Fires of differing intensities rapidly select distinct soil fungal communities in a Northwest US ponderosa pine forest ecosystem

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ABSTRACT

Environmental change and long-term fire management in the western United States have created conditions that facilitate high-intensity burn areas in forested systems. Such burns may have dramatic effects on the soil microbial communities. In this study, we utilized experimental infrastructure in the Pringle Falls Experimental Forest in Oregon, where ten pairs of sites were assigned to either high burn (HB) or low burn (LB) intensity treatments to examine fungal community responses. In these treatments, understory shrubs and logging debris were masticated and broadcast burned (LB) or piled logs were fully combusted (HB) in a paired design. The burn treatments generated soil temperatures of ∼100 °C (LB) or up to 700 °C (HB) at the soil surface. We sampled soils (0–10 cm) one week before and three weeks after ignition and Illumina MiSeq-analyzed fungal Internal Transcribed Spacer 1 (ITS1) PCR-amplicons to deeply dissect the fungal communities. Our data indicate dramatic and rapid responses in community diversity and evenness in the HB treatment, with similar responses, but to a lesser degree, in the LB treatment. Nonmetric Multidimensional Scaling (NMS) ordinations and analyses of taxon frequencies reveal a substantial community turnover and corresponding replacement of the dominant basidiomycetes by ascomycetes in the HB treatment. Similar trends were visible, but weaker in the LB treatments. These coarse-level taxonomic responses were attributable to a few fire-responsive fungi, particularly Operational Taxonomic Units (OTUs) assigned to *Pyronema* sp. and *Morchella* sp., whose frequencies increased more than 100-fold following the HB treatment. Our study highlights the strong and rapid fungal fire responses and differences among fires of different intensities. As the high intensity fires – such as those represented here by the HB treatment – tend to be spatially confined and limited in scale, we emphasize their potential to generate distinct patches that may substantially contribute to beta diversity on small scales. Further, these data lead to questions about fungal community recovery (return to community state preceding the fire) and the importance of patch dynamics following a fire as well as function of post-fire communities and ecosystem services that they may provide.

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1. Introduction

Fires are a significant disturbance in forested ecosystems (Cairney and Bastias, 2007) and burn annually an average of ∼40,000 km² in North America (Giglio et al., 2006) and ∼2000 km² in Europe (Schelhaas et al., 2003). There is a trend of increased fire frequency and intensity that has been predicted to escalate as a result of warmer and drier climatic conditions in the future (Balshi et al., 2009; Flannigan et al., 2009; Pechony and Shindell, 2010) and these changes are already becoming evident in the Western United States (Miller et al., 2009; Westerling

et al., 2006). Additionally, extended periods of fire suppression combined with limited thinning management may further exaggerate the probability of intense, stand-replacing wildfires. More intense fires that include intensely burned areas or areas with more abundant intensely burned patches as a result of whole downed log combustion are also likely to increase.

Although wildfires may represent one of the most widespread and potentially destructive disturbances in forested ecosystems, low-intensity fires also are used in forest management to reduce fuel loads, remove fire-sensitive vegetation, and release nutrients bound in litter (Waldrop et al., 1992; Glitzenstein et al., 1995; Harden et al., 2003; Certini, 2005; Callaham et al., 2012). Areas that burn with greater intensity inhibit re-invading vegetation and persist "weed free" longer than lightly burned areas (Hebel et al.,

2009), thus facilitating conifer establishment desired by silviculture (Cooper, 1960, 1961; White, 1985). In contrast to this potential benefit, high intensity fires may degrade plant seed and fungal propagule banks as well as alter soil nutrient and water availability, thus affecting post-fire community re-establishment above- and below-ground (Rowe, 1983; Amaranthus and Trappe, 1993; Bond and van Wilgen, 1996; Cairney and Bastias, 2007). In addition, high intensity soil heating volatilizes soil nutrients and causes soil organism mortality (Neary et al., 1999) including beneficial root-associated mycorrhizal fungi that may be particularly sensitive to fire (Dahlberg et al., 2001; Cairney and Bastias, 2007; Holden et al., 2013). Fire disturbance affects soil microbial and fungal communities directly through removal of fire-sensitive taxa from the propagule pools (Oliver et al., 2015b), and indirectly through plant mediated responses, such as changes in the flow of recent photosynthates to below-ground pools, or shifts in soil chemistry (*e.g.*, Neary et al., 1999; Certini, 2005). As a result, fire disturbances often lead to a selection for communities enriched in fire adapted – or phoenicoid (Carpenter and Trappe, 1985) – fungi that rapidly respond to heat stimulus (Adamczyk et al., 2012) and produce abundant fruiting bodies (Adamczyk et al., 2012) or mycelia (Bettucci and Alonso, 1995; Chen and Cairney, 2002).

Fire intensities vary at the landscape level as a result of different environmental conditions such as landscape position, local weather, season of the fire, fuel load, and soil moisture (Certini, 2005; Glass et al., 2008). Fires also produce heterogeneous microsite mosaics, whose abiotic and biotic properties are a result of burn intensity at small scales (Cairney and Bastias, 2007). Whereas rapidly moving surface fires may not generate lethal temperatures in the soil, as suggested by mycorrhizal colonization soon after fire (Horton et al., 1998; Baar et al., 1999; Korb et al., 2003), soil temperatures that far exceed the lethal threshold for fine roots and most soil organisms can be generated beneath burning slash piles (Massman and Frank, 2004), masticated fuels (Busse et al., 2010), or downed wood and logs (Monsanto and Agee, 2008). Large soil temperature changes during heating volatilize soil C and nutrients, cause mortality of soil microbes, and may shift species composition (Bååth et al., 1995; Pietikäinen et al., 2000; Knicker, 2007; Bormann et al., 2008; Hebel et al., 2009; Brown et al., 2013; Oliver et al., 2015b). For example, Korb et al. (2004) reported an 18%, 20%, and 9% reduction in soil C, N, and P, respectively, inside intensely burned slash pile scars in a ponderosa pine forest in Arizona, compared to the soil outside the burn scars. Hebel et al. (2009) reported even greater nutrient losses (71%, 69%, and 71% less total soil C, N, and plant available P, respectively) under combusted logs compared to less severely burned soil. Such dramatic changes in soil nutrients are likely coupled with shifts in microbial communities.

