Forest Ecology and Management 544 (2023) 121160

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Distinct fungal and bacterial responses to fire severity and soil depth across a ten-year wildfire chronosequence in beetle-killed lodgepole pine forests

Marcos V. Caiafa[a,*], Amelia R. Nelson[b], Thomas Borch[b,c], Holly K. Roth[c], Timothy S. Fegel[d], Charles C. Rhoades[d], Michael J. Wilkins[b], Sydney I. Glassman[a,*]

[a] *Department of Microbiology and Plant Pathology, University of California Riverside, United States*
[b] *Department of Soil and Crop Sciences, Colorado State University, United States*
[c] *Department of Chemistry, Colorado State University, United States*
[d] *USDA Forest Service, Rocky Mountain Research Station, United States*

ARTICLE INFO

Keywords:
Fire
Rocky Mountains
Pinus contorta
Microbes
qPCR
Illumina MiSeq

ABSTRACT

Lodgepole pine forests are under threat due to wildfires of increasing severity and frequency coupled with tree mortality from insect outbreaks. Soil microbial communities, which drive biogeochemical cycles and partner in mycorrhizal symbiosis with lodgepole pines, play critical roles in the ability of these forests to survive and regenerate in the face of simultaneous global change threats. How soil microbial communities are influenced by fire severity and soil depth and how they recover over time in lodgepole pine forests with existing insect-driven mortality remains an open question. Here, we sampled two soil depths (0–5 and 5–15 cm) and various burn severities across a ten-year wildfire chronosequence in the Southern Rocky Mountains. We used qPCR of 18S and 16S rRNA genes to assess changes in fungal and bacterial abundance and ITS2 and 16S amplicon sequencing to assess fungal and bacterial richness and composition. Our results show that: 1) higher severity fires led to larger reductions of both fungal and bacterial abundance and richness, 2) the impact of fire on fungal and bacterial communities was modulated by soil depth, with more severe impacts in shallower soils 3) both fungal and bacterial communities exhibit a partial recovery of abundance and species richness in older fires, 4) fire severity is the main driver of fungal and bacterial community structure but its effect varied across time, 5) pyrophilous "fire-loving" fungi and bacteria exhibit an increased abundance in burned plots, particularly in recent fires, and 6) symbiotic ectomycorrhizal fungi are particularly hard hit by the compound effect of the beetle-driven tree mortality and wildfires. They exhibit a consistently low abundance and richness in the high severity plots which did not recover over time, and unburned plots have a depauperated ectomycorrhizal community.

1. Introduction

Wildfires are important natural disturbances that drive biodiversity in forested ecosystems worldwide (Bowman et al., 2009; Keeley et al., 2011). Natural wildfire regimes have well-described impacts on soil biogeochemistry (Johnson and Curtis, 2001; Nave et al., 2011) and animal and plant communities (He et al., 2019). Although fires are a natural component of many healthy forests, their size, frequency and severity has increased in recent decades and is predicted to continue increasing with climate change and the growth of wildland-urban interface (Archibald et al., 2013; Stephens et al., 2014; Radeloff et al., 2018). High severity fires cause an increase in erosion (Benavides-Solorio and MacDonald, 2005), soil carbon and nitrogen losses (Pierson et al., 2019), and nutrient and sediment export in stream water (Rhoades et al., 2011). Severe wildfires combined with prior disturbance or post-fire climatic stress can delay ecosystem recovery for many decades (Chambers et al., 2016; Stevens-Rumann et al. 2018) and may cause lasting changes in vegetation types (Parks et al., 2019). Vegetation recovery after fires of unprecedented size and severity is further constrained by dispersal limitation of propagules of both plants and their symbiotic microbial partners (Gill et al., 2022).

Soil microbial communities regulate many biogeochemical processes and are critical to post-fire ecosystem recovery (Fierer, 2017; Crowther et al., 2019; Pérez-Valera et al., 2020). Owing to their symbiotic relation with 80–90% of plant species, and their role in nutrient uptake, mycorrhizal fungi are especially relevant to post-fire forest vegetation

---

* Corresponding authors.
E-mail addresses: marcosvc@ucr.edu (M.V. Caiafa), sydneyg@ucr.edu (S.I. Glassman).

https://doi.org/10.1016/j.foreco.2023.121160
Received 24 February 2023; Received in revised form 30 May 2023; Accepted 1 June 2023

and soil recovery (Smith and Read, 1997; Brundrett and Tedersoo, 2018). Likewise, changes in both soil fungal and bacterial communities affect post-fire organic matter decomposition and nutrient cycling (Semenova-Nelsen et al., 2019; Yang et al. 2020).

The response of soil microbes to wildfire is influenced by fire severity (Holden et al., 2016; Whitman et al. 2019; Nelson et al., 2022), time since fire (Kipfer et al., 2011; Pulido-Chavez et al., 2021), interactions with host mortality from pathogens (Metz et al., 2011), and soil depth, with microbes typically being more impacted in surface soils, which experience hotter temperatures (Qin and Liu, 2021; Barbour et al., 2022). High severity fires reduce microbial biomass (Dooley and Treseder, 2012), richness (Pressler et al., 2019), and alter community composition by promoting pyrophilous fire specialists (Seaver, 1909; Enright et al., 2022; Fox et al., 2022) at the expense of other microbial taxa with less tolerance of post-fire conditions. Studies examining the effect of fire on mycorrhizal fungal richness at the local scale exhibit contrasting results (Taudière et al., 2017). However, wildfires generally reduce root colonization (Dove and Hart, 2017) and change community structure (Glassman et al., 2016; Owen et al., 2019). In the case of severe wildfires, it may take a decade or more for those communities to recover to the pre-fire conditions in Western North America forests (Twieg et al., 2007; Pulido-Chavez et al., 2021) and could take up to two decades to recover after high severity fires in Mediterranean shrublands (Pérez-Valera et al., 2018). Fires also tend to shift fungal composition from Basidiomycota to Ascomycota dominance (Cairney and Bastias, 2007; Semenova-Nelsen et al., 2019) with Ascomycota fungi such as *Pyronema* and *Geopyxis* fruiting rapidly after fires (Fox et al., 2022). Severe wildfires can also affect bacterial communities by reducing biomass and richness and shifting the dominance of Proteobacteria and Acidobacteria and enriching Firmicutes and Actinobacteria (Whitman et al., 2019; Enright et al., 2022; Nelson et al., 2022; Pulido-Chavez et al., 2023). Certain bacterial taxa such as the Actinobacteria *Arthrobacter* and the Proteobacteria *Massilia* increase in abundance after severe wildfires in forest ecosystems (Whitman et al., 2019). Conversely, low severity fires in California grasslands have shown to have no effect on bacterial richness (Glassman et al., 2023) and studies in both grasslands and scrublands indicate that the impact of fire on bacterial communities decrease with depth (Barbour et al., 2022).

Increasing drought and warming temperatures have augmented the frequency and severity of fires across the western United States (Parks et al., 2018), where many forests are dominated by lodgepole pine (*Pinus contorta*) (Lotan and Critchfield, 1990). Insect-driven tree mortality has also become more common with climate change (Anderegg et al., 2022), and lodgepole pine is no exception. Over the last 20 years, lodgepole pines have been subject to infestation by the mountain pine beetle (*Dendroctonus ponderosae*) (Raffa et al., 2008), which can lead to tree mortality of more than 80% (Collins et al., 2011; Diskin et al., 2011; Rhoades et al., 2013).

High tree mortality following pine beetle outbreaks leads to alterations in carbon storage (Kurz et al., 2008), nitrogen cycling (Griffin et al., 2011; Rhoades et al., 2017) and soil microbiomes (Ferrenberg et al., 2014; Treu et al., 2014; Mikkelson et al., 2016; Pec et al., 2017). Symbiotic ectomycorrhizal (ECM) fungi, which form obligate and diverse symbioses with *P. contorta* (Talbot et al., 2014) are particularly sensitive to tree mortality and their abundance and richness are reduced after beetle outbreaks (Treu et al., 2014; Pec et al., 2017). While soil bacterial communities appear to be more resistant to beetle-induced tree mortality than fungi (Ferrenberg et al., 2014), heavily impacted forest (~85% tree mortality) have been shown to have an increased bacterial alpha diversity and significant compositional changes throughout the different infestation phases (Mikkelson et al., 2016). How these already stressed lodgepole pine forests and their associated soil microbiomes will recover after high severity wildfires over time remains an open question. Indeed, a better understanding of microbial community and functional resilience, or recovery over time, in the face of multiple global change stressors is increasingly urgent (Rhoades et al., 2018; Stevens-Rumann et al. 2018; Rillig et al., 2019). The burned, beetle-decimated *P. contorta* forests of Colorado and Wyoming present an opportunity to investigate ecosystem recovery from compound disturbances that are common throughout western North America and many regions of the globe.

Here, we studied how fire severity and soil depth influence the temporal recovery of bacterial and fungal abundance, richness, and composition across a ten-year wildfire chronosequence in lodgepole pine-dominated forests that had previously experienced high mortality due to beetle outbreaks. Using a combination of quantitative PCR of 16S and 18S rRNA genes and Illumina MiSeq of 16S and ITS2 amplicons, we tested whether the magnitude and persistence of post-fire changes in soil microbial abundance, species richness, and composition of both fungi and bacteria are sensitive to fire severity, soil depth, and time, and how this recovery is mediated by beetle-driven tree mortality. We hypothesized that: (1) increasing fire severity will correlate with larger changes in the abundance, richness and composition of microbial communities and the persistence of those changes, (2) the effect of fire severity will be stronger in fungi than bacterial and will be modulated by soil depth, (3) recovery of microbial communities will be affected by the time since pine beetle outbreak when each wildfire happen, (4) wildfires will differentially impact fungal guilds with largest impacts on symbiotic ECM fungi, and (5) wildfires will promote the growth of pyrophilous fungi and bacteria, which will persist during the first years after fire.

2. Methods

2.1. Study area, plot design and soil collection

Sampling was conducted in five lodgepole pine-dominated (*P. contorta*) forests of the Southern Rocky Mountains located in Colorado and Wyoming that burned between 2010 and 2020. Our experimental design consisted in a time-for-space substitution and sites were selected based on time since fire and similarity in stand structure (same co-occuring species, closed canopy, mature forest of ~ 1000 trees/ha) and soils. The fire chronosequence included the Church’s Park (2010), Beaver Creek (2016), Ryan (2018), Badger Creek (2018) and Mullen (2020) fires ranging in elevation from 2612 to 3044 m (Fig. S1, Table S1). Soils are well to excessively drained, loamy Alfisols and Inceptisols (Fletcher, 1981; Alstatt and Miles, 1983; Reckner, 1998). The lodgepole pine-dominated forests we sampled experienced a severe mountain pine beetle outbreak with 75% average overstory tree mortality prior to burning (Kayes and Tinker, 2012; Rhoades et al., 2020). Annual aerial insect detection monitoring and previous local research observed that beetle activity began about 2005 and continued for 3–4 years (Chapman et al., 2012; Rhoades et al., 2013, 2018, 2022; Meddens & Hicke, 2014). Since it is not possible to assign precise stand-level infestation dates we assume that all sites were infested in 2005 and thus had been dead for 5 to 15 years at the time of the wildfires. The outbreak affected large diameter lodgepole pine, but not co-occurring tree species (subalpine fir: *Abies lasiocarpa,* Engelmann spruce: *Picea engelmannii*, quaking aspen: *Populus tremuloides*) or small diameter lodgepole pine (Rhoades et al., 2017).

On 29–30 July 2021, we sampled low and high severity burned areas and adjacent unburned forests at each of the five fires. At each fire site, three or four burn transects were selected within each burn severity class using remotely sensed comparisons of pre- and post-fire greenness, and then field validated with standard indices of soil burn severity. Fire severity classes were assigned based on ground cover, ash color and depth, soil structure, presence of roots, and soil water repellency (Parsons et al., 2010). Along each transect, three 1-m^2 plots were established at 15 m intervals along each transect. After removing O-horizon material (litter and duff), three mineral soil replicates were collected in each plot from the 0–5 cm (“shallower”) and 5–15 cm depths (“deeper”). A total of 288 soil samples were collected (5 wildfires along the chronosequence × 3 severities × 3–4 transects × 2 depths × 3 replicates). Soil samples were collected using a 15 cm long soil corer, then shallower and deeper soil were separated. The soil corer was cleaned with 70% ethanol between sample. Soils were transported on dry ice and then stored at −80° C. Soil was then shipped overnight to UC Riverside and stored at −80° C until DNA extraction.

