Recovering lost ground: Effects of soil burn intensity on nutrients and ectomycorrhiza communities of ponderosa pine seedlings

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ABSTRACT

Fuel accumulation and climate shifts are predicted to increase the frequency of high-severity fires in ponderosa pine (*Pinus ponderosa*) forests of central Oregon. The combustion of fuels containing large downed wood can result in intense soil heating, alteration of soil properties, and mortality of microbes. Previous studies show ectomycorrhizal fungi (EMF) improve ponderosa seedling establishment after fire but did not compare EMF communities at different levels of soil burn intensity in a field setting. For this study, soil burn intensity effects on nutrients and EMF communities were compared at Pringle Falls Experimental Forest, La Pine, Oregon. Twelve replicate sites were used, each with three treatments: high intensity soil burn from large downed wood combustion (HB), low intensity soil burn (LB), and unburned control (UB). Temperatures lethal to fungi were detected at 0-cm, 5-cm, and 10-cm depths in HB soils and 0-cm depth in LB soils. Ponderosa pine seedlings planted post-burn were harvested after four months for EMF root tip analysis. We found: (a) greater differences in soil properties and nutrients in HB soils compared to LB and UB soils; (b) no differences in EMF richness and diversity among treatments; (c) weak differences in community composition based on relative abundance between UB and either burn treatments; and (d) EMF composition in HB and LB treatments correlated with soil carbon and organic matter contents. These results support the hypothesis that the combustion of large downed wood can alter the soil environment directly beneath it. However, an EMF community similar to LB soils recolonized HB soils within one growing season. Community results from both burn treatments suggest an increase in patchy spatial distribution of EMF. We hypothesize that quick initiation of EMF recolonization is possible depending on the size of high intensity burn patches, proximity of low and unburned soil, and survival of nearby hosts. The importance of incorporating mixed fire effects in fuel management practices will help to provide EMF refugia for ponderosa pine forest regeneration.

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1. Introduction

Fire provides many benefits to forest ecosystems by consuming accumulated vegetation and releasing nutrients into the soil. Over the past century, humans have actively suppressed wildfires to prevent damage to human infrastructure and natural resources. As a result, fire exclusion has led to an unprecedented overgrowth of vegetation (Fulé et al., 1997; Safford et al., 2012). The accumulated vegetation acts as fuel when fire returns to a forest, resulting in hotter and more destructive fires (Kaufmann et al., 2005). Climate shifts in conjunction with fuel accumulation are contributing to an increase in the frequency and size of high severity fires

and length of fire season in the ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) forests of central Oregon (Covington, 2000; Hessburg et al., 2005; Westerling et al., 2005; Millar and Stephenson, 2015). This outlook has created a need for an increased comprehension of the effects of fire on soil ecosystems and their implications for post-fire ponderosa pine regeneration.

The impact of a fire can be classified by burn severity, the "degree to which a site has been altered or disrupted by fire" (NWCG, 2003). The degree of severity can be determined by assessing the physical, chemical, and ecological changes observed post-fire that occur as a direct result of combustion (Keeley, 2009). Burn severity is a product of burn intensity, i.e., the amount of heat energy measured by temperature and duration of heating (NWCG, 2003; Keeley, 2009). The term *soil burn intensity* directly refers to the heat absorbed by the ground during a fire. The size, quantity, arrangement, and quality of the fuel in contact with the

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forest floor influence the depth and degree of soil burn intensity (Busse et al., 2013).

Large downed wood increases soil burn intensity (Busse et al., 2013)—but what role does it play in the post-fire effects and recovery of ponderosa pine forests? In many forest ecosystems decaying downed wood can provide habitat for organisms as well as shade, water, and growing substrate for plants (Maser and Trappe, 1984; Franklin et al., 1987; Fukasawa, 2012). The natural accumulation of large downed wood in ponderosa pine forests was historically managed and maintained by periodic fire (Fitzgerald, 2005). In the environment created post-fire, the combustion of large downed wood can form a mineral soil seedbed temporarily void of competing vegetation for ponderosa pine seedlings (White, 1985). However, large downed wood may also have negative effects on soil. Greater belowground degradation of some soil properties occurs as a result of high intensity soil burning (Neary et al., 1999). Soil nutrients may be volatized or leached at higher temperatures, making them less accessible for plants and microbes (Neary et al., 1999; Bormann et al., 2008). Water repellant layers form during intense soil heating and can contribute to soil erosion (DeBano, 2000). High soil burn intensity can also reduce water content and elevate soil pH (Certini, 2005; Neary et al., 2005), creating a less favorable environment for some plants and microbes.

High soil burn intensity can also directly affect soil microbes, including ectomycorrhizal fungi (EMF) (Holden et al., 2013). Ectomycorrhizal fungi form symbiotic relationships with the roots of host trees and shrubs where water and nutrients are exchanged for the tree's carbohydrates. Through hyphal networks, EMF expand the area of soil from which a tree can attain resources. Ectomycorrhizal fungi can also prevent post-disturbance nutrient leaching, aid in soil stabilization, and supply host trees in depleted soils (Claridge et al., 2009; van der Heijden et al., 2015). In the absence of an EMF symbiont, some conifer species are unable to establish and thrive (Miller et al., 1998).

Ectomycorrhizal fungi can be sensitive to heating by fire. Fungal mortality occurs at temperatures around 60 °C and above (Neary et al., 1999). While the insulating properties of soil help to buffer heat penetration from fire (Neary et al., 2005), the depth can vary depending on soil type, moisture, and other factors (Agee, 1996; Smith et al., 2004). Some EMF produce spores that can withstand higher temperatures (Baar et al., 1999; Peay et al., 2009). Whereas these spores can serve as sources of post-fire inoculum (Cairney and Bastias, 2007), successional dynamics and the length of time needed for recovery are poorly understood. Measures of EMF diversity such as species richness and relative abundance have been used as indicators for recovery of an EMF community (Taylor, 2002). The presence of a diverse EMF community can support the growth and survival of the host plants with which they associate (Barker et al., 2013).

Ectomycorrhizal fungi form an obligate association with ponderosa pine roots that assists trees during drought and provides protection from root pathogens (Read, 1998; Peterson et al., 2004). The first growing season is critical for pine seedlings; EMF colonization during this time can determine seedling success (Horton et al., 1998; Baar et al., 1999; Barker et al., 2013). Previous observational and greenhouse studies have shown EMF also improve ponderosa seedling growth and survival after fire but did not investigate community composition among different levels of soil burn intensity in a field setting (Miller et al., 1998).

Current research gaps expose the question: Does soil burn intensity alter early EMF recruitment on ponderosa pine seedlings? The goal of this study was to investigate first-growing season effects of high intensity soil burning from the combustion of large downed wood in ponderosa forests. To do this, we conducted an in-situ experiment with three treatments: high soil burn intensity (HB), low soil burn intensity (LB), and unburned control (UB). We expected to find (a) greater differences in soil properties and nutrient contents in soils subjected to HB treatment in comparison with LB and UB treatments; (b) lower EMF richness and diversity on ponderosa pine seedlings grown in HB soils compared to LB and UB soils; (c) greater differences in EMF constancy and relative abundance in HB soils in comparison with LB and UB soils; and (d) differences in EMF composition in HB plots that would correlate with differences in HB soil properties and nutrient contents.

2. Materials and methods

2.1. Study area

We conducted our research at the Pringle Falls Experimental Forest on the eastern slope of the Cascade Range in Central Oregon (43°42′N, 121°37′W). Pringle Falls is located about 48 km southwest of the city of Bend, in the Deschutes National Forest. Operated by the United States Department of Agriculture-United States Forest Service, the Experimental Forest is part of a national network of outdoor laboratories dedicated for silviculture, insect, disease, fire, and climate change research. Originating from a stand-replacing fire in 1845, the Pringle Falls Experimental Forest has experienced over a century of fire exclusion and infrequent thinning (Youngblood et al., 2004).