Meta-analyses (Holden and Treseder, 2013) estimate that soil microbial biomass declines on average ~30% following fires. These meta-analyses, however, found few studies to evaluate soil microbial community responses to varying fire intensities. As a result, they concluded that there is an urgent need for deeper community analyses that identify fire-responsive and fire-tolerant taxa – or those that establish soon after fire. Further, it is important to understand what are the impacts of fire intensity – characterized either by the temperatures that they generate or duration of the high temperatures – on the communities and their responses to fire. The community responses tend to be more visible and more extreme after high intensity burning (Jiménez Esquilín et al., 2007; Hebel et al., 2009). Many studies have evaluated microbial biomass responses to fire, but studies specifically targeting fungal communities and their compositional responses to fire are few (Cairney and Bastias, 2007; Holden and Treseder, 2013). As a result,

these authors call for detailed fungal community analyses in the context of fire disturbance.

In this study, we utilized an experimental infrastructure in the Pringle Falls Experimental Forest in Oregon, wherein ten pairs of sites were assigned to either high burn (HB) or low burn (LB) intensity treatments to examine fungal community responses to high and low intensity fires. We acquired samples before and three weeks after ignition to explicitly evaluate how the fungal community richness, diversity and composition changed following the fire. Further, we aimed to identify components of the fungal community that respond positively to fire and increase in their frequency following the burn. Whereas high intensity burning may decimate the soil-inhabiting microbial communities, areas of high intensity are often spatially confined and may provide open niche space for establishment of ruderal taxa that benefit from this competitive release (Adamczyk et al., 2012) or select the fire-dependent, phoenicoid fungi (Carpenter and Trappe, 1985), whose propagules may be strongly stimulated by soil heating (Monti, 1992; Kipfer et al., 2010; Simonovicova et al., 2014). To follow immediate fire responses of soil fungi, we compared communities, their richness, diversity and composition before and after burning as well as between sites that had been exposed to high or low intensity burning.

2. Materials and methods

2.1. Study site

We utilized a research infrastructure established within the 1430 ha Lookout Mountain Unit (43°42′N, 121°37′W) of the Pringle Falls Experimental Forest in central Oregon located in the Deschutes National Forest ~48 km southwest of Bend, Oregon. The soils are classified as Xeric Vitricryands in the La Pine Soil Series and consist of well-drained, loamy, coarse sands combined with volcanic ash deposits from the eruption of Mount Mazama ~7000 years ago. Winters are cold and summers are hot and dry resulting in average annual temperatures of about 6.4 °C. The precipitation typically occurs as winter snow and averages 519 mm annually (Youngblood et al., 2004).

This fire intensity study was conducted within a southeast-facing, 199 ha prescribed burn area at an elevation of ~1372 m. The stand, dominated by ponderosa pine (*Pinus ponderosa* Douglas ex. Lawson), originated largely following a stand-replacing forest fire in 1845. A hundred years of fire suppression and exclusion combined with limited low thinning management ~40 years ago has led to large areas of closed-canopy, high density stands that have a high probability of mountain and western pine beetle outbreaks and/or additional stand-replacing wildfires. Following a summer thinning in 2011, the non-commercial material and brush (understory of bitterbrush (*Purshia tridentata* Pursh) and snowbrush Ceanothus (*Ceanothus velutinus* Dougl. Ex Hook)) were masticated in 2012 using a Takeuchi TL 150 rubber track loader (Takeuchi Manufacturing, Pendergrass, GA, USA) with a Fecon mulcher head (Fecon, Lebanon, OH, USA).

2.2. Burn treatments

The high intensity burn (HB) treatments were created by the complete combustion of "mega-logs" (~1.5–2 m wide, 8–10 m long, 1 m high) as described in Smith et al. (in press). Briefly, timber from the 2011 harvest was used to construct "mega-logs" that approximate the footprint and volume of large downed logs by stacking logs and placing them in parallel for maximal soil contact and minimal airspace. These mega-logs were covered in plastic and

left to cure for two years – until spring 2013, after which they had a decay class 1 or 2 (low decay, bark and twigs intact; Maser et al., 1979). Logistics dictated the mega-log placement in the landscape; the necessity of areas accessible with log-lifting machinery and available nearby logs resulted in a non-random placement.

In spring 2013, ten mega-logs meeting the size criteria, tight stacking of logs to minimize airspace and bottom logs in contact with soil were selected for the HB treatment. Adjacent to each mega-log and ~20 m from its center, we established 2 m wide and 10 m long low intensity burn (LB) treatments on which the existing fuel was broadcast burned at the time of mega-log combustion as described in Cowan (2015). The United States Department of Agriculture (USDA) Forest Service (FS) Bend-Fort Rock Ranger District prescribe-burned the site on May 14th, 2013. Mega-logs and the surrounding forest floor were ignited using drip torches and fire accelerant (Heat Source Slash Burner, Wildfire Environmental Inc., Lachine, Canada). Weather conditions on the day of burn were light W to NW winds, clear skies, 12–19 °C (dry bulb), and 25–40% relative humidity. Under those conditions, 10 and 100 h fuels were the primary carriers of the fire. Flame lengths were 0.6–1.8 m with a 12–18 m flame zone depth.

2.3. Soil sampling

We sampled the ten, paired HB and LB treatment plots five days before the ignition. We returned to the sites three weeks after ignition to sample each of the treatment plots. After removing the O horizon (where present – the HB treatments never had O horizons post-fire), one core of mineral soil (1–10 cm) was sampled with a 6.35 cm (diam.) impact-coring device with 10 cm liners (AMS Inc., American Falls, Idaho). Soil samples were placed in plastic ziplock bags and transported on ice until cold room storage at 4 °C. A subsample for molecular analyses was transferred into a 15 ml Falcon tube (Corning Inc., Corning, New York) and stored at −20 °C.