2.2. DNA extraction, amplification, and sequencing

Genomic DNA was extracted from soil using QIAGEN DNeasy PowerSoil Pro (QIAGEN, Germantown, MD, USA) kit following the manufacturer's protocol. Samples that yielded unusable concentrations were re-extracted introducing a modification in which 100 μL of ATL buffer was added to 700 μL of CD1 solution during the lysis step and incubated at 4° C overnight. To identify fungi, we amplified the rDNA internal transcribed spacer region 2 (ITS2) using the primers ITS4-fun and 5.8 s (Taylor et al., 2016). To identify bacteria, we amplified the V4 region of the 16S rRNA gene using the primers 515F and 806R (Caporaso et al., 2011). Although 16S primers amplify both archaea and bacteria, for simplicity, we refer to 16S results as bacteria since archaea contributed < 1% of sequencing reads. Fungal and bacterial libraries were prepared using the Dual-Index Sequencing Strategy (DIP)(Kozich et al., 2013) with PCR1 amplifying gene-specific primers and PCR2 ligating the DIP barcodes for Illumina sequencing. PCR1 conditions for fungi were 94 °C (2 min), followed by 32 cycles of 94 °C (20 s), 55 °C (20 s), 68 °C (1 min) with a final extension at 68 °C (2 min) using 5 μL of undiluted DNA, 6.5 μL of Ultra-Pure Sterile Molecular Biology Grade Water (Genesee Scientific, San Diego, CA, USA), 12.5 μL of 2x AccuStart ToughMix (Quantabio, Beverly, MA, USA), and 0.5 μL each of the 10 μM ITS4-fun and 5.8 s primers. PCR1 conditions for bacteria were 94 °C (2 min), followed by 31 cycles of 94 °C (20 s), 55 °C (20 s), 68 °C (45 s) with a final extension at 68 °C (2 min) using 1 μL of 1:10 diluted DNA, 10.5 μL of Ultra-Pure water, 12.5 μL of 2x AccuStart ToughMix, and 0.5 μL each of the 10 μM 515F and 806R primers. PCR1 products were then cleaned with AMPure XP magnetic beads (Beckman Coulter Inc., Brea, CA, USA) following manufacturers' protocols. The DIP PCR2 primers containing the barcodes and adaptors for Illumina sequencing were ligated to the amplicons during PCR2 in a 25 μL reaction containing 2.5 μL of the 10 μM DIP PCR2 primers, 6.5 μL of ultra-pure water, 12.5 μL of 2x Accustart ToughMix, and 1 μL of PCR1 product. Thermocycler conditions for PCR2 for fungi and bacteria were 94 °C for 2 min followed by 9 cycles of 94 °C (30 s), 60 °C (30 s), and 72 °C for (1 min). Products of PCR2 were then pooled for each amplicon based on gel electrophoresis band strength as in Glassman et al., (2018) and each pool was then cleaned with AMPure XP magnetic beads and checked for quality and quantity with the Agilent Bioanalyzer 2100. Based on Bioanalyzer results, fungal and bacterial samples were pooled at a 3:2 ratio (0.6 units for fungi to 0.4 units for bacteria) prior to sequencing, and two separate Illumina MiSeq v3 2x300 bp runs were required to accommodate all samples, which were sequenced at the University of California Riverside Institute for Integrative Genome Biology.

2.3. Fungal and bacterial abundance

We used quantitative (q) PCR to estimate fungal and bacterial small ribosomal subunit copy number as a proxy of abundance. We targeted the 18S rDNA for fungi using the FungiQuant-F/FungiQuant-R primers (Liu et al., 2012) and the 16S rDNA for bacteria using the Eub338/Eub518 primers (Fierer et al., 2005). qPCR reactions were performed in triplicate with 1 μL of DNA added to 9 μL of qPCR master mixer containing 1 μL of 0.05 M Tris-HCl ph8.3, 1 μL of 2.5 mM MgCl2 (New England BioLabs; NEB; Ipswich, MA, USA), 0.5 μL of 0.5 mg/mL BSA, 0.5 μL of 0.25 mM dNTPs (NEB), 0.4 μL of both forward and reverse primer at 0.4 μM, 0.5 μL of 20X Evagreen Dye (VWR), 0.1 μL of Taq DNA polymerase (NEB) and 4.6 μL of molecular grade water. qPCR reactions were run in 384 well plates on a CFX384 Touch Real-Time PCR Detection System starting at 94 °C (5 min), followed by 40 cycles of a denaturing step at 94 °C (20 s), annealing step at 50 °C for fungi or 52 °C for bacteria (30 s), and an extension step at 72 °C (30 s). Fungal and bacterial copy numbers were generated as previously established (Pulido-Chavez et al., 2023).

2.4. Bioinformatics

Illumina MiSeq sequencing data were processed using Qiime2 version 2020.8 (Bolyen et al., 2019). FastQ files from the two Illumina sequencing runs were each de-multiplexed and then forward and reverse primers were removed using cutadapt (Martin, 2011). Denoising was done using DADA2 to remove chimeric sequences and low-quality regions and to produce Amplicon Sequence Variants (ASVs) (Callahan et al., 2016). Then, DADA2 outputs from the two libraries were merged for downstream processing. Taxonomic assignments were done using Qiime2 Naïve Bayes Blast + and the reference database UNITE version 8.3 for fungi (Kõljalg et al., 2005) and the reference database SILVA version 132 for bacteria (Quast et al., 2013) (accessed on 18 March 2022). Sequences not assigned to the Kingdom Fungi or assigned to mitochondria and chloroplast for bacteria were removed from the ASV tables before subsequent analysis. We assigned functional ecological guilds to each fungal ASV using FUNGuild (Nguyen et al., 2016). Further analysis of fungal guilds retained ASVs in taxa with confidence levels of "probable" and "highly probable" and ASVs classified as multiple guilds were discarded. All sequences were deposited at NCBI Sequence Read Archive under BioProject accession number PRJNA922564.

2.5. Statistical analyses

All statistical analyses were performed using R version 4.1.1 (R Core Team, 2021) and statistical codes are available at https://github.com/mvcaiafa/fire-chronosequence. The two Illumina runs resulted in 17.2 M fungal and 7.6 M bacterial sequences with an average of with an average of 58,855 fungal and 26,020 bacterial sequences/sample. To account for uneven sequencing depth, we took a conservative approach and rarefied ASV tables to a depth of 6,124 sequences/sample for fungi and 5,321 sequences/sample for bacteria. This approach enabled us to retain the largest number of samples and sequencing depth within each dataset. Observed species richness was estimated using package BiodiversityR (Kindt and Coe, 2005). To assess the effect of fire site as a proxy of time since fire (Church's Park 2010, Beaver Creek 2016, Badger Creek 2018, Ryan 2018, and Mullen 2020), severity (control, low and high), and depth (shallower and deeper) on bacterial and fungal abundance and richness we fitted a total of 48 statistical models (12 each for fungal and bacterial abundance and richness). Fungal and bacterial abundance were log transformed. The effect of fire site is primarily our measure of time since fire although it also incorporates all environmental variables that may have differed including time since beetle outbreaks and plant mortality in the years pre-fire. We used generalized mixed effect models (GLMM) with a gamma or negative binomial distribution using the lme4 (Bates et al., 2015) and MASS (Venables and Ripley, 2002) packages. Model selection was made via comparison of Akaike Information Criterion (AIC). All models contained "plot" as a random effect. To assess the effect of site, fire severity and soil depth we use single term deletion of the best GLMM. By deleting single terms, we can assess the contribution of each term on the goodness of fit of the model.

To test whether the fire site, severity and sample depth influenced the fungal and bacterial community composition, we performed a nonparametric permutational multivariate ANOVA (PERMANOVA) (Anderson, 2001) using the adonis2 function in the vegan package (Oksanen et al., 2019) with the Bray-Curtis dissimilarity metric. We tested the differences in multivariate dispersion among severity, fire sites and depth using the betadisper function (Anderson, 2006). Results were visualized using Non-Metric Multidimensional Scaling (NMDS). We then plotted the relative abundance of ASVs of sequence read abundance greater than 5% for fungi and 2% for bacteria. To identify pyrophilous taxa that positively responded to fires, we used DESeq analysis. We used DESeq2 using phyloseq (McMurdie and Holmes, 2013) to identify the taxa at the genus (fungi) and phylum (bacteria) level that respond positively or negatively to a treatment (control vs. high severity). To test how different species responded to high severity fires, we fitted a GLM based on the negative binomial distribution using the DESeq function of the DESeq2 package (Love et al., 2014). We used a Kruskal-Wallis test to evaluate the effect of fire severity on the richness of different fungal guilds.

3. Results

3.1. Sequencing data

Overall, the two Illumina Miseq runs resulted in 17,185,707 fungal sequences and 7,597,940 bacterial sequences with an average of 58,855 fungal and 26,020 bacterial sequences/sample and a total of 10,970 fungal ASVs and 35,627 bacterial ASVs. After rarefaction, the total number of ASVs was 7,754 for fungi and 29,601 for bacteria. From the 7754 fungal ASV present in the rarefied table, 3843 were not assigned to any guild and 1358 were discarded because were assigned to more than one guild or were assign with a low level of confidence.

3.2. Effects of fire severity, soil depth and fire site on microbial abundance

GLMMs revealed that fungal abundance was primarily affected by fire severity, followed by fire site, then soil depth (Table S2), whereas bacterial abundance was significantly affected by fire site then severity with depth having no statistical effect (Table S3). Aside from the most recent fire (2020 Mullen), burn severity had a greater effect on microbial abundance in the more recent fires in the shallower soils (Fig. 1). High severity fire reduced bacterial and fungal abundance relative to control plots in all sites in both shallower (bacteria: 31–92%; fungi: 85–98%) and deeper soils (bacteria: 14–64%; fungi: 54–87%) although changes for bacteria were not significant in deeper soils (Fig. 1; Table S4). High severity fires in general had larger impacts on shallower (0–5 cm deep) than deeper (5–15 cm) soils, and shallower samples in control plots typically harbored higher microbial abundance than deeper samples. In contrast to high severity fires, low severity fires had smaller reductions in abundance compared to control plots (bacteria: 28–85% in shallower and 5–55% in deeper; fungi: 15–97% in shallower and 74–79% in deeper) and in fact led to increased abundance in two cases for bacteria and one for fungi (Table S4).