A 199 ha area of Lookout Mountain was designated for the study located in a forest stand that was thinned from below (two years prior) to a residual tree density approximating 75% of the maximum recommended stocking level, the site occupancy threshold for competition induced mortality and risk of bark beetle outbreak (Cochran et al., 1994; Youngblood, 2009). The study area ranges from flat to gently sloping terrain (0–20%, southeast aspect) at elevations of 1340–1440 m. Ponderosa pine is the dominant tree species, with a stand density index of 107 and an average basal area of 16.8 m^2 ha^{-1} (Youngblood, 2009). The dominant shrubs of the understory plant communities are bitterbrush (Purshia tridentata Pursh) and snowbrush ceanothus (Ceanothus velutinus Dougl. ex Hook) typical of a ponderosa pine/bitterbrush/Idaho fescue (Festuca idahoensis) plant association (Simpson, 2007). The forest floor includes pine needle litter and duff averaging about 3 cm in depth. Soils are 62–148 cm in depth (to bedrock) and consist of well- to excessively-drained loamy coarse sands and volcanic ash deposits from the eruption of Mount Mazama 7700 years ago (http://websoilsurvey.nrcs.usda.gov/app/help/citation.htm; Powers and Wilcox, 1964). The soils are classified as Xeric Vitricryands in the La Pine Soil Series (Soil Survey Staff, 2014) and the density of pumice components averages 81% (Klug et al., 2002). Hot, dry summers and cold winters typify the climate of the region. The mean annual precipitation is 519 mm, usually arriving in the form of winter snow, and annual temperatures average 6.4 °C (Youngblood et al., 2004).

2.2. Experimental design

We established 12 sites throughout the study area in the summer of 2011. Sites were non-randomly assigned to areas with open canopies for maneuverability of log-lifting machinery. Parallel stacks of large downed logs ("mega-log") were constructed to simulate large diameter coarse woody debris that can be found in ponderosa pine ecosystems. Mega-logs were covered with plastic tarps and left to cure over the following two years. At each of the 12 replicate sites, we established a site center and three plots: high soil burn intensity (HB), low soil burn intensity (LB), and an unburned control (UB). The three plots were located 10 m from the site center, equidistant from one another in a pinwheel design (Fig. 1). HB plots were assigned to mega-log locations. We
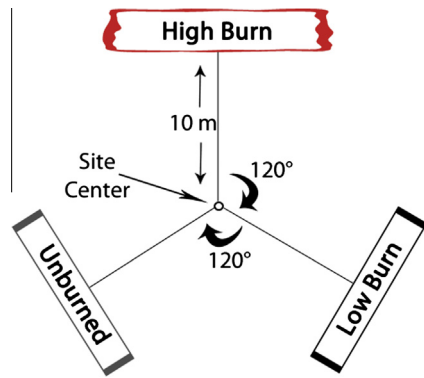
Fig. 1. Site design showing three plots located 10 m from the site center, oriented in haphazard cardinal direction. High Burn (HB) = high soil burn intensity, Low Burn (LB) = low soil burn intensity, and Unburned (UB) = unburned control (n = 12 sites).

Fig. 2. Example of high intensity burn treatment (HB) applied by the combustion of a parallel stack of large downed logs. Photo credit: Ariel D. Cowan.

Fig. 3. Mean maximum temperature (°Celsius) recorded under low intensity (Low burn) and high intensity (High burn) soil burn treatments at 0, 5, 10, and 30 cm depth from plot center (n = 9). Approximate lethal temperature threshold for fungi is 60 °C (Neary et al., 1999). Temperatures of 10 and 30 cm depths in Low burn treatment were not recorded. Error bars denote ±1 standard error.

maximum temperature (Fig. 3) and mean duration above 60 °C, the approximate lethal threshold for fungi (Neary et al., 1999). Temperature recording methods and statistical analysis are available in Smith et al. (in press).

2.3. Soil sampling

We returned to the sites one week after the burn to collect soil samples. After removing the O horizon (where present), mineral soil was collected at 0–10 cm, 10–20 cm, and 20–30 cm depths from 10 of 12 sites. Soils were sampled from the 10 sites that met selection criteria including minimal underlying rocky substrate that would prevent tree seedling planting, thermocouple installation, and soil sampling. Soil cores were taken from the center of each plot (30 soil cores, 90 soil samples) using a 6.35 cm diameter × 30.4 cm length impact coring device containing three 10 cm liners (AMS Inc., American Falls, Idaho). Each soil sample, containing a volume of 179.2 cm³, was placed in a plastic zip-lock bag and kept on ice in a cooler until cold room storage at 4 °C. Forest floor depth, the depth of litter and duff above mineral soil, was recorded from the center of each plot.

Soil samples were processed in July of 2013 and were analyzed by the Page-Dumroese Lab at the Rocky Mountain Research Station, Moscow Forestry Sciences Laboratory, Moscow, Idaho. Samples were dried, sieved (2 mm mesh), and mechanically homogenized with a Spex Mixer Mill (Metuchen, New Jersey) before being processed as described in Cerise et al. (2013). Analysis included total nitrogen (N), total carbon (C), soil organic matter (SOM), pH, total extractable calcium (Ca), total extractable magnesium (Mg), percent water content (%MC), total bulk density (BD) and fine-fraction bulk density (FineBD). Soils were weighed, dried at 105 °C for 24 h and reweighed to calculate %MC. Total C and N were evaluated by dry combustion at 950 °C on a Leco TruSpec CN determinator (St. Joseph, Michigan). Bray phosphorus (Bray-P) samples were analyzed using methods described in Amacher et al. (2003), first undiluted to check Bray-P range then re-analyzed at 1:10 dilutions on over-range samples. The pH neutral 1 M ammonium acetate method (Helmke and Sparks, 1996) was used to extract Ca and Mg before analysis on a Perkin Elmer 5100PC AA Spectrometer (Waltham, MA, USA). Mineral soil C, N, Bray-P, Ca, Mg, and SOM contents were corrected for rock fragment content and converted from percentages to units of Mg/ha (C, SOM)

randomly assigned the LB and UB plots to the remaining two sides of the pin-wheel with the flip of a coin.

High burn treatments were created by the complete combustion of mega-logs during a prescribed burn (Fig. 2). The dimensions of each mega-log ranged from 1.5 to 2 m wide, 8 to 10 m long, and 0.7 to 1.2 m in height. Individual logs had a decay class of 1–2 (low decay, bark and twigs intact) (Maser et al., 1979). Moisture contents of logs are available in Smith et al. (in press).

To mimic the footprint of a mega-log, we established 2 m wide and 10 m long plots for LB and UB treatments. LB treatments were applied through the broadcast burning of the pre-existing fuels. Pre-treatment fuels in LB plots consisted of fuel size classes 1, 10, and 100 h fuels (0–7.6 cm) (Brown et al., 1982). A 2 m wide fire line was constructed outside the perimeter of UB plots to protect them from burning during the prescribed fire. The construction of the fire lines included removal of surface organic matter down to mineral soil in order to disrupt fuel continuity and fire spread.

The USDA-FS Bend-Fort Rock Ranger District conducted the prescribed burn on May 14th of 2013. Mega-logs and the surrounding forest floor were ignited using drip torches and fire accelerant (Heat Source Slash Burner, Wildfire Environmental Inc.). Weather conditions for the day were light W to NW winds, clear skies, 12–19 °C (dry bulb), and 25–40% relative humidity. Under heading conditions, 10 and 100 h fuels were the primary carriers of the fire. Flame lengths were 0.6–1.8 m (2–6 ft) with a 12–18 m (40–60 ft) flame zone depth. Survival of mature ponderosa pine trees adjacent to all sites was approximately 99%.

