1] · **Melanie D. Jones** [4]

Received: 4 September 2014 / Accepted: 29 October 2015 / Published online: 7 November 2015

Abstract Forest ecosystems of the Pacific Northwest of the USA are changing as a result of climate change. Specifically, rise of global temperatures, decline of winter precipitation, earlier loss of snowpack, and increased summer drought are altering the range of *Pinus contorta*. Simultaneously, flux in environmental conditions within the historic *P. contorta* range may facilitate the encroachment of *P. ponderosa* into *P. contorta* territory. Furthermore, successful pine species migration may be constrained by the distribution or co-migration of ectomycorrhizal fungi (EMF). Knowledge of the linkages among soil fungal diversity, community structure, and environmental factors is critical to understanding the organization and stability of pine ecosystems. The objectives of this study were to establish a foundational knowledge of the EMF communities of *P. ponderosa* and *P. contorta* in the Deschutes National Forest, OR, USA, and to examine soil characteristics associated with community composition. We examined EMF root tips of *P. ponderosa* and *P. contorta* in soil cores and conducted soil chemistry analysis for *P. ponderosa* cores. Results indicate that *Cenococcum geophilum*, *Rhizopogon salebrosus*, and *Inocybe flocculosa* were dominant in both *P. contorta* and *P. ponderosa* soil cores. *Rhizopogon* spp. were ubiquitous in *P. ponderosa* cores. There was no significant difference in the species composition of EMF communities of *P. ponderosa* and *P. contorta*. Ordination analysis of *P. ponderosa* soils suggested that soil pH, plant-available phosphorus (Bray), total phosphorus (P), carbon (C), mineralizable nitrogen (N), ammonium (NH_4), and nitrate (NO_3) are driving EMF community composition in *P. ponderosa* stands. We found a significant linear relationship between EMF species richness and mineralizable N. In conclusion, *P. ponderosa* and *P. contorta*, within the Deschutes National Forest, share the same dominant EMF species, which implies that *P. ponderosa* may be able to successfully establish within the historic *P. contorta* range and dominant EMF assemblages may be conserved.

Keywords Climate change · Ectomycorrhizal communities · Pine species migration · *Pinus contorta* · *Pinus ponderosa*

Electronic supplementary material The online version of this article (doi:10.1007/s00572-015-0668-x) contains supplementary material, which is available to authorized users.

✉ Jane E. Smith
jsmith01@fs.fed.us

[1] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

[2] Present address: Department of Biology, Boston University, 5 Cummington Mall, Boston, MA 02215, USA

[3] US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331, USA

[4] Biology Department, Institute for Biodiversity, Resilience and Ecosystem Services, University of British Columbia, Okanagan campus, Kelowna, British Columbia V1V 1V7, Canada

Introduction

Forest ecosystems of the Pacific Northwest are changing as a result of the effects of climate change (Vose et al. 2012). The rise of global temperatures, decline of winter precipitation, earlier loss of snowpack, and increased summer drought are altering the range of economically and ecologically important tree species, such as lodgepole pine (*Pinus contorta* Douglas ex Loudon), a species that thrives in cold, continental climates. Additional stressors, such as concurrent bark beetle infestations, are contributing to the demise of this widely distributed early seral stage tree species. A recent study based on climate change models suggests that lodgepole pine will

decline in the NW USA by the end of the twenty-first century (Coops and Waring 2011). As climate change transforms the lodgepole pine zone into a warmer drier environment, drought-tolerant tree species such as ponderosa pine (*Pinus ponderosa* Lawson) may establish within the historic lodgepole pine range (Coops and Waring 2011).

Tree species migration is a complex process involving ecological linkages between the belowground and aboveground components of ecosystems. For a tree species to most effectively compete in a particular region, environmental conditions such as temperature, precipitation, water availability, photosynthetic capacity, and soil conditions must be at an optimal level to favor one tree species over another. In addition, trees need to form symbiotic relationships with mycorrhizal fungi for optimal survival and growth (Jones and Smith 2004). Successful migration of pine species may be constrained by the distribution or comigration of belowground fungal symbionts (Perry et al. 1990; Nunez et al. 2009; Pringle et al. 2009; Dickie et al. 2010; Peay et al. 2010; Wolfe and Pringle 2011). The impacts of climate change may alter belowground fungal communities (Pickles et al. 2012) so that they may be a limiting factor in tree migration. Furthermore, knowledge of the linkages among soil fungal diversity, community structure, and environmental factors is critical to understanding of the organization and stability of pine ecosystems (Simard and Austin 2010; Karst et al. 2014).

Mycorrhizal fungi establish obligate mutualistic relationships with pine. The host tree provides photosynthetically fixed carbon (C) to the fungi, while the fungi in turn translocate soil nutrients such as nitrogen (N) and phosphorus (P) to the tree. Ectomycorrhizal fungi (EMFs) form an external sheath of hyphae around the fine roots of the host tree and extend mycelia outward into the soil reaching greater soil volumes than roots of trees alone could access (Smith and Read 2008). Furthermore, EMFs are a critical component of the forest ecosystem because they link aboveground and belowground components of biogeochemical cycles in forest ecosystems (Treseder and Allen 2000). Specifically, fungi are known to be important players in the decomposition and mineralization of organic matter (Schimel and Bennett 2004; Phillips et al. 2013). Nitrogen, P, and C are key nutrients in soil systems and are important for fungal nutrition. The availability of these nutrients is known to control mycorrhizal fungal abundance because plants invest more C in mycorrhizal fungi when N and P are limiting to plant growth (Mosse and Phillips 1971; Treseder 2004). Conversely, colonization by EMF declines if N or P availabilities increase in the soil (Jones et al. 1990; Read 1991). Belowground biogeochemical dynamics contributing to the availabilities of N, P, and C in the soil may, in turn, drive EMF community composition (Lilleskov et al. 2002; Treseder 2004).

Ecological specificity is a result of biotic and abiotic factors that control the ability of plants to form relationships with particular fungi in the soil and also plays a role in EMF community formation (Molina et al. 1992). In specificity phenomenon theory, mycorrhizal fungi may vary in host specificity from narrow (associating only with a single plant genus or family) (Massicotte et al. 1994; Bruns et al. 2002) to broad (associating with a diversity of plant genera, families, and orders) (Molina and Trappe 1982a, b). Conversely, host receptivity defines the numbers and diversity of mycorrhizal fungi that are accepted by a particular host. The interactions among host specificity, host receptivity, and ecological specificity are important to consider when examining the formation of EMF communities in host-specific soil systems (Pickles et al. 2015). Indeed, mycorrhizae play a key role in the establishment of plant species in a particular environment and the presence or absence of particular mycorrhizal fungi might determine the composition of plant species in forest stands (Weber et al. 2005; Nunez et al. 2009).

Lodgepole pine is currently a widely distributed tree species in eastern OR, USA. The *P. contorta* zone, found on the pumice plateau, formed as a result of the eruption of Mount Mazama 6600 years ago (Volland 1985). Previous studies of lodgepole pine EMF species in other systems have found *Cenococcum geophilum*, *Thelephora* spp., *Suillus* spp., *Russula* spp., and *Piloderma* spp. dominating the community composition (Bradbury et al. 1998; Durall et al. 1999; Byrd et al. 2000; Douglas et al. 2005; Jones et al. 2012). The *P. ponderosa* zone extends in a 55–65-km-wide range within the pumice/ash deposits from Mount Mazama, located south of Bend, OR (Simpson 2007). Overall, few studies have been conducted of EMF on ponderosa pine (Kotter and Farentinos 1984; Stendell et al. 1999; Barroetaveña et al. 2005, 2007), with very few studies on the mycorrhizal fungi of pine east of the Cascade Range in OR (Wright 1957, 1963, 1971; Smith et al. 2004, 2005; Fujimura et al. 2005). No previous study has characterized these communities in central OR using molecular tools.