3.3. Effects of fire severity, soil depth and fire site on microbial richness

GLMMs revealed that fungal richness was primarily affected by the interaction of fire severity with fire site followed by the interaction of fire severity with depth (Fig. 2A–B; Table S5). This means that fire severity had different effects on fungal richness by site and depth, with typically stronger impacts in shallower than deeper soils and larger reductions in richness in the more recent fires in shallower soils (Fig. 2B). Similarly, bacterial richness was primarily affected by the interaction of fire severity with fire site, followed by the interaction of depth and fire

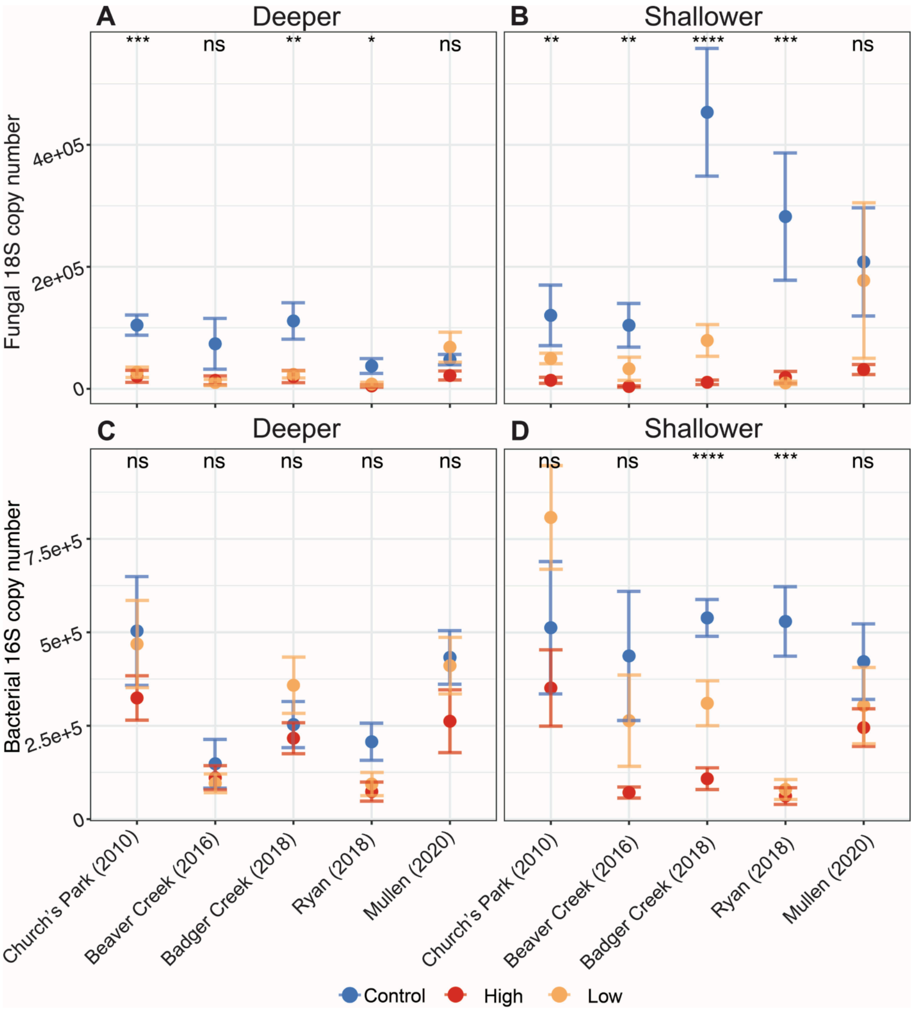

Fig. 1. Change in mean per sample 18S copy number to estimate fungal abundance (A–B) and 16S copy number to estimate bacterial abundance (C–D) across a fire chronosequence among low and high severity versus control plots, collected at 0–5 cm (shallower samples) and 5–15 cm (deeper samples). Points represent per sample means with standard error bars. The effect of fire severity on microbial abundance at each site was tested using a Kruskal-Wallis test. ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$.

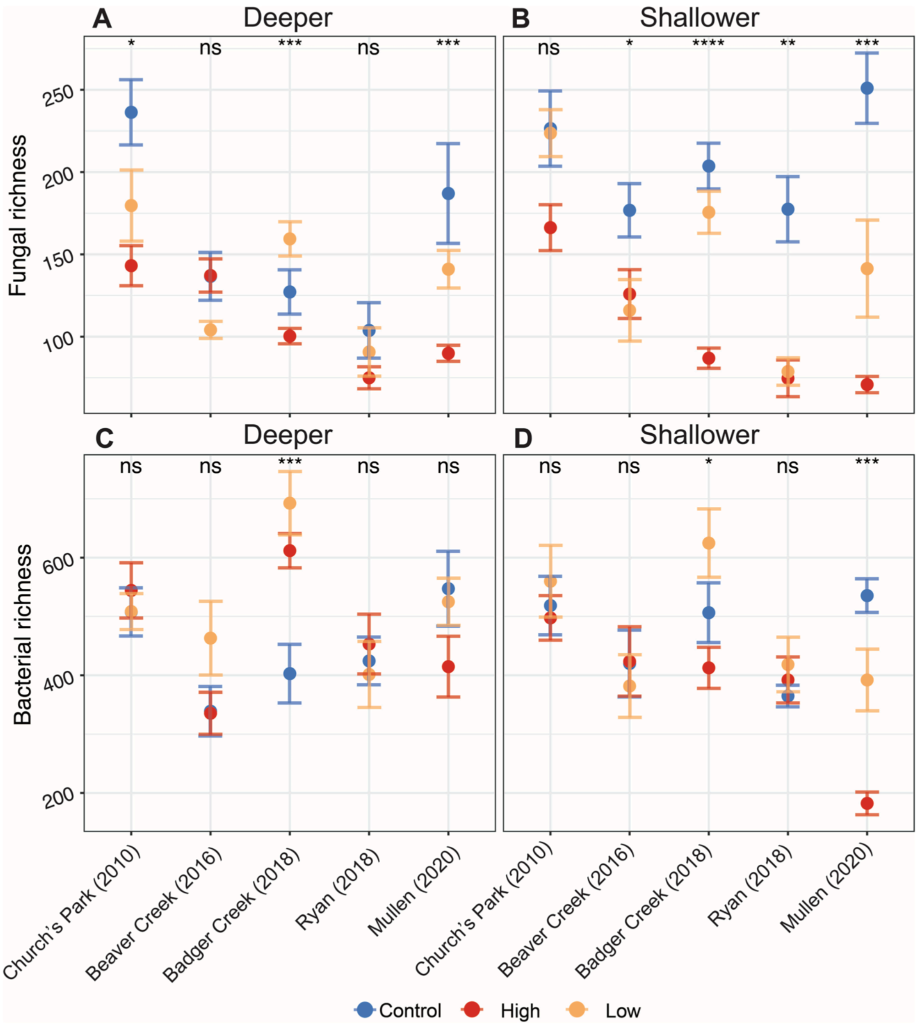

Fig. 2. Change in mean per sample species richness of A) fungi in deeper and B) shallower samples and bacteria in C) deeper and D) shallower samples across a fire chronosequence among low severity, high severity and control plots, collected at 0–5 cm (shallower samples) and 5–15 cm (deeper samples). Points represent per sample means with standard error bars. The effect of fire severity on microbial richness was tested for each site using a Kruskal-Wallis test. ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$.

site, then by the interaction of fire severity with depth (Table S6). In deeper soils, bacterial richness was only impacted by severity in one site (Fig. 2C), but in shallower soils, bacterial richness was more affected in the recent than older fires (Fig. 2D). In general, fire severity had larger impacts on fungal than bacterial richness, richness was more affected in shallower than deeper soils, and in a few cases low severity fire increased richness relative to control (Fig. 2; Table S7). While the impacts of fire severity in deeper soils were more mixed (Fig. 2A and C), the reduction in fungal (Fig. 2B) and bacterial (Fig. 2D) richness was more pronounced in more recent fires.

3.4. Changes in fungal and bacterial communities across the fire chronosequence

Fungal community structure was significantly affected by fire severity, fire site, soil depth, and the interactions of fire severity with fire site and soil depth (Fig. 3A, Fig. 4A; Table S8). Specifically, the effect of fire severity on community composition decreased with time since fire, with the amount of variance explained reduced from 23% to 17% from the newest to oldest fire (Fig. 3B; Fig. S2). Multivariate dispersion was significantly different among severity treatments but not among sites or soil depths (Table S8), with dispersion highest in high and low severity plots and lowest in control plots. This means that samples from high severity plots are more heterogeneous than samples from control plots. In samples from high severity plots (Fig. 4A), fungal communities grouped by site explained 23% of the variation. In contrast, fungal communities at unburned control plots showed a greater overlap across sites with only 15% of the variation explained by site. This is an indication that fungal communities changed more significantly across fire site (representing mainly time since fire) in high severity plots but not in control plots. Depth had small (3–4%) but significant impact on fungal composition that increased slightly with fire severity (Fig. S3).

In the case of bacteria, community composition was primarily affected by the fire site and severity, followed by the interaction of severity with fire site and fire site with depth (Fig. 3B, Fig. 4C; Table S9). Like fungi, the effect of fire severity on bacterial community composition decreased with time since fire, with variance explained reduced from 21% to 14% from newest to oldest fire (Fig. 3D; Fig. S4). Also, Multivariate dispersion of bacterial communities was not affected by severity, sites, or soil depth (Table S9), indicating bacterial communities across sites, severity plots and depths were equally dispersed. In samples from high severity plots (Fig. 4B), bacterial communities grouped by site explained 17% of variation, compared to 11% in unburned control plots, meaning that bacterial composition became more variable across time in burned compared to control plots. The impact of depth on bacterial composition increased with fire severity with depth explaining 7.2% of variation in control plots versus 9.6 % in high severity plots (Fig. S5).

3.5. Changes in relative taxonomic composition across fire severity and fire site

The relative sequence abundance of both fungal and bacterial taxa varied across fire severity and fire site (Fig. 5). In the case of fungi, some Ascomycota genera such as *Calyptrozyma, Coniochaeta, Oidiodendron,*

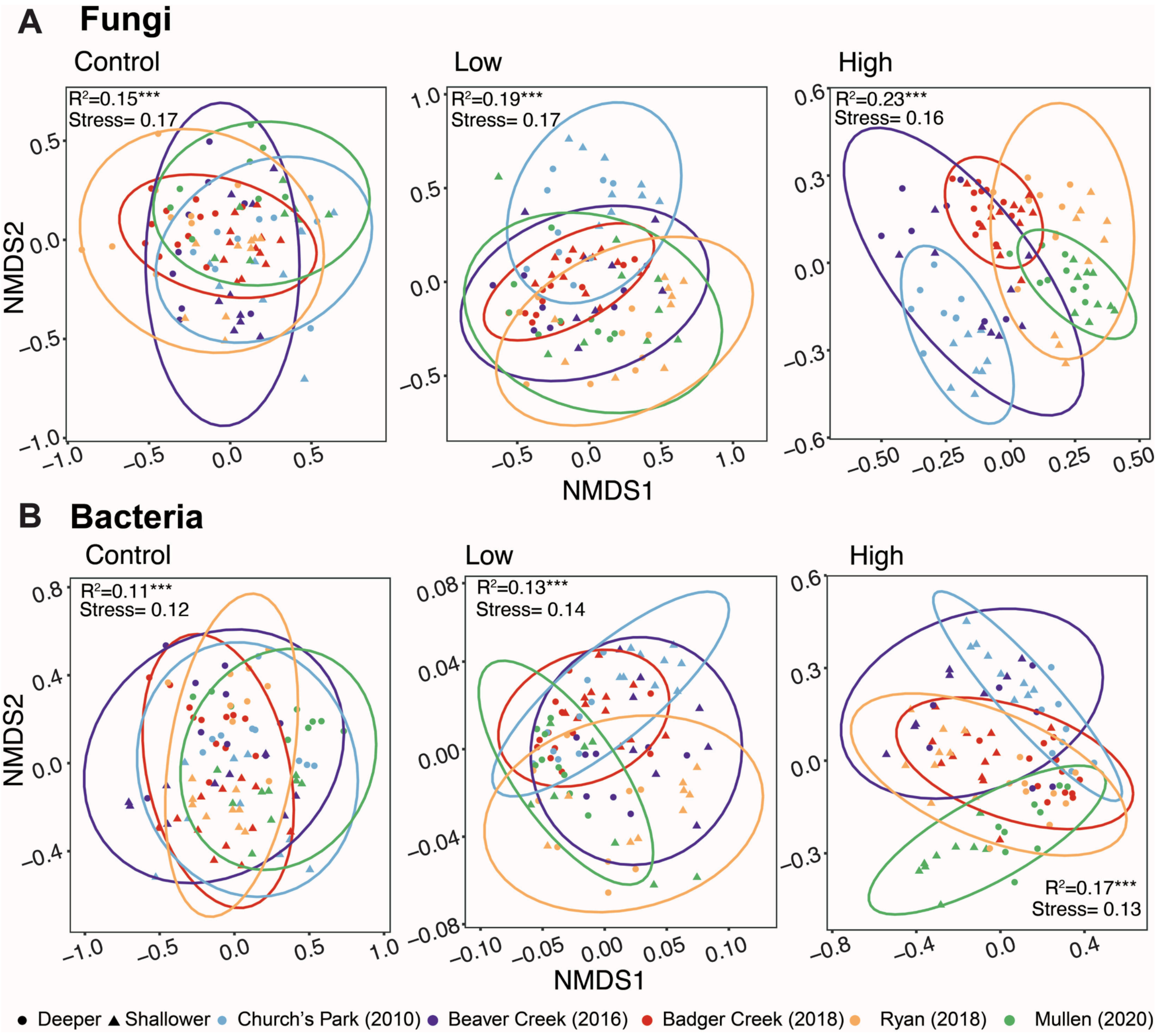

Fig. 3. Non-metric multidimentional scaling (NMDS) ordination and R^2 values across sites of fungal (A–B) and bacterial (C–D) communities. NMDS of A) fungi and C) bacteria colored by fire severity at all five sites of the wildfire chronosequence. Fire severities are represented by different colors and soil depth by shape. Effect of fire severity on fungal and bacterial communities was tested using a PERMANOVA. ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$. R^2 values indicate the variation in community structure explained by fire severity at each site.