Thermocouple probes recorded soil temperatures within LB and HB plots. Temperature data points were analyzed for mean
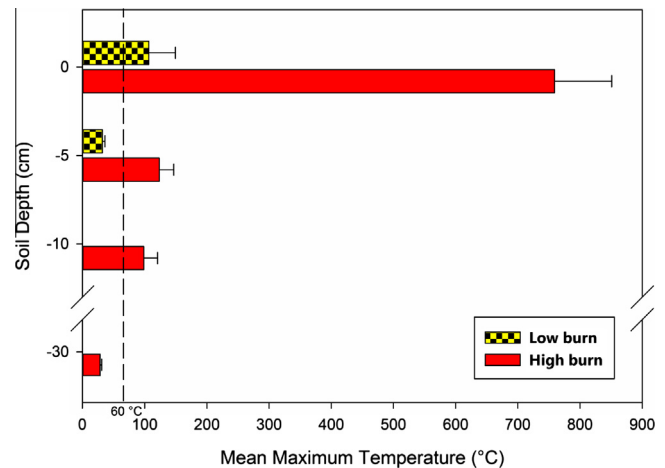
and kg/ha (N, Bray-P, Ca, Mg) using fine-fraction bulk density values (Andraski, 1991; Page-Dumroese et al., 1999; Klug et al., 2002). Total bulk density, fine fraction bulk density, and gravimetric rock-fragment contents are reported in Supplemental Table A1.

2.4. Planting and root tip assessment

Eight days after the burn, we planted ponderosa pine seedlings at each plot in all 12 sites. Two-year-old Q-plug +1.5 (containerized for first 6 months) seedlings were obtained from the same central OR *Pinus ponderosa* stock (PIPO-01-0136-553-89 SB) from a Forest Service-operated nursery in Coeur d'Alene, Idaho. Two-year-old seedlings, as opposed to seed, were planted to assure the survival of a large quantity of seedlings for the study (Rose and Haase, 2006). Approximately thirty seedlings were planted in two rows within each plot, 50 cm apart and 50 cm from the plot perimeter. Surface woody debris was removed to facilitate planting. Vexar tubes were secured around each seedling to protect them from herbivory.

An assumption of this study is that nursery EMF growing with the seedlings before planting were infrequent and out-competed once transplanted in the field (Dahlberg and Stenström, 1991). To account for possible nursery-derived ectomycorrhizas, a subset of seedlings were evaluated before planting using the methods described below and in Section 2.5. All seedlings sampled lacked visible ectomycorrhizas. *Wilcoxina mikolae* (Chin S. Yang & H.E. Wilcox) Chin S. Yang & Korf and *Laccaria proxima* (Boud.) Pat. DNA was detected in a pre-planting evaluation and was therefore removed from the data set referred to in Section 2.5.

Seedlings were harvested in September 2013, four months after planting. Three randomly selected seedlings were carefully removed from each plot (108 seedlings total) using a tree-planting shovel. Seedlings were stored at 4 °C and examined within one month of harvest. Roots were kept in plastic bags with a small portion of the surrounding soil remaining attached. Prior to examination, roots were separated from each seedling at the root collar and washed in de-ionized water. Roots were then cut into 1.5–2 cm fragments, mixed around and evenly dispersed on a grid with 2.5 cm^2 spacing. Colonized root tips were obtained from the center of randomly selected grid squares until a total of 100 root tips were collected from an individual seedling (Jones et al., 2008). Root tips were examined with a 10x stereomicroscope (Zeiss Stemi SV6, Jena, Germany) and grouped by morphological type (morphotype) by seedling using methods described in Barker et al. (2013) and the Colour Atlas of Ectomycorrhizae (Agerer, 1997). Morphotypes were based primarily on colour, mantle surface texture, rhizomorph features, and branching pattern. Ectomycorrhizas with slight differences in appearance were separated into several morphotypes and later pooled by plot for data analysis if warranted by identification with molecular methods. Ectomycorrhizas of a single morphotype from a given seedling were placed in individual plastic centrifuge tubes and stored in 2× cetyltrimethylammonium bromide (CTAB) at −20 °C until molecular analysis.

2.5. Molecular analysis

Sigma Extract-N-Amp™ kit (Sigma Aldrich, St. Louis, Missouri) was used to extract DNA from one root tip per morphotype from each examined seedling. The extracted DNA was used in polymerase chain reaction (PCR) amplifications of internal transcribed spacer regions (ITS) using primers ITS 1F and ITS 4 (White et al., 1990). We also used ascomycete specific primers ITS 1F-ITS 4A (Larena et al., 1999) and basidiomycete specific primers ITS 1F-ITS 4B (Gardes and Bruns, 1993) in separate reactions in an effort to isolate multiple species found on the same root tip

(Kennedy et al., 2012; Bogar and Kennedy, 2013) in which case results from both primer sets were pooled. PCR reactions contained 0.16 µl GoTaq® (Promega, Madison, Wisconsin), 5 µl of 5× PCR buffer, 2 µl of 10× deoxynucleotide triphosphates (dNTPs), 0.85 µl of MgCl, 0.5 µl of bovine serum albumin (BSA), 1 µl of the DNA template, 0.2 µL of each primer, and 10.35 µl of molecular grade water. PCR cycling parameters consisted of a 2-min denaturation at 95 °C followed by 30 cycles of 94 °C for 30 s, 50 °C for 1 min, 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. PCR products were visualized under UV light on a 2.5% agarose gel treated with Gel-Red™ (Biotium, Hayward, California). When a sample failed to amplify, another root tip from the same morphotype was used for molecular analysis. DNA from PCR products were purified using ExoSAP-IT® (Affymetrix, Santa Clara, California) and quantified for sequencing using a Qubit fluorometer (Invitrogen, Carlsbad, California).

A total of 513 purified PCR samples were sent to the University of Kentucky Advanced Genetics Technology Center (UK-AGTC) for sequencing. Direct sequencing of PCR products was performed by the Sanger reaction using the ABI Big Dye terminator v. 3.1 cycle sequencing kit (Applied Biosystems, Foster City, California) on an ABI 3730xl DNA Analyzer. ITS 1F primer was used to sequence PCR products in the forward direction. DNA sequences were compiled and analyzed using Geneious® v6.1.7. Regions with primer motifs of more than 4% chance of error per base were trimmed from sequences. Sequences were assembled into contigs of ⩾99% similarity. We performed sequence identity searches using the Nucleotide Basic Local Alignment Search Tool (nBLAST) from the National Center for Biological Information (NCBI) database (www.ncbi.nlm.nih.gov). Taxonomic names (taxa) were generally assigned to morphotypes using the following sequence identity criteria: ⩾98% ID value similarity for species, 96–97.9% similarity for genera, 90–95.9% similarity for families, and ⩾80% query cover for all matches. Taxa were also assigned when sequences were found to be consistent with the top ten identity matches. Sequences below 90% identity similarity were named by the closest consensus of taxonomic order. Species identification criteria were set at higher percentages compared to the typical 97% cutoff in order to increase accuracy of assigned species names (Nilsson et al., 2012).

Exploration types were assigned to the identified taxa using the web-based information system for characterization and determination of ectomycorrhizae (DEEMY). Exploration types describe differences in EMF hyphal development and the distance extramatrical mycelia can spread from a colonized root (Agerer, 2001; Peay et al., 2011; DEEMY). For simplification purposes, we combined the various exploration types described by Agerer (2001) into four types to classify taxa identified in our study. Long distance exploration types have the longest range of mycelial length and have a reported ability to spread up to several decimeters, linking with other compatible mycelia to form a network for nutrient transport (Agerer, 2001). Medium fringe exploration types form mycelial and hyphal fans at medium distances while medium smooth types form uniform mycelial strands that are smooth in appearance (Agerer, 2001). Short distance exploration types form short hyphae that emanate from the ectomycorrhizal structure (Agerer, 2001).

2.6. Statistical analyses

Soil nutrient data was analyzed in RStudio v.0.97.318. After investigating the soil nutrient data distributions, all had adequately met the assumptions of the statistical methods except for total carbon (C), magnesium (Mg), and calcium (Ca). Data for C, Mg, and Ca were natural log-transformed for use in the linear mixed model and back-transformed for ratio inference in treatment comparison. An extension of a two-way analysis of variance

was used that included a repeated measures (autoregressive 1) linear mixed model. Variations between sites, plots, and soil depths were accounted for in the model. Mean soil nutrient differences among treatments and their confidence intervals were estimated from the model. *P*-values and confidence intervals were adjusted using False Discovery Rate (FDR) adjustments (Benjamini and Hochberg, 1995) to account for multiple comparisons. Since detection of differences can be considered difficult for field experiments with a small sample size (Steel and Torrie, 1980), comparisons were considered significant at α = 0.1.