2.4. DNA extraction, PCR amplification, and sequencing

Total genomic DNA was extracted from ~0.25 g subsamples using PowerSoil DNA Isolation Kit (MoBio, Carlsbad, California) following the manufacturer's instructions and stored at −20 °C until PCR amplification. The DNA was quantitated with an ND1000 spectrophotometer (NanoDrop Technologies, Wilmington, Delaware) and standardized to 25 ng/μl for PCR amplification of the Internal Transcribed Spacer (ITS1) region of the ribosomal RNA gene cluster. The ITS1 region was chosen because it is highly variable and optimal for the shorter reads available with the paired-end Illumina MiSeq. The amplicons were generated with the forward primer ITS1F (5′ – CTTGGTCATTTAGAGGAAGTAA – 3′; Gardes and Bruns, 1993) and reverse primer ITS2 (5′ – GCTGCGTTCTTCATC-GATGC – 3′; White et al., 1990). All PCR reactions were performed in triplicate 20 μl reaction volumes with the following amounts/-concentrations: 40 ng DNA template (1.6 μl), 200 μM dNTPs, 1 μM of both forward (ITS1f) and reverse (ITS2) primers, 2 μl 10× of buffer containing 3.5 mM $MgCl_2$, 0.5% Bovine Serum Albumin (BSA), 11.22 μl molecular biology grade water, and 0.4 units (0.08 μl) of Platinum Taq DNA polymerase (Invitrogen, Carlsbad, CA). PCR cycling parameters included an initial denaturing at 94 °C for 3 min, followed by 30 cycles of denaturing at 94 °C for 45 s, annealing at 50 °C for 1 min and extension at 72 °C for 1 min 30 s, and a final extension at 72 °C for 10 min.

The three technical replicates (120 in total) per experimental unit (40 in total) were cleaned using Zymo Clean & Concentrator system (Zymo Research, Irvine, CA) following the manufacturer's protocol and combined per experimental unit. The cleaned amplicons were quantitated using the Qubit dsDNA high sensitivity assay kit (ThermoFisher Scientific, Grand Island, New York) and the DNA concentrations adjusted to 10 nM for library preparations. The samples were submitted to the Center for Genome Research and Biocomputing at Oregon State University (Corvallis, OR), where Illumina specific adapters and indices were added using a NEBNext® DNA MasterMix (Protocol E6040, New England Biolabs Inc., Ipswich, MA, USA) and sequenced using a MiSeq Reagent Kit v3 (Illumina, San Diego, CA, USA) with 600 cycles. Paired fastq files (BioProject PRJNA325522; BioSamples SAMN05237557 – SAMN05237596) are available in the Sequence Read Archive at NCBI (www.ncbi.nlm.nih.gov).

2.5. Sequence analysis

The sequence data were analyzed using mothur software (v. 1.33.1; Schloss et al., 2009). After initial contig construction, the paired-end read library contained 4,547,868 sequences. The data were screened to remove contigs with any ambiguous bases, any disagreements with PCR primers, sequences shorter than 250 bp, or homopolymers longer than 8 bp (2,186,830 remaining sequences). The sequences were truncated to 250 bp, near identical sequences preclustered to reduce potential sequencing bias (Huse et al., 2008) and screened for chimeras (uchime; Edgar et al., 2011). After quality control and removal of chimeras, the experimental units were subsampled to an equal 8578 sequences. A pairwise distance matrix was calculated and sequences clustered into Operational Taxonomic Units (OTUs) at 97% sequence similarity. Low frequency OTUs (representing ⩽ 10 sequences) that may be PCR and/or sequencing artifacts were removed (Tedersoo et al., 2010; Brown et al., 2015; Oliver et al., 2015a) resulting in a total of 345 OTUs and 337,376 total sequences in the dataset. The 345 OTUs were assigned to taxa using the Naïve Bayesian Classifier at 97% sequence similarity (Wang et al., 2007) and the UNITE taxonomy reference (http://unite.ut.ee/repository.php) as implemented in mothur. We calculated Good's coverage, observed (S_{Obs}) and extrapolated (Chao1) richness, diversity (1-D or compliment of Simpson's diversity index and Shannon's diversity index H′), and evenness (Simpson's equitability or E_D and Shannon's evenness or E_H) using mothur.

2.6. Statistical analyses

Our pre- and post-burn analyses as well as low and high intensity burns were arranged in a strict pairwise design, wherein pre-burn samples were collected within the location of the forthcoming burn and low and high intensity burns were spatially located adjacent for a total ten replicates per each treatment. To be faithful to the error structure dictated by the design, as well as to avoid concerns emerging from non-normality and heteroscedasticity, we chose nonparametric two-tailed Wilcoxon Signed Rank tests for paired samples to test for differences in diversity and richness estimators across treatments to detect any effects of the burns (pre-burn vs. post burn) and across the paired burns of different intensities (low vs. high intensity). It is of note that our non-parametric tests were largely congruent with paired t-tests and, where they differed, the differences were mainly on marginally different treatment effects (data not shown). To also test for potential and unexpected differences between the locations selected for low and high intensity burns, we compared them before the burn. All these analyses were conducted in JMP® (version 10.0.0).

To detect compositional differences in fungal communities across treatments, we first derived a Bray-Curtis distance matrix and compared treatments by permutation-based nonparametric MANOVA (PerMANOVA; Anderson, 2001) in PC-ORD (version 6.19; McCune and Mefford, 2011). To visualize these community

data clouds, we estimated Nonmetric Multidimensional Scaling (NMS) axis scores for two ordination axes that represented 72.9% of the variation to obtain a stress of 12.42. To identify OTUs that may have increased or decreased in frequency after fire, we tested for differences in OTU frequencies in our data set using nonparametric Wilcoxon Ranked Sign tests in JMP®. We also used Indicator Species Analysis (calculated with the method of Dufrene and Legendre (1997) in PC-ORD. As the more conservative Wilcoxon Ranked Sign tests are complementary to the indicator taxon analyses, we only discuss the Wilcoxon Ranked Sign tests here but provide both for comparison in the supplements (Supplementary Table S1).

3. Results

3.1. General fungal community data description

The dataset initially contained 4,547,868 sequences. After quality control, subsampling to equal number of sequences per experimental unit, and removal of a total of 4087 low frequency OTUs ($\leqslant$10 sequences) we included a total of 345 OTUs and 337,376 sequences in the final analyses. Although numerous, the rare OTUs (represented by $\leqslant$10 sequences across the entire data set) accounted for only a minor proportion of the dataset (5744 sequences; 1.7%). Similarly, a small proportion (19,292 sequences; 63 OTUs; 5.7%) of sequences were assigned to Kingdom Fungi but remained unclassified at the phylum level or below. Communities overall were dominated by Basidiomycota (158,486 sequences, 47.0%; 135 OTUs, 36.2%), followed by Ascomycota (104,124 sequences, 30.9%; 112 OTUs, 30.8%) and basal lineages – mainly taxa formerly assigned to Zygomycota (55,474 sequences, 16.4%; 35 OTUs, 16.4%). The communities were strongly dominated by a single OTU (OTU1 with affinity to *Geminibasidium hirsutum*) in Wallemiomycetes representing 80,800 sequences (24.0% of the total). However, burning had a strong impact on the soil-inhabiting fungal communities even at the coarsest of levels of taxonomic hierarchy; we will discuss these responses below. We also provide a complete taxon list with estimates of their abundance before and after the HB and LB treatments as a supplement (Supplemental Table S2).

