

Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a ponderosa pine forest

Suzanne M. Owen^{a,b,e,*}, Adair M. Patterson^c, Catherine A. Gehring^c, Carolyn H. Sieg^b, L. Scott Baggett^d, Peter Z. Fulé^a

^a School of Forestry, Northern Arizona University, PO Box 15018, Flagstaff, AZ, 86011, United States

^b USDA Forest Service: Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ, 86001, United States

^c Department of Biological Sciences and Merriam-Powell Center of Environmental Research, Northern Arizona University, Flagstaff, AZ, 86011, USA

^d USDA Forest Service: Rocky Mountain Research Station, 240 W Prospect Rd, Fort Collins, CO, 80526, United States

^e USDA Forest Service: Pacific Northwest Research Station, 620 SW Main ST, Suite 502, Portland, OR, 97205, USA

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ABSTRACT

Over the past three decades, wildfires in southwestern US ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have increased in size and severity. These wildfires can remove large, contiguous patches of mature forests, alter dominant plant communities and increase woody debris, potentially altering fungal community composition. Additionally, post-fire conditions may shift dominant fungal functional groups from plant-symbiotic ectomycorrhizal (EM) fungi to more decomposer saprotrophic fungi. We investigated the long-term (13 years post-wildfire) effect of fire severity on 1) fungal sporocarp density, functional groups and community composition and 2) EM colonization and community composition from naturally regenerating ponderosa pine seedlings on the Pumpkin Fire that burned in 2000 in Arizona, USA. Plots were located in four burn severity classes: unburned, moderate-severity, and two high-severity (defined as 100% tree mortality) classes, either adjacent to residual live forest edges (edge plots), or >200 m from any residual live trees (interior plots). We found that high-severity burn plots had a unique sporocarp community composition, and a shift in dominant sporocarp functional groups, with 5–13 times lower EM sporocarp densities, and 4–7 times lower EM sporocarp species richness compared to unburned and moderate-severity plots. In contrast, saprotrophic sporocarp densities and richness were similar among burn severity classes, even with the large amount of coarse wood in the high-severity burn patches. Regenerating ponderosa pine seedlings had similar EM colonization and richness among severity classes, yet high-severity interior plots had a different community composition and a lower relative abundance of EM species compared to moderate-severity burn plots. Taken together, our results suggest that large patches of high-severity fire have long-term consequences for both EM sporocarp and root tip communities. Because EM fungal species vary in function, the limited species pool available in interior high-severity burn patches may influence pine recovery.

1. Introduction

Wildfire size and severity are predicted to increase in many forest ecosystems, with rising temperatures and altered fuel conditions, leading to increased tree mortality in coming decades (Jolly et al., 2015; Abatzoglou and Williams, 2016; Kitzberger et al., 2017; Krofcheck et al., 2018). Large-scale changes in fire behavior are driven by climate changes, such as increased temperature and droughts, particularly in areas with high fuel loads (Shive et al., 2013; Sieg et al., 2017; Yocom

Kent et al., 2017). Wildfires with large patches of high-severity fire, along with warmer climates are forecasted to cause widespread conifer mortality and extensive shifts in plant species distributions in many forest ecosystems (Rehfeldt et al., 2006; McDowell et al., 2016; Abatzoglou and Williams, 2016; Flatley and Fulé, 2016; Stevens-Rumann et al., 2018). These studies predict long-term consequences for above-ground communities, but knowledge of the effects of increased fire severity on soil biota, such as fungi, are limited.

It is critical to understand how severe fire can influence soil fungi,

* Corresponding author. School of Forestry, Northern Arizona University, PO Box 15018, Flagstaff, AZ, 86011, United States.

E-mail address: suzanne.m.owen@usda.gov (S.M. Owen).

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including ectomycorrhizal (EM) fungi and saprotrophic fungi, because they may influence ecosystem resilience due to their diverse functions as plant mutualists and decomposers (Buscardo et al., 2015; Gehring et al., 2017; Yang et al., 2018). Ectomycorrhizal fungi increase water and nutrient uptake for their plant hosts in return for carbon, and saprotrophic fungi play an important role in nutrient cycling and are responsible for decomposing wood, plant litter, and soil organic matter (SOM) (Cairney and Meharg, 2002; Smith and Read, 2008). A direct consequence of fire is heat-induced mortality from high soil temperatures; however, some fungal species are more resilient to heat, especially in the form of spores (Peay et al., 2009; Kipfer et al., 2010; Carlsson et al., 2014). Fire can select for heat-tolerant EM and saprotrophic species that have likely evolved within historically fire-prone ecosystems (Carlsson et al., 2014; Kipfer et al., 2010; Glassman et al., 2016). Fire can indirectly influence saprotrophic community composition by changing the structure and chemistry of soil and litter (Ficken and Wright, 2017; Bhatnagar et al., 2018). For example, increased log cover could increase white and brown rot decomposers; alternatively, increased herbaceous plant C inputs could favor different guilds of saprotrophic fungi (Zhou and Hyde, 2002; Ficken and Wright, 2017; Bhatnagar et al., 2018). Fire can also indirectly alter EM communities and reduce EM inoculum by causing host mortality or shifting dominant plant communities (Buscardo et al., 2011; Peay et al., 2012; Peay and Bruns, 2014; Pec et al., 2017). While fire may directly and indirectly influence both EM and saprotrophic fungal communities, there is still much to learn about whether or not increased fire severity, including expansive patches of tree mortality will have long-term effects on both EM and saprotrophic fungal communities.

Previous studies have shown variable effects of high-severity fire on fungal communities. Fungal recovery after high-severity wildfires may be influenced by time since fire, and distance from available plant hosts (Visser, 1995; Treseder et al., 2004; Kipfer et al., 2011; Holden et al., 2013). For example, EM and saprotrophic sporocarp richness were low 6 years post-fire, but recovered 41 years after stand-replacing wildfire from a chronosequence study in a Jack pine (*Pinus banksiana* Lamb.) forest (Visser, 1995). Recovery of EM inoculum after high-severity fires may also be dependent on the proximity of surviving hosts, and nearby inoculum sources such as hyphae and spores may contribute to post-fire seedling colonization (Nara, 2006; Teste et al., 2009; Peay et al., 2012; Peay and Bruns, 2014). Lower EM densities and richness are expected after high-severity fires from the lack of tree hosts, especially at greater distances from surviving trees (Dickie and Reich, 2005; Peay et al., 2012; Buscardo et al., 2011). Contrary to EM species, saprotrophic sporocarp densities and richness are predicted to increase following high-severity fires because of diverse substrates such as herbaceous and woody debris that accumulate with time after snags fall and understory litter accumulates, and could favor a variety of decomposers (Egger, 1986; Matheny et al., 2015). Given the increasing size and severity of recent fires in some forest types, especially in the southwestern US, a better understanding is needed of how large patches of high-severity fire, far from surviving plant hosts, influence the recovery of fungal communities over time.

Wildfires in southwestern US ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have increased in size and severity, leaving large, contiguous patches of tree mortality (often ≥ 100 ha) (Dillon et al., 2011; Singleton et al., 2019). Ponderosa pine forests are one of the dominant forest types in the semi-arid western US, and large high-severity burn patches are in stark contrast to the low-to moderate-severity wildfires that dominated the historical fire regime in ponderosa pine forests (Covington and Moore, 1994; Fulé et al., 1997; Moore et al., 2004). High-severity fires in ponderosa pine forests reduce dominant tree cover and increase log cover for extended periods of time (Roccaforte et al., 2012; Chambers et al., 2016; Owen et al., 2017). The limited studies on the effects of high-severity wildfires on fungal communities in ponderosa pine forests have yielded contrasting results.