We compared EMF community composition using richness, Simpson's diversity index, relative abundance, and constancy. PC-ORD v.5.12 was used to calculate richness and Simpson's diversity values based on relative abundance (McCune and Grace, 2002). First and second order jackknife estimates were calculated to compare richness estimates amongst treatments (Palmer, 1991). Relative abundance was calculated as the number of root tips colonized by a given taxon in a plot divided by the total number of root tips sampled from a plot (three seedlings = 300 root tips per plot). Constancy was calculated as the percentage of plots in which a taxon occurred. For taxa found present in all three treatments, relative abundance and constancy were compared among treatments in a two-way analysis of variance with a linear mixed model in RStudio v.0.97.318. Differences between treatments and their confidence intervals were estimated from the model. *P*-values and confidence intervals were FDR-adjusted and comparisons were considered significant at α = 0.1.

For non-parametric multivariate analysis, EMF relative abundance and soil nutrient content were compared among treatments in non-metric multidimensional scaling (NMS) ordinations in PC-ORD v.5.12. The environmental variable matrix included site (block), treatment, pH, %MC, SOM, C, N, Bray-P, Ca, Mg, C:N ratio, and forest floor depth. Using the Sørenson (Bray-Curtis) distance measure, a random starting configuration, and 500 runs with real data, a stable two-dimensional solution was found after 91 iterations and passed a Monte Carlo significance test ($p = 0.019$). Under the default settings, the PC-ORD's Multi-Response Blocked Permutations (MRBP) function was used to conduct pair-wise comparisons among all three treatments. MRBP comparisons were considered significant if both (a) the probability of a smaller or equivalent δ to the observed δ was $p \leqslant 0.05$; and (b) the chance-corrected within-group agreement (*A*) was <0.1 (McCune and Grace, 2002). Indicator species analysis was used to identify taxa that were detected to be most abundant and constant in a particular treatment (McCune and Grace, 2002; Dufrêne and Legendre, 1997). Indicator values were tested with 1000 randomizations in a Monte Carlo test and were considered significant at $p \leqslant 0.05$.

3. Results

3.1. Soil environment

The soil environment conditions we tested did not differ statistically among the three treatments at either 10–20 cm or 20–30 cm
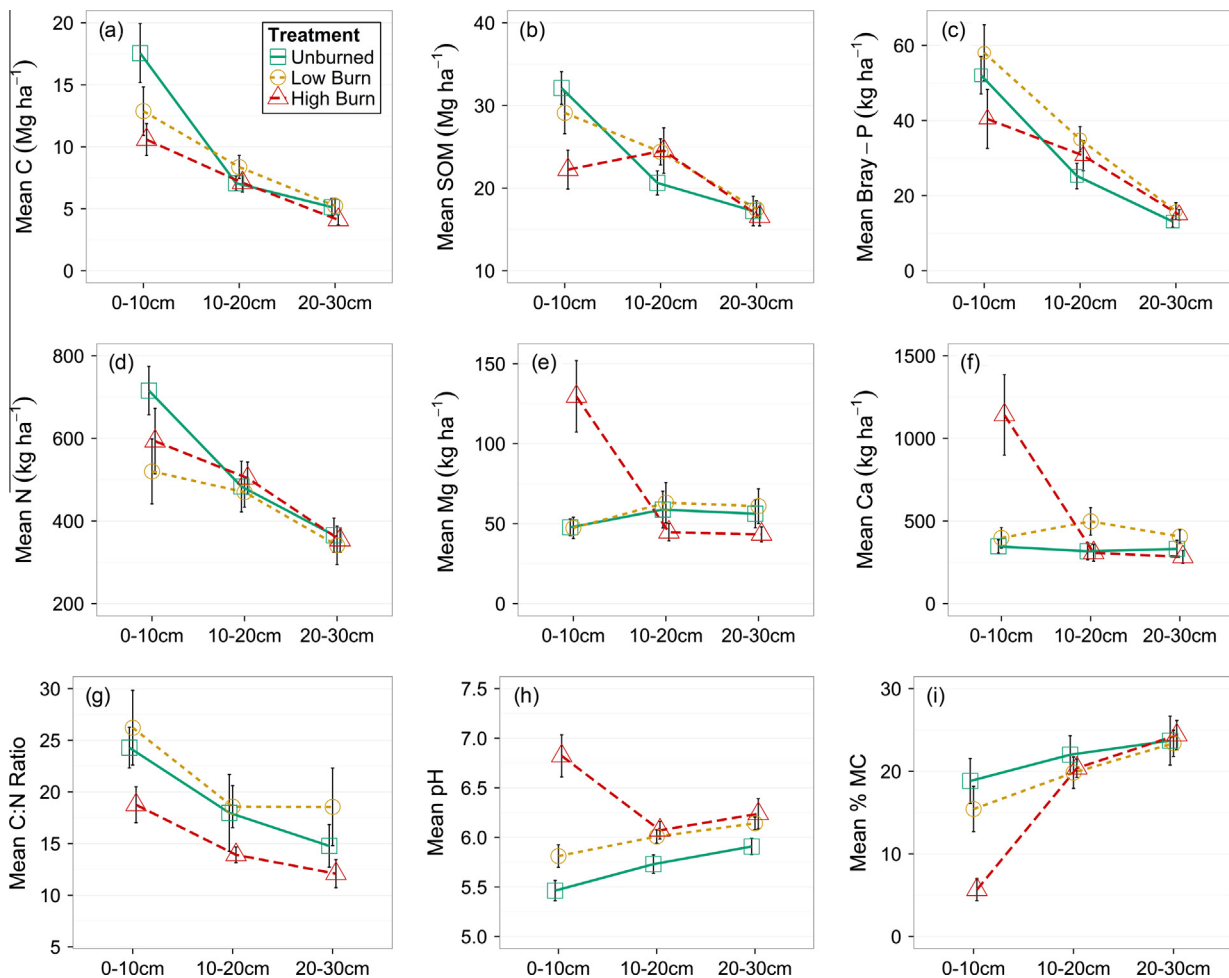

Fig. 4. Post-burn soil properties and nutrient contents from the center of unburned, low soil burn intensity (Low Burn), and high soil burn intensity (High Burn) plots at all three soil depths (*n* = 10). Small figures denoted by lowercase letters: (a) mean carbon (C); (b) mean soil organic matter (SOM); (c) mean Bray phosphorus (Bray-P); (d) mean nitrogen (N); (e) mean magnesium (Mg); (f) mean calcium (Ca); (g) mean C:N ratio; (h) mean pH; and (i) mean percent moisture content (%MC). Error bars denote ±1 standard error.

Table 1

Estimated mean and median differences in post-burn soil properties and nutrient contents compared among all three treatments at 0–10 cm depth. Estimated differences (Estimate), degrees of freedom (DF), FDR-adjusted p-values, lower and upper confidence intervals (CI) are reported. Statistical significance of p-value at $\alpha = 0.1$ are shown in bold.