The main objective of this observational study was to establish baseline information about the EMF communities of ponderosa pine and lodgepole pine in the Deschutes National Forest of central OR. Furthermore, we investigated the role of soil chemistry and its relationship with EMF community structure on ponderosa pine because ponderosa pine is one of the tree species expected to replace lodgepole pine under future climate change conditions. The information gathered through this study provides insights into the driving forces behind the formation of EMF communities in pine, supplementing the current knowledge for developing management strategies in a system anticipated to shift with impending climate change.

Materials and methods

Study area and sampling design

This study was conducted east of the Oregon Cascade Mountain Range in the Deschutes National Forest (OR, USA;

Fig. 1). Sites consisted of intermixed lodgepole pine and ponderosa pine stands of the south-central OR pumice zone; no other EMF tree hosts were present. Understory shrub communities included *Arctostaphylos patula* Greene, *Purshia tridentata* Pursh DC, *Festuca idahoensis* Elmer, and *Ceanothus velutinus* Douglas ex Hook (Franklin and Dyrness 1988).

Locations of remnant old-growth intermixed ponderosa and lodgepole pine stands with similar stand structure on the Deschutes National Forest were acquired (Chaylon Shuffield, personal communication; Shuffield 2011) and used to establish 17 sites for this study (Fig. 1 and Table 1). Ponderosa pine greater than 150 years old and lodgepole pine greater than 100 years old accounted for less than 5 and 3 %, respectively, of the total contemporary density (Shuffield 2011). Seven ponderosa pine trees, with diameters ranging from approximately 17 to 30 cm, were selected for soil coring in a random direction (selected trees were a minimum of 50 m apart) at each site. Five of the seven cores were randomly selected for use in the study. A total of 85 cores (1 core × 5 trees × 17 sites) were processed to capture mycorrhizal symbionts in the root zone. Ponderosa pine trees were randomly selected and located at least three canopy diameter lengths away from any lodgepole pine tree to exclude non-ponderosa ECM roots. We expected very few lodgepole pine roots in these samples, given that the density of lodgepole pine roots is very low more than 8 m from the bole (Parsons et al. 1994). Selected ponderosa pine trees were flagged, marked with paint, and their GPS coordinates were recorded. In addition, between 1 and 5 soil cores from 16 pure lodgepole stands (26 total soil cores) were collected to compare and contrast with the EMF communities of ponderosa pine. Most lodgepole stands were within the vicinity of our ponderosa pine stands in the Deschutes National Forest. All soil cores were taken at the tree crown edge of the selected tree.

Table 1 *Pinus ponderosa* study site locations with elevation

Site	Latitude (N)	Longitude (W)	Elevation (m)
4380	43° 43′ 46″	121° 34′ 15″	1306
BHB	43° 26′ 06″	121° 17′04″	1438
C1	43° 44′ 34″	121° 45′ 00″	1358
C4ER	43° 36′ 00″	121° 42′ 05″	1315
C6A	43° 39′ 43″	121° 51′ 33″	1400
C6B	43° 40′ 11″	121° 50′ 51″	1396
C7	43° 45′ 29″	121° 38′ 51″	1345
C8	43° 41′ 57″	121° 22′ 38″	1451
DEAD LOG	43° 35′ 04″	120° 54′ 59″	1546
FIN. BUTTE	43° 36′ 36″	121° 23′ 22″	1480
FIRE BUTTE	43° 38′ 52″	120° 59′ 11″	1561
HWY31	43° 28′ 24″	121° 23′ 26″	1435
ICE CAVE	43° 35′ 07″	121° 03′ 15″	1490
KB	43° 26′ 06″	121° 21′ 02″	1452
LB	43° 46′ 45″	121° 10′ 45″	1829
MOFF. BUTTE	43° 30′ 29″	121° 27′ 11″	1326
PB	43° 47′ 28″	121° 25′ 07″	1322

Soil core collection and processing

The upper duff layer, consisting primarily of pine needles, was removed, and a soil corer (5 cm diameter) was used to sample to a depth of 10 cm. Each core was placed into a ziplock plastic bag and kept in a cooler on ice while in the field and

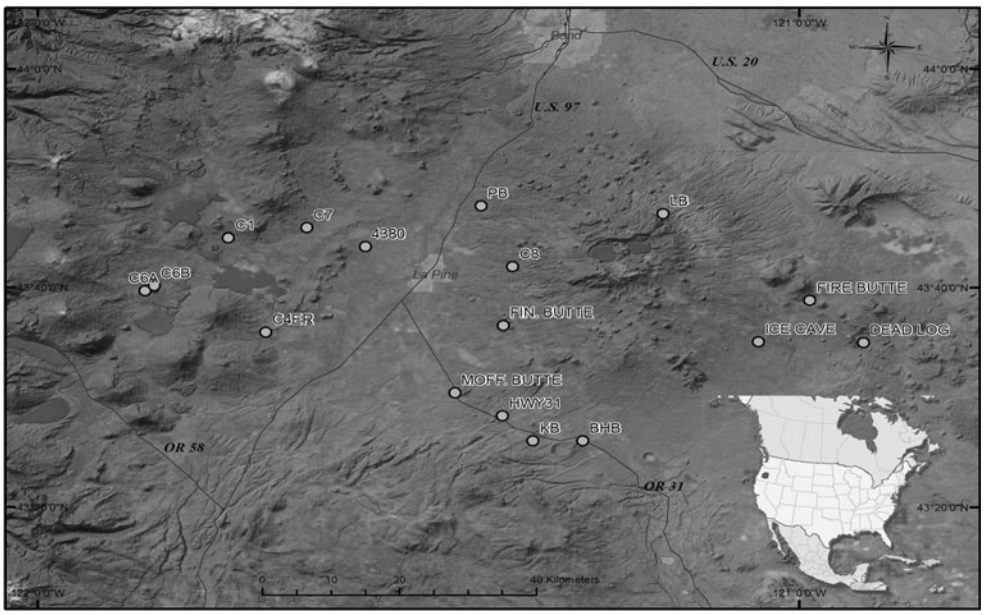


Fig. 1 Satellite image map showing the general area of study and ponderosa pine sampling locations on the Deschutes National Forest, OR, USA

at 4 °C during the week of collection. At the end of the week, soil cores were transported back to the lab within 1 day and stored in a cold room (4 °C) until processing. All soil core samples were collected on July 2011.

Soil cores were processed from July 2011 to September 2011. Soil was sieved (2 mm) out of each core sample, and the remaining roots were washed with water and examined with stereomicroscopy at 10X magnification. All live EMF root tips were collected per core and grouped based on morphological characteristics such as color, shape, and surface hyphal formations (Agerer 1987–2003). The total number of EMF root tips in each core was recorded for five soil cores from each site. One clean tip of each morphotype per core was placed into a 0.5-mL tube, air-dried overnight, and used for DNA extraction.

DNA extraction, amplification, and sequencing

DNA was extracted from dried EMF root tips using the Sigma Extract-N-Amp™ Kit (Sigma, Dorset, UK). A crushed dried root tip was placed into a 0.5-mL tube, and 10 μL of extraction solution was added. The sample was then incubated at 95 °C for 10 min in a thermocycler (Bio-Rad DNA Engine PTC 0200). Following the incubation, 20 μL of dilution solution was added to the extraction solution and lightly vortexed. Samples were stored at −20 °C until amplification by polymerase chain reaction (PCR). DNA amplification was carried out in 15 μL reactions using Promega GoTaq™ (Promega Madison, WI, USA) and universal fungal primers ITS1f and ITS4 (White et al. 1990). Amplifications were performed with initial denaturation at 95 °C for 2 min, followed by 35 cycles of 94 °C for 30 s, 50 °C for 1 min, and 72 °C for 90 s, with a final extension of 72 °C for 10 min. Successful PCR products (i.e., non-double band results with minimum 400 bp) were purified using ExoSAP-IT™ (USB, Cleveland, OH, USA) following manufacturer's instructions. Positive amplicons were directly sequenced at the University of Washington on an ABI 3730xl DNA analyzer using ABI reagents (Applied Biosystems Foster City, CA, USA).