and *Penicillium* and the Basidiomycota *Naganishia* responded positively to fire through increased relative abundances in both low and high severity plots (Fig. 5A), a finding supported through DESeq analysis (Fig. 6). Well-described pyrophilous fungi such as the Basidiomycota *Pholiota* and the Ascomycota *Pyronema* showed a significant positive response to fire and the increased abundance of pyrophilous fungi can be observed up to five years after fire (2016–2020) (Fig. 5A, Fig. 6). Conversely, ectomycorrhizal genera such as the Basidiomycota *Cortinarius*, *Inocybe* and *Piloderma* were in high relative abundance only in control or low severity plots and showed a strongly negative response to high severity fires (Fig. 5A, Fig. 6). Fires generally reduced the relative abundance of Basidiomycota and increased the abundance of Ascomycota. This was particularly noticeable in the 2018 Badger Creek and Ryan fires.

Fire severity differentially affected the relative abundances of fungal functional groups (Fig. 7). Primarily, ECM fungi, which already had low richness in control plots, were significantly reduced in low and high severity plots to an average of <5 species per sample in high severity plots, and this did not improve over time (Fig. 7A). Indeed, high severity plots at the 2010 Church's Park fire site had one of the lowest ECM fungal richness measurements despite being the oldest fire. Conversely, saprotrophic and plant pathogenic fungi show a less clear trend, generally being reduced in high severity plots relative to control plots, but with relative abundance of certain taxa increasing in burned plots at some sites (Fig. 7B and 7D; Fig S6). While species richness of ericoid mycorrhizal (ERM) was generally reduced by fire, relative abundances of this guild increased in burned plots at the Beaver Creek and Badger Creek fires (Fig. 7C; Fig. S6). For saprotrophic, plant pathogenic, and ERM fungi, there were large decreases in high severity compared to control plots in the recent fires in shallower soils (Fig. 7B-D). However, in contrast to ECM fungi, saprotrophic and plant pathogenic fungi tended to recover over time.

For bacteria, increases in the relative abundances of Actinobacteria and Firmicutes were coupled to decreasing relative abundances of Acidobacteria and Proteobacteria in both low and high severity plots (Fig. 5B). Gemmatimonadetes also increased in abundance in low and

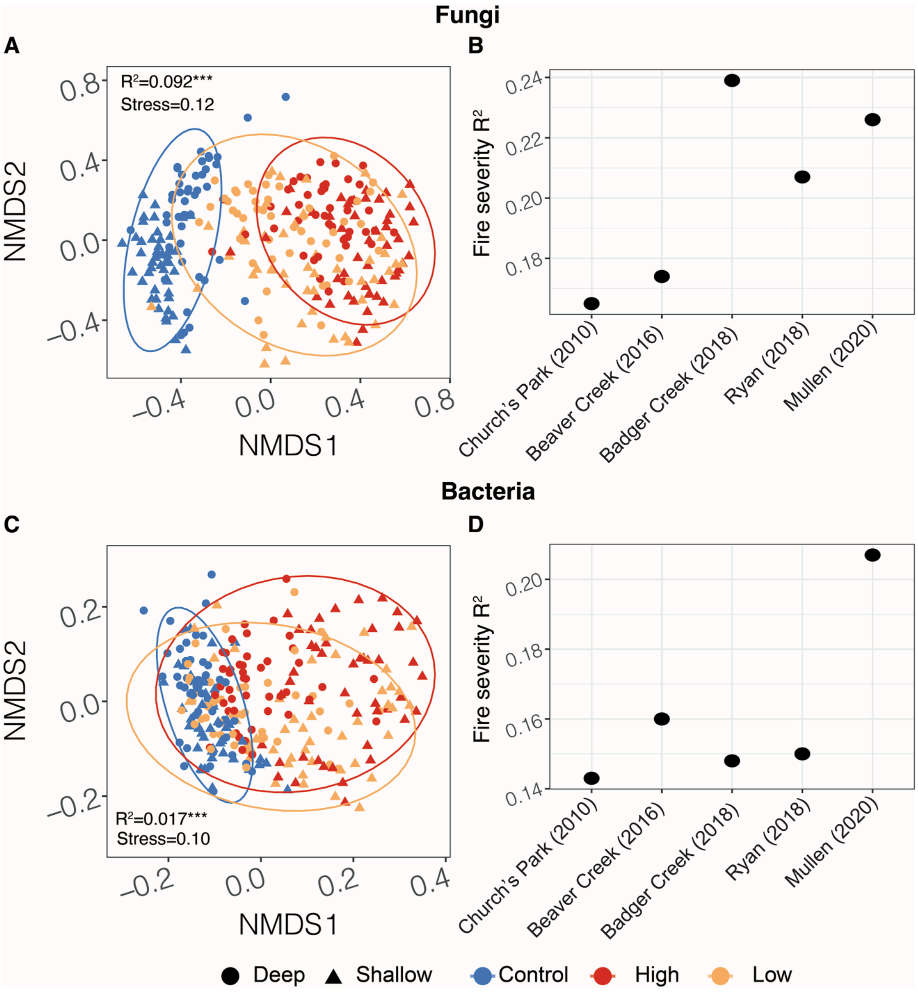

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of A) fungal and B) bacterial communities at unburned control, low severity and high severity plots using the Bray-Curtis dissimilarity metric. Fire sites are represented by different colors and soil depth by shape. Effect of fire site on fungal and bacterial communities was tested using a PERMANOVA. ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$.

high severity plots in the older fires. DESeq analysis indicated that some genera such as *Blastococcus* (Actinobacteria)*,* Paenibacillus and Alicyclobacillus (Firmicutes), *Massilia* (Proteobacteria), *Modestobacter* (Actinobacteria)*, Noviherbaspirillum* (Proteobacteria) and *Pedobacter* (Bacteroidetes) positively responded to high severity fires (Fig. 8). The increased abundance of these pyrophilous bacteria can be observed up to five years after fire (2016–2020).

4. Discussion

We documented the temporal succession of fungal and bacterial communities across a ten-year fire chronosequence in lodgepole pine-dominated subalpine forests in the Southern Rocky Mountains that had previously experienced high levels of insect-driven mortality. Our results demonstrate that increasing fire severity correlates with a larger reduction in fungal and bacterial abundance, species richness, and significant changes in community composition, but these effects are modulated by time and soil depth. As expected, deeper soils were less impacted by fire, and the impact of fire severity on microbial composition tended to decrease over time since fire. However, while the species richness of fungal and bacterial communities partially recovered, they did not return to unburned levels even 10 years after fire. We detected the increased abundance of pyrophilous fungi and bacterial in high severity plots, which persisted for at least 5 years after fire. Additionally, we found that ECM fungi were reduced from already low levels in high severity fires, and their richness did not recover over time, suggesting that the compound effect of beetle-driven tree mortality and wildfires could delay forest recovery.

Here, we highlight a unique finding that symbiotic ECM fungi are particularly hard hit by multiple global change disturbances. Like previous studies (Dove and Hart, 2017; Pulido-Chavez et al., 2021; Enright et al., 2022), we found a consistent reduction in richness and relative sequence abundance of ECM fungi in burned plots. However, it is worth noting that ECM species richness in control plots in some sites was lower than reported ECM richness in other pine forests not infested with bark beetles (Talbot et al., 2014; Pec et al., 2017; Pulido-Chavez et al., 2021). For example, there were on average 12 ECM taxa per plot in unburned and uninfested *P, ponderosa* plots of Washington state (Pulido-Chavez et al., 2021) and *P. contorta* plots in Yosemite, CA yielded a total of 110 species of ECM in the soil and 49 in the spore bank (Glassman et al., 2015). While our sites yielded an average of 11 ECM taxa per plot and 108 ECM taxa per site, the Mullen site, where the beetle-killed host trees had been dead for the longest period before the fire, had only 7 ECM taxa per sample on average in the unburned plots and a total of 88 ECM taxa in the whole site. Lower ECM richness and relative abundance have been attributed to tree mortality caused by pine beetle outbreaks (Treu et al., 2014; Pec et al., 2017). The response of ECM fungi to fire is particularly important for forests recovery as these fungi are obligate symbionts with all pines, including *P. contorta* (Brundrett and Tedersoo, 2018). Indeed, planted pine species in the Southern hemisphere cannot colonize and

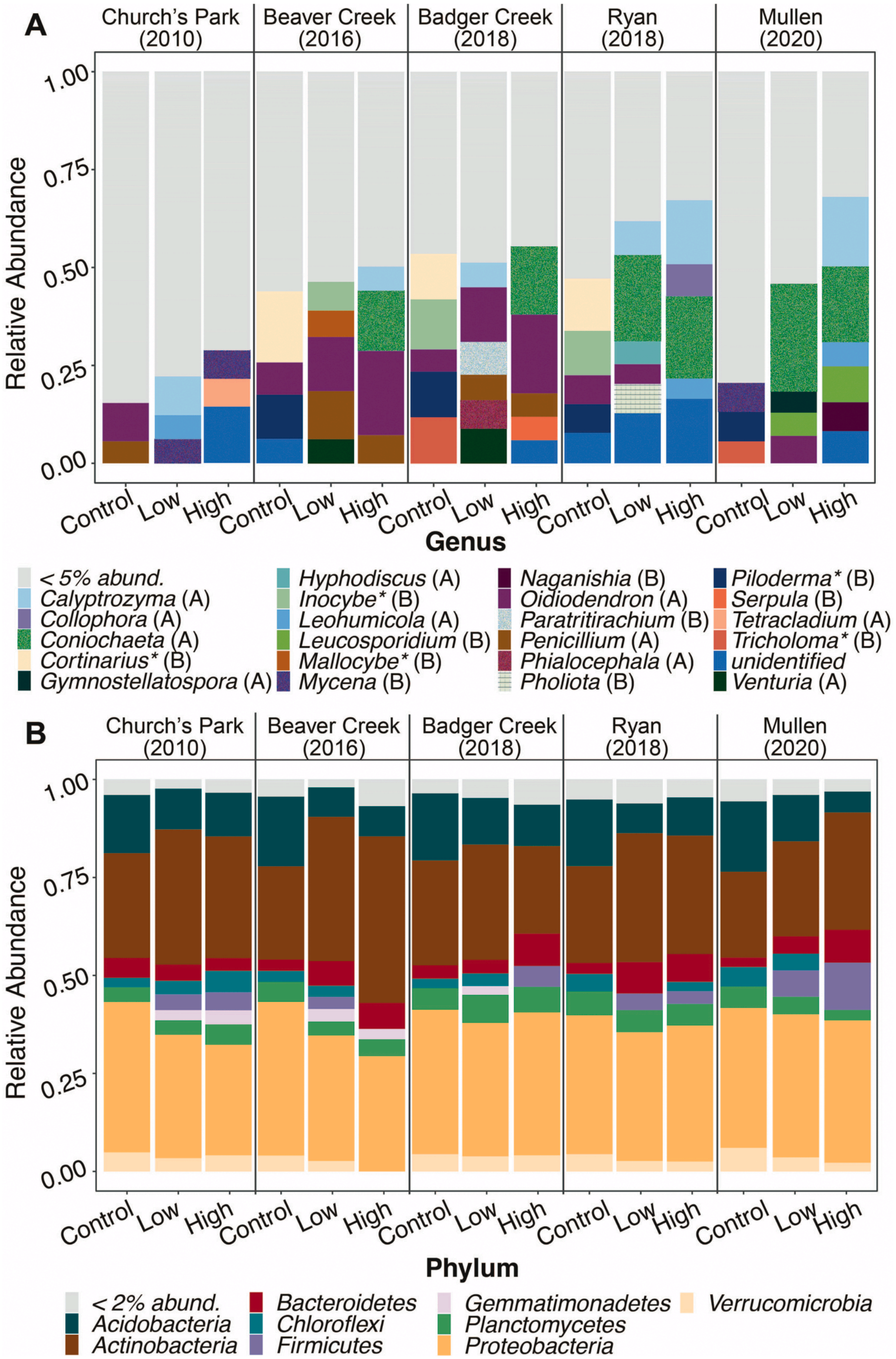

Fig. 5. Relative sequence abundance of microbial communities across fire chronosequence for A) fungal genera with more than 5% sequence abundance (ectomycorrhizal fungi denoted with an asterisk), B) bacterial phyla with more than 2% sequence abundance at each fire severity treatment at all five sites. Fungi in the phylum Ascomycota represented with A and in the Basidiomycota with B.