3.2. Effect of burn intensity on richness and diversity

Overall, Good's coverage (99.7 ± 0.001% across all treatments) indicated a rather complete capture of the common community components. Coverage did not differ between the two fire intensity treatments either before or after burning, but differed or tended to differ between samples collected before and after HB or LB treatments (Table 1). None of the richness or diversity estimators differed ($P \geqslant 0.3223$, Table 1) between the two fire treatments before the fire (Fig. 1, Table 1) indicating their similarity before

the burn treatments. Similarly, the observed and extrapolative richness estimators remained similar after the fire between the two intensities (Fig. 1A and B; Table 1). In contrast to richness, fire affected diversity estimators differently between the two fire treatments: while there was no difference in the Simpson or Shannon diversity estimators before the burns ($P \geqslant 0.8457$), the HB treatment had lower diversity than LB after the fire ($P = 0.0020$) (Fig. 1C and D, Table 1). Evenness estimators derived from these diversity estimators responded correspondingly. While evenness based on either Simpson's D or Shannon's H′ did not differ before the fire ($P \geqslant 0.3223$, Table 1), evenness was lower (-H′/lnJ) or tended to be lower (E_D) in the HB than in the LB treatment (Fig. 1E and F, Table 1) after burning.

The richness, diversity, or evenness estimators responded strongly to burn treatments. Observed (S_{Obs}) and extrapolated richness (Chao1) declined following the HB and LB treatments (Fig. 1A and B, Table 1). The observed richness declined by 47.2% after the HB and 36.1% after the LB treatment. Similarly, diversity declined after both fire intensity treatments (Fig. 1C and D): Simpson's complement declined by 62.2% and 11.9% and Shannon's diversity by 68.8% and 20.2% in HB and LB treatments, respectively. These declines in richness and diversity were mirrored in declines in evenness in the HB treatment but not in the LB treatment (Fig. 1E and F, Table 1). The evenness estimators based on Simpson's diversity declined by 52.1% and based on Shannon's diversity by 63.6% in the HB treatment.

3.3. Effect of burn intensity on soil fungal communities

Soil communities differed among the treatments (PerMANOVA: F = 6.47, P = 0.0002, R² = 0.35). Pairwise comparisons indicated that while the communities did not differ among the treatments before the burns ($t = 1.13$, $P = 0.1734$), fire – both low and high intensity – resulted in a soil fungal community shift (Fig. 2). The LB treatment led to a significant ($t = 1.33$, $P = 0.0296$), yet rather minor, community shift (Fig. 2). In contrast, the HB treatment dramatically altered the community composition ($t = 3.33$, $P = 0.0002$; Fig. 2). Further, the post-fire communities following the HB and LB treatments were distinct from each other ($t = 3.01$, $P = 0.0004$; Fig. 2) suggesting fire intensity dependent effects on soil fungal communities.

3.4. Fire responsive taxa

We combined nonparametric two-tailed Wilcoxon Ranked Sign tests with indicator taxon analyses to identify OTUs that responded to burning, but present only the more conservative non-parametric paired sample tests here (see Supplemental Table S1 for both analyses). Only two frequent OTUs (4 – *Pyronema domesticum*; 66 – *Morchella sextelata*) among the 43 that occurred in counts greater than 1000 (>0.3% of the sequences included in the final analyses) across the dataset increased in relative abundance after

Table 1

Good's coverage, observed (S_{Obs}) and extrapolated (Chao1) richness, diversity [Simpson's complement (1-D), Shannon's index (H′)], and evenness [Simpson's equitabililty (E_D), Shannon's evenness ($-$H′/J)] (mean ± standard deviation). The latter four columns provide pairwise tests for before (pre-) and after (post-) the fire manipulation in the high intensity (HB) or low intensity (LB) burns. |S| is the test variable for two-tailed Wilcoxon Ranked Sign test with it's associated P-value.