Previous studies have found short-term reductions in fungal biomass

and richness and/or altered community composition after high-severity fire or repeated burning in ponderosa pine forests (Hart et al., 2005; Reazin et al., 2016; Glassman et al., 2016). For example, a high-severity wildfire in a ponderosa pine forest reduced both EM richness and density and favored a *Rhizopogon* species 1 month post-fire, compared to pre-fire (Glassman et al., 2016). In contrast, EM richness, diversity and community composition were similar across different fire severities and unburned areas within one year post-fire in a different ponderosa pine forest (Cowan et al., 2016). In this latter study, EM fungi quickly recovered and colonized planted ponderosa pine seedlings after high-severity fire, but study sites were approximately 10–20 m from nearby live host-trees (Cowan et al., 2016), and this may not be the case for large patches of fire-caused mortality, isolated from surviving trees. Additionally, high-severity fire altered the saprotrophic community composition associated with ponderosa pine logs up to 4 years post-fire, from a culturing study (Kurth et al., 2013), and reduced saprotrophic richness 1 year post-fire in Canadian boreal forests, in a study using high-throughput sequencing (HTS) (Day et al., 2019). Various methods such as culturing and HTS measure different fractions of fungal communities, each having benefits and potential biases (see Tóth and Barta, 2010; Nilsson et al., 2019). Both above- and below-ground fungal assessments, including sporocarp surveys are still valuable because they include the saprotrophic community, a greater EM species richness than sampling root tips alone, and sporocarp production can be more sensitive to environmental changes than belowground EM or saprotrophic species found within logs (Last et al., 1979; Gardes and Bruns, 1996; Tóth and Barta, 2010). It is unclear how fungal communities, including both aboveground EM and saprotrophic sporocarps and belowground EM root tips, will recover in large high-severity burn patches, often >200 m from any live tree, and over 10 years post-fire.

To understand the long-term effect of fire severity on fungal communities, we assessed both aboveground sporocarps (fruiting EM and saprotrophic fungi found at the soil surface) and belowground EM fungi colonizing the root tips of naturally regenerating ponderosa pines, 13 years after the 2000 Pumpkin Fire near Flagstaff, AZ. The Pumpkin Fire was chosen because it had extensive patches of high-severity fire, as well as moderate-severity fire, and nearby unburned areas. Because of the extensive patch size and tree mortality, distance from forest edges, and increased surface fuels, we hypothesized that compared to moderate-severity and unburned areas, high-severity burn patches will have: H₁) greater saprotrophic and lower EM sporocarp density; H₂) greater saprotrophic and lower EM sporocarp species richness and a distinct sporocarp community composition; and H₃) regenerating ponderosa pine seedlings with similar EM colonization rates, but lower richness, and a distinct EM community composition. Additionally, we expected seedlings in high-severity patches to have a community dominated by species with resistant propagules (e.g. *Wilcoxina* or *Rhizopogon*), similar to Glassman et al. (2016), but lacking some species capable of long-distance hyphal exploration associated with hyphal networks, compared to those from moderate-severity or unburned areas (Agerer, 2001). Finally, we expected these differences in fungal composition in high-severity burn patches to be more pronounced with greater distances from surviving trees.

2. Materials and methods

2.1. Study sites and plot design

We investigated the long-term effect of fire severity on fungal communities 13 years after the 2000 Pumpkin Fire in northern Arizona. The Pumpkin Fire burned approximately 6500 ha, including 1400 ha of high-severity fire on the Kaibab and Coconino National Forests (<http://www.mtbs.gov/>; Fig. 1A). We define high-severity as 100% tree mortality. Our plots ranged from 2350 to 2600 m elevation. The mean 15 year (2001–2015) post-fire annual precipitation was 57.7 cm and the mean temperature was 7.2 °C (Prism Climate Group: <http://prism.oregonso>

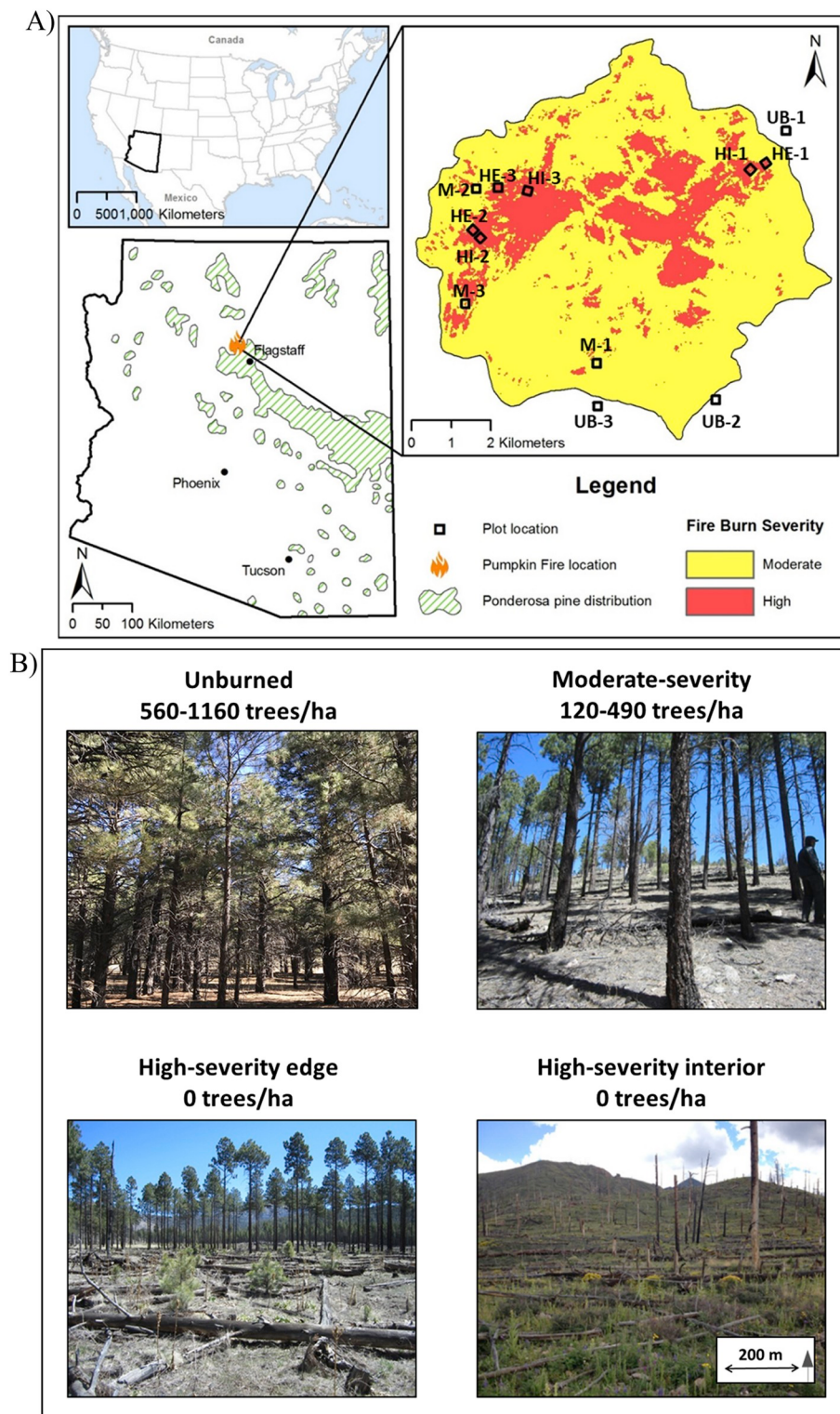


Fig. 1. A) Location of 4-ha study sites within different burn severity classes on the 2000 Pumpkin Fire, Arizona, USA. Study areas are to scale, and UB = unburned, M = moderate-severity, HE = high-severity edge, and HI = high-severity interior. Smaller quadrats for quantifying fungal communities were randomly selected within each of these study areas. B) Photographs of different burn severity classes, including unburned (560–1160 trees/ha), moderate-severity (120–490 trees/ha), high-severity edge (0 trees/ha) and high-severity interior (0 trees/ha) plots, for a total of twelve 4-ha plots. High-severity edge plots were established adjacent to forest edges, and high-severity interior plots were established at least 200 m from any live tree.