establish without co-colonization or co-invasion of ECM fungal partners (Nuñez et al., 2009). Following slash pile burns, ECM fungal root colonization on *P. contorta* was reduced for up to a decade (Rhoades et al., 2021), and pine recolonization post-fire remains limited for more than 50 years (Rhoades and Fornwalt, 2015) in sites near our study area. Considering that a large proportion of the lodgepole pine stands in the study area were killed in the early 2000 s and remained as snags for years (Rhoades et al., 2018; Audley et al., 2021). It is likely that this reduced ECM colonization is due to lack of fungal propagules (Gill et al 2022), which were not present to disperse in from nearby unburned plots. Thus, reduced ECM fungal diversity caused by the compound effect of beetle outbreaks and fire might hinder the recovery of these forests. This was particularly noticeable in Church's Park (Fig. 6A) where, unlike previous studies (Pulido-Chavez et al., 2021), the ECM community in the burned plots has a very low richness even though soil samples were collected more than 10 years post-fire. Considering that the forests in Church's Park burned 3–5 years after the beetle outbreaks, it is possible that ECM communities were already depauperated before the fire preventing much post-fire recovery.

Regardless of fire site and previous history of mountain pine beetle infestation, severity remained the largest explanatory variable of both bacterial and fungal community composition, and while these effects

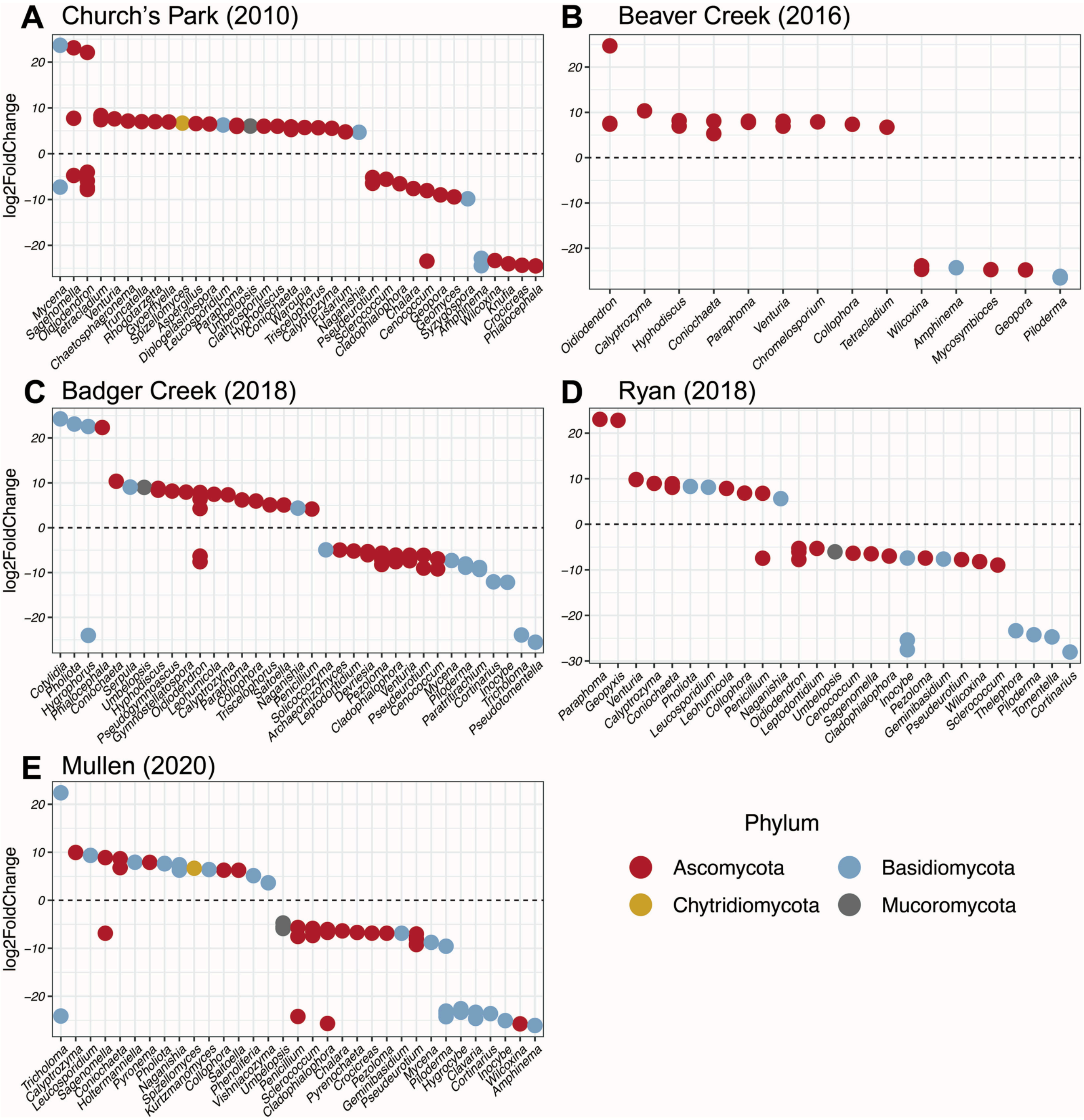

Fig. 6. DESeq analysis showing the differential representation of significantly abundant fungal ASV's between high severity burned and unburned control plots across the five sites of the fire chronosequence. Representations are based on a negative binomial regression at the genus level. Each dot represents a taxon, colored by phylum and labeled by genus. Positive values represent a positive response to fire while negative values represent a negative response to fire. Only probabilities with a differential abundance at $p < 0.001$ are included.

decreased over time, they were still large and persistent even after 10 years post-fire. This is consistent with previous studies in temperate and boreal forests that suggest that it can take between 12 and 18 years for microbial communities to return to the pre-fire conditions (Treseder et al., 2004; Twieg et al., 2007; Kipfer et al., 2011). While microbial communities across the five sites did not return to the pre-fire conditions even after 10 years post-fire, community composition in high severity plots was significantly different across fire site whereas communities in control plots show a greater overlap across fire sites (Fig. 4), indicating post-fire succession of microbial communities. Previous fire chronosequence studies in pine forests that did not experience large levels of beetle-induced mortality documented similar temporal community turnover after wildfires (Kipfer et al., 2011; Pulido-Chavez et al., 2021). When analyzing sites individually (Figs. S2 and S4), fire severity explained a larger proportion of variability in community composition in the more recent fires. Thus, it appears that the influence of fire severity on community composition attenuates over time.

It is important to note that the use of space-for time substitutions has some limitations. Since it is not always possible to account for all site-specific variation, distinguishing time and site effects can be challenging. We made efforts to limit inter-site variation by selecting sites in the same region, with similar stand structure, elevation, and soil types. Also, by including unburned controls in each site, we can better distinguish time from site effects. Thus, differences from burned to control

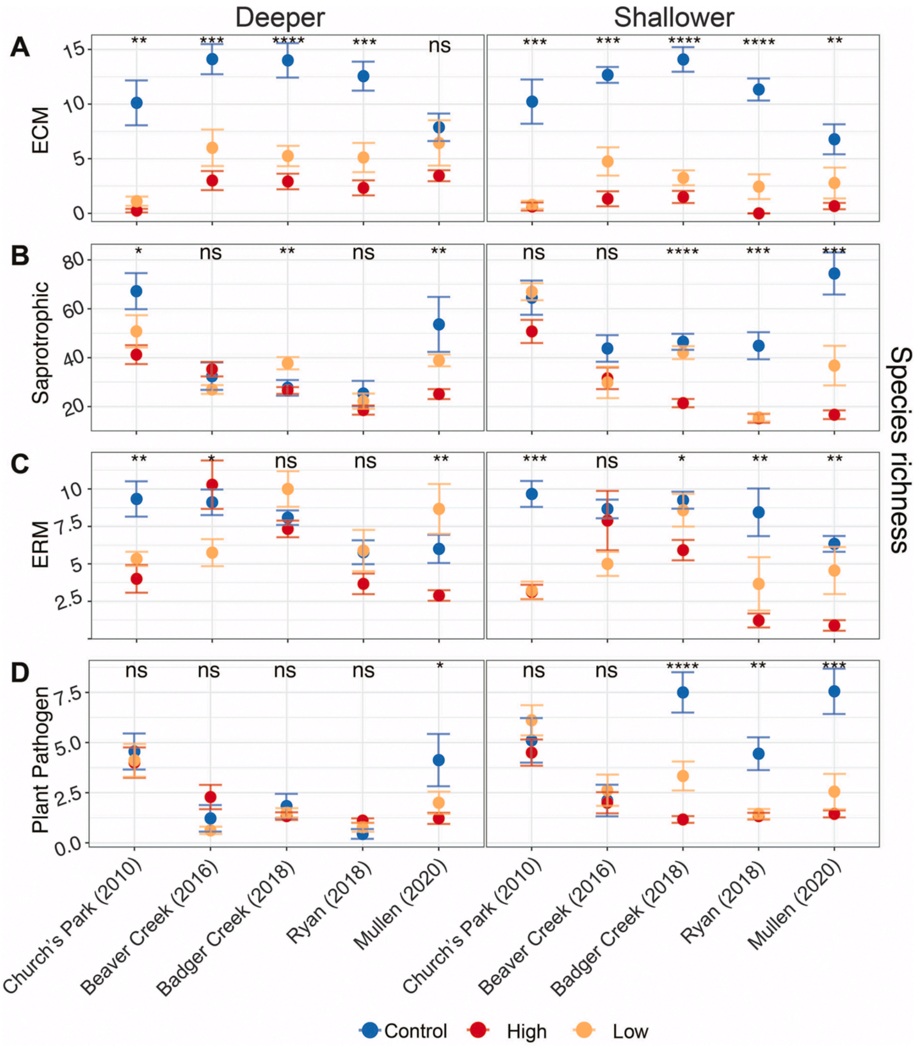

Fig. 7. Change in species richness of A) ectomycorrhizal (ECM) fungi, B) saprotrophic fungi, C) ericoid mycorrhizal (ERM) fungi and D) plant pathogenic fungi across a fire chronosequence among low severity, high severity and control plots, collected at 0–5 cm deep (shallower samples) and 5–15 cm deep (deeper samples). Points represent per sample means with standard error bars. The effect of fire severity at each site was tested using a Kruskal-Wallis test. ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****: $p < 0.0001$.

plots among sites can be attributed to time since fire. Due to the unpredictable nature of wildfires, space-for-time have been critical to study post-fire recovery (Turner, 2010; Kashian et al., 2013).