Chromatograms were examined, edited, and corrected manually using Geneious Pro 5.5.6 (Drummond et al. 2008). Sequences were assembled into operational taxonomic units (OTUs) using the Assembly feature of Geneious Pro by setting the minimum overlap identity parameter to 97 %. Sequences were entered into the National Center for Bioscience Informatics (NCBI) Basic Local Alignment Search Tool (BLAST) to determine fungal sequence identities. Names were assigned to OTUs using sequence similarity criteria of ≥97 % for species, ≥95 % for genera, and ≤95 % to family. When possible, sequences that were 97 % or more identical were assigned the same OTU. Quality assurance measures led us to further examine sequences using the Alignment feature of Geneious Pro. Parameters were set to use MAFFT v6.814b alignment tool with the algorithm set to "auto." Once aligned, sequences were manually cross-checked to determine whether they could be assigned to the same OTU. For this analysis, BLAST hits for *C. geophilum* were grouped into one OTU. A representative sequence from each mycorrhizal taxon for each host by site and tree number is present in GenBank as accessions KT800056-KT800279 for ponderosa pine (Supplementary Table 1) and KT800280-KT800376 for lodgepole pine (Supplementary Table 2).

Soil chemistry

For chemical analysis, soil was sieved (2 mm) from each ponderosa pine core sample, composited by site, homogenized, and air-dried. All soil chemistry analyses were conducted at the Oregon State University Central Analytical Lab, following the methods of Horneck et al. (1989). Soil pH was tested using a 1:2 soil to water ratio. The dilute acid-fluoride method was used to analyze P-Bray. Ammonium (NH_4) and nitrate (NO_3) were extracted using 2 N KCL (Horneck et al. 1989) and quantified using an Alpkem Flow Solution autoanalyzer, Astoria 305D (Technicon Instruments, Saskatoon, Canada). Mineralizable N, or the fraction of organic N that can potentially be mineralized by soil microbes to produce NH_4 and NO_3 (Robertson et al. 1999), was measured using the anaerobic incubation method. Total N was measured using the Kjeldahl procedure. Total Kjeldahl P (TKP) was digested in a solution of sulfuric acid, potassium sulfate, and a catalyst. The resulting orthophosphate was quantified using an Astoria Pacific flow solution analyzer. Total carbon and N were measured following pure oxygen combustion on a Leco CNS-2000 Macro Analyzer.

Statistical analysis

Data structure

The presence-absence matrices constructed for analysis of EMF communities were based on data from 81 ponderosa pine soil cores, because 4 out of the 85 cores failed to give reliable sequences. All matrices that included lodgepole pine data had a total of 26 cores in the matrix.

Species accumulation curve

Species accumulation curves for rarefaction analysis were generated using the sample-based estimator of EstimateS (Colwell 2013). The *P. ponderosa* ectomycorrhiza species richness curve was based on the full 81-sample data set. The *P. contorta* richness curve was generated by using the extrapolation feature for samples 27–81.

Multivariate analyses of OTU presence and absence

Multiresponse permutation procedures (MRPPs) (Mielke and Berry 2001) with the Sørensen distance measure (PC-ORD software version 6.0; McCune and Mefford 2011) were used to test the null hypothesis of no difference in EMF OTU community composition between samples of lodgepole pine and ponderosa pine roots. The resulting A statistic represents the chance-corrected within-group agreement and is a measure of effect size (McCune and Grace 2002). When $A=0$, the groups are no more or less different than expected by chance; when $A=1$, all sample units are identical within each group. A stratified random sample approach was used to account for differences in the number of samples between ponderosa pine and lodgepole pine. The "random sample" option of PC-ORD was used to select 26 random cores out of the total 81 ponderosa pine soil cores at each of 1000 iterations. A bootstrapped confidence interval was calculated for the MRPP statistic to estimate the variability within groups by repeatedly sampling the data over 1000 iterations. Non-metric multidimensional scaling was used to provide a graphical representation of community relationships between ponderosa pine and lodgepole pine. The Sørensen distance measure was used to calculate similarities in communities, and the settings in PC-ORD were set on "autopilot mode" which included a random starting configuration and a maximum number of iterations of 500 with 100 runs with real data. The final instability criterion was set to 0.000001.

A non-metric multidimensional scaling (NMS) ordination with the same configurations was also generated for ponderosa pine communities, and a joint plot of environmental variables was superimposed on the ordination. The proportion of variance represented by each axis is based on the R^2 between distance in the ordination space and distance in the original space. The R^2 values of environmental variables plotted on the NMS ordination axes were determined by linear regression that was carried out using StatView software v5.1 (SAS Institute 1999). Only those environmental variables that had a significant R^2 value (≤ 0.1) when regressed with ordination axis values were plotted. The environmental variables included in the joint plot (Fig. 5) are listed in Table 3. Averages were calculated for each environmental variable, and relative standard deviations were calculated to provide a measure of sampling spread that was comparable between

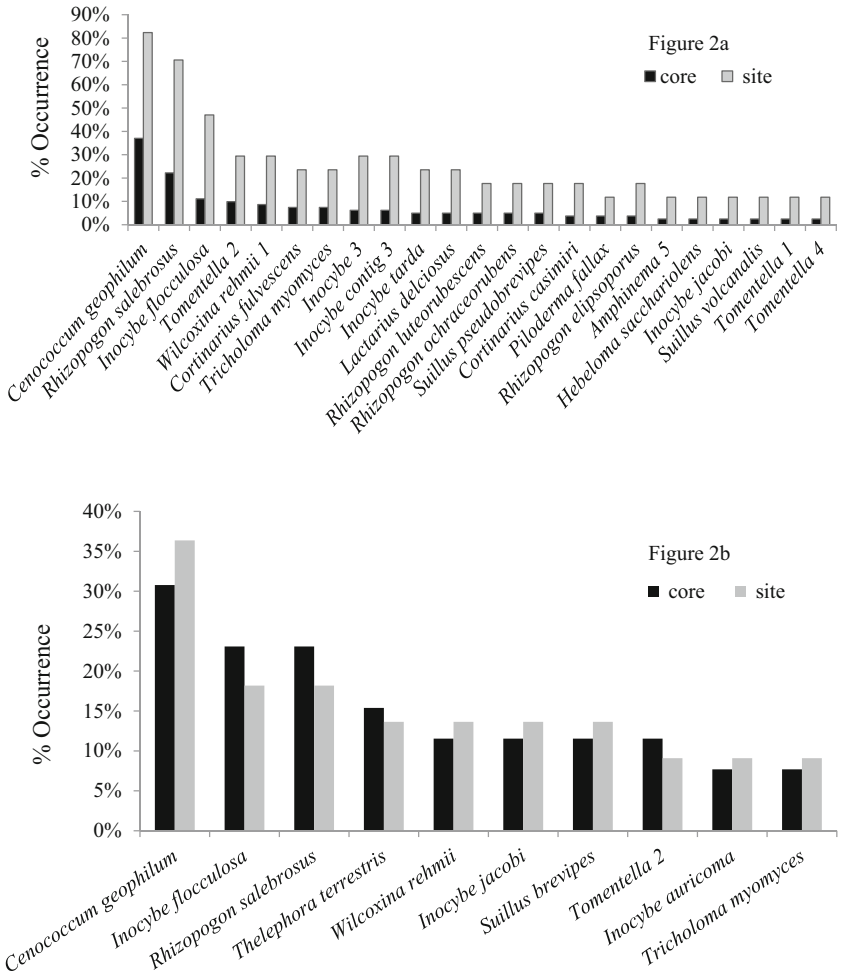


Fig. 2 **a** Occurrence of dominant ectomycorrhizal fungus operational taxonomic units (OTUs) in *Pinus ponderosa* forests. Data are presented by percentage of soil cores the taxa occurred in (*black*, $n=81$) and percentage of sites (*gray*, $n=17$). Ectomycorrhizal fungus OTU names are for closest BLAST match. **b** Occurrence of dominant ectomycorrhizal fungus OTUs in *P. contorta* forests. Data are presented by percentage of soil cores the taxa occurred in (*black*, $n=26$) and percentage of sites (*gray*, $n=16$). Ectomycorrhizal fungus OTU names are for the closest BLAST match