Parameter	HB Pre	HB Post	LB Pre	LB Post	HB Pre vs. Post |S|[P]	LB Pre vs. Post |S|[P]	Pre HB vs. LB |S|[P]	Post HB vs. LB |S|[P]
Good's coverage	0.998 ± 0.001	0.998 ± 0.001	0.997 ± 0.001	0.998 ± 0.001	|S| = 18.50[0.0645]	|S| = 27.50[0.0020]	|S| = 10.50[0.3223]	|S| = 2.50[0.8457]
Richness (S_{Obs})	80.46 ± 16.56	42.46 ± 22.92	87.32 ± 14.75	55.84 ± 13.78	|S| = 25.50[0.0059]	|S| = 26.50[0.0039]	|S| = 10.50[0.3223]	|S| = 13.50[0.1934]
Richness (Chao1)	104.28 ± 13.42	56.51 ± 24.54	111.40 ± 21.23	74.81 ± 20.48	|S| = 26.50[0.0039]	|S| = 26.50[0.0039]	|S| = 9.50[0.3750]	|S| = 14.50[0.1602]
Simpson Diversity (1-D)	0.84 ± 0.11	0.32 ± 0.18	0.83 ± 0.07	0.73 ± 0.09	|S| = 27.50[0.0020]	|S| = 21.50[0.0273]	|S| = 2.50[0.8457]	|S| = 27.50[0.0020]
Simpson Evenness (E_D)	0.10 ± 0.04	0.05 ± 0.03	0.08 ± 0.03	0.08 ± 0.03	|S| = 26.50[0.0039]	|S| = 0.50[1.0000]	|S| = 10.50[0.3223]	|S| = 17.50[0.0840]
Shannon Diversity (H′)	2.53 ± 0.58	0.79 ± 0.47	2.46 ± 0.40	1.96 ± 0.34	|S| = 27.50[0.0020]	|S| = 22.50[0.0195]	|S| = 1.50[0.9219]	|S| = 27.50[0.0020]
Shannon Evenness ($-$H′/lnJ)	0.58 ± 0.11	0.21 ± 0.10	0.55 ± 0.08	0.49 ± 0.07	|S| = 27.50[0.0020]	|S| = 14.50[0.1602]	|S| = 5.50[0.6250]	|S| = 27.50[0.0020]
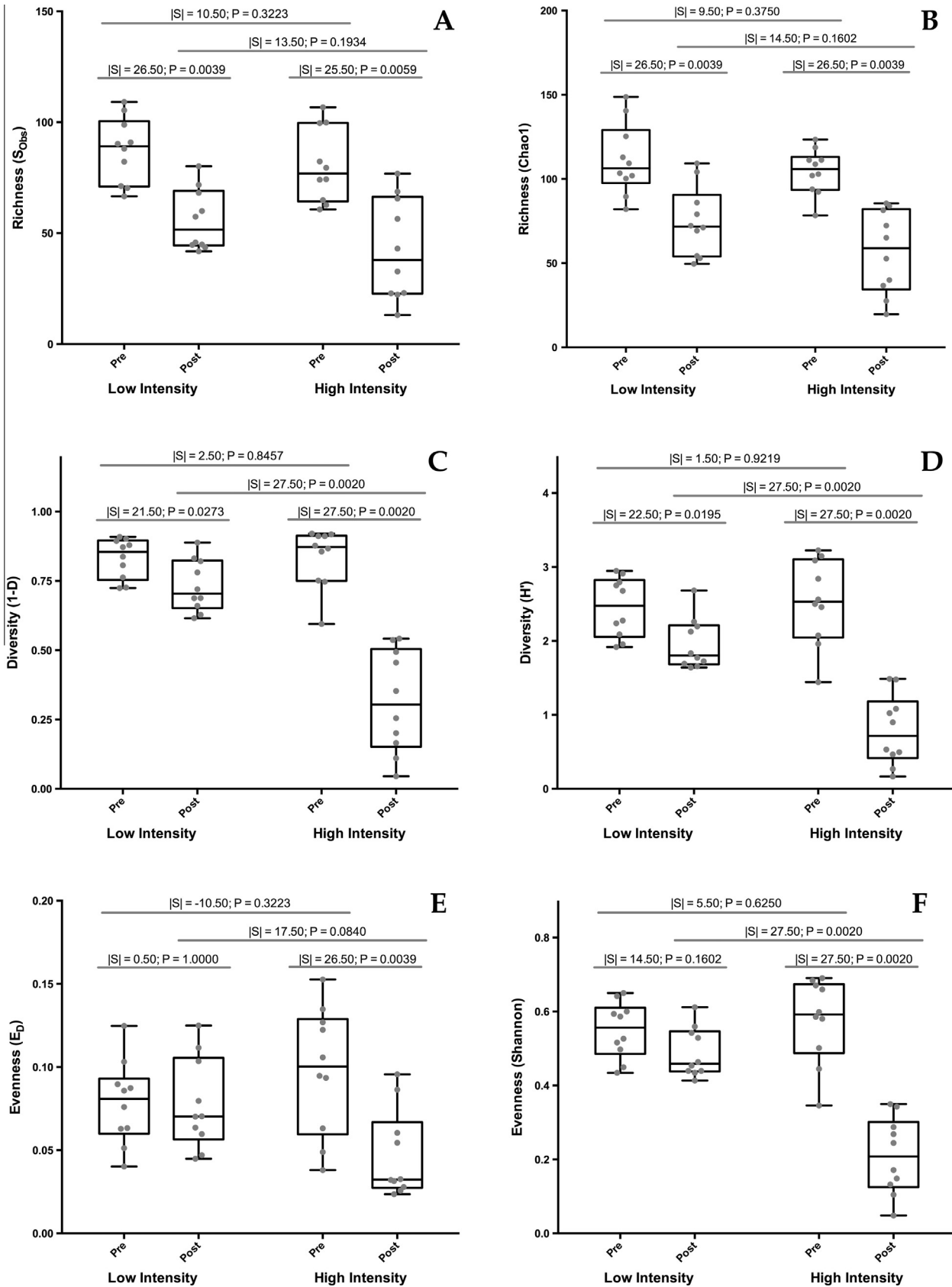
Fig. 1. Observed (S_{Obs}, A) and extrapolated richness (Chao 1, B), diversity (complement of Simpson's diversity – 1-D, C; Shannon's diversity – H′, D), and evenness (Simpson's equitability E_D, E; Shannon's evenness, F) before and after high or low intensity fire treatments. Also included are results of non-parametric pairwise two-tailed Wilcoxon Ranked Sign tests (test variable |S| with its corresponding probability) testing for differences among the four treatment combinations. The data indicate that both low and high intensity fires lead to a decline in richness and diversity, whereas only high intensity fires have a strong effect on the community evenness.
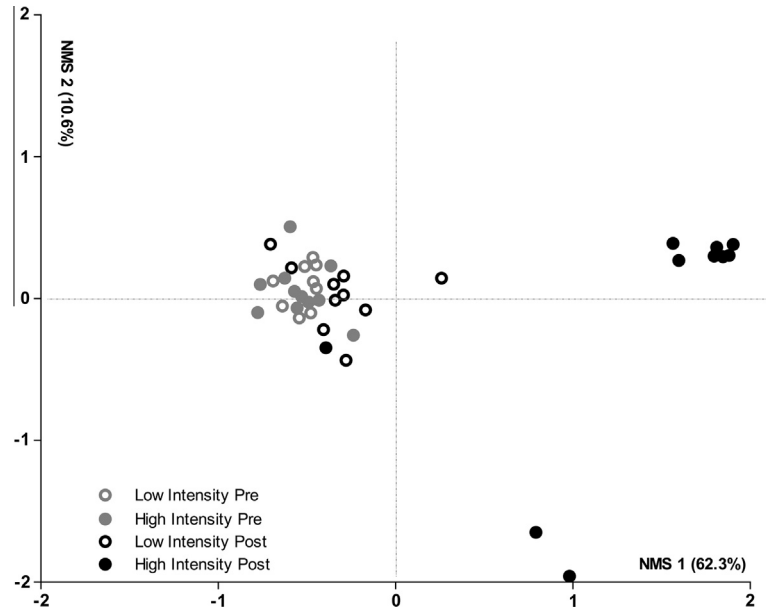
Fig. 2. Non-metric Multidimensional Scaling (NMS) ordination of areas before (gray symbols) and after (black symbols) low (open symbols) or high (closed symbols) intensity burning. The NMS ordination was optimally resolved on two axes (stress = 12.42) that represented 62.3% and 10.6% of the variability for a total of 72.9%. Permutation-based MANOVA indicated significantly different communities ($F = 6.47$, $P = 0.0002$) across the four treatment combinations. Subsequent pairwise comparisons indicated that communities did not differ before the fire treatments ($t = 1.13$, $P = 0.1734$) and that pre- and post-fire communities differed after both low ($t = 1.33$, $P = 0.0296$) and high ($t = 3.33$, $P = 0.0002$) intensity fire treatments. The post-fire communities after low and high intensity fire treatment also differed from each other ($t = 3.01$, $P = 0.0004$).