Overall, the effect of fire severity across the fire sites was more noticeable in fungal communities than bacterial communities, likely owing to the higher sensitivity of fungi to fire especially the ECM fungi. Previous studies in non-beetle impacted forests also reported larger turnover in fungal than bacterial communities (Enright et al., 2022; Pérez-Valera et al., 2018; Pulido-Chavez et al., 2023; Whitman et al., 2019;). Chronosequence studies in Mediterranean and temperate forests also showed that bacterial communities recovered faster than fungal communities after perturbation (Bárcenas-Moreno et al., 2011; Sun et al., 2017). Interestingly, another form of symbiotic fungi, ericoid (ERM) mycorrhizal fungi, also had lowest richness at the site with the longest lag between tree mortality from beetles and wildfire (Mullen), and richness remained depressed in burned compared to control plots in the oldest site (Church's Park), suggesting a lack of recovery over time. In particular, the ERM genus *Oidiodendron* displayed relative abundance increases in burned plots (low and high severity) at two of the fires (Beaver and Badger Creek). ERM fungi form symbiotic associations with plants in the families Ericaceae and Diapensiaceae (Brundrett and Tedersoo, 2018). In the study area, ERM fungi are likely associated to *Vaccinium scoparium*, a common understory shrub in forested areas of the Rocky Mountains (Rhoades et al., 2015). *Vaccinium* cover is reduced following forest harvesting (Fornwalt et al., 2018) and burning in these forests (Rhoades and Fornwalt, 2015) and may remain depressed in non-forested openings for decades after disturbance. Due to their higher saprotrophic capabilities, ERM fungi may survive without a host as free-living saprobes and could be more resilient to disturbances including fire (Ward et al., 2022). In contrast to ECM and ERM fungi, plant pathogens increased in richness overtime and so did saprobes in shallower soils, indicating a higher resilience to fire in beetle killed forests. Interestingly, some taxa that are well known pyrophilous fungi from other burned ecosystems (Fox et al., 2022), also increased in abundance in soils from the recent fires sampled here, such as the Ascomycota *Coniochaeta, Pyronema* and *Penicillium*. Similarly, some yeast forming fungi such as *Calyptrozyma* that we found to increase after fire are known to inhabit oligotrophic and stressful environments and have also been reported to be abundant after wildfires in boreal forests (Day et al., 2019; Whitman et al., 2019; Pérez-Izquierdo et al., 2021).

We also found evidence for increased abundance of pyrophilous bacteria in high severity plots, with post-fire changes in community composition persisting for years, although they were more pronounced in recent fires. In burned plots, there was a reduction in the relative abundance of Proteobacteria and Acidobacteria and an increase in the relative abundance of Actinobacteria and Firmicutes compared to the control plots (Fig. 5B). Firmicutes, known to be thermotolerant and form endospores, have been found to increase in abundance after fire in many ecosystem types (Enright et al., 2022; Filippidou et al., 2016; Pérez-Valera et al., 2020; Pulido-Chavez et al., 2023). Our DESeq results indicate that some bacteria such as the Actinobacteria *Blastococcus* and *Modestobacter,* the Firmicute *Paenibacillus,* the Proteobacteria *Massilia*

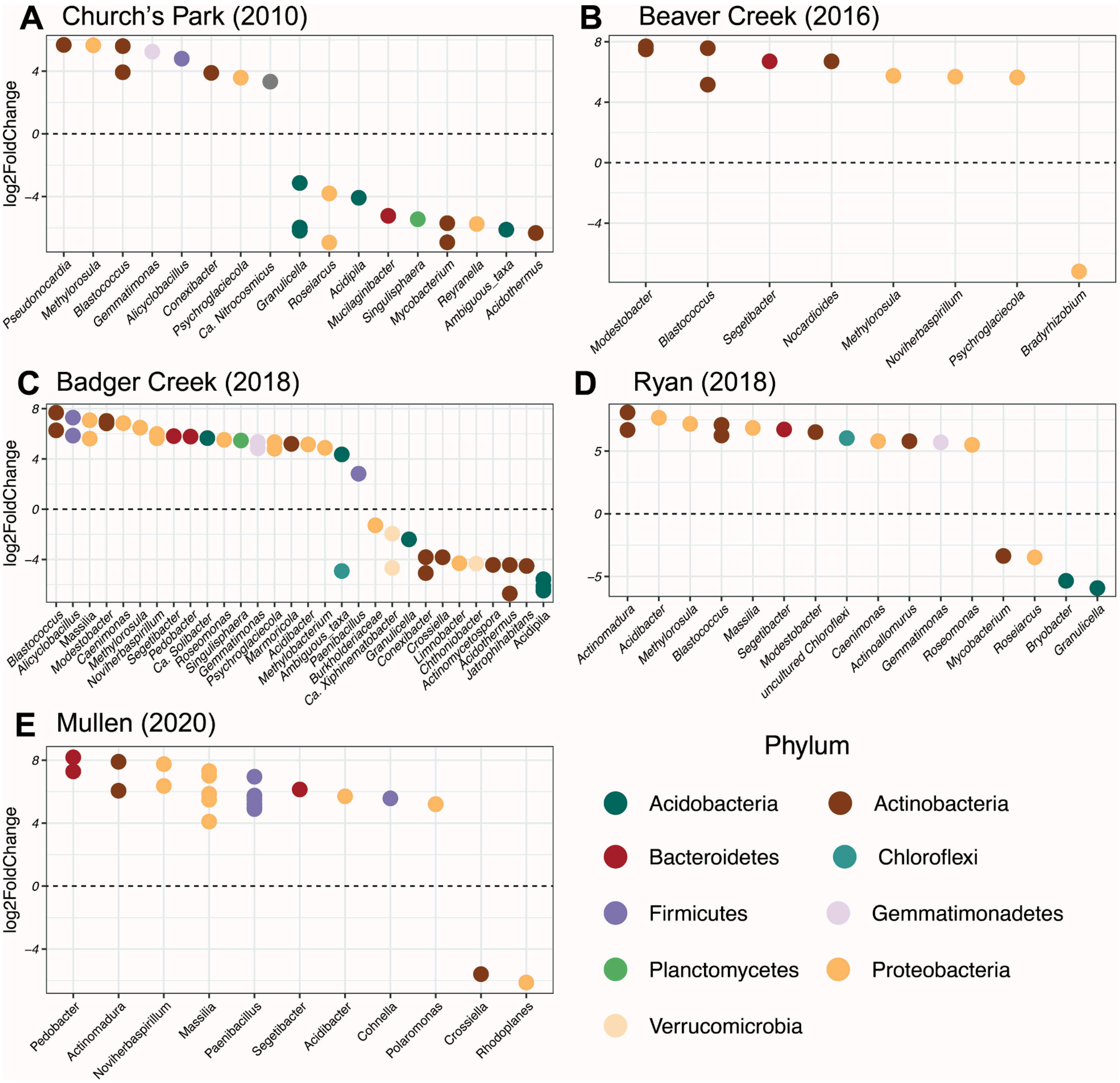

Fig. 8. DESeq analysis showing the differential representation of significantly abundant bacterial ASV's between high severity burned and unburned control plots across the five sites of the fire chronosequence. Representations are based on a negative binomial regression at the genus level. Each dot represents a taxon, colored by phylum and labeled by genus. Positive values represent a positive response to fire while negative values represent a negative response to fire. Only probabilities with a differential abundance at $p < 0.01$ are included.

and *Noviherbaspirillum,* and the Bacteroidetes *Pedobacter* responded positively to fire, with changes that persisted for several years post-fire. These taxa have consistently been found to increase in burned soils (Enright et al., 2022; Nelson et al., 2022; Pulido-Chavez et al., 2023; Whitman et al., 2019) and likely benefit from traits such as fast growth, thermotolerance and utilization of pyrogenic substrates that facilitate their colonization of post-fire environments (Enright et al., 2022). We found that differences in bacterial communities between burned and unburned plots declined over time.

Overall, fire reduced both fungal and bacterial abundance, with larger impacts on fungi than bacteria, and impacts on fungal abundance tending to become less pronounced over time. While there are reasons to be cautious when interpreting abundance estimates obtain from qPCR, which measures gene copy number and is only a proxy of abundance, our results were largely in line with a *meta*-analysis that also found that high severity fires reduced microbial abundance and that fires tended to reduce fungal more than bacterial abundance (Dooley and Treseder, 2012). We found similar trends even in a lower severity Southern California grassland fire (Glassman et al., 2023). Fungal abundance was reduced towards deeper soils in control plots, however, this trend was not observed in bacteria. Previous studies in unburned soils have shown that microbial biomass tends to decrease with depth (Fierer et al., 2003; Fierer, 2017). The lack of a strong depth effect on bacterial abundance might be due to the relatively shallow depth of the collected soils. Nonetheless, bacterial communities in the deeper soil layer (5–15 cm) were generally less sensitive to fire than fungal communities at the same depth. The higher sensitivity of fungi to fire at deeper soils may be because some fungal genets (individual) tend to form mycelia that grow across the two soil depths. Thus, even fungi in the deeper soil would be impacted by fire. In agreement with our results, Qin and Liu, (2021) reported fungi tend to be more sensitive to fire than bacteria and another study in a California grassland found that impact of environmental change on bacterial communities decreased with soil depth (Barbour et al., 2022). Furthermore, experimental burns have shown that soil depth variation as little as 5 cm can results in differences in maximum temperature of more than 100 °C (Bruns et al., 2020).

Fungal and bacterial species richness was affected by the interaction of fire severity, fire site, and soil depth. Previous studies in pine-dominated forests have shown a reduction in microbial richness after high severity fire (Whitman et al. 2019; Pulido-Chavez et al., 2021; Nelson et al., 2022). We found that differences in fungal richness between burned and unburned plots persisted for more than 10 post-fire years, with the most pronounced differences for the more recent fires (2018–2020) (Fig. 2). Interestingly, this pattern was weaker for bacterial communities, with significant differences only between burned and unburned plots at only two sites (Badger Creek 2018 and Mullen 2020). In a few cases, bacterial richness was slightly higher than unburned controls. Low severity fires have been shown to have little or no impact on bacterial richness (Kranz and Whitman, 2019; Glassman et al., 2023), thus, the increased bacterial richness in some low severity plots is likely due to the proliferation of pyrophilous bacteria in these soils. Niche heterogeneity created by fire and low mortality could result in an increased species richness after fire (Pulido-Chavez et al., 2023). Despite the differences in richness between burned (low and high severity) and control, we observed a partial recovery of both fungal and bacterial richness over time. A similar trend has been observed in other fire chronosequence studies in pine-dominated forests (Kipfer et al., 2011; Pulido-Chavez et al., 2021). Yet, fungal richness might also be influenced by the beetle-driven tree mortality in the years pre-fire. Beetle outbreaks has been shown to reduce the richness of saprotrophic and ectomycorrhizal fungi (Pec et al., 2017) and a large portion of the pine trees in our study sites had been dead for up to 15 years before the wildfires. Therefore, low richness in some unburned plots could be due to high tree mortality.

5. Conclusions

Our chronosequence approach tracked the partial recovery of abundance and species richness in older fires and found that shifts in community composition persisted in both bacteria and fungi even after ten years post-fire. We also detected an increased abundance of pyrophilous fungi and bacteria in the recent fires. While long-lasting effects of wildfire on microbial community composition have been reported in numerous ecosystems, it is important to note that the forests studied here had already experienced high beetle induced mortality prior to fires, which compounded to severely reduce ECM fungi more than just fire alone and led to ECM fungal richness not recovering over time. Ecosystems getting hit consecutively by multiple global change factors will likely have synergistic negative impacts on forest recovery in many systems across the globe.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank the rangers at the Medicine Bow-Routt National Forests for their assistance in site selection and access. This work was supported by a USDA NIFA award #2021-67019-34608 (to M.J.W, C.C.R, T.B. and S.I.G.) and US National Science Foundation Division of Environmental Biology Awards #2114870 (S.I.G.) and #2114868 (to M.J.W. and T.B.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121160.

References

Alstatt, D., Miles, R.L., 1983. Soil survey of Grand County area, Colorado. USDA Soil Conservation Service and Forest Service and Colorado Agriculture Experiment Station. U.S. Government Printing Office.