	Estimate	DF	FDR-adjusted p-value	Lower CI	Upper CI
C					
UB vs LB	1.43[a]	18.00	0.24	0.93	2.20
UB vs HB	1.66[a]	18.00	**0.08**	1.02	2.71
LB vs HB	1.16[a]	18.00	0.51	0.84	1.60
N					
UB vs LB	195.57	18.00	0.19	−24.57	415.70
UB vs HB	122.34	18.00	0.60	−72.31	316.98
LB vs HB	−73.23	18.00	0.88	−252.52	106.06
C:N ratio					
UB vs LB	0.97[a]	18.00	0.88	0.71	1.34
UB vs HB	1.30[a]	18.00	0.28	0.93	1.82
LB vs HB	1.34[a]	18.00	0.28	0.89	2.02
SOM					
UB vs LB	3.01	18.00	0.48	−2.33	8.34
UB vs HB	9.88	18.00	**0.01**	2.51	17.25
LB vs HB	6.88	18.00	**0.08**	0.35	13.40
Bray-P					
UB vs LB	0.91[a]	18.00	0.73	0.63	1.31
UB vs HB	1.58[a]	18.00	0.16	0.96	2.60
LB vs HB	1.73[a]	18.00	0.13	0.97	3.08
Mg					
UB vs LB	1.06[a]	18.00	0.86	0.76	1.48
UB vs HB	0.41[a]	18.00	**<0.001**	0.26	0.66
LB vs HB	0.39[a]	18.00	**<0.001**	0.23	0.66
Ca					
UB vs LB	0.91[a]	18.00	0.73	0.62	1.33
UB vs HB	0.36[a]	18.00	**0.001**	0.20	0.65
LB vs HB	0.39[a]	18.00	**0.002**	0.23	0.67
pH					
UB vs LB	−0.35	18.00	**0.04**	−0.65	−0.05
UB vs HB	−1.36	18.00	**<0.001**	−1.91	−0.80
LB vs HB	−1.01	18.00	**<0.001**	−1.50	−0.52
%MC					
UB vs LB	3.40	18.00	0.83	−3.58	10.38
UB vs HB	13.16	18.00	**0.003**	4.59	21.74
LB vs HB	9.76	18.00	**0.02**	2.18	17.35
Forest floor depth					
UB vs LB	1.50	18.00	**0.01**	0.57	2.43
UB vs HB	2.95	18.00	**<0.001**	2.02	3.88
LB vs HB	1.45	18.00	**0.01**	0.52	2.38

$n = 10$.
[a] Ratio of median values after back transformation.

depths (Fig. 4). Soil environment and nutrient analysis results are in reference to the 0–10 cm depth (Table 1). We did not detect differences in median Bray phosphorus (Bray-P), mean total nitrogen (N), and median C:N ratios (Fig. 4c, d, and g; Table 1).

Forest floor depth differences were detected among all treatments post-burn (Fig. 5). Mean forest floor depth was estimated to be 2.95 cm greater in UB plots compared to HB plots, 1.5 cm greater in UB plots compared to LB plots, and 1.45 cm greater in LB plots compared to HB plots (Fig. 5, Table 1).

3.2. EMF composition

A total of 66 fungal taxa were identified from 403 root tip samples (81% sequence success rate) at all 10 sites (Supplemental Table A2, Supplemental Table A3). We were unable to detect statistical differences in EMF taxon richness and Simpson's diversity index (Table 2). The first-order and second-order jackknife estimates for UB plots were 48.3 and 57.6 taxa, respectively.
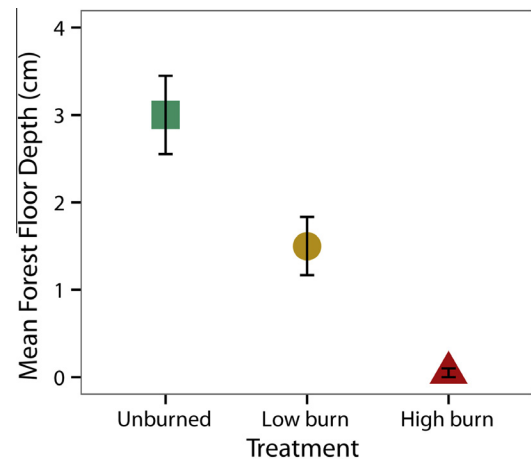

Fig. 5. Post-burn forest floor depth from the center of unburned, low soil burn intensity (Low Burn), and high soil burn intensity (High Burn) plots. Error bars denote ±1 standard error. $n = 10$.

Table 2

Mean richness and Simpson's diversity by treatment. ±1 standard error. $n = 12$.

	UB	LB	HB
Richness	7.4 ± 0.7	8.4 ± 0.8	6.6 ± 0.5
Simpson's diversity	0.68 ± 0.04	0.74 ± 0.02	0.64 ± 0.06

First-order and second-order jackknife estimates for LB plots were 66.4 and 80.8 taxa, respectively. First-order and second-order jackknife estimates for HB plots were 49 and 62.9 taxa, respectively. For all treatments, first-order and second-order jackknife estimates were 103.8 and 129.3 taxa, respectively. The taxa area curves (Fig. 6) and jackknife estimates suggest that we failed to capture the total taxon richness of our sites (Palmer, 1991). The continuous increase in a curve, without leveling, demonstrates incomplete identification of all taxa present. The overall EMF richness we observed was about 50% of the jackknife estimates.
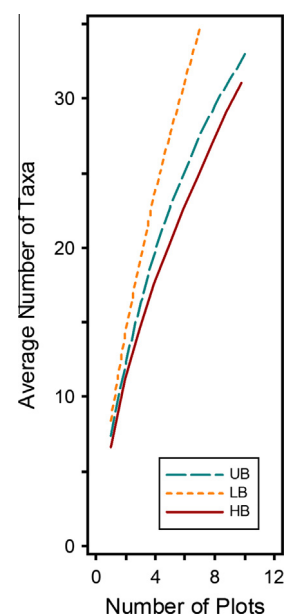

Fig. 6. Taxa area curves of average number of ectomycorrhizal fungi (EMF) taxa identified by number of plots in each treatment. Long-dashed line represents unburned plots (UB), short-dashed line represents low intensity burned plots (LB), and solid line represents high intensity burned plots (HB). $n = 66$ taxa.

Only 21% of taxa were detected in all three treatments (Supplemental Table A2). Five taxa were detected in only UB and LB plots. Four taxa were detected in only LB and HB plots while five taxa were detected in both HB and UB plots. A total of nine taxa were found to be unique to seedlings grown in UB plots. Twenty two taxa were found to be unique to LB plots. A total of seven taxa were found to be unique to HB plots. Mean relative abundances of taxa identified more than two times are reported in Fig. 7. We detected a greater number of distinct dominant taxa in UB plots than in LB

and HB plots (Fig. 7). Constancy (percent occurrence among plots) of taxa identified more than two times or occurring in more than one treatment is reported in Fig. 8.

Out of 403 identified root tips, 70% were classifiable by exploration type using the information available on DEEMY (www.deemy.de). Taxa detected only in LB plots included EMF of all four exploration types, whereas taxa detected only in HB plots were comprised of long or unknown exploration types (Supplemental Table A2). Taxa detected only in UB plots included
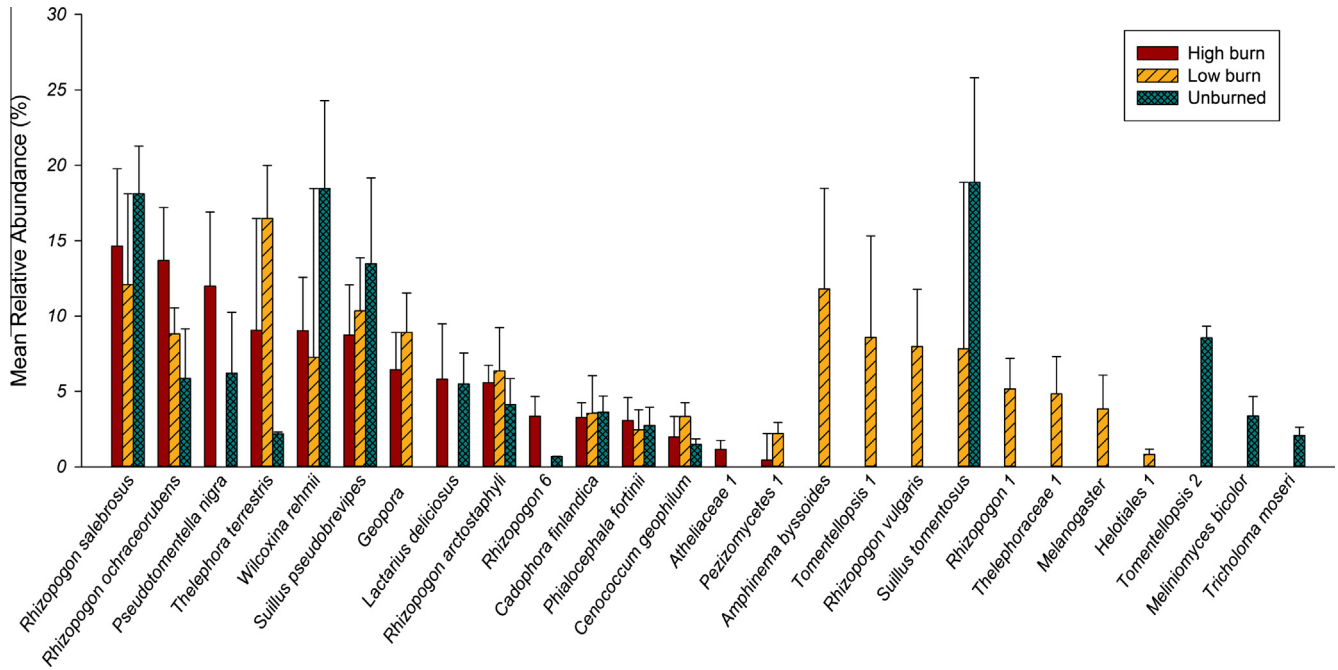