the HB treatment, suggesting that they benefitted from the fire (Fig. 3). An additional three, less frequent OTUs (6 – *Mucor circinelloides*; 12 – unclassified fungus; 60 – *Fusarium solani*) among the 293 that were detected in the HB treatment increased in frequency. Similarly, the LB treatment favored few – total of four – frequent OTUs (4 – *Pyronema domesticum*; 14 – unknown Pezizomycete; 66 – *Morchella sextelata*; 68 – *Trichophaea abundans*). Two additional low frequency OTUs increased in frequency after the LB

treatment (6 – *Mucor circinelloides*; 115 – uncultured fungus). It is notable that two frequent (4 and 66) and one less frequent OTU (6) that increased following the fire overlapped between the two intensity treatments (Supplemental Table S1).

We also observed a total of 32 OTUs that declined in relative abundance following the HB treatment. Approximately half of these (a total of fifteen) were among the 43 most frequent OTUs (Fig. 3A) indicating a shift from and decline in the pre-fire
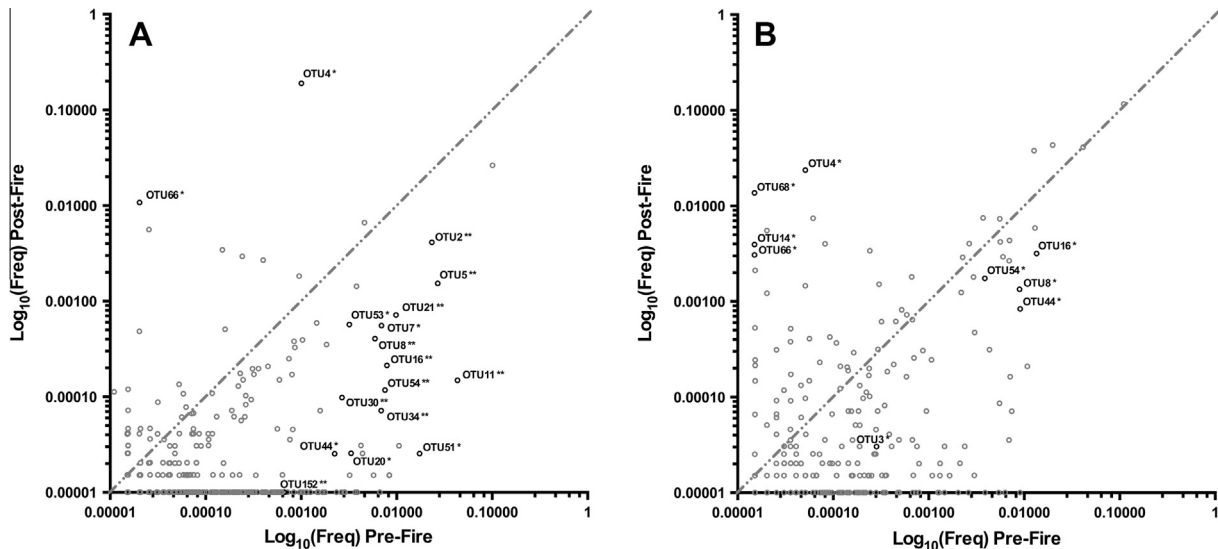
Fig. 3. Operational Taxonomic Unit (OTU) frequencies (log₁₀-transformed) before (x-axis) and after (y-axis) a high (A) or low (B) intensity fire. The dashed line indicates equal frequencies before and after fire; OTUs above the line were more frequent in the post-fire communities, those below the line were more frequent in the pre-fire communities. OTUs with counts >1000 identified by Wilcoxon Ranked Sign tests as fire responsive are highlighted by black symbols. Asterisks following the OTU identifier indicate level of significance (* – $0.01 \leqslant P < 0.05$; ** – $0.001 \leqslant P < 0.01$). The responsive OTUs identified in the figures are 2 – *Umbelopsis nana*; 3 – *Mortierella* sp.; 4 – *Pyronema domesticum*; 5 – *Paratritirachium curvibasidium*; 7 – *Sagenomella diversispora*; 8 – uncultured *Cladophialophora*; 11 – *Umbelopsis* sp.; 14 – unknown Pezizomycete; 16 – *Phialocephala europea*; 20 – *Mortierella marburgensis*; 21 – Fungal sp.; 30 – *Umbelopsis* sp.; 34 – Microbotryomycetes sp.; 44 – *Mortierella* sp.; 47 – *Mortierella* cf. *hyalina*; 51 – unclassified; 53 – *Tremellomyces* sp.; 54 – *Wilcoxina rehmii*; 66 – *Morchella sextelata*; 68 – *Trichophaea abundans*; 152 – *Rhizopogon vulgaris*. Complete list of the responsive OTUs is available in Supplemental Table 1.

dominants. Similarly to the community-wide NMS analyses, the responses to LB treatment were more subtle: four frequent (OTUs that occurred in counts greater than 1000 in our data set) and an additional sixteen low frequency OTUs declined in frequency compared to the pre-burn conditions (Fig. 3B, Supplemental Table S1). Three high frequency OTUs (8 – uncultured *Cladophialophora*; 16 – *Phialocephala europea*; 44 – *Mortierella* sp.) and five low frequency OTUs (47 – *Mortierella* cf. *hyalina*; 72 – unculturable fungus; 121 – unculturable fungus; 127 – unculturable ascomycete; 140 – *Cladophialophora minutissima*) responded negatively in both HB and LB treatments. In general, OTUs that declined in frequency following the fire included soil-inhabiting Zygomycetes (OTUs with affinities to the genus *Mortierella* or family Umbelopsidaceae), uncultured or unclassified fungi, putatively mycorrhizal OTUs (*e.g.*, OTUs in genera *Inocybe*, *Rhizopogon*, and *Tomentella*), and a variety of likely saprobic ascomycetes (Supplemental Table S1).