tate.edu/. Accessed 10/7/16). This region receives most of its annual moisture from late-summer monsoon rains that typically occur July–August and from winter precipitation. We sampled both aboveground sporocarps and belowground root tips a single time and reached all plots through August–September 2013. During the time of our field sampling, late-summer moisture was higher than average (mean precipitation for July: 173.3 mm, August: 103.1 mm, and September: 105.9 mm) compared to the 15 year post-fire average (July: 75.5 mm, August: 95.0 mm, and September: 51.5 mm; Prism Climate Group). The soils

were derived from basalt and ranged from shallow gravelly sandy loam to moderately deep cobbly clay loam on our study plots (WebSoil Survey: <http://websoilsurvey.nrcs.usda.gov>. Accessed 10/5/16). The unburned and pre-fire overstory vegetation was dominated by ponderosa pine. Common understory species included the bunch grasses, such as mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.); forbs, such as spreading fleabane (*Erigeron divergens* Torr. & A. Gray) and silvery lupine (*Lupinus argenteus* Pursh); and shrubs including Woods' rose (*Rosa woodsii* Lindl. var. *ultramontana* (S. Watson) Jeps.) and Fendler's

Ceanothus (*Ceanothus fendleri* A.).

We used Monitoring Trends in Burn Severity (MTBS, 2013) maps with field validation to identify different burn severities and unburned sites for plot selection. We established 4-ha (200 × 200 m) plots in four severity classes, including “unburned” (UB), “moderate-severity” (M), “high-severity edge” (HE) and “high-severity interior” (HI) plots, and used ArcGIS 10.1 (ESRI, 2012) to randomly select three replicates for a total of twelve 4-ha plots (Fig. 1A). Unburned plots were selected near the other plots and they were not burned in a wildfire or managed fire for the past 50 + years, as determined by comparison to fire records (Crouse, 2019). Unburned areas had high tree densities, ranging from 560 to 1160 trees/ha. Moderate-severity plots were chosen from areas that resulted in a spatial heterogeneity of post-fire surviving trees ranging from 120 to 490 trees/ha, including some patches of high-severity fire <1 ha in size. Both high-severity edge and interior plots had 100% tree mortality from the wildfire, but high-severity edge plots were established adjacent to forest edges or residual live trees (within approximately 1–200 m), and high-severity interior plots were established where no surviving trees were found within at least 200 m to over 400 m from the plot boundaries. Ponderosa pine seedling densities were lower in high-severity interior plots than edge plots. High severity plots had an average of 20 ponderosa pine seedlings/ha (interior burn patch) to 73 seedlings/ha (near forest edges), and regeneration was spatially heterogeneous (Owen et al., 2017; see Fig. 1B). All burn plots had higher understory forb (averaging >50%) and coarse woody debris (averaging 18%) cover, but similar litter (>90%; mostly herbaceous) and bare ground (1–4%) cover, compared to unburned plots with an average of ~31% forb, < 2% coarse woody debris, 89% litter (mostly pine needles), and ~3% bare ground cover (Owen, 2019). To understand the effects of fire severity on fungal communities, we surveyed aboveground sporocarps within smaller quadrats located in each 4-ha plot, and we destructively sampled ponderosa pine seedlings outside each 4-ha plot, described in more detail below.

2.2. Measuring post-fire sporocarp communities

To test the first hypothesis that high-severity burn patches will have greater saprotrophic and lower EM density compared to moderate-severity or unburned areas, we surveyed post-fire sporocarps and determined their functional status. We surveyed aboveground sporocarps in August–September 2013, within 2 X 2-m quadrats surrounding 30 regenerating ponderosa pine seedlings (ranging from 4 to 11 years old) across different fire severities and unburned areas, for a total of 360 quadrats. The quadrats were set up around randomly selected ponderosa pine seedlings (using a random number generator) from all spatially mapped seedlings in each 4-ha plot (Owen et al., 2017). We counted all individual sporocarps within each quadrat, collected multiple reference specimens of each morphotype, recorded the substrate (bare ground, litter, or log) they were found on, and dried specimens at room temperature in the laboratory at the Rocky Mountain Research Station, Flagstaff, AZ until identification as described below.

To test the second hypothesis that sporocarp richness and diversity would be lower in the high-severity burn patches compared to moderate-severity or unburned areas, we identified sporocarps to the species level based on their morphology using a mushroom key (Arora, 1986), and used molecular techniques when species could not be keyed out and to test some specimens for keying accuracy. To identify sporocarps using molecular techniques, we extracted DNA from each sporocarp using a Thermo MagJET Plant gDNA Kit (Thermo Fisher Scientific Baltics UAB, Vilnius, Lithuania) according to the manufacturer's instructions. We amplified extracted DNA by polymerase chain reaction (PCR) using a fungal specific ITS-1F and ITS4 primer pair as in White et al. (1990). This primer pair, which targets the internal transcribed spacer (ITS) region of rDNA also includes the 5.8S, and portions of the 18S and 28S rRNA genes in the fungal genome (Horton and Bruns, 2001). We sequenced DNA on an ABI 3730xl Genetic Analyzer (Applied

Biosystems, Foster City, California) from each sporocarp in the Environmental Genetics and Genomics (EnGGen) laboratory at Northern Arizona University, Flagstaff, AZ. The resulting sequences were assembled in BioEdit version 7.0.5.3 (Hall, 1999) and in Pregap4 of the Staden Package (Staden et al., 1998). The consensus sequences from Pregap4 were used in Genbank BLAST® searches on the NCBI website (Altschul et al., 1990) and UNITE database (Kõljalg et al., 2013). We used percentage query coverage, percentage maximum identity, and bit score data to identify the closest match to references in GenBank. Sequence similarity of ≥98% was used for species level identity and 95–97% for genus level identity (Kõljalg et al., 2013). We aligned sequences from a similar genus against one another using MEGA version 7.0 (Kumar et al., 2016) and considered them different species if they had ≥ 2% base pair dissimilarity. We determined sporocarp species richness from each quadrat. To test whether functional groups of sporocarps will differ in the high-severity burn patches compared to moderate-severity or unburned areas, we separated species into different functional groups (either EM or saprotrophic) based on common consensus from past studies (e.g., Tedersoo et al., 2006; Tedersoo and Smith, 2013).

To analyze sporocarp density and richness, we used generalized linear mixed models (GLMM) in SAS 9.4 (SAS PROC GLIMMIX®, 2017), with fire-severity as a fixed effect and site location (see three replicate locations on Fig. 1A) as a random effect. Total, EM, and saprotrophic density and richness of sporocarps were analyzed with GLMMs with a negative binomial distribution and log-link function. If significant differences were found, the post hoc Tukey–Kramer HSD test was used on least-squares means for subsequent pair-wise comparisons (Kramer, 1956).