Anderegg, W.R.L., Chegwidden, O.S., Badgley, G., Trugman, A., Cullenward, D., Abatzoglou, J.T., Hicke, J., Freeman, J., Hamman, J.J., Lawler, J., 2022. Future climate risks from stress, insects and fire across US forests. Ecol. Lett. 25 (6), 1510–1520.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1046/j.1442-9993.2001.01070.x.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x.

Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L., Bradstock, R.A., 2013. Defining pyromes and global syndromes of fire regimes. Proc. Natl. Acad. Sci. U.S.A. 110 (16), 6442–6447.

Audley, J.P., Fettig, C.J., Steven Munson, A., Runyon, J.B., Mortenson, L.A., Steed, B.E., Gibson, K.E., Jørgensen, C.L., McKelvey, S.R., McMillin, J.D., Negrón, J.F., 2021. Dynamics of beetle-killed snags following mountain pine beetle outbreaks in lodgepole pine forests. For. Ecol. Manage. 482, 118870.

Barbour, K.M., Weihe, C., Allison, S.D., Martiny, J.B.H., 2022. Bacterial community response to environmental change varies with depth in the surface soil. Soil Biol. Biochem. 172, 108761 https://doi.org/10.1016/j.soilbio.2022.108761.

Bárcenas-Moreno, G., García-Orenes, F., Mataix-Solera, J., Mataix-Beneyto, J., Bååth, E., 2011. Soil microbial recolonisation after a fire in a Mediterranean forest. Biol. Fertil. Soils 47, 261–272. https://doi.org/10.1007/s00374-010-0532-2.

Bates, D., Mächler, M., Zurich, E., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Benavides-Solorio, J.D.D., MacDonald, L.H., 2005. Measurement and prediction of post-fire erosion at the hillslope scale, Colorado Front Range. Int. J. Wildland Fire 14, 457–474. https://doi.org/10.1071/WF05042.

Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A., Alexander, H., Alm, E.J., Arumugam, M., Asnicar, F., 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat. Biotechnol. 37, 852–857.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J. E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J., 2009. Fire in the earth system. Science 324, 481–484. https://doi.org/10.1126/science.1163886.

Brundrett, M.C., Tedersoo, L., 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. 220, 1108–1115. https://doi.org/10.1111/nph.14976.

Bruns, T.D., Chung, J.A., Carver, A.A., Glassman, S.I., Suen, G., 2020. A simple pyrocosm for studying soil microbial response to fire reveals a rapid, massive response by Pyronema species. PLoS One 15 (3), e0222691.

Cairney, J.W.G., Bastias, B.A., 2007. Influences of fire on forest soil fungal communities. Can. J. For. Res. 207–215. https://doi.org/10.1139/X06-190.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat. Methods 13, 581–583. https://doi.org/10.1038/nmeth.3869.

Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Lozupone, C.A., Turnbaugh, P.J., Fierer, N., Knight, R., 2011. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. Proc. Natl. Acad. Sci. U.S.A. 108 (supplement_1), 4516–4522.

Chambers, M.E., Fornwalt, P.J., Malone, S.L., Battaglia, M.A., 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. For. Ecol. Manage. 378, 57–67. https://doi.org/10.1016/j.foreco.2016.07.001.

Chapman, T.B., Veblen, T.T., Schoennagel, T., 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93, 2175–2185. https://doi.org/10.1890/11-1055.1.

Collins, B.J., Rhoades, C.C., Hubbard, R.M., Battaglia, M.A., 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. For. Ecol. Manage. 261, 2168–2175. https://doi.org/10.1016/j.foreco.2011.03.016.

Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. Science 365. https://doi.org/10.1126/science.aav0550.

Day, N.J., Dunfield, K.E., Johnstone, J.F., Mack, M.C., Turetsky, M.R., Walker, X.J., White, A.L., Baltzer, J.L., 2019. Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada. Glob. Chang. Biol. 25, 2310–2324. https://doi.org/10.1111/gcb.14641.

Diskin, M., Rocca, M.E., Nelson, K.N., Aoki, C.F., Romme, W.H., 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. Can. J. For. Res. 41, 782–792. https://doi.org/10.1139/x10-247.

Dooley, S.R., Treseder, K.K., 2012. The effect of fire on microbial biomass: A meta-analysis of field studies. Biogeochemistry 109, 49–61. https://doi.org/10.1007/s10533-011-9633-8.

Dove, N.C., Hart, S.C., 2017. Fire reduces fungal species richness and in situ mycorrhizal colonization: A meta-analysis. Fire Ecology 13, 37–65. https://doi.org/10.4996/fireecology.130237746.

Enright, D.J., Frangioso, K.M., Isobe, K., Rizzo, D.M., Glassman, S.I., 2022. Mega-fire in redwood tanoak forest reduces bacterial and fungal richness and selects for pyrophilous taxa that are phylogenetically conserved. Mol. Ecol. 31, 2475–2493. https://doi.org/10.1111/mec.16399.

Ferrenberg, S., Knelman, J.E., Jones, J.M., Beals, S.C., Bowman, W.D., Nemergut, D.R., 2014. Soil bacterial community structure remains stable over a 5-year chronosequence of insect-induced tree mortality. Frontiers in Microbiology 5. https://doi.org/10.3389/fmicb.2014.00681.

Fierer, N., 2017. Embracing the unknown: Disentangling the complexities of the soil microbiome. Nat. Rev. Microbiol. 15, 579–590. https://doi.org/10.1038/nrmicro.2017.87.

Fierer, N., Schimel, J.P., Holden, P.A., 2003. Variations in microbial community composition through two soil depth profiles. Soil Biol. Biochem. 35, 167–176. https://doi.org/10.1016/S0038-0717(02)00251-1.

Fierer, N., Jackson, J.A., Vilgalys, R., Jackson, R.B., 2005. Assessment of soil microbial community structure by use of taxon-specific quantitative PCR assays. Appl. Environ. Microbiol. 71, 4117–4120. https://doi.org/10.1128/AEM.71.7.4117-4120.2005.

Filippidou, S., Wunderlin, T., Junier, T., Jeanneret, N., Dorador, C., Molina, V., Johnson, D.R., Junier, P., 2016. A combination of extreme environmental conditions favor the prevalence of endospore-forming firmicutes. Front. Microbiol. 7, 1–11. https://doi.org/10.3389/fmicb.2016.01707.

Fletcher, L.A., 1981. Soil survey of Jackson County area, Colorado. USDA Soil Conservation Service and Forest Service and Colorado Agriculture Experiment Station. U.S. Government Printing Office.

Fornwalt, P.J., Rhoades, C.C., Hubbard, R.M., Harris, R.L., Faist, A.M., Bowman, W.D., 2018. Short-term understory plant community responses to salvage logging in beetle-affected lodgepole pine forests. For. Ecol. Manage. 409, 84–93. https://doi.org/10.1016/j.foreco.2017.10.056.

Fox, S., Sikes, B.A., Brown, S.P., Cripps, C.L., Glassman, S.I., Hughes, K., Semenova-Nelsen, T., Jumpponen, A., 2022. Fire as a driver of fungal diversity — A synthesis of current knowledge. Mycologia 114 (2), 215–241.

Gill, N.S., Turner, M.G., Brown, C.D., Glassman, S.I., Haire, S.L., Hansen, W.D., Pansing, E.R., St Clair, S.B., Tomback, D.F., 2022. Limitations to Propagule Dispersal Will Constrain Postfire Recovery of Plants and Fungi in Western Coniferous Forests. BioScience. doi:10.1093/biosci/biab139.

Glassman, S.I., Peay, K.G., Talbot, J.M., Smith, D.P., Chung, J.A., Taylor, J.W., Vilgalys, R., Bruns, T.D., 2015. A continental view of pine-associated ectomycorrhizal fungal spore banks: A quiescent functional guild with a strong biogeographic pattern. New Phytol. 205, 1619–1631. https://doi.org/10.1111/nph.13240.

Glassman, S.I., Levine, C.R., Dirocco, A.M., Battles, J.J., Bruns, T.D., 2016. Ectomycorrhizal fungal spore bank recovery after a severe forest fire: Some like it hot. ISME J. 10 (5), 1228–1239. https://doi.org/10.1038/ismej.2015.182.

Glassman, S.I., Weihe, C., Li, J., Albright, M.B.N., Looby, C.I., Martiny, A.C., Treseder, K. K., Allison, S.D., Martiny, J.B.H., 2018. Decomposition responses to climate depend on microbial community composition. Proc. Natl. Acad. Sci. U.S.A. 115 (47), 11994–11999.

Glassman, S.I., Randolph, J.W.J., Saroa, S.S., Capocchi, J.K., Walters, K.E., Pulido-Chavez, M.F., Larios, L., 2023. Prescribed versus wildfire impacts on exotic plants and soil microbes in California grasslands. Appl. Soil Ecol. 185, 104795 https://doi.org/10.1016/j.apsoil.2022.104795.

Griffin, J.M., Turner, M.G., Simard, M., 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For. Ecol. Manage. 261, 1077–1089. https://doi.org/10.1016/j.foreco.2010.12.031.

He, T., Lamont, B.B., Pausas, J.G., 2019. Fire as a key driver of Earth's biodiversity. Biol. Rev. 94, 1983–2010. https://doi.org/10.1111/brv.12544.

Holden, S.R., Rogers, B.M., Treseder, K.K., Randerson, J.T., 2016. Fire severity influences the response of soil microbes to a boreal forest fire. Environ. Res. Lett. 11 (3), 035004.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manage. 140, 227–238. https://doi.org/10.1016/S0378-1127(00)00282-6.

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., Ryan, M.G., 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. Ecol. Monogr. 83, 49–66. https://doi.org/10.1890/11-1454.1.

Kayes, L.J., Tinker, D.B., 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. For. Ecol. Manage. 263, 57–66. https://doi.org/10.1016/j.foreco.2011.09.035.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16 (8), 406–411.

Kindt, R., Coe, R., 2005. Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre.

Kipfer, T., Moser, B., Egli, S., Wohlgemuth, T., Ghazoul, J., 2011. Ectomycorrhiza succession patterns in Pinus sylvestris forests after stand-replacing fire in the Central Alps. Oecologia 167, 219–228. https://doi.org/10.1007/s00442-011-1981-5.

Kõljalg, U., Larsson, K.H., Abarenkov, K., Nilsson, R.H., Alexander, I.J., Eberhardt, U., Erland, S., Høiland, K., Kjøller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A.F.S., Tedersoo, L., Vrålstad, T., Ursing, B.M., 2005. UNITE: A database providing web-based methods for the molecular identification of ectomycorrhizal fungi. New Phytol. 166, 1063–1068. https://doi.org/10.1111/j.1469-8137.2005.01376.x.

Kozich, J.J., Westcott, S.L., Baxter, N.T., Highlander, S.K., Schloss, P.D., 2013. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the miseq illumina sequencing platform. Appl. Environ. Microbiol. 79, 5112–5120. https://doi.org/10.1128/AEM.01043-13.

Kranz, C., Whitman, T., 2019. Short communication: Surface charring from prescribed burning has minimal effects on soil bacterial community composition two weeks post-fire in jack pine barrens. Appl. Soil Ecol. 144, 134–138. https://doi.org/10.1016/j.apsoil.2019.07.004.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452, 987–990. https://doi.org/10.1038/nature06777.

Liu, C.M., Kachur, S., Dwan, M.G., Abraham, A.G., Aziz, M., Hsueh, P.-R., Huang, Y.-T., Busch, J.D., Lamit, L.J., Gehring, C.A., Keim, P., Price, L.B., 2012. FungiQuant: a broad-coverage fungal quantitative real-time PCR assay. BMC Microbiol. 12 (1), 255.

Lotan, J.E., Critchfield, W.B., 1990. Pinus contorta Dougl. ex. Loud. lodgepole pine, in: Silvics of North America. US Department of Agriculture Forest Service Washington, DC, pp. 302–315.

Love, M.I., Huber, W., Anders, S., 2014. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biol. 15 https://doi.org/10.1186/s13059-014-0550-8.

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet. Journal 17, 10–12.