The fire responsive taxa led to a community turnover across multiple levels of taxonomic hierarchy. Although the Basidiomycetes dominated the communities in the entire dataset, the burn treatments resulted in substantial shifts in the communities even on the coarsest levels of taxonomy, especially following the HB treatment. In the samples collected before the HB treatment, Basidiomycetes and fungi assigned to the former phylum Zygomycota composed 59.4 ± 10.9% and 23.7 ± 11.3% of the communities, respectively. However, the proportion of Basidiomycetes declined over fivefold (9.3 ± 22.2% after the high intensity burns) and Zygomycete frequency declined approximately ten-fold (2.3 ± 2.1% after the high intensity burns) (Wilcoxon Ranked Sign test for paired samples: Basidiomycota: S = 26.50, $P = 0.0039$; Zygomycota: S = 27.50, $P = 0.0020$). Ascomycetes (13.3 ± 7.3% in the high intensity samples before burns) largely replaced these two groups and increased in frequency (S = −24.50, P = 0.0098) resulting in strongly Ascomycete-dominated communities (75.0 ± 35.2%) after the HB treatment. Similar responses were not as obvious in the LB treatments. Yet, Basidiomycetes composed 70.1 ± 10.4% of the communities in the samples destined for LB treatment and declined to 49.2 ± 19.2% after the treatment (pre- vs. post-burn: S = 22.50, P = 0.0195). While the Ascomycete frequency increased from 12.5 ± 4.6 to 22.2 ± 17.4% following the LB treatment, these responses were not supported by our non-parametric Wilcoxon Ranked Sign tests (pre- vs. post-burn: S = −10.50, P = 0.3223). The other phyla – including the unclassified fungi – did not change in frequency following the LB treatment. The observed community shifts were strongly driven by a few OTUs that increased dramatically in frequency following the fire, perhaps best exemplified by OTU4 (affinity to *Pyronema domesticum*) and OTU66 (*Morchella sextelata*), whose mean frequencies increased more than 250- and 1000-fold after the HB treatment, respectively. Both were rare prior to the burn (OTU4: 0.2 ± 0.7%; OTU66: $0.2 \times 10^{-6} \pm 0.7 \times 10^{-6}\%$ of sequences), but dominated the communities after the HB treatment (OTU4: 61.0 ± 42.7%; OTU66: 2.6 ± 3.0% of sequences), suggesting most likely mycelial expansion into the intensely burned soil substrates. Both also increased following the LB treatment but to a lesser extent (OTU4: 6.5 ± 16.4%; OTU66: 0.9 ± 1.4% of sequences).

4. Discussion

Forest fires are a common large-scale disturbance (Giglio et al., 2006; Schelhaas et al., 2003) and fire frequency and intensity are likely increasing (Balshi et al., 2009; Flannigan et al., 2009; Pechony and Shindell, 2010). Thus, it is important to understand the soil community fire responses and the differences in these responses to fires of differing intensities. We evaluated community responses to low and high intensity fire and compared soil fungal communities before and after burning in a well replicated and rigidly designed experiment in the Pringle Falls Experimental Forest in Oregon. Our data indicate strong and rapid community turnover largely attributable to a few post-fire ascomycetes that within days strongly dominate the post-fire communities after replacing the formerly dominating basidiomycetes. This large contribution of the few strong dominants also drove declines in evenness and diversity, whereas the richness estimators tended to be less sensitive, perhaps because of the arrival of propagules that can contribute to a large number of low frequency taxa (Chen and Cairney, 2002). Although both high and low intensity fire treatments resulted in detectable community shifts and shared post-fire dominants (*i.e.,* species of *Morchella* and *Pyronema*), the fire responses were more distinct in the high intensity treatment that resulted in communities confined to small landscape patches that included distinct fungal communities and that likely contribute to biological diversity through generation of unique niches for soil organisms.

Soil microorganisms are essential to nutrient cycling and plant health. Yet, only a limited number of studies have dissected their community responses to a fire disturbance in great detail (Dahlberg et al., 2001; Cairney and Bastias, 2007; Holden and Treseder, 2013). Our data indicate distinct fungal community responses and are consistent with results of many others (Johnson and Curtis, 2001; Treseder et al., 2004; Mack et al., 2008; Amiro et al., 2010; Goulden et al., 2011; Brown et al., 2013; Holden et al., 2013; Rincón et al., 2014; Oliver et al., 2015b) and conclusions of broader meta-analyses (Dooley and Treseder, 2012; Holden and Treseder, 2013). Intense fires tend to have greater impacts and longer lasting effects than low intensity fires (Dahlberg et al., 2001; Carter and Foster, 2004; Certini, 2005). Indeed, microbial community responses tend to be more visible and extreme after intense burning (Jiménez Esquilín et al., 2007; Hebel et al., 2009). Our data corroborate this pattern and showed distinct soil fungal community shifts towards a few strong post-fire dominants after a high intensity burning. Similar responses were also detectable following a low intensity fire that lead to increase in the same common dominant post-fire ascomycetes, albeit to a far lesser degree. Both low and high intensity fire treatments highlighted the extremely rapid response of the phoenicoid fungi – in our case just three weeks following the fire.

Recent studies suggest shifts towards greater fire intensity and frequency in the Western United States (Westerling et al., 2006; Miller et al., 2009). As a result, it is necessary to understand the soil community fire responses and the differences in these responses to fires of differing intensities. This is important in the context of wildfires, but also in the context of prescribed fires used to manage fuel loads and vegetation (Waldrop et al., 1992; Glitzenstein et al., 1995; Harden et al., 2003; Certini, 2005; Callaham et al., 2012). The prescribed burning often aims for controllable low fire intensities, whereas wildfires frequently maintain longer durations and higher intensities and may include areas with completely combusted logs such as those mimicked here by the mega-logs. Although differences in fire intensities are important, as indicated by our data, the mosaic of patches that incorporates areas of high and low fire intensities may be even more so. Our fire responsive taxa, particularly the post-fire dominants, were often present only in low frequencies or even below detection level before burning (Supplemental Table S2). The high intensity fires favor few low frequency taxa that contribute to biological diversity in the scale of these landscape patches. We consider it likely that the mycelia of these post-fire dominants rapidly expand from either deeper in the soil profile or from adjacent areas that are at the margins of the intense burns with lethal temperatures. It is important to note that the HB treatments implemented here maintained temperatures higher than 60 °C for more than six hours and a peak temperatures of up to over 700 °C on the surface and ~100 °C at 10 cm depth (Smith et al., in press). These temperatures combined

with their duration are likely to strongly select for the fire adapted phoenicoid fungi.