To test the latter part of the second hypothesis, that high-severity burn patches have unique sporocarp communities compared to moderate-severity or unburned areas, we used permutational multivariate analysis of variance (PERMANOVA); and to visualize differences in communities among burn severity classes, we used a redundancy analysis (RDA) in R v.3.4.1, library vegan, function rda (Oksanen et al., 2018; R Core Team, 2018; Ter Braak, 1994). The ordination axes represent distances showing how similar or dissimilar each community is by proximity of the data points in environmental space. All PERMANOVA analyses, including pairwise comparisons, used original counts with a Hellinger distance, which is insensitive to double zeros because the metric does not place importance on the mutual absence of a species (Legendre and Legendre, 2012). If PERMANOVA results were significant, we then calculated dispersion (a measure of beta diversity) as measured by individual dissimilarity from the burn severity group centroid in multivariate space, described by Anderson et al. (2006), and used indicator species analysis (indicator value = frequency X relative abundance) to determine if particular species were driving community differences (McCune and Grace, 2002).

Finally, to understand if log or tree canopy cover could be driving community differences in sporocarp community composition within each quadrat, we measured percent cover of coarse woody debris (CWD) (dead woody materials, including logs and branches ≥ 7.62 cm diameter) using a go/no-go gauge (Brown, 1974), and overstory tree canopy cover using a GRS vertical densitometer (Geographic Resource Solutions, Arcata, California, USA), taking the average of 5 readings/quadrat at each corner and center of each quadrat. We overlaid vectors on our ordination from a second matrix, consisting of CWD and overstory cover variables, and used Hellinger distance as an assessment of these environmental gradients to determine any correlation with differences in sporocarp communities.

2.3. Measuring EM fungi colonizing regenerating ponderosa pine seedlings

To test the third hypothesis, we destructively sampled three naturally regenerating ponderosa pine seedlings outside each 4-ha plot (for a total of 36 seedlings) to measure EM colonization and community composition. We removed an average of 20 cm of roots from each

seedling to measure fungal occurrence and frequency as shown by EM mycorrhizal root tips using a dissecting microscope, examined roots at 40X magnification, and quantified the percentage of live and dead EM root tips, as well as live and dead non-colonized root tips (Gehring and Whitham, 1994). We surveyed 60–200 root tips per sample. To test for differences in percent EM colonization among ponderosa pine seedlings, we divided the percentage data by 100 and used a GLMM with a log-link function and a beta distribution in SAS 9.4 (SAS PROC GLIMMIX©, 2017).

We identified EM fungi both morphologically and with molecular techniques. We recorded different morphotypes based on different colors, shapes, and hyphal arrangements (Horton and Bruns, 2001) and froze them at -20°C for future molecular analysis. DNA was extracted from 2 to 3 representatives of each morphotype from each seedling using similar methods as described above for sporocarps. We tested for differences in richness, community composition and dispersion among burn severity classes using the same statistical methods described for the sporocarps. Also, to understand if seedling growth and age is correlated with EM colonization and richness, we measured seedling diameter at the root collar (DRC), estimated seedling pith age (by counting growth rings from a cross-section of the stem). We used partial correlation analysis to determine any association between % colonization and richness and seedling growth, while adjusting for the effect of age, in SAS 9.4 (SAS PROC CORR, 2017). Lastly, to understand if regenerating seedlings were associated with EM fungi with different hyphal exploration types, we categorized EM genera into short, medium or long exploration types according to Agerer (2001, 2006), and Tedersoo and Smith (2013).

3. Results

3.1. Fire severity and EM sporocarps

EM sporocarp densities were lower in both edge and interior high-severity burn plots compared to the unburned and moderate severity plots, partially supporting our first hypothesis (EM density: $F = 12.01$, $p < 0.01$; Fig. 2A). Ectomycorrhizal sporocarp densities were approximately 5–13 times lower in the high-severity burn plots compared to the unburned and moderate-severity plots. Additionally, the proportion of EM to saprotrophic sporocarps was much lower in the high-severity burn plots compared to the unburned and moderate-severity plots (Fig. 2A). We did not find any sporocarps in 133 of the total 360 quadrats (26–39% of the unburned and moderate-severity plots, and 44–49% of the high-severity plots had no visible aboveground sporocarps). Similar to sporocarp densities, EM sporocarp richness was lower in both high-severity burn plots compared to the unburned and moderate severity plots, partially supporting our second hypothesis (EM richness: $F = 17.20$, $p < 0.01$; Fig. 2B). Average EM sporocarp richness was 4–7 times lower in both edge and interior high-severity burn plots, compared to the unburned and moderate-severity plots (Fig. 2B).

Some dominant EM sporocarps found in the unburned and moderate-severity plots were missing from the high-severity burn plots (Appendix Table S1). The most abundant EM species was *Hygrophorus speciosus*, found in 30 quadrats, but absent from both the edge and interior high-severity quadrats. Other common EM fungal species included *Russula brevipes* + *Hypomyces lactifluorum* (from here on referred to by common name “lobster mushroom”), *Inocybe geophylla* var. *lilacina*, and *Clavulina cristata* (all missing from high-severity burn plots; Appendix Table S1). Some EM fungal genera found in the unburned and moderate-severity plots, such as *Suillus*, *Amanita*, and most *Russulas*, were also not found in the high-severity plots, except *Russula xerampelina*, which was found in one high-severity edge quadrat (Appendix Table S1).

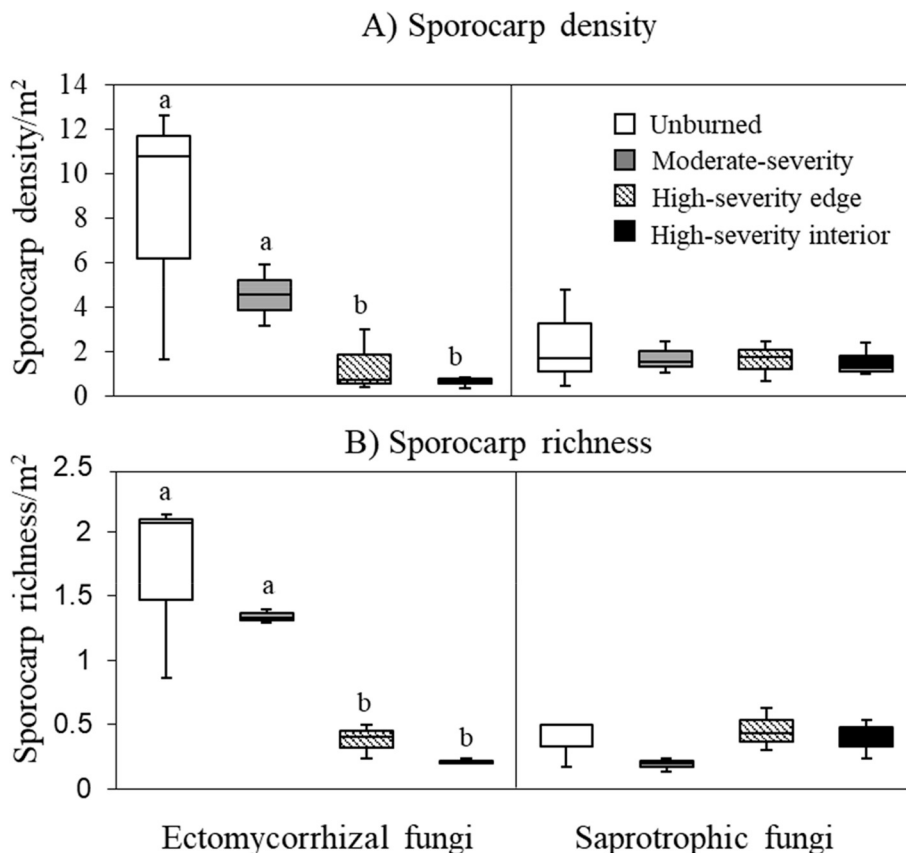


Fig. 2. Total and ectomycorrhizal sporocarp A) density and B) richness were lower in the high-severity burn plots compared to the unburned and moderate severity plots. No differences were found in saprotrophic sporocarp density or richness among burn severity classes. White boxes = unburned, gray boxes = moderate-severity, patterned boxes = high-severity edge, and black boxes = high-severity interior plots. Boxplots represent the variation between sites, and span the first to the third quartile. A center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.