Fig. 7. Percent mean relative abundance for ectomycorrhizal fungi (EMF) taxa occurring more than once in at least one of three treatments (*n* = 66 taxa in 12 sites). Error bars denote ±1 standard error.
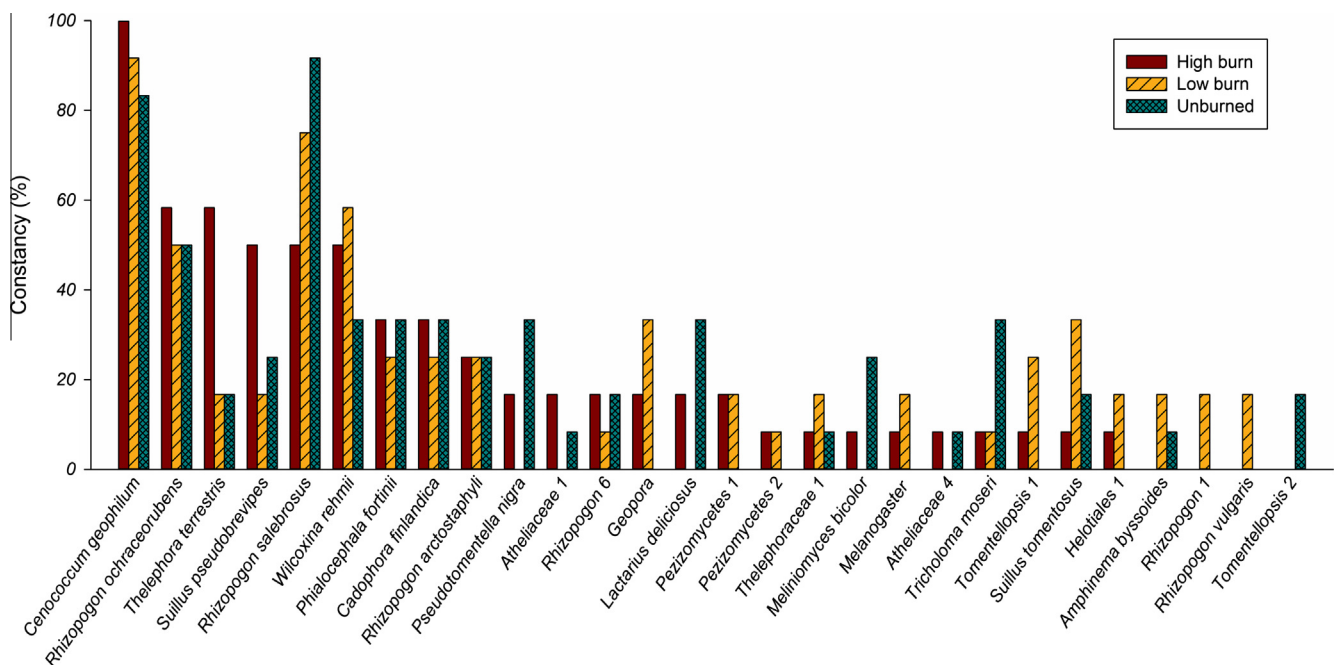

Fig. 8. Percent constancy for ectomycorrhizal fungi (EMF) taxa occurring in more than one of three treatments or more than once in at least one of three treatments (*n* = 66 taxa in 12 sites).

medium and short exploration types (Supplemental Table A2). Mean relative abundance of all identified exploration types are reported in Fig. 9.

Multi-Response Blocked Permutation Procedures (MRBP) results showed EMF composition (relative abundance and constancy) differed by treatment ($p = 0.01$), yet the effect size was small ($A = 0.03$). There was evidence of a difference in taxa composition between HB and UB plots (FDR-adjusted $p = 0.02$) with a small effect size ($A = 0.06$). There was also evidence of a difference in taxa composition between LB and UB plots (FDR-adjusted $p = 0.01$) with a small effect size ($A = 0.07$). We were unable to detect differences in taxa composition between LB and HB plots (FDR-adjusted $p = 0.86$, $A = -0.01$). For the Indicator Species Analysis, *Rhizopogon salebrosus* AH Sm. was found to be a significant indicator for UB plots (FDR-adjusted $p = 0.01$, indicator value (IV) = 64.3) (Fig. 10).
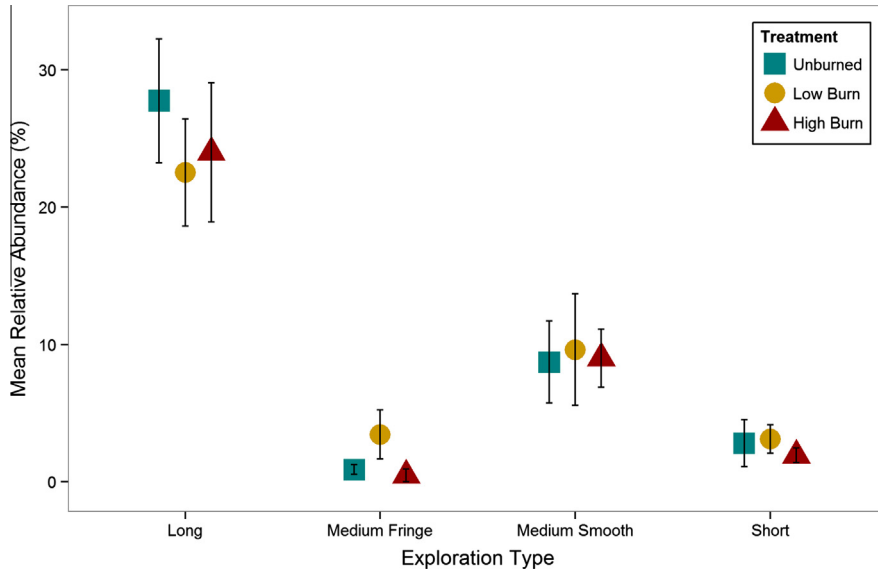