McMurdie, P.J., Holmes, S., Watson, M., 2013. Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. PLoS One 8 (4), e61217.

Meddens, A.J.H., Hicke, J.A., 2014. Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA. For. Ecol. Manage. 322, 78–88. https://doi.org/10.1016/j.foreco.2014.02.037.

Metz, M.R., Frangioso, K.M., Meentemeyer, R.K., Rizzo, D.M., 2011. Interacting disturbances: wildfire severity affected by stage of forest disease invasion. Ecol. Appl. 21 (2), 313–320.

Mikkelson, K.M., Lozupone, C.A., Sharp, J.O., 2016. Altered edaphic parameters couple to shifts in terrestrial bacterial community structure associated with insect-induced tree mortality. Soil Biology and Biochemistry 95, 19–29. https://doi.org/10.1016/j.soilbio.2015.12.001.

Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2011. Fire effects on temperate forest soil C and N storage. Ecological 21 (4), 1189–1201.

Nelson, A.R., Narrowe, A.B., Rhoades, C.C., Fegel, T.S., Daly, R.A., Roth, H.K., Chu, R.K., Amundson, K.K., Young, R.B., Steindorff, A.S., Mondo, S.J., Grigoriev, I.V., Salamov, A., Borch, T., Wilkins, M.J., 2022. Wildfire-dependent changes in soil microbiome diversity and function. Nat. Microbiol. 7 (9), 1419–1430.

Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol. 20, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006.

Nuñez, M.A., Horton, T.R., Simberloff, D., 2009. Lack of belowground mutualisms hinders Pinaceae invasions. Ecology 90, 2352–2359. https://doi.org/10.1890/08-2139.1.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package.

Owen, S.M., Patterson, A.M., Gehring, C.A., Sieg, C.H., Baggett, L.S., Fulé, P.Z., 2019. Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a ponderosa pine forest. Soil Biol. Biochem. 139, 107616 https://doi.org/10.1016/j.soilbio.2019.107616.

Parks, S.A., Holsinger, L.M., Panunto, M.H., Jolly, W.M., Dobrowski, S.Z., Dillon, G.K., 2018. High-severity fire: Evaluating its key drivers and mapping its probability across western US forests. Environ. Res. Lett. 13 (4), 044037.

Parks, S.A., Dobrowski, S.Z., Shaw, J.D., Miller, C., 2019. Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. Ecosphere 10. https://doi.org/10.1002/ecs2.2651.

Parsons, A., Robichaud, P.R., Lewis, S.A., Napper, C., Clark, J.T., 2010. Field Guide for Mapping Post-Fire Soil Burn Severity.

Pec, G.J., Karst, J., Taylor, D.L., Cigan, P.W., Erbilgin, N., Cooke, J.E.K., Simard, S.W., Cahill, J.F., 2017. Change in soil fungal community structure driven by a decline in ectomycorrhizal fungi following a mountain pine beetle (Dendroctonus ponderosae) outbreak. New Phytol. 213 (2), 864–873.

Pérez-Izquierdo, L., Clemmensen, K.E., Strengbom, J., Granath, G., Wardle, D.A., Nilsson, M.-C., Lindahl, B.D., Gilliam, F., 2021. Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest. J. Ecol. 109 (1), 504–518.

Pérez-Valera, E., Verdú, M., Navarro-Cano, J.A., Goberna, M., 2018. Resilience to fire of phylogenetic diversity across biological domains. Mol. Ecol. 27, 2896–2908. https://doi.org/10.1111/mec.14729.

Pérez-Valera, E., Verdú, M., Navarro-Cano, J.A., Goberna, M., 2020. Soil microbiome drives the recovery of ecosystem functions after fire. Soil Biol. Biochem. 149, 107948.

Pierson, D.N., Robichaud, P.R., Rhoades, C.C., Brown, R.E., 2019. Soil carbon and nitrogen eroded after severe wildfire and erosion mitigation treatments. Int. J. Wildland Fire 28, 814–821. https://doi.org/10.1071/WF18193.

Pressler, Y., Moore, J.C., Cotrufo, M.F., 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128, 309–327. https://doi.org/10.1111/oik.05738.

Pulido-Chavez, M.F., Alvarado, E.C., DeLuca, T.H., Edmonds, R.L., Glassman, S.I., 2021. High-severity wildfire reduces richness and alters composition of ectomycorrhizal fungi in low-severity adapted ponderosa pine forests. For. Ecol. Manage. 485, 118923.

Pulido-Chavez, M.F., Randolph, J.W.J., Zalman, C., Larios, L., Homyak, P.M., Glassman, S.I., 2023. Rapid bacterial and fungal successional dynamics in first year after chaparral wildfire. Mol. Ecol. 32 (7), 1685–1707.

Qin, Q., Liu, Y., 2021. Changes in microbial communities at different soil depths through the first rainy season following severe wildfire in North China artificial Pinus tabulaeformis forest. J. Environ. Manage. 280, 111865 https://doi.org/10.1016/j.jenvman.2020.111865.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. Nucleic Acids Res. 41 https://doi.org/10.1093/nar/gks1219.

R Core Team, 2021. R: A Language and Environment for Statistical Computing.

Radeloff, V.C., Helmers, D.P., Kramer, H.A., Mockrin, M.H., Alexandre, P.M., Bar-Massada, A., Butsic, V., Hawbaker, T.J., Martinuzzi, S., Syphard, A.D., Stewart, S.I., 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. Proc. Natl. Acad. Sci. U.S.A. 115 (13), 3314–3319.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions, BioScience.

Reckner, R., 1998. Soil survey of the Albany County area, Wyoming. USDA Natural Resources Conversation Service and University of Wyoming Agriculture Experiment Station, the Forest Service and the Department of Interior Bureau of Land Management. U.S. Government Printing Office.

Rhoades, C.C., Entwistle, D., Butler, D., 2011. The influence of wildfire extent and severity on streamwater chemistry, sediment and temperature following the Hayman Fire, Colorado. Int. J. Wildland Fire 20, 430–442. https://doi.org/10.1071/WF09086.

Rhoades, C.C., Fegel, T.S., Zaman, T., Fornwalt, P.J., Miller, S.P., 2021. Are soil changes responsible for persistent slash pile burn scars in lodgepole pine forests? For. Ecol. Manage. 490, 119090.

Rhoades, C.C., Fegel, T.S., Hubbard, R.M., Chambers, M.E., 2022. Limited seed viability in long-dead serotinous lodgepole pine trees in the Southern Rockies, USA. For. Ecol. Manage. 526, 120565 https://doi.org/10.1016/j.foreco.2022.120565.

Rhoades, C.C., Fornwalt, P.J., 2015. Pile burning creates a fifty-year legacy of openings in regenerating lodgepole pine forests in Colorado. For. Ecol. Manage. 336, 203–209. https://doi.org/10.1016/j.foreco.2014.10.011.

Rhoades, C.C., McCutchan, J.H., Cooper, L.A., Clow, D., Detmer, T.M., Briggs, J.S., Stednick, J.D., Veblen, T.T., Ertz, R.M., Likens, G.E., Lewis, W.M., 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. Proc. Natl. Acad. Sci. U.S.A. 110 (5), 1756–1760.

Rhoades, C.C., Hubbard, R.M., Elder, K., 2017. A Decade of Streamwater Nitrogen and Forest Dynamics after a Mountain Pine Beetle Outbreak at the Fraser Experimental Forest, Colorado. Ecosystems 20, 380–392. https://doi.org/10.1007/s10021-016-0027-6.

Rhoades, C.C., Pelz, K.A., Fornwalt, P.J., Wolk, B.H., Cheng, A.S., 2018. Overlapping bark beetle outbreaks, salvage logging and wildfire restructure a lodgepole pine ecosystem. Forests 9, 1–15. https://doi.org/10.3390/f9030101.

Rhoades, C.C., Hubbard, R.M., Hood, P.R., Starr, B.J., Tinker, D.B., Elder, K., 2020. Snagfall the first decade after severe bark beetle infestation of high-elevation forests in Colorado, USA. Ecol. Appl. 30 https://doi.org/10.1002/eap.2059.

Rillig, M.C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C.A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J., Yang, G., 2019. The role of multiple global change factors in driving soil functions and microbial biodiversity. Science 366, 886–890. https://doi.org/10.1126/science.aay2832.

Seaver, F.J., 1909. Studies in Pyrophilous Fungi—I. The Occurrence and Cultivation of Pyronema. Mycologia 1, 131–139. https://doi.org/10.1080/00275514.1909.12020584.

Semenova-Nelsen, T.A., Platt, W.J., Patterson, T.R., Huffman, J., Sikes, B.A., 2019. Frequent fire reorganizes fungal communities and slows decomposition across a heterogeneous pine savanna landscape. New Phytol. 224, 916–927. https://doi.org/10.1111/nph.16096.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis. Academic Press, London.

Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G., van Wagtendonk, J.W., 2014. Temperate and boreal forest mega-fires: Characteristics and challenges. Front. Ecol. Environ. 12, 115–122. https://doi.org/10.1890/120332.

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., Lloret, F., 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21 (2), 243–252.

Sun, S., Li, S., Avera, B.N., Strahm, B.D., Badgley, B.D., Löffler, F.E., 2017. Soil bacterial and fungal communities show distinct recovery patterns during forest ecosystem restoration. Appl. Environ. Microbiol. 83 (14) https://doi.org/10.1128/AEM.00966-17.

Talbot, J.M., Bruns, T.D., Taylor, J.W., Smith, D.P., Branco, S., Glassman, S.I., Erlandson, S., Vilgalys, R., Liao, H.-L., Smith, M.E., Peay, K.G., 2014. Endemism and functional convergence across the North American soil mycobiome. Proc. Natl. Acad. Sci. U.S.A. 111 (17), 6341–6346.

Taudière, A., Richard, F., Carcaillet, C., 2017. Review on fire effects on ectomycorrhizal symbiosis, an unachieved work for a scalding topic. For. Ecol. Manage. 391, 446–457. https://doi.org/10.1016/j.foreco.2017.02.043.

Taylor, D.L., Walters, W.A., Lennon, N.J., Bochicchio, J., Krohn, A., Caporaso, J.G., Pennanen, T., Cullen, D., 2016. Accurate estimation of fungal diversity and abundance through improved lineage-specific primers optimized for Illumina amplicon sequencing. Appl. Environ. Microbiol. 82 (24), 7217–7226.

Treseder, K.K., Mack, M.C., Cross, A., 2004. Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. Ecol. Appl. 14, 1826–1838. https://doi.org/10.1890/03-5133.

Treu, R., Karst, J., Randall, M., Pec, G.J., Cigan, P.W., Simard, S.W., Cooke, J.E.K., Erbilgin, N., Cahill, J.F., 2014. Decline of ectomycorrhizal fungi following a mountain pine beetle epidemic. Ecology 95 (4), 1096–1103.

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849. https://doi.org/10.1890/10-0097.1.

Twieg, B.D., Durall, D.M., Simard, S.W., 2007. Ectomycorrhizal fungal succession in mixed temperate forests. New Phytol. 176, 437–447. https://doi.org/10.1111/j.1469-8137.2007.02173.x.

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S. Statistics and Computing. New York: Springer.

Ward, E.B., Duguid, M.C., Kuebbing, S.E., Lendemer, J.C., Bradford, M.A., 2022. The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests. New Phytol. 235 (5), 1701–1718.

Whitman, T., Whitman, E., Woolet, J., Flannigan, M.D., Thompson, D.K., Parisien, M.A., 2019. Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. Soil Biol. Biochem. 138, 107571 https://doi.org/10.1016/j.soilbio.2019.107571.

Yang, S., Zheng, Q., Yang, Y., Yuan, M., Ma, X., Chiariello, N.R., Docherty, K.M., Field, C. B., Gutknecht, J.L.M., Hungate, B.A., Niboyet, A., le Roux, X., Zhou, J., 2020. Fire affects the taxonomic and functional composition of soil microbial communities, with cascading effects on grassland ecosystem functioning. Glob. Chang. Biol. 26, 431–442. https://doi.org/10.1111/gcb.14852.