3.2. Fire severity and saprotrophic sporocarps

Contrary to our first hypothesis, no differences were found in saprotrophic sporocarp densities among burn severity classes (saprotrophic density: $F = 1.43$, $p = 0.19$; Fig. 2A). Mean saprotrophic densities ranged from 1.5 to 2.3 sporocarps/m² among all severity classes. Additionally, no differences were found in saprotrophic sporocarp richness among severity classes (saprotrophic richness: $F = 1.53$, $p = 0.21$; Fig. 2B). Similar to sporocarp densities, the proportion of EM to saprotrophic sporocarp richness was much lower in the high-severity burn plots compared to the unburned and moderate-severity burn plots (Fig. 2B).

Common saprotrophic species included *Vascellum curtisii* (found in 20 quadrats, in all severity classes), a *Psathyrella* sp. (only found in high-severity burn plots), and *Gloeophyllum sepiarium* (common in high-severity plots and found in one unburned plot; Appendix Table S1). Most of the saprotrophic species known to decompose forest litter were found in the unburned plots, whereas the high-severity edge and interior plots had more white-rot and brown-rot species, associated with logs (Appendix Table S1). Finally, we found one species that is parasitic to some trees, *Armillaria ostoyae*, in the high-severity interior plots (Appendix Table S1).

3.3. Sporocarp community composition

Both edge and interior high-severity burn plots had a different sporocarp community composition compared to unburned and moderate-severity plots, supporting our second hypothesis (PERMANOVA: $F = 3.92$, $P < 0.01$; Fig. 3). Pairwise PERMANOVA comparisons show high-severity plots had a different sporocarp community composition compared to unburned and moderate-severity plots ($p < 0.01$ for both), and there was a trend for different community composition between high-severity edge and interior plots, as well as unburned and moderate-severity plots ($p = 0.06$ for both). Both % overstory tree canopy cover and CWD vectors were significantly correlated with axis dbRDA1 ($p < 0.01$ for both), but explained very little of the variance in community composition between the two high-severity burn plots and moderate-severity and unburned plots (see low R^2 values; Fig. 3).

Species dispersion differed among severity classes ($F = 6.53$, $p < 0.01$; average distance to centroid: unburned = 0.77 moderate-

severity = 0.74, high-severity edge = 0.61, high-severity interior = 0.57). Pairwise PERMANOVA comparisons show sporocarp dispersion on high-severity edge and interior plots were similar to one another ($p = 0.91$), as well as unburned and moderate-severity plots ($p = 0.96$). There was a trend for similar dispersion between high-severity edge and moderate-severity plots ($p = 0.06$), and high-severity edge plots had lower dispersion than unburned ($P = 0.02$). Finally, high-severity interior plots had lower dispersion than both unburned and moderate-severity plots ($p = 0.01$ for both). There were no significant indicator species when analyzing all 360 quadrats, including many zero-inflated plots, but when collapsing data into the large plot level ($n = 3$), there were significant indicator species from different functional groups. Two indicator species for the unburned areas were *Suillus kaibabensis* ($I = 64.5$, $p = 0.04$) and a lobster mushroom ($I = 59.5$, $p = 0.05$), and for moderate-severity burn areas, they were *Russula sanguinea* ($I = 60.0$, $p = 0.02$) and *Clavulina cristata* ($I = 78.6$, $p = 0.04$). An indicator species for the high-severity edges was *Gloeophyllum sepiarium* ($I = 78.6$, $p = 0.04$), and there were no indicator species for the high-severity interior areas.

3.4. EM fungi colonizing ponderosa pine seedlings

Percent live EM fungal colonization in regenerating ponderosa pine seedlings was similar among burn severity classes ($F = 1.48$, $p = 0.24$; Appendix S2A), supporting our third hypothesis. The percentage of live EM root tips from regenerating ponderosa pine roots ranged from 23 to 32% colonization (Appendix Fig. S2A). The percentage of total (live + dead) EM colonization ($F = 1.89$; $p = 0.15$), and total non-colonized root tips ($F = 1.28$; $p = 0.30$) were also similar among severity classes (data not shown).

Ectomycorrhizal root tip species richness ($F = 1.42$, $p = 0.26$; Appendix Fig. S2B) was similar among severity classes, contrary to our third hypothesis. Although the average species richness/seedling was similar among severity classes (ranging from 2 to 3.4/seedling; Appendix Fig. S2B), the total number of EM species colonizing regenerating ponderosa pine seedlings on the plot-level was much lower in the high-severity interior plots compared to the other severity classes, especially the moderate-severity plots (Fig. 4). The total number of root-tip EM species at the plot level were: unburned = 13, moderate-severity = 15, high-severity edge = 9, and high-severity interior = 7 (Fig. 4).

We identified 24 different EM species colonizing ponderosa pine roots (Table 1). The unburned plots had five unique species (*Boletales* sp., *Inocybe chelanensis*, *Russula integriformis*, *Russula sanguinea*, and a *Tricholoma* sp.), the moderate-severity plots had seven unique species, and the high-severity interior had one unique species, *Inocybe* sp. (Table 1). Also, a *Wilcoxina* sp. was only found in both of the high-severity burn plot types, but absent from the unburned and moderate-severity plots. Similar to the sporocarp results, species from the genus *Russula* were mostly found in the unburned and moderate-severity plots, and absent from high-severity interior plots, but *R. brevipes* was found on one high-severity edge seedling. We found a large discrepancy between species that were found colonizing ponderosa pine roots and those found as fruiting sporocarps. Only six out of the 24 species found colonizing ponderosa pine roots were also found as fruiting sporocarps in the same burn severity classes (Table 1). We expected both high-severity plots to have different ponderosa pine EM root tip communities compared to moderate-severity and unburned plots; however, only the high-severity interior and moderate-severity EM community composition differed ($p = 0.02$), but all other burn severity classes were similar ($p > 0.10$; PERMANOVA pairwise comparisons; Fig. 5). There were trends for EM dispersion differences among severity classes ($F = 2.95$, $p = 0.05$), and for lower EM dispersion on high-severity interior compared to moderate-severity plots ($p = 0.07$). An indicator species for moderate-severity plots was a *Sebacina* sp. ($IV = 33.3$, $p = 0.04$), and there was a trend for indicator species for the high-severity interior plots (*Cenococcum geophilum*: $IV = 37.6$, $p = 0.08$, and *Inocybe nitidiuscula*: $IV = 25$,

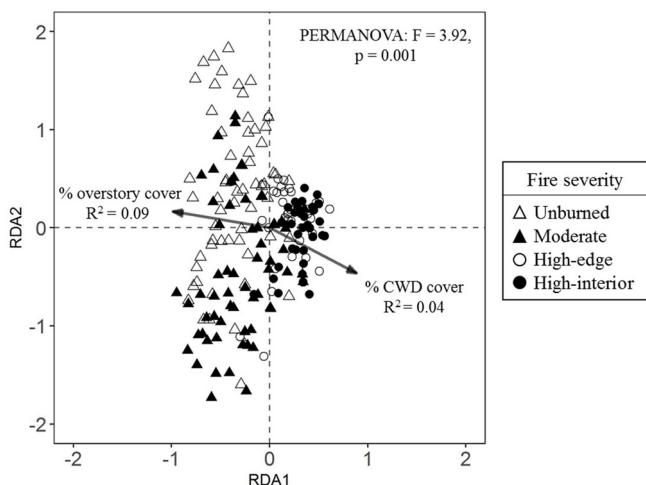


Fig. 3. A redundancy analysis (RDA) and PERMANOVA results show high-severity edge and interior plots have a different sporocarp community composition compared to unburned and moderate-severity plots. The closer two symbols are together, the more similar the communities are. Both % overstory tree canopy cover and coarse woody debris (CWD) vectors (arrows) were significant, however they explained very little of the variance in community composition. White triangles = unburned, black triangles = moderate-severity, white circles = high-severity edge, and black circles = high-severity interior.