different measures in order to help identify soil parameters that display the greatest and least amounts of variation. Relative standard deviations were particularly useful for data exploration.

Linear regression was used to examine relationships between species richness and soil chemistry. To meet the assumptions of normality and homogenous variance (Sabin and Stafford 1990), species richness was square root transformed. Analyses were carried out with StatView software v5.1 (SAS Institute 1999).

Results

Ectomycorrhizal community structure of ponderosa pine and lodgepole pine

This observational study, conducted to determine the similarities between the EMF communities of ponderosa pine and lodgepole pine, yielded 437 usable DNA sequences of which 320 representative sequences from across the study sites were submitted to GenBank (Supplementary Information). In total, 237 OTUs were identified, with 173 found only in ponderosa pine, 94 only in lodgepole pine, and 31 were shared by the two tree species (Supplementary Information). Dominant (top three most abundant) OTUs of both pine species in this system were *C. geophilum* Fr., *Inocybe flocculosa* Saccardo, and *Rhizopogon salebrosus* A.H. Smith (Fig. 2a, b). Species accumulation curves generated using EstimateS showed a significant difference between *Pinus ponderosa* (PIPO) and *Pinus contorta* (PICO) when the EMF richness for 81 samples was estimated because the 95 % confidence intervals did not overlap (Fig. 3).

NMS ordination (Fig. 4) and MRPP tests showed that EMF communities did not differ between ponderosa pine and lodgepole pine at the species level (MRPP $A=0.001$, $p=0.68$, 90 % CI $-0.002<A<0.006$). Only 6 % of 1000 bootstrap samples demonstrated a significant difference in community composition between pine species.

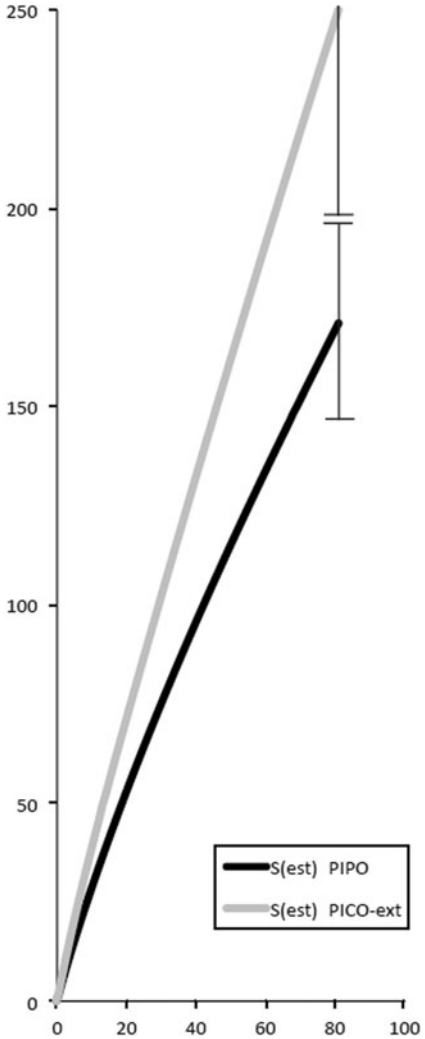


Fig. 3 Species accumulation curves generated using the rarefaction sample-based estimator of EstimateS. The *Pinus ponderosa* ectomycorrhiza species richness curve (S(est) PIPO) is based on the full 81-sample data set. The *P. contorta* ectomycorrhizal species richness curve (S(est) PICO-ext) is based on extrapolation for samples 27–81. The 95 % confidence intervals (*vertical bars*, upper PICO bar not shown) indicate a significant difference between PIPO and PICO when the richness for 81 samples is estimated

Chemistry of soil surrounding ponderosa pine trees

Soil chemistry variables with the highest variability across ponderosa pine sites were NO_3, NH_4, mineralizable N, P-Bray, and C, with relative standard deviations greater than 23 %. By contrast, we observed low variability in pH across our sites, with a relative standard deviation of about 3 %.

Relationships between EMF communities on ponderosa pine and environmental variables

Our NMS ordination resulted in three dimensions, which explained 70 % of the variation in ponderosa pine EMF community data set by site. Axis 1 explained 17 % of the variation, axis 2 explained 25 % of the variation, and axis 3 explained 28 % of the variation. The strongest environmental variables related to ponderosa pine EMF composition were mineralizable N, P-Bray, NO_3, NH_4, C, TKP, and elevation. Elevation was positively correlated with axis 3, and NO_3 and NH_4 were negatively correlated with axis 1 (Fig. 5 and Tables 2 and 3). Mineralizable N and P-Bray were positively correlated with axis 3 (Fig. 5 and Tables 2 and 3). We found a significant positive linear relationship between mineralizable N and square root EMF species richness ($p=0.04$, $Y=1.436+0.021*$ X, $R^2=0.234$; Fig. 6).

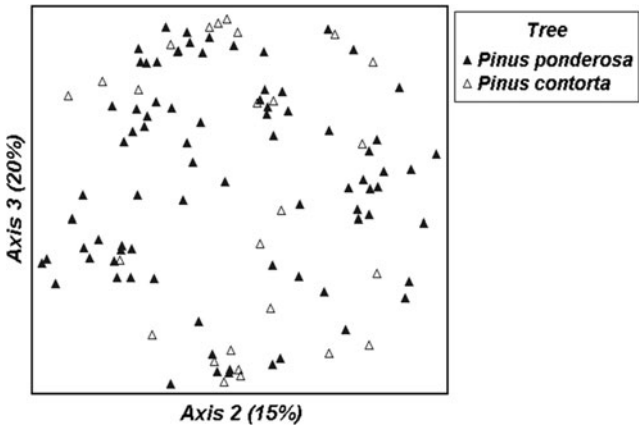


Fig. 4 NMS ordination of *Pinus ponderosa* and *P. contorta* soil cores in ectomycorrhizal fungus (EMF) species space. Multiresponse permutation procedure (MRPP) tests showed that EMF communities did not differ between the pine species for the full EMF OTU data set

Discussion

Most abundant EMF of ponderosa pine and lodgepole pine

The ascomycete *C. geophilum* was widespread across sites and the most encountered EMF colonizing roots in ponderosa pine and lodgepole pine soil cores. These findings are consistent with the morphological examination of ponderosa pine root tips in OR by Ernest Wright (Wright 1963, 1971). It is not surprising that *Cenococcum* formed a dominant type of ectomycorrhiza in our study since the *C. geophilum* [*Cenococcum graniforme* (Sow.) Fred and Winge] species complex is considered the world's most widely distributed ectomycorrhizal fungus (Massicotte et al. 1992).