Fig. 9. Mean relative abundance of ectomycorrhizal fungi (EMF) taxa identified by hyphal exploration types "long", "medium fringe", "medium smooth", and "short" based on the exact or most closely related taxa from information available on DEEMY (www.deemy.de) or Peay et al., 2011. Error bars denote ±1 standard error. n = 36 taxa in 12 sites (70% of identified root tips).
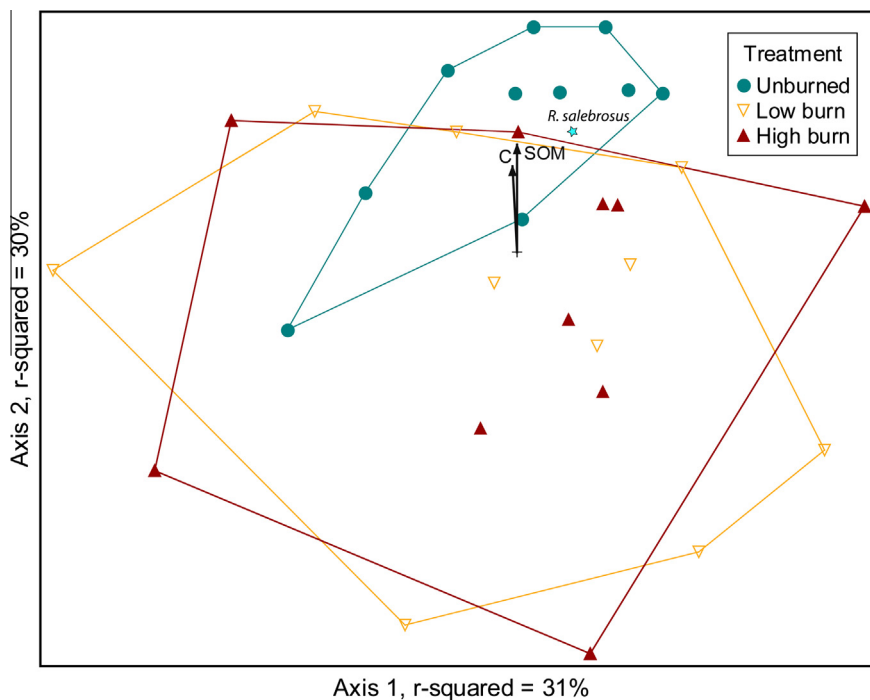

Fig. 10. Graphic results of non-metric Multidimensional Scaling (NMS) ordination according to relative abundance of ectomycorrhizal taxa (n = 66 taxa). Filled circles represent unburned plots, empty inverted triangles represent low soil burn intensity plots, and filled triangles represent high soil burn intensity plots. Lines connecting points outline region of graph where plots of the same treatment are located. Nutrient contents correlated with species composition are displayed as overlay vectors in the direction of increasing linear correlation (joint plot cutoff $r^2 \geqslant 0.2$). Star represents *Rhizopogon salebrosus*, a significant indicator of unburned plots.

3.3. EMF and soil nutrient correlations

Ordination results, displayed as plots in taxa space, provided two axes (Fig. 10). R^2 is the proportion of variance (in the Sørenson distance matrix) among plots explained by the axes. The two axes explained 61% of the variation in EMF composition among plots. Results from the NMS ordination found considerable overlap in taxa composition among LB and HB plots and none of the three treatments were completely isolated or dissimilar in taxa composition from one another. Total carbon (C) and soil organic matter (SOM) were the only soil nutrients found to correlate with plots based on taxa composition (Fig. 10). Both C and SOM aligned with axis 2 ($r^2 = 0.3$) and increase in content from the bottom to the top of the graph. Most of the unburned plots are in the top half of the graph and therefore are correlated with higher C and SOM contents. Alternatively, both LB and HB plots occupy space in the graph correlated with low to moderate C and SOM contents.

4. Discussion

4.1. Forest floor and mineral soil differences

As hypothesized, HB soils differed from UB and LB soils in several of the variables we measured though only at shallow depths. A steep vertical temperature gradient (Fig. 3) resulting from the insulating properties of soil (DeBano, 2000) restricted soil nutrient effects to 0–10 cm. Increases in ash contributed to an increase in mineral soil pH (Neary et al., 1999; Choromanska and DeLuca, 2001), which can support biological recovery (Knicker, 2007) but can also directly affect nutrient availability (Agee, 1996). Our inability to detect differences in Bray-P may have been due to P bound by pH and cations, rendering P insoluble (McDowell et al., 2003). Despite this effect, a greater release of macronutrients Ca and Mg was observed in HB plots. Calcium and Mg have high ion potentials which lower the probability of post-fire leaching (Agee, 1996).

Similar to previous studies (Fernández et al., 1997; Knicker, 2007), high intensity soil burning resulted in decreases in C and SOM, both of which begin to break down at around 100 °C (Agee, 1996). The dramatically higher temperatures we observed in HB plots volatilized C and organic matter-derived nutrients, thus depriving fungal communities of important sources of nutrition. A decrease in C can lower C:N ratios, though the observed C:N ratios in HB soils were within the typical range for mycorrhizal growth (C:N of ~3:1–51:1) (Strickland and Rousk, 2010). Carbon and SOM degradation can also produce water repellent layers which may have formed just above the 5 cm depth at HB plots where temperatures reached 175–280 °C (DeBano, 2000). Low burn plots did not reach water repellency-producing temperatures and therefore may have maintained an erosion-resistant and water-absorbent habitat for EMF.

Changes in soil nitrogen from burning are often complex (Agee, 1996; Monleon et al., 1997). We believe the large variability in N content in our results was responsible for our inability to detect N differences among treatments. Some of the variation may be attributed to the timing of our soil sample collection. Collection of samples one week after the burn may not have provided sufficient time for ash and released nutrients to leach into the mineral soils. This issue may have been more pronounced in LB soils where the forest floor was not completely consumed and could have temporarily intercepted ash and delayed nutrient release (Hart et al., 2005). Precipitation, which would have aided in nutrient filtration into the mineral soil, did not occur in the time between the burn and soil sampling.

4.2. EMF community differences

Our results suggest that EMF can survive or recolonize HB soils within one growing season despite effects on soil properties. Due to our inability to detect differences among treatments, we reject our hypothesis of reductions in EMF richness and diversity in HB plots. By comparison, our community composition results were complicated. We were able to detect a pattern that distinguished unburned from burned communities, though composition differences had a small effect size (magnitude of differences between groups) and therefore may not have been biologically significant. Whereas differences in C and SOM correlated with taxa composition (Fig. 10), a large proportion of the variation in EMF composition remained unexplained.

We suggest several potential explanations for the observed similarities in the HB and LB EMF communities. The relatively small patch of high burn soil at each site was likely influenced by the low intensity burning that occurred in the surrounding soil. However, we argue that these conditions mimic realistic wildfire events in which surface flames ignite large downed logs. Additionally, our inability to detect community differences may have been due to a small sample size constrained by mega-log construction and a feasible area for same-day prescribed burning. We also acknowledge that the technique of using morphotyped groupings of root tips for molecular identification may have limited our ability to detect rare EMF species (Sakakibara et al., 2002). Despite this limitation, and the typically high spatial variability in EMF communities (Jonsson et al., 1999; Grogan et al., 2000; Peay and Bruns, 2014), we were able to identify dominant and ubiquitous taxa among the three treatments. Alternatively, sampling variability may have increased with either burn treatment, posing a challenge in our ability to detect EMF composition differences and total taxa richness.

4.3. The role of refugia and recolonization mechanisms

Frequent low severity fires historically occurred in central Oregon ponderosa pine forests (Fitzgerald, 2005; Graham and Jain, 2005; Hessburg et al., 2005) and it is likely that the local EMF community is adapted to soil heating at shallow depths. However, the lethal temperatures we recorded in HB soils penetrated deeper than in LB soils and directly affected where most EMF live (Swezy and Agee, 1991; Cromack et al., 2000; Reazin et al., 2016). If the extreme temperatures we observed altered the EMF community in the top 10+ cm of soil, how did HB and LB plots contain similar EMF communities?

Knowing the primary colonization or dispersal mode of EMF taxa can give us insight into post-fire succession. Of all the taxa we identified, *Rhizopogon salebrosus* was found to be the most abundant. *Rhizopogon* species specialize in colonization of disturbed habitat, are widely distributed throughout the soil, and are prolific producers of hypogeous sporocarps (truffles) (Molina et al., 1999; Taylor and Bruns, 1999; Smith et al., 2002, 2005). Spores can be dispersed by small mammals and remain viable in the soil for decades (Claridge et al., 2009; Kennedy et al., 2009; Nguyen et al., 2012). The abundance of *R. salebrosus* in our UB plots might also be explained as a response to disturbance from thinning operations that occurred at all sites two years prior. Nevertheless, Garcia et al. (2016) found *R. salebrosus* to be a dominant EMF species in soil sampled from undisturbed pine forests in central Oregon.