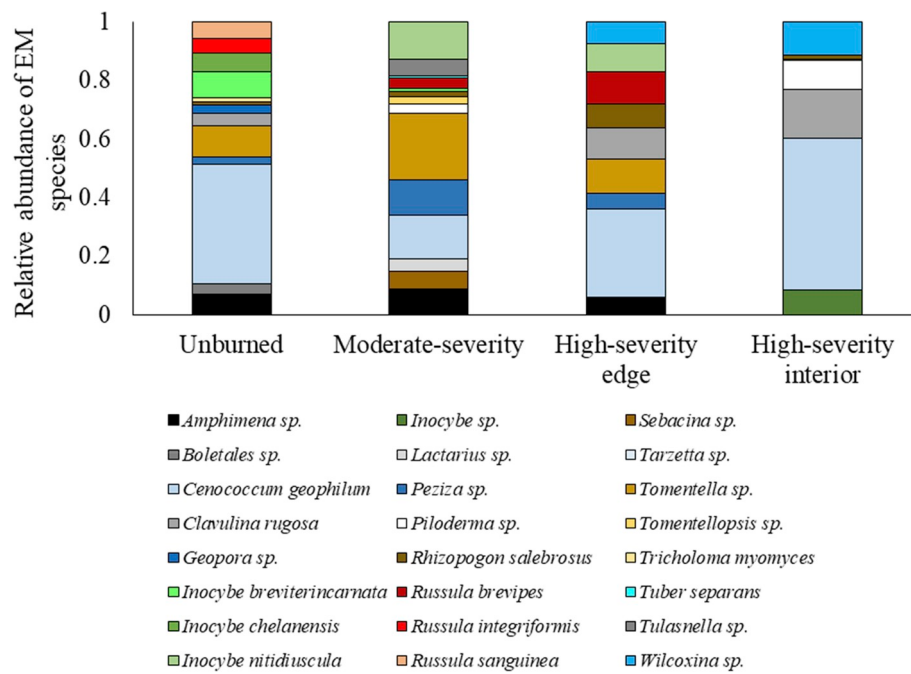


Fig. 4. Mean relative abundance (proportion) of EM species colonizing regenerating ponderosa pine seedlings in unburned, moderate-severity, high-severity edge and high-severity interior plots. Some taxonomy groups are separated by color, e.g. Ascomycetes are shown in shades of blue, *Russulaceae* in shades of red, and *Inocybaceae* in shades of green.

Table 1

EM species identified from regenerating ponderosa pine seedlings from the 2000 Pumpkin Fire, and their presence in each treatment (UB = unburned, M = moderate-severity, HE = high-severity edge, and HI = high-severity interior). Species were identified from the best BLAST match to ITS sequences (% is percentage similarity of query to published reference sequence, and score is an evaluation of query and reference sequence alignment based on their length and number of gaps); phylum: A = Ascomycete or B = Basidiomycete. Hyphal exploration type based on our observation and [Agerer \(2001, 2006\)](#).

EM species ID	Best BLAST match	Presence in treatment	% Identity	% Query	Accession number	Phylum	Hyphal exploration type
<i>Amphimena</i> sp.	Uncultured <i>Agaricomycetidae</i>	UB, M, HE	98	99	FJ554011.1	B	Medium
<i>Boletales</i> sp.	Uncultured <i>Boletales</i>	UB	98	99	FJ554030.1	B	Long
<i>Cenococcum geophilum</i>	<i>Cenococcum geophilum</i>	UB, M, HE, HI	92	95	LC095057.1	A	Short
<i>Clavulina</i> sp.	Uncultured <i>Clavulina</i>	UB, M, HE, HI	97	99	KP645350.1	B	Medium
<i>Geopora</i> sp.	Uncultured <i>Geopora</i>	UB, HI	99	96	LC013727.1	A	Short
<i>Inocybe breviterincarnata</i>	<i>Inocybe breviterincarnata</i>	UB*, M	98	98	JQ408750.1	B	Short
<i>Inocybe chelanensis</i>	<i>Inocybe chelanensis</i>	UB*	99	99	HQ604403.1	B	Short
<i>Inocybe nitidiuscula</i>	<i>Inocybe nitidiuscula</i>	M*, HE*	97	92	HE862959.1	B	Short
<i>Inocybe</i> sp.	<i>Inocybe</i> sp.	HI	98	99	JQ319695.1	B	Short
<i>Lactarius</i> sp.	Uncultured <i>Lactarius</i>	M	99	99	FJ552816.1	B	Medium
<i>Peziza</i> sp.	Uncultured ectomycorrhizal fungus	UB, M, HE	99	98	JN704833.1	A	Short
<i>Piloderma</i> sp.	<i>Piloderma</i> sp.	M	99	85	KT800234.1	B	Short
<i>Rhizopogon salebrosus</i>	<i>Rhizopogon salebrosus</i>	UB, M, HE, HI	99	99	HQ914340.1	B	Long
<i>Russula integriformis</i>	<i>Russula integriformis</i>	UB	99	98	KP783458.1	B	Medium
<i>Russula brevipes</i>	<i>Russula brevipes</i>	M*, HE	99	100	FJ845429.1	B	Medium
<i>Russula sanguinea</i>	<i>Russula sanguinea</i>	UB*	96	99	FJ845434.1	B	Medium
<i>Sebacina</i> sp.	Uncultured <i>Sebacina</i>	M	99	99	JN704824.1	B	Short
<i>Tarsetta</i> sp.	Uncultured <i>Tarsetta</i>	M	97	81	KF041371.1	A	Medium
<i>Tomentella</i> sp.	Uncultured <i>Tomentella</i>	UB, M, HE	99	98	HQ271387.1	B	Short
<i>Tomentellopsis</i> sp.	Uncultured ectomycorrhizal fungus	M	98	99	AY702814.1	B	Medium
<i>Tricholoma myomyces</i>	<i>Tricholoma myomyces</i>	UB*	95	99	FJ845443.1	B	Medium
<i>Tuber separans</i>	<i>Tuber separans</i> isolate	M	99	97	HM485388.1	A	Short
<i>Tulasnella</i> sp.	Uncultured <i>Tulasnellaceae</i>	M	98	99	JQ994403.1	B	Short
<i>Wilcoxina</i> sp.	Uncultured <i>Pyronemataceae</i>	HE, HI	99	99	FJ553830.1	A	Short

*Species were also found fruiting in these treatments.