Post-fire ascomycetes – particularly members of the order Pezizales – and their rapid fruiting that may take place as soon as in a few weeks and continue for up to two years post-fire have been previously documented in great detail (*e.g.*, Petersen, 1970; Wicklow, 1975; Warcup, 1990; Fujimura et al., 2005; Adamczyk et al., 2012). Our data corroborated these findings, but also emphasize the rapid response. The post-fire fungi have been recorded in studies focusing on fires at landscape levels (*e.g.*, Friedrich, 2001; Dahlberg, 2002; Rincón et al., 2014) as well as in smaller scales such as in campfire sites (Adamczyk et al., 2012). Our high throughput sequencing data corroborated these observations: conservative nonparametric tests identified taxa in the families Pyronemataceae and Morchellaceae (both Pezizales) as being among those whose frequencies increased following burning. Further, our data highlighted the expedient response of the phoenicoid taxa: within three weeks after ignition, these post-fire fungi had established a strong dominance in the soil community, particularly in the areas with high intensity fire. Our field observations were also in concert with laboratory experiments that have found that some species of Pyronemataceae grow in soils gradually heated to >100 °C and that heat-resistant Pyronemataceae appear in soils regularly influenced by the fire (Monti, 1992; Kipfer et al., 2010; Simonovicova et al., 2014). These taxa commonly grow on bare or burned soils and decaying wood debris (Doveri, 2011). While the post-fire fungi are mainly ascomycetes, they also include basidiomycetes and/or basal fungi formerly assigned to Zygomycota (Petersen, 1970; Dahlberg, 2002). Consistent with these observations, our data indicated that some basal fungi – members of the genus *Mucor* – also responded positively to the burning regardless of the fire intensity. Overall, a total of five OTUs increased in frequency following the high intensity burn and six following the low intensity burns.

In addition to these fungi whose frequencies increased following the fires, our data indicated a greater number of taxa that declined post-fire. These taxa included a heterogeneous mix of common soil-inhabiting fungi (including species of Mortierellaceae and Umbeliopsidaceae), common saprobes (*e.g.,* species of *Penicillium*), as well as some putative ectomycorrhizal taxa (*e.g., Rhizopogon* and *Wilcoxina*). It is also notable that the high intensity fire in particular led to the replacement of the formerly dominant basidiomycetous component by the post-fire taxa, suggesting a substantial community turnover following the fire even at the coarsest levels of taxonomy.

Many post-fire fungi can form new mycorrhizal associations soon after a fire (Egger and Paden, 1986; Vrålstad et al., 1998; Dahlberg, 2002; Rincón et al., 2014), whereas saprobic post-fire fungi may mineralize nutrients and stabilize soil moisture (Egger and Paden, 1986). However, it is unlikely that many ectomycorrhizal taxa would have established the strong dominance that we observed just three weeks after the intense burning. Therefore, the functional shifts in the belowground communities may be even more important than the community shifts alone. Sun et al. (2015) combined high throughput sequencing and functional gene arrays (GeoChip; Tu et al., 2014) in a recent fire chronosequence study. Their data suggested that wildfires had community level consequences both on the richness and composition, but also on the function of the soil-inhabiting fungal communities. While our study may clearly indicate community shifts following recent fire disturbance and concomitant shifts in the dominant community constituents as well as community diversity metrics, further studies are mandatory to better understand the functional consequences of these compositional shifts.

Our study clearly identified fire-responsive taxa that rapidly establish distinct post-fire communities, particularly following a high intensity burning. However, it also opens a few additional questions. These include questions about the sources of post-fire communities, the duration of the fire effects, and the time required to return to the pre-disturbance, pre-fire communities, or perhaps the alternate trajectories that may result from fires of different intensities. Very little is known about the sources that establish the distinct post-disturbance communities following fire (but see Bettucci and Alonso, 1995; Taylor and Bruns, 1991; Chen and Cairney, 2002; Buscardo et al., 2010). Post-fire species may have inactive spores present in soil that germinate only after exposure to fire (*e.g.*, Jalaluddin, 1967; El Abyad and Webster, 1968; Taylor and Bruns, 1999; Buscardo et al., 2010), or may establish from airborne propagules (Chen and Cairney, 2002). We speculate that it is most likely a combination of air-borne sources and – to a much larger extent – a rapid mycelial expansion from either buried propagule bank or perimeters of the intensely burned areas that lead to the community turnover resulting from the rapid responses to fire disturbance. These speculations are consistent with our observations of the low frequency of post-fire dominants in the pre-fire communities and the fast establishment of the post-fire community.

In contrast to rapid colonization by the post-fire fungi, return of soil fungal communities to pre-fire states (recovery) may be a slow process. Although the system resistance (capacity to maintain function through change – Pimm, 1984; Tilman and Downing, 1994) to high intensity fires is likely low, the resilience (capacity to recover function following change – Pimm, 1984; Tilman and Downing, 1994) remains an unanswered question. Meta-analysis by Dooley and Treseder (2012) and fire chronosequence study in Alaskan boreal forest ecosystems (Holden et al., 2013) suggest that more than ten years may be required for post-fire community recovery. Even low intensity prescribed fires that shift soil fungal community composition may require extended periods of time for recovery. Oliver et al. (2015b) deeply dissected fungal communities in soils under coniferous stands on the Piedmont of central Georgia (USA) that had been under a long-term prescribed burn regime. They concluded that recovery to a pre-disturbance community state required more than a decade, despite the low intensity fires implemented in the course of the prescribed fire management. If these low intensity prescribed fires lead to communities that remain distinct over several years, it is interesting to hypothesize on the community trajectories that follow intense fires: do the landscape units that experience the intense fire remain in a unique trajectory that distinguishes them from areas that burn simultaneously but at lower intensity, or do both fire intensities converge to a community or system state similar to that preceding the fire disturbance? These trajectories remain an open question, but fire studies similar to ours permit direct comparisons of pre- and post-fire conditions and better understanding the system recovery and community trajectory over longer periods of time.

Acknowledgements

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.2016.07.002.

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