The basdiomycete *R. salebrosus* was also abundant in our samples. *Rhizopogon* spp. are typical on root systems of *Pinus*. This genus is considered the most species-rich of all hypogeous fruiting EMF, with the largest number of *Rhizopogon* species occurring in Pinaceae-dominated areas of the Pacific northwestern USA (Molina and Trappe 1994; Massicotte et al. 1999; Kennedy and Bruns 2005). In greenhouse experiments, ponderosa pine was shown to form ectomycorrhizae with several *Rhizopogon* species including *R. arctostaphylli*, *R. ellenae*, *R. salebrosus* (as *subcaerulescens*), *R. truncatus*, *R. rubescens*, and *R. flavofibrillosus* (Massicotte et al. 1994, 1999). While our results are consistent with those of the greenhouse study at the genus level, our studies showed additional types of *Rhizopogon* mycorrhizae on field-grown pine roots at the species level.

We have not encountered published reports of *I. flocculosa* sporocarps being found in association with ponderosa pine or lodgepole pine. On mycorrhizae, however, we detected *I. flocculosa* as an abundant species with both *P. ponderosa* and *P. contorta*. ITS sequencing allowed for the detection of species in an area with sporadic fruitings of sporocarps. Documenting the correlation between sporocarp production and EM abundance of species would take long-term monitoring in order to include the infrequent years of abundant fruitings. Overall, the results of this study are consistent with the idea that dominance by a few species is a common feature of EMF communities (Gehring et al. 1998; Luoma et al. 2006).

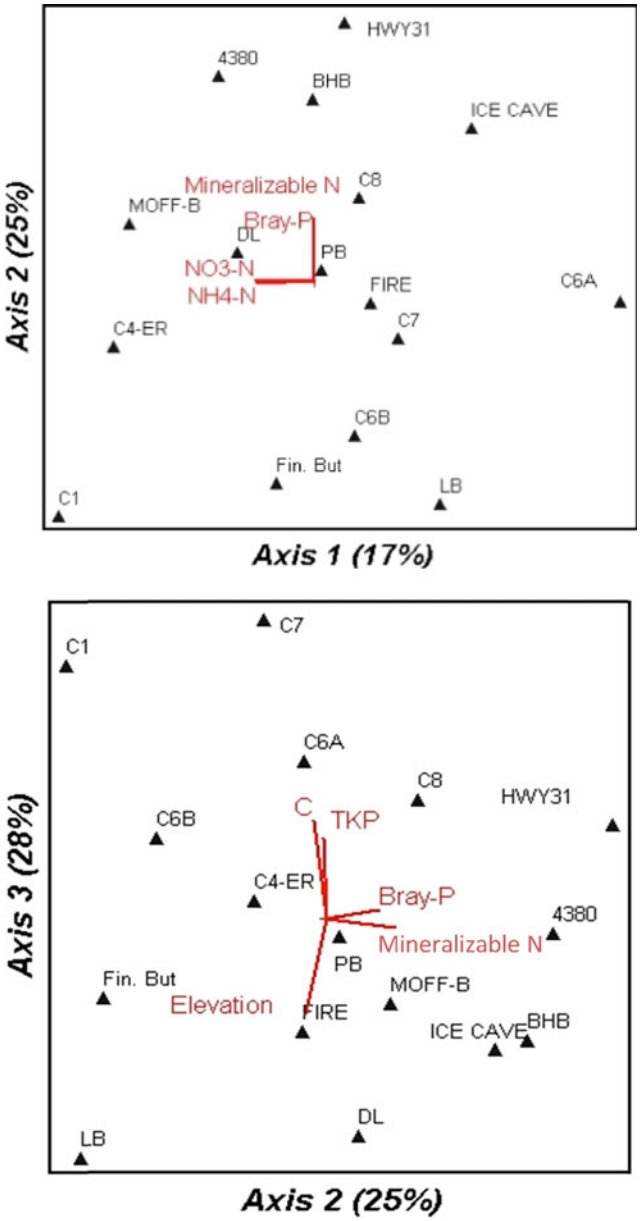


Fig. 5 NMS ordinations of ponderosa pine sites in ectomycorrhizal fungus species space with superimposed joint plots of environmental variables. *Vectors* show direction and magnitude of correlation between the ordination of sites and significant environmental variables (Table 3). Axis 1 explained 17 % of the variation in ordination scores, Axis 2 explained 25 % of the variation, and Axis 3 explained 28 % of the variation. Site and variable abbreviations are defined in Tables 1 and 3

Table 2 Chemistry of soils sampled at the 17 study sites in the Deschutes National Forest, OR

Site	pH	P-Bray	NO_3-N	NH_4-N	Mineralizable N	C	TKN	TKP
4380	6.8	37	0.2	0.2	10.7	1.55	509.2	749.2
BHB	6.6	42	0.5	0.4	18.1	1.47	470.3	585.2
C1	6.7	32	0.6	0.6	13.5	1.94	508.9	664.9
C4ER	6.5	37	0.3	0.4	9.7	1.92	530.9	561.5
C6A	6.4	33	0.2	0.2	11.9	2.71	680.0	525.0
C6B	6.6	34	0.3	0.3	10.5	1.91	464.6	548.2
C7	6.4	63	0.3	0.5	18.2	2.68	615.4	888.1
C8	6.7	55	0.2	0.3	21.7	1.75	546.5	705.0
DEAD LOG	6.6	33	0.9	0.4	24.1	1.03	563.5	423.4
FIN. BUTTE	6.3	60	0.5	0.5	14.7	2.43	748.1	739.5
FIRE BUTTE	6.7	37	0.6	0.3	23.8	1.21	536.0	468.9
HWY 31	6.8	80	0.6	0.3	22.8	2.18	644.3	569.5
ICE CAVE	6.6	54	0.2	0.6	22.2	1.58	467.7	550.0
KB	6.3	65	9.0	1.4	33.1	2.54	914.6	473.3
LB	6.9	31	0.4	0.3	9.1	1.64	571.7	579.1
MOFF. BUTTE	6.6	71	0.9	0.8	27.1	2.49	821.3	534.8
PB	6.8	49	0.4	0.2	12.5	1.48	413.5	671.2
Average	6.6	47.7	1.0	0.5	17.9	1.9	588.6	602.2
RSD	2.7	32.6	219.3	65.6	39.4	27.1	23.0	19.8

Values are means of five soil cores, each taken under a different ponderosa pine, at each site. Average and relative standard deviation (RSD) are calculated for each chemistry variable

Common mycorrhizal networks

Given that the EMF communities of the two pine species are so similar, it is reasonable to assume that ponderosa pine and lodgepole pine form common mycorrhizal networks (CMNs) (Molina and Trappe 1982b; Simard and Durall 2004) in the study area. Common mycorrhizal networks may be especially important for an ecosystem that is expected to transition with climate change because established CMNs may be beneficial for the survival of replacement tree seedlings, such as those of ponderosa pine. Common mycorrhizal networks may enhance EMF seedling survival and growth (Nara 2006; McGuire 2007) and may facilitate distribution of

Table 3 Environmental variables and respective R^2 values associated with NMS ordination axes

Code	Variable	R^2 values with ordination axes		
		Axis 1	Axis 2	Axis 3
pH	Soil pH	0.01	0.04	0.07
Bray P	Bray phosphorus	0.000	**0.18***	0.03
NO_3–N	Nitrate	**0.21****	0.001	0.14
NH_4–N	Ammonium	**0.21***	0.01	0.002
Mineralizable N	Mineralizable nitrogen	0.002	**0.23****	0.03
C	Carbon	0.02	0.04	**0.37*****
TKN	Total nitrogen	0.001	0.008	0.001
TKP	Total phosphorus	0.004	0.01	**0.30****
Elevation	Site elevation	0.16	0.07	**0.36*****