$p = 0.09$). The amount of EM ascomycetes ($F = 0.39$, $p = 0.79$) and basidiomycetes ($F = 0.36$, $p = 0.81$) colonizing seedlings did not differ among severity classes; however, the total number of ascomycetes compared to basidiomycetes was higher within the high-severity interior sites (Table 1, Appendix Fig. S3). The EM communities in all burn severity classes were dominated by taxa with short hyphal exploration types, and the relative abundance of short, medium and long hyphal exploration types was similar among severity classes (Table 1, Appendix

Fig. S4), contrary to our hypothesis.

Finally, regenerating ponderosa pine seedling age was correlated with growth measured by diameter at root collar (DCR) ($F = 83.6$; $p < 0.001$, Appendix Fig. S5); therefore age was used as a covariate in our correlation analyses. Ponderosa pine seedling age ($p = 0.65$) and DCR ($p = 0.58$) did not differ among severity classes and there were no significant relationships between % EM colonization ($p = 0.47$), or EM richness ($p = 0.24$) and ponderosa pine seedling DCR growth (data not

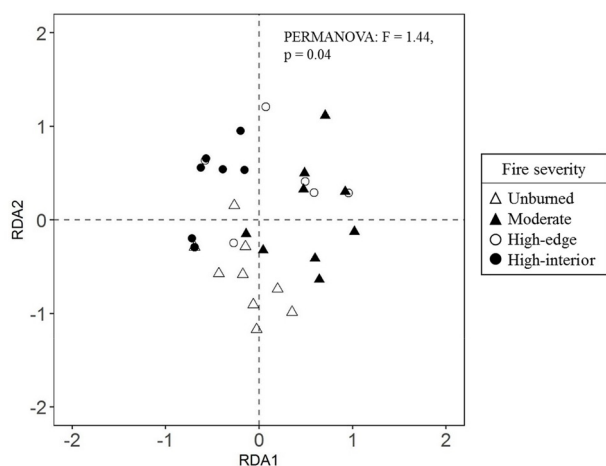


Fig. 5. A redundancy analysis (RDA) PERMANOVA results show a difference in ponderosa pine root tip EM community composition between the high-severity interior and moderate-severity plots. The closer two symbols are together, the more similar the communities are. White triangles = unburned, black triangles = moderate-severity, white circles = high-severity edge, and black circles = high-severity interior.

shown).

4. Discussion

4.1. Fire effects on EM sporocarps

We found low EM sporocarp densities and richness over ten years after severe fire compared to unburned and moderate-severity plots in a ponderosa pine forest, similar to the findings of [Salo and Kouki \(2018\)](#), but contrary to [Mediavilla et al. \(2014\)](#) in different forest types. These results may be attributed to altered resources and site conditions, lack of suitable hosts, and the successional status of species. Lower EM sporocarp density and richness on high-severity burn plots does not necessarily indicate an absence of certain species, but may be attributed to inadequate conditions for sporocarp production. Sporocarp production is highly dependent on sufficient carbohydrate sources and moisture, and sporocarp production is sensitive to air and soil temperatures ([Lange, 1978](#); [O'Dell et al., 1999](#); [Smith and Read, 2008](#)), and the harsh site conditions in the high-severity burn sites, characterized by a lack of overstory canopy cover (exposure to intense sunlight, and very little wind protection) could have contributed to the lack of sporocarps. Our sporocarp survey was conducted during a very wet year, and low numbers of fruiting sporocarps in severely burned areas could mean conditions are rarely good 13 years after high-severity fire, and this could apply to saprotrophic species as well. Other possibilities for the differences in EM composition found among burn severities apply to both EM sporocarps and roots tips, discussed further below.

4.2. Fire effects on saprotrophic sporocarps

Our study found similar saprotrophic sporocarp density and richness among burn severity classes, even with increased log cover on burned sites. These findings may be explained by time since fire, substrate quality of burned wood, or sampling methods ([Sun et al., 2015](#); [Bhatnagar et al., 2018](#); [Nilsson et al., 2019](#)). Others have shown that some species of pyrophilous “fire-loving” fungi are known to produce sporocarps only in the first 1–2 years after fire, but sporocarp production can decrease with time since fire ([Robinson et al., 2008](#); [Claridge et al., 2009](#)). Alternatively, [Dejene et al. \(2017\)](#) found reduced saprotrophic sporocarp density and richness within the first few years after high-severity fire, but both recovered to similar levels as unburned areas

over time. A change in the structure, chemical composition, substrate quality, and spatial variability of woody debris could also alter the presence of some saprotrophic fungi ([Zhou and Hyde, 2002](#); [Dove and Keeton, 2015](#); [Ficken and Wright, 2017](#); [Bhatnagar et al., 2018](#)). Finally, these results could be attributed to our sampling methods that could be biased toward species that fruit, or site conditions that may influence a species' ability to fruit. While saprotrophic density and richness were similar, we found the composition of saprotrophic species varied among burn severity classes.

The unburned sites (characterized by high tree densities and a thick forest floor) had more litter-decomposing saprotrophic sporocarps, and high-severity burn sites (characterized by stumps and downed logs) had more sporocarps capable of brown- and white-rot decomposition. Two of the most abundant saprotrophic species were *Vascellum curtisii*, a puffball found in all severity classes and associated with litter and areas of disturbance ([Terashima et al., 2004](#)), and a *Psathyrella* sp., only found on the high-severity burn plots; some members of this genus are brown-rot fungi, associated with logs ([Padamsee et al., 2008](#)). Two species, *Gloeophyllum sepiarium* and a *Crassisporium* sp., were mostly found in the high-severity burned plots, and have a preference for fruiting on burned litter or wood ([Carlsson et al., 2014](#); [Matheny et al., 2015](#)). Other species unique to the high-severity edge plots included an *Agrocybe* sp., a *Cystoderma* sp., and *Entoloma iodiolens*, and evidence suggests they are white-rot species ([Singer, 1977](#); [Noordeloos, 1981](#); [Berg and Verhoef, 1998](#)). One of the saprotrophic species unique to the high-severity interior plots was *Armillaria ostoyae*, and it was the only tree pathogen we found on our plots, and others have found that logs or stumps can be habitats for potential fungal tree pathogens ([Garbelotto, 2004](#); [van der Wal et al., 2017](#)). There were no live trees on the high-severity burn plots and they also had a much higher proportion of saprotrophic to EM fungi than unburned and moderate-severity plots, both comprised of mature, live trees. Others have found that saprotrophic fungi are less susceptible to severe fire than EM fungi ([Holden et al., 2016](#); [Sun et al., 2015](#); [Day et al., 2019](#)).

4.3. EM sporocarps and root tip community composition

We found very little overlap between EM sporocarp and root tip species composition, but fire-severity influenced both. The difference in above- and belowground species composition is a common finding in previous studies, and [Gardes and Bruns \(1996\)](#) suggest that resource allocation to produce fruiting sporocarps varies among species; some species may not produce sporocarps, and abundant fruiterers could rely more on saprotrophic energy sources. The difference in both EM sporocarp and root tip community composition between high-severity burns and other severity classes may be partially explained by distance from mature EM hosts ([Dickie and Reich, 2005](#); [Buscardo et al., 2011](#); [Peay et al., 2012](#)). Numerous studies show EM fungi are sensitive to high-severity fires, similar to our findings ([Treseder et al., 2004](#); [Kipfer et al., 2011](#); [Holden et al., 2013](#); [Glassman et al., 2016](#); [Reazin et al., 2016](#)). Evidence suggests that EM inoculum can become limited, and community composition can differ farther from live forest edges ([Dickie and Reich, 2005](#); [Peay et al., 2012](#)). For example, [Dickie and Reich \(2005\)](#) found lower EM colonization of *Quercus macrocarpa* seedlings at greater distances from mature forest edges (>16 m), and did not find any *Russula* species past 12 m from the forest edge, yet *Cenococcum geophilum* was the most common species found at all distances. Although we did not find a difference in EM inoculum among severity classes, members of the genus *Russula* were absent from the high-severity interior burn patches as either sporocarps or root tips, and *C. geophilum* was found colonizing ponderosa pine roots in all severity classes. Further, the high-severity interior patches had a lower EM root tip species pool and community dispersion compared to the moderate-severity burn plots.