Spore dispersal of *Rhizopogon* spp. and other taxa can contribute to early successional EMF colonization (Ashkannejhad and Horton, 2006; Galante et al., 2011; Horton et al., 2013; Peay et al., 2011; Peay and Bruns, 2014). However, our detection of similar taxa in

all three treatments may suggest that pre-existing spore banks or mycelia are a more likely source of inoculum than newly dispersed spores. Similarly, Jonsson et al. (1999) found common taxa before and after fire events where host plants survived, suggesting that spore dispersal is less important for EMF recolonization after fires with low host mortality.

Heat-resistant spores and sclerotia likely contributed to the recolonization of burned soils. *Cenococcum geophilum*, a drought tolerant species capable of producing sclerotia (Massicotte et al., 1992), was detected in all three treatments though in low abundance. Several studies support the theory that heat-resistant spores are the main source of EMF in burned soils (Horton et al., 1998; Baar et al., 1999; Taylor and Bruns, 1999). However, mycelial spread may have been limited in these studies due to host tree mortality. In contrast, most host trees and shrubs in the vicinity of our sites remained alive. Izzo et al. (2006) identified heat-resistance up to 75 °C in *Rhizopogon*, *Cenococcum*, and *Wilcoxina* propagules but did not test at the temperatures reached in our HB plots. In LB plots, heat-resistant propagules may have survived below the surface in large enough numbers to colonize seedlings, possibly explaining the steeper taxa area curve, larger jackknife estimates, and greatest number of unique taxa detected in LB compared to UB and HB plots (Fig. 6; Supplemental Table A2).

Besides colonization by spores, *Rhizopogon* and *Suillus* spp. have the ability to spread via mycelia over longer distances than many other EMF (Simard et al., 1997; Peay et al., 2011). Long distance types were detected in great abundance in all three treatments, suggesting mycelia play a large role in colonization. Nevertheless, this finding may be a product of pre-existing low root densities in ponderosa pine forest systems where long distance exploration types may be better adapted (Peay et al., 2011). Besides this consideration, long distance EMF were well-represented in UB soils and were therefore likely to colonize LB and HB soils before less-abundant short distance EMF such as *Cenococcum geophilum*.

Although we do not provide direct evidence to support the greater likelihood of mycelial colonization over spore colonization, other research has supported the theory of extensive mycelial genets associated with pine species that have large carbon budgets and the capability to out-compete other EMF for resources (Bonello et al., 1998). Bonello et al. (1998) roughly estimated a mycelium growth rate for a large *Suillus pungens* genet of *at least* 0.5 m per year, the approximate distance each ponderosa pine seedling was from the perimeter of treatments in this study. Theoretically, any surviving mycelia or host roots existing below the heated soil (>10 cm depth) would be in even shorter distance to the roots of planted seedlings than the perimeter of treatments at the soil surface.

Whether by spores or mycelia, deep soil inoculum might play an important role in the recolonization of burned soils. Non-lethal temperature increases experienced by HB soils deeper than 10 cm may have stimulated spores to germinate. Alternatively, mycelia from deep root ectomycorrhizas might rise through the soil column to inoculate seedling roots and provide increased access to nutrient pools (Rosling et al., 2003; Tedersoo et al., 2003; Genney et al., 2006). Pezizomycetes spp. 1, 2, and *Geopora* were found in both burn treatments and may have originated from deeper in the soil profile (Vrålstad et al., 1998). Phoenicoid or heat-stimulated fungi, such as some Pezizomycetes spp., may fill functional roles in water-limited post-fire soils (Persiani and Maggi, 2013; Tedersoo et al., 2013) and may support post-fire plant communities (Oliver et al., 2015). Additionally, drought-adapted EMF can extend their mycelia into further depths of the soil in search of moisture where they may inadvertently survive a fire event (Genney et al., 2006). It should also be noted that greenhouse studies using burned soil obtained from field sites would not have the advantage of these alternative sources of inoculum experienced in natural systems. Future studies can investigate the influence of deep soil inoculum through a depth-stratified approach to EMF root or soil analysis.

4.4. The role of downed fuel

The mega-log combustion used in our HB treatments mimicked the approximate size and shape of exposed soil that would result from the combustion of a large downed log. Because of the sheer amount of fuel in one space, the long duration of plant lethal temperatures (Neary et al., 1999; Busse et al., 2013) created a gap in vegetation. Despite the obvious downsides of forest floor consumption and alteration of the soil environment, the reduction in plant competition would be advantageous for ponderosa pine seedlings (Graham and Jain, 2005). The area previously occupied by a downed log also offers direct access to the mineral soil and a release of macronutrients for a seedling's first year (Monleon et al., 1997). This situation may provide sufficient time for the seedling to establish a taproot to obtain the moisture below.

The distribution of downed fuels influences the size and location of burned soil patches in a fire event. We hypothesize that EMF recolonization success depends on the size of high burned soil areas and proximity to low and unburned soils. Not surprisingly, we see this occurrence in nature. Wildfires typically produce a mosaic of burn severities across a landscape (Hessburg et al., 2005; Ryan et al., 2013). Large contiguous patches of high soil burn severity would appear to be rare due to stochastic fuel distributions in direct contact with the forest floor. However, where downed fuels are in direct contact, our study shows that EMF are somewhat resilient on this localized scale. If a seedling growing in high intensity burned soil is colonized by EMF, it can obtain essential nutrients from beyond that patch of soil via EMF mycelia (Peay et al., 2011; Buscardo et al., 2012).

Regardless of direct soil effects, heavy fuels loads can contribute to large scale host mortality (Agee, 1996). If surviving host trees are important sources of EMF inoculum, then large scale tree mortality from severe fires may be of concern for post-fire regeneration. Tree seedling colonization by EMF species is facilitated by existing mycorrhizal networks via nearby mature trees and shrubs (Fleming, 1983; Buscardo et al., 2011). Ponderosa pine seedlings growing in high intensity burned soils may have a similar advantage if a surviving mature ponderosa pine or other host is in the vicinity. Even in high severity wildfires with areas of 100% tree mortality, variation exists in the localized effect on the fungal community (Rincón and Pueyo, 2010). In those cases, the mortality of all hosts may have a larger effect on EMF communities than the changes to the soil environment itself (Southworth et al., 2011)—unless the multiple forms of inoculum can persist until a host seed germinates or a seedling is planted.

Extreme fire weather can be the ultimate determinant of host mortality; nonetheless, management goals that aim to increase heterogeneity in fuel distribution can potentially promote patches of surviving host trees and shrubs supporting EMF refugia. Management activities such as thinning and prescribed burning not only improve heterogeneous fuel distributions but may also improve forest health by reducing competition, thereby increasing the ability of host trees to provide carbon for EMF networks which in turn can support an establishing tree seedling population (Egli et al., 2010; Southworth et al., 2011; Buscardo et al., 2012; Anderson and Lake, 2013).

5. Conclusions

High intensity soil burning from large downed log combustion had a greater effect on soil properties and nutrient contents than

low intensity soil burning. Despite this effect, the area of high intensity burned soil was small enough to be colonized by common EMF taxa within one growing season. The proximity of unburned and low burned soils and mycelial networks from surviving hosts may have aided in the speed of this process as sources of inoculum.

The detrimental impacts of fire on soil microbes are often used as an argument for reducing fuels and fire severity. However, this argument must be qualified in order to acknowledge the complexity of fire effects and the timescale of recovery. Burn severity patch size and host survival may be more important to consider than the degree of soil burn intensity. Fuel reduction treatments, such as thinning and prescribed burning, in ponderosa pine forests can maintain EMF refugia by controlling burn severity patch size and host mortality before extreme fire events occur. By maintaining refugia, not all areas previously occupied by large downed logs will result in long-term sterilization. Reduced plant competition and access to nutrient pools via ectomycorrhizal networks might make the narrow footprints of combusted logs nurseries for ponderosa pine seedlings. In turn, intact EMF communities could contribute to the regeneration success and resilience of ponderosa pine forests.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.07.030. These data include Google maps of the most important areas described in this article.

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