Figure 4 displays the significant variables in conjunction with the ordination of ponderosa pine EMF communities at the sample locations

Significant r^2 values in bold, *$p \leq 0.1$, **$p \leq 0.05$, ***$p \leq 0.01$

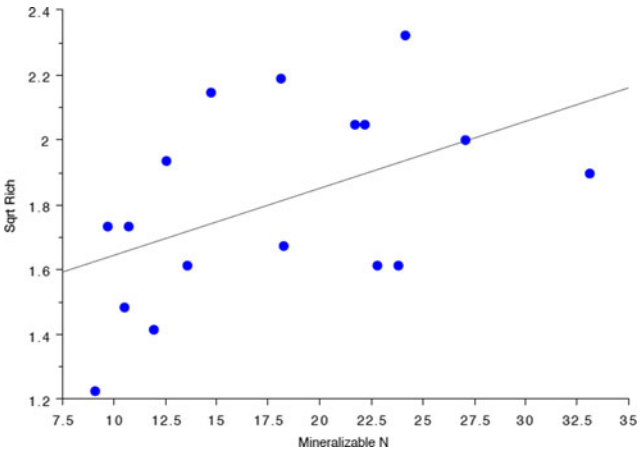


Fig. 6 Linear relationship between mineralizable N and the square root of mean species richness per soil core of ectomycorrhizal fungi colonizing ponderosa pine roots at 17 sites in the Deschutes National Forest; $Y=1.436+0.021^*$ X, $R^2=0.23$, $p=0.04$

resources within the system (Simard and Durall 2004). Furthermore, seedlings that can tap into a CMN are more likely to survive in stressed or harsh environments (Borchers and Perry 1990; Horton et al. 1999; Marler et al. 1999). In forests prone to stand-replacing wildfires, dominance by broad-host-ranging fungi was also reported in mixed stands of lodgepole pine and Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) (Cullings et al. 2000). Thus, in the face of climate-induced loss of lodgepole pine from mixed stands, survival of ponderosa pine seedlings may be enhanced by usurping mycorrhizal networks previously established with lodgepole pine.

Relationship between elevation and EMF communities

Our NMS analysis (Fig. 5) indicates that elevation may be a factor driving EMF community structure in ponderosa pine. An elevation gradient may create microclimate variations in qualities such as moisture availability that may be more amenable to the colonization of certain EMF over others. Although elevation gradients are frequently correlated with xeric to mesic gradients in ecosystems (Allen and Peet 1990), the scope of this study did not include measurements of elevation gradients and further study would be needed to determine whether there is a correlation between the elevation gradient and a moisture gradient in these sites.

Soil chemistry

Soil environments can act as habitat filters for EMF communities (Pickles et al. 2015). The results of our NMS analysis suggest that mineralizable N, NO_3, NH_4, P-Bray, TKP, and C are the main biogeochemical driving factors for the community composition in ponderosa pine sites. Nitrogen, P, and C are essential nutrients that are used by EMF, and the results of this study are consistent with other studies indicating that N, P, and C are driving biogeochemical factors of EMF communities in soil (Trudell and Edmonds 2004; Kranabetter et al. 2009b; Fox et al. 2013; Horton et al. 2013; Lim and Berbee 2013).

The results of simple linear regression showed that species richness increased as mineralizable N increased (Fig. 6). Kranabetter et al. (2009a) found a similar relationship when studying natural N gradients of a southern boreal forest. The results may suggest that EMF communities are more adapted to productive, N-rich environments. Alternatively, drought is a characteristic of harsh sites with low N availability and may require stress-tolerant EMF species; the simplicity of N forms (primarily organic N, rather than NH_4^+ and NO_3) on poor sites also precludes many EMF species. This suggests that N availability is a strong driver of EMF community and therefore an important soil property to consider in the implications of climate change. Alternatively, belowground competition may be driving the relationship between species richness and mineralizable N. In a system where mycorrhizal fungi are present, root nitrifiers, heterotrophs, and other microbial organisms may also exist. If there is a release of inorganic N as a result of mineralization, it cannot be assumed that this will be taken up by mycorrhizal fungi and tree roots alone (Brady and Weil 2002). Fungi may have to compete with all organisms in the system for inorganic nitrogen (Norton and Firestone 1996); thus, trees may invest in many species of fungi as a way to create a competitive advantage.

Conclusions

We found that ponderosa pine and lodgepole pine, located within the Deschutes National Forest, share the same dominant EMF species in pure lodgepole and mixed ponderosa/lodgepole pine stands (Fig. 4). This finding implies that ponderosa pine may be able to successfully establish within the historic lodgepole pine range in a climate change scenario and dominant EMF assemblages may be conserved. Note that this is not necessarily the case for other pairs of conifers (Pickles et al. 2015), so this conclusion should not be generalized. Furthermore, temporal studies would be necessary to confirm this, because the extent of host specificity/receptivity between these two pine species may be context-dependent (Karst et al. 2014). Therefore, further study is needed to establish that EMF communities are also similar in pure ponderosa and pure lodgepole stands.

Furthermore, our findings indicate that *P. contorta* stands have the capacity to harbor more EMF species than *P. ponderosa* stands, based on rarefaction analysis (Fig. 3). If the *P. contorta* stands do indeed exhibit higher EMF species density than *P. ponderosa* stands, then species richness per unit area may be lower under a climate that is projected to favor conversion to *P. ponderosa*. However, we also had a higher success rate in obtaining EMF OTUs from *P. contorta* than from *P. ponderosa* (PICO 73 % and PIPO 52 %). In view of this result, we must be cautious in ascribing higher EMF species richness to *P. contorta* stands. The steeper slope of the *P. contorta* accumulation curve may be the result of higher rates of detecting EMF species in each sample. A slightly lower rate of accumulation in *P. contorta* stands would negate the statistical significance of the difference between the stand types.

Ponderosa pine and lodgepole pine might be forming CMN in the soil system, and knowledge of the presence of fungal networks may prove helpful to forest managers. For example, if an assisted migration approach is considered as a management strategy (Kranabetter et al. 2012), EMF networks may help enhance EMF seedling survivorship and growth in this system. In addition, the results of this study indicate the availabilities of C, N, and P in this system affect the formation of

EMF communities, which in turn are essential for the survival of migrating tree species.

Acknowledgments This research was made possible with funding received from the National Science Foundation Graduate Research Fellowship Program and the USDA Forest Service Pacific Northwest Research Station. Mention of trade or firm names does not constitute an endorsement by the US Department of Agriculture. We thank Levi Davis, Tara Jennings, Doni McKay, and Joyce Eberhart for the lab assistance and Norman Forsberg for the field assistance. Thanks to Mary Berbee for the help with data analysis, Ed Mitchell and Bruce McCune for the help with the statistical analysis, and Kelly Christiansen for the GIS assistance. The comments of Greg Brenner, Paul Doescher, Marty Kranabetter, Pablo Martin-Pinto, and two anonymous reviewers greatly improved this manuscript.