In addition to distance from EM-hosts, the successional stage of fungi may help explain differences in EM communities in high-severity burn

plots. There is evidence that early-, multi- (persisting throughout the lifetime of forest stands) and late-successional EM species persist at different stages of forest development (Visser, 1995; Nara et al., 2003). Some early-successional species (e.g., *Thelephora*, *Cenococcum*) typically colonize seedlings and their C demand is lower than older successional species (Visser, 1995; Agerer, 2001). We found that *C. geophilum* was most abundant on root tips from high-severity interior plots. Some late successional fungi that were absent from high-severity interior burn plots, including *Russula* and *Amanita* species, are associated with developed soil organic layers and with older and larger trees that provide more carbon, and they do not germinate well in early-successional conditions, even if host roots are present (Visser, 1995; Nara et al., 2003; Dickie et al., 2013). Long distance EM exploration types can connect with other mycelia to form common mycorrhizal networks (CMNs) for nutrient transfer, yet they require more carbon than short distance types (Agerer, 2001, 2006; Tedersoo and Smith, 2013). Evidence suggests that short-distance EM exploration types dominate in dry-forest pine seedlings, because we found a much higher relative abundance of this type in all ponderosa pine seedlings compared to medium- or long-distance exploration types, similar to the findings of Patterson et al. (2019) for *Pinus edulis* seedlings.

Ectomycorrhizal heat-tolerance, or spore longevity and dispersal could also play a role in post-fire recovery and may help explain the low species pool and community dispersion found colonizing seedlings from the high-severity interior burn plots (Kipfer et al., 2010; Glassman et al., 2015, 2016). Recent research suggests that fire could be acting as a selective agent for certain EM species (Rincón and Pueyo, 2010; Kipfer et al., 2010; Rincón et al., 2014; Glassman et al., 2016). Common EM fungi found colonizing seedlings from the high-severity plots on our study sites were from the genera *Rhizopogon*, *Cenococcum* and *Wilcoxina*, that others have shown can survive high heat (Peay et al., 2009; Kipfer et al., 2010). Some EM species produce sexual spores (*Rhizopogon*) or asexual chlamydospores (*Wilcoxina*) and sclerotia (*Cenococcum*) that can stay dormant for some time, or are prolific producers and contribute to early successional EM-host establishment (Glassman et al., 2015, 2016). Seedling colonization was similar among burn severity classes in our study, but seedlings far from inoculum sources, may be dependent on EM species that survive the fire. Spores of certain species of *Wilcoxina* and *Rhizopogon* are viable for at least 6 years and some may be viable for decades (Bruns et al., 2009; Nguyen et al., 2012). Additionally, a high concentration of spores fall near fruiting mushrooms (Galante et al., 2011), and some can be dispersal-limited within distances of <1 km (Peay et al., 2012), especially *Basidiomycota* far from forest edges (Peay and Bruns, 2014). Spores can also be distributed by rodents and larger mammals (Theimer and Gehring, 2007; Ashkannejhad and Horton, 2006). However, low concentrations of EM spores and timing of spore dormancy could limit successful colonization (Bruns et al., 2009; Peay and Clemmensen, 2018).

4.4. EM fungi were resilient after moderate-severity fire

Although high-severity fire had lasting effects on fungal communities, areas of moderate-severity fire had comparable fungal composition as unburned areas, consistent with previous studies (Jonsson et al., 1999; Korb et al., 2003; Curlevski et al., 2011; Southworth et al., 2011). These results suggest that EM fungi are mostly resilient after low-moderate severity fire. The natural fire regime for SW ponderosa pine forests is characterized by mostly frequent, low-moderate-severity fires (Covington and Moore, 1994; Fulé et al., 1997), and fungal communities have likely evolved within this fire-prone forest (Carlsson et al., 2014; Glassman et al., 2016). Moderate-severity plots had a different sporocarp and EM community composition, higher dispersion, and a large EM species pool colonizing ponderosa pine seedlings compared to the interior high-severity burn plots. Our findings stress that fungal communities may be resilient after moderate-severity fire, but large patches of high-severity fire may limit fungal recovery, even 13 years

post-fire.

4.5. Implications and research needs

While we did not find that high-severity fires limited saprotrophic sporocarps or EM colonization rates and richness, we did find that large patches of high-severity fire could have long-term consequences for EM sporocarp communities and EM root tip species pools, which may influence ecosystem resiliency and forest productivity. In contrast, the moderate-severity burn sites from our study had fungal communities comparable to the unburned areas, which is promising for management that includes thinning and prescribed burning with the goal of reducing the potential for high-severity fires (Hart et al., 2018). Managers may want to retain some large branches and logs in high-severity burn patches because others have shown they encourage both regeneration and EM and saprotrophic fungi (Sánchez Meador and Moore, 2010; Rajala et al., 2011). Similarly, we observed most post-fire pine regeneration and fruiting sporocarps near logs in the high-severity burn areas in our study. Also, we did not find evidence that reduced root tip EM species in the high-severity interior plots affected seedling growth; seedling growth may be driven more by nurse objects, such as fallen logs, as well as light availability or soil conditions (Pearson, 1950; Owen, 2019). Finally, managers may want to prioritize the protection of surviving trees within or surrounding large burn patches to conserve future pine seed and EM sources (Peay et al., 2010; Stephens et al., 2018). Our study gives important insights on both above- and below-ground fungal communities in large high-severity burn patches, including those >200 m from surviving EM-host trees, but it also had some limitations. Limitations to our study include the exclusion of some early spring and belowground fruiting species from our assessment and limited temporal and spatial sampling to a single fire. More research is needed to fully understand the long-term effects of severe fire on fungal communities and their role in post-fire recovery.

There are some gaps in our understanding of the effects of fire on fungal communities and the relationship between EM fungi and ponderosa pines. First, more studies are needed on how fire affects saprotrophic fungi because they are an understudied functional group in most forest ecosystems (reviewed in McMullan-Fisher et al., 2011). Future studies could include approaches along with sporocarp surveys to determine if saprotrophs are present after high-severity fires (e.g. culturing, see Kurth et al., 2013; or HTS techniques, see Nilsson et al., 2019). Second, more research is needed on understanding the benefits of EM to ponderosa pine. Most evidence of mycorrhizal influence on ponderosa pine growth or survival come from early greenhouse experiments (Riffle and Tinus, 1982; Steinfeld et al., 2003; Barroetaveña et al., 2016), but there is still uncertainty about the relative benefits or costs of EM fungi for regenerating seedlings (Smith and Read, 2008; Smith et al., 2009). Additionally, we need a better understanding of “fire-adapted” EM species and if they are functionally similar to other EM species, and if post-fire missing species are important to pine recovery and survival. Species of EM fungi missing after *P. edulis* mortality were important to *P. edulis* seedling growth in SW forests near our study sites (Mueller et al., 2019). Pine genotype and drought-tolerant EM species may play a role in recovery in future climates (Gehring et al., 2017; Patterson et al., 2019).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.107616>.

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