References

Agerer R (1987–2003) Colour atlas of ectomycorrhizae. Einhorn, Schwäbisch Gmünd

Allen RB, Peet RK (1990) Gradient analysis of forests of the Sangre de Cristo Range, Colorado. Can J Bot 68(1):193–201. doi:10.1139/b90-026

Barroetaveña C, Rajchenberg M, Cázares E (2005) Mycorrhizal fungi in *Pinus ponderosa* introduced in Central Patagonia (Argentina). Nova Hedwigia 80(3–4):453–464. doi:10.1127/0029-5035/2005/0080-0453

Barroetaveña CE, Cázares E, Rajchenberg M (2007) Ectomycorrhizal fungi associated with ponderosa pine and Douglas-fir: a comparison of species richness in native western North American forests and Patagonian plantations from Argentina. Mycorrhiza 17(5):355–373. doi:10.1007/s00572-007-0121-x

Borchers SL, Perry DA (1990) Growth and ectomycorrhiza formation of Douglas-fir seedlings grown in soils collected at different distances from pioneering hardwoods in southwest Oregon clear-cuts. Can J For Res 20(6):712–721. doi:10.1139/x90-094

Bradbury SM, Danielson RM, Visser S (1998) Ectomycorrhizas of regenerating stands of lodgepole pine (*Pinus contorta*). Can J Bot 76(2):218–227. doi:10.1139/cjb-76-2-218

Brady NC, Weil RR (2002) The nature and properties of soils, 13th edn. Prentice-Hall, Upper Saddle River. doi:10.1016/S0167-8809(02)00230-X

Bruns TD, Bidartondo MI, Taylor DL (2002) Host specificity in ectomycorrhizal communities: what do the exceptions tell us? Integr Comp Biol 42(2):352–359. doi:10.1093/icb/42.2.352

Byrd KB, Parker VT, Vogler DR, Cullings KW (2000) The influence of clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming, and Gallatin National Forest, Montana. Can J Bot 78(2):149–156. doi:10.1139/cjb-78-2-149

Colwell RK (2013) EstimateS: statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates

Coops NC, Waring RH (2011) A process-based approach to estimate lodgepole pine (*Pinus contorta* Dougl.) distribution in the Pacific Northwest under climate change. Clim Chang 105(1):313–328. doi:10.1007/10584-010-9861-2

Cullings KW, Vogler DR, Parker VT, Finley SK (2000) Ectomycorrhizal specificity patterns in a mixed *Pinus contorta* and *Picea engelmannii* forest in Yellowstone National Park. Appl Environ Microbiol 66(11):4988–4991. doi:10.1128/AEM.66.11.4988-4991.2000

Dickie IA, Bolstridge N, Cooper JA, Peltzer DA (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. New Phytol 187(2):475–484

Douglas RB, Parker VT, Cullings KW (2005) Belowground ectomycorrhizal community structure of mature lodgepole pine and mixed conifer stands in Yellowstone National Park. For Ecol Manag 208(1):303–317. doi:10.1016/j.foreco.2004.12.011

Drummond AJ, Ashton B, Cheung M, Heled J, Kearse M, Moir R, Stones-Havas S, Wilson A (2008) Geneious Pro v4. 5.5

Durall D, Jones MD, Wright EF, Kroeger P, Coates KD (1999) Species richness of ectomycorrhizal fungi in cutblocks of different sizes in the Interior Cedar-Hemlock forests of northwestern British Columbia: sporocarps and ectomycorrhizae. Can J For Res 29(9):1322–1332. doi:10.1139/cjfr-29-9-1322

Fox MD, Tackaberry LE, Drouin P, BergeronY BR, Massicotte HB, Chen HY (2013) Microbial community structure of soils under four productivity classes of aspen forests in northern British Columbia. Ecoscience 20(3):264–275. doi:10.2980/20-3-3611

Franklin JF, Dyrness CT (1988) Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis

Fujimura KE, Smith JE, Horton TR, Weber NS, Spatafora JW (2005) Pezizalean mycorrhizas and sporocarps in ponderosa pine (*Pinus ponderosa*) after prescribed fires in eastern Oregon, USA. Mycorrhiza 15(2):79–86. doi:10.1007/s00572-004-0303-8

Gehring CA, Theimer TC, Whitham TG, Keim P (1998) Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. Ecology 79(5):1562–1572. doi:10.2307/176776

Horneck DA, Hart JM, Topper K, Koepsell B (1989) Methods of soil analysis used in the soil testing laboratory at Oregon State University. Oregon State University Agricultural Experiment Station SM 89:4

Horton TR, Bruns TD, Parker VT (1999) Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. Can J Bot 77(1):93–102. doi:10.1139/cjb-77-1-93

Horton BM, Glen M, Davidson MJ, Ratkowsky D, Wardlaw TJ, Mohammed C (2013) Temperate eucalypt forest decline is linked to altered ectomycorrhizal communities mediated by soil chemistry. For Ecol Manag 302:329–337. doi:10.1016/j.foreco.2013.04.006

Jones MD, Smith SE (2004) Exploring functional definitions of mycorrhizas: are mycorrhizas always mutualisms? Can J Bot 82(8):1089–1109. doi:10.1139/B04-110

Jones MD, Durall DM, Tinker PB (1990) Phosphorus relationships and production of extrametrical hyphae by two types of willow ectomycorrhizas at different soil phosphorus levels. New Phytol 115(2):259–267. doi:10.1111/j.1469-8137.1990.tb00451.x

Jones MD, Phillips LA, Treu R, Ward V, Berch SM (2012) Functional responses of ectomycorrhizal fungal communities to long-term fertilization of lodgepole pine *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands in central British Columbia. Appl Soil Ecol 60:29–40. doi:10.1016/j.apsoil.2012.01.010

Karst J, Randall MJ, Gehring CA (2014) Consequences for ectomycorrhizal fungi of the selective loss or gain of pine across landscapes. Botany 92:855–865. doi:10.1139/cjb-2014-0063

Kennedy PG, Bruns TD (2005) Priority effects determine the outcome of ectomycorrhizal competition between two *Rhizopogon* species colonizing *Pinus muricata* seedlings. New Phytol 166(2):631–638. doi:10.1111/j.1469-8137.2005.01355x

Kotter MM, Farentinos RC (1984) Formation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. Mycologia 76(4):758–760

Kranabetter J, Durall D, MacKenzie W (2009a) Diversity and species distribution of ectomycorrhizal fungi along productivity gradients of a southern boreal forest. Mycorrhiza 19(2):99–111. doi:10.1007/s00572-008-0208-z

Kranabetter J, Friesen J, Gamiet S, Kroeger P (2009b) Epigeous fruiting bodies of ectomycorrhizal fungi as indicators of soil fertility and

associated nitrogen status of boreal forests. Mycorrhiza 19(8):535–548

Kranabetter J, Stoehr M, O'Neill GA (2012) Divergence in ectomycorrhizal communities with foreign Douglas-fir populations and implications for assisted migration. Ecol Appl 22(2):550–560. doi:10.1007/s00572-009-0255-0

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM (2002) Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83(1):104–115. doi:10.1890/0012-9658

Lim S, Berbee ML (2013) Phylogenetic structure of ectomycorrhizal fungal communities of western hemlock changes with forest age and stand type. Mycorrhiza 23(6):473–486. doi:10.1007/s00572-013-0488-9

Luoma DL, Stockdale CA, Molina R, Eberhart JL (2006) The spatial influence of Douglas-fir retention trees on ectomycorrhiza diversity. Can J For Res 36:2561–2573. doi:10.1139/x06-143

Marler MJ, Zabinski CA, Callaway RM (1999) Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology 80(4):1180–1186. doi:10.2307/177065

Massicotte H, Trappe J, Peterson RL, Melville LH (1992) Studies on *Cenococcum geophilum*. II. Sclerotium morphology, germination, and formation in pure culture and growth pouches. Can J Bot 70(1):125–132. doi:10.1139/b92-017

Massicotte HB, Molina R, Luoma DL, Smith JE (1994) Biology of the ectomycorrhizal genus, *Rhizopogon* II. Patterns of host-fungus specificity following spore inoculation of diverse hosts grown in monoculture and dual culture. New Phytol 126(4):677–690. doi:10.1111/j.1469-8137.1994.tb02962.x

Massicotte HB, Melville LH, Peterson RL, Molina R (1999) Biology of the ectomycorrhizal fungal genus, *Rhizopogon*, IV. Comparative morphology and anatomy of ectomycorrhizas synthesized between several *Rhizopogon* species on ponderosa pine (*Pinus ponderosa*). New Phytol 142(2):355–370. doi:10.1046/j.1469-8137.1999.00392.x

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

McCune B, Mefford MJ (2011) PC-ORD. Multivariate analysis of ecological data. MjM Software Design Gleneden Beach, OR

McGuire KL (2007) Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88(3):567–574. doi:10.1890/05-1173

Mielke PW Jr, Berry KJ (2001) Permutation methods: a distance function approach. Springer, New York

Molina R, Trappe JM (1982a) Patterns of ectomycorrhizal host specificity and potential among Pacific Northwest conifers and fungi. For Sci 28(3):423–458

Molina R, Trappe JM (1982b) Lack of mycorrhizal specificity by the ericaceous hosts *Arbutus menziesii* and *Arctostaphylos uva-ursi*. New Phytol 90:495–509

Molina R, Trappe JM (1994) Biology of the ectomycorrhizal genus, *Rhizopogon* I. Host associations, host-specificity and pure culture syntheses. New Phytol 126:653–675

Molina R, Massicotte H, Trappe JM (1992) Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning: an integrative plant-fungal process. Chapman and Hall, New York, pp 357–423

Mosse B, Phillips J (1971) The influence of phosphate and other nutrients on the development of vesicular-arbuscular mycorrhiza in culture. J Gen Microbiol 69(2):157

Nara K (2006) Ectomycorrhizal networks and seedling establishment during early primary succession. New Phytol 169(1):169–178. doi:10.1111/j.1469-8137.2005.01545.x

Norton JM, Firestone MK (1996) N dynamics in the rhizosphere of *Pinus ponderosa* seedlings. Soil Biol Biochem 28(3):351–362. doi:10.1016/0038-0717(95)00155-7

Nunez MA, Horton TR, Simberloff D (2009) Lack of belowground mutualisms hinders Pinaceae invasions. Ecology 90(9):2352–2359

Parsons WF, Miller SL, Knight DH (1994) Root-gap dynamics in a lodgepole pine forest: ectomycorrhizal and nonmycorrhizal fine root activity after experimental gap formation. Can J For Res 24(8):1531–1538

Peay KG, Garbelotto M, Bruns TD (2010) Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91(12):3631–3640

Perry D, Borchers JG, Borchers SL, Amaranthus MP (1990) Species migrations and ecosystem stability during climate change: the belowground connection. Conserv Biol 4(3):266–274. doi:10.1111/j.1523-1739.1990.tb00288.x

Phillips LA, Ward V, Jones MD (2013) Ectomycorrhizal fungi contribute to soil organic matter cycling in sub-boreal forests. ISME J 8(3):699–713. doi:10.1038/ismej.2013.195

Pickles BJ, Egger KN, Massicotte HB, Green DS (2012) Ectomycorrhizas and climate change. Fungal Ecol 5(1):73–84. doi:10.1016/j.funeco.2011.08.009

Pickles BJ, Gorzelak MA, Green DS, Egger KN, Massicotte HB (2015) Host and habitat filtering in seedling root-associated fungal communities: taxonomic and functional diversity are altered in "novel" soils. Mycorrhiza. doi:10.1007/s00572-015-0630-y

Pringle A, Bever JD, Gardes M, Parrent JL, Rillig MC, Klironomos JN (2009) Mycorrhizal symbioses and plant invasions. Annu Rev Ecol Evol Syst 40:699–715

Read DJ (1991) Mycorrhizas in ecosystems—nature's response to the "law of the minimum". In: Hawksworth DL (ed) Frontiers in mycology. CAB International, Wallingford, pp 101–130

Robertson GP, Wedin D, Groffman PM, Blair JM, Holland EA, Nadelhoffer KJ, Harris D (1999) Soil carbon and nitrogen availability: nitrogen mineralization, nitrification and carbon turnover. In: Robertson GP, Bledsoe CS, Coleman DC, Sollins P (eds) Standard soil methods for long term ecological research. Oxford University Press, New York, pp 258–271

Sabin T, Stafford SG (1990) Assessing the need for transformation of response variables. Forest Research Lab, Oregon State University. Special Publication 20, 31 p

SAS Institute (1999) StatView software v5.1. SAS Institute, Cary

Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. Ecology 85(3):591–602. doi:10.1890/03-8002

Shuffield CD (2011) Overstory composition and stand structure shifts within inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone. MS Thesis, Oregon State University, Corvallis, OR

Simard SW, Austin ME (2010) The role of mycorrhizas in forest soil stability with climate change. In: Simard SW (ed) Climate change and variability. InTech p 275–302. doi: 10.5772/9813

Simard SW, Durall DM (2004) Mycorrhizal networks: a review of their extent, function, and importance. Can J Bot 82(8):1140–1165. doi:10.1139/b04-116

Simpson M (2007) Forested plant associations of the Oregon East Cascades, USDA, Forest Service, Pacific Northwest Region, Tech Pap R6-NR-ECOL-TP-03-2007, 602 p

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic Press, New York, New York

Smith JE, McKay D, Niwa CG, Thies WG, Brenner G, Spatafora JW (2004) Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. Can J For Res 34(12):2477–2491. doi:10.1139/X04-124

Smith JE, McKay D, Brenner G, McIver J, Spatafora JW (2005) Early impacts of forest restoration treatments on the ectomycorrhizal

fungal community and fine root biomass in a mixed conifer forest. J Appl Ecol 42(3):526–535. doi:10.1111/j.1365-2664.2005.01047.x

Stendell ER, Horton TR, Bruns TD (1999) Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycol Res 103(10):1353–1359. doi:10.1017/S0953756299008618

Treseder KK (2004) A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol 164(2):347–355. doi:10.1111/j.1469-8137.2004.01159.x

Treseder KK, Allen MF (2000) Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. New Phytol 147:189–200. doi:10.1046/j.1469-8137.2000.00690.x

Trudell SA, Edmonds RL (2004) Macrofungus communities correlate with moisture and nitrogen abundance in two old-growth conifer forests, Olympic National Park, Washington, USA. Can J Bot 82(6):781–800. doi:10.1139/b04-057

Volland LA (1985) Plant associations of the central Oregon pumice zone, USDA, Forest Service, Pacific Northwest Region Tech Rep 217 p

Vose JM, Peterson DL, Patel-Weynand T (2012) Effects of climatic variability and change on forest ecosystems: a comprehensive science synthesis for the U.S. Forest Sector. USDA, Forest Service Pacific Northwest Research Station, Portland, OR, Gen Tech Rep PNW-GTR-870

Weber A, Karst J, Gilbert B, Kimmins JP (2005) Thuja plicata exclusion in ectomycorrhiza-dominated forests: testing the role of inoculum potential of arbuscular mycorrhizal fungi. Oecologia 143(1):148–156

White TJ, Bruns TD, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic, London, pp 315–322

Wolfe BE, Pringle A (2011) Geographically structured host specificity is caused by the range expansions and host shifts of a symbiotic fungus. ISME J 6(4):745–755

Wright E (1957) Importance of mycorrhizae to ponderosa pine seedlings. For Sci 3(3):275–280

Wright E (1963) Ectotrophic mycorrhizae on pine seedlings in Oregon. Ecology 44(1):173–175

Wright E (1971) Mycorrhizae on douglas fir and ponderosa pine seedlings. Oregon State Univ, For Res Lab, Res Bulletin 13, paper 670, 35 p