

Stand age and fire return interval shape soil microbial communities in young, postfire lodgepole pine stands

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ABSTRACT

As wildfire activity increases globally, understanding how soil microbial communities vary in young postfire forests and the effect of short fire-return intervals on these communities becomes increasingly important for anticipating postfire ecosystem function. We asked how soil bacterial and fungal communities varied during early postfire stand development in lodgepole pine (*Pinus contorta* var. *latifolia*) forests, and whether a short-interval (16 yr) reburn altered those trajectories. We sampled soils in 6-, 22-, and 34-year-old stands in Grand Teton National Park (Wyoming, USA) and used high-throughput sequencing to assess community composition, environmental drivers, and fire responsive taxa. Bacterial and fungal community composition shifted with stand age under typical fire return intervals. For fungi, Ascomycetes declined in relative abundance with stand age whereas Basidiomycetes increased, consistent with the expected increase in ectomycorrhizal fungi associated with lodgepole pine. Litter mass and soil nutrient properties explained 28.6 % and 23.9 % of variance in bacterial and fungal community composition, respectively. Following the short-interval stand-replacing fire, bacterial communities in 6-year-old stands closely resembled nearby stands (22-year-old) that did not reburn, whereas fungal communities more closely resembled nearby 6-year-old stands that burned in the historical long (>100 yr) fire-return interval. These results suggest that microbial recovery during early stand development in postfire forests is shaped by changes in resource availability, and that short fire-return intervals may have greater effects on fungi than on bacteria.

1. Introduction

Warmer temperatures, earlier snowmelt, and longer fire seasons are increasing fire frequency, size, and severity, thereby transforming swaths of mature conifer forests into young postfire stands (Abatzoglou and Williams, 2016; Boer et al., 2020; Bond and Keeley, 2005; Bowman, 2020; McDowell et al., 2020; Parks et al., 2018; Westerling, 2016; Westerling et al., 2006). This shift toward early seral forests alters ecosystem structure and function (Swanson et al., 2011; Turner, 2010) and may reshape the soil microbial communities that regulate key ecosystem processes like carbon (C) and nitrogen (N) cycling (Fierer et al., 2007). However, how environmental characteristics shape soil microbial communities during early succession (i.e., during the window of aggradation prior to reaching peak productivity) is uncertain (Bardgett and van der Putten, 2014; Jansson and Hofmockel, 2020). This is a critical knowledge gap as the likelihood of young forests burning at

high severity before recovering from previous fire (i.e., “short-interval (SI)” fires) in systems historically shaped by long fire-return intervals rises (Baltzer et al., 2021; Prichard et al., 2017; Turner et al., 2019; E. Whitman et al., 2019; Woollet et al., 2022). It is unclear whether there are consistent patterns of soil microbial community structure and composition during the early decades of stand development, what factors explain such patterns, and how these patterns change with SI fires.

High-severity, stand-replacing wildfire affects soil microbial communities through direct and indirect mechanisms (Agbeshie et al., 2022; Certini, 2005; Keeley, 2009; Mataix-Solera et al., 2011). Directly, microbial biomass and diversity are typically reduced through increased soil temperatures and subsequent cell death (Johnson et al., 2023; Pressler et al., 2019; Q. Wang et al., 2012), although these effects may be limited to the upper few centimeters (Busse et al., 2010; Turner et al., 1999). Indirectly, fire alters soil properties (e.g., pH, moisture retention, and nutrient availability), competition (amongst microbes and between

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microbes and plants), and the biomass and composition of plant communities (e.g., death of symbiotic mycorrhizal hosts and changes in litter inputs and quality; Ferrenberg et al., 2013; Hart et al., 2005). In conifer forests, fungal diversity and abundance often decline rapidly after fire and community composition shifts from Basidiomycetes and symbiotic mycorrhizal fungi to Ascomycetes and saprotrophic fungi (Adkins et al., 2020; Day et al., 2019; Dooley and Treseder, 2012; Holden et al., 2013; Kipfer et al., 2011; Pulido-Chavez et al., 2021; Twieg et al., 2007). Bacterial responses are less consistent, with diversity and richness either declining (Sáenz de Miera et al., 2020) or remaining stable (Pressler et al., 2019; T. Whitman et al., 2019) after severe fire. As forests recover and succession proceeds, the direct effects of fire diminish, and environmental and biotic factors likely play a stronger role in shaping soil microbial community composition (Albert-Belda et al., 2023; Johnson et al., 2023; Zhou et al., 2017).

Fire fundamentally reshapes soil microbial communities, but knowledge of how long changes initiated by fire persist and how they change through early forest development is limited (Dove et al., 2020; McLauchlan et al., 2020). Changes caused by fire vary in how long they last in different ecosystems and can range from months or years (e.g., pH, nutrient status) to decades (e.g., plant biomass) (Certini, 2005; Hart et al., 2005). As forests recover from fire and plant biomass increases, litter inputs also increase and the source of carbon microbes are accessing may change (Pellegrini et al., 2020). Inputs from litter and roots are a main source of C into soil pools and help regulate microbial communities and soil processes (Dove et al., 2019). The carbon source selects for microbes that fit different niches, so if forest soil carbon sources vary among stand-age classes, the composition of forest soil microbial communities may also differ (Feng et al., 2022). While much research on whole community and individual taxa responses has focused on the days to months following fire, some bacterial taxa (e.g., operational taxonomic units or OTUs from the genera *Massilia*, *Blastococcus*, *Arthrobacter*) remain enriched several years after fire, though to a lesser extent than in the first year (Whitman et al., 2022). By five years, bacterial communities begin to resemble those in unburned areas, and the link between taxa with traits that foster postfire survival (e.g., fast growth potential which is important in the short term) and high-severity fire is weakened (Whitman et al., 2022). How long fire-adapted taxa persist through early stand development or following repeat fires is unknown, or if short-interval fires select for different microbial communities altogether.

Climate change is driving novel fire regimes, including SI fires in forests adapted to infrequent (>100 yr) high-severity fires, which can alter soil chemical and physical properties, extracellular enzyme activity, and microbial respiration (Agbeshie et al., 2022; Dove et al., 2020; Knelman et al., 2015; Pellegrini et al., 2020). Short-interval fires may disrupt soil microbial communities that develop after typical fire-return intervals and are resistant or resilient to fire (Shade et al., 2012). This is important because the state of the soil microbial community when disturbance occurs can influence ecosystem response and recovery (Jansson and Hofmockel, 2020). This influence of past disturbance on the soil microbial community response to more recent disturbance has been seen for fire, and other disturbances like drought, logging, and herbivory (Hinojosa et al., 2019; Kostenko et al., 2012; G. D. Martin et al., 2022; Norris et al., 2023). Much of the research on microbial resilience to changing fire regimes comes from low-severity fire systems experiencing high-severity burns, where increased severity can reduce microbial biomass, alter microbial composition, and potentially slow postfire recovery by disrupting plant-microbe interactions (Adkins et al., 2020; Pulido-Chavez et al., 2021; Weber et al., 2014). In such ecosystems, fire-adapted fungi and bacteria can persist, but their composition may shift due to altered resource availability and competition dynamics (Nelson et al., 2022; Whitman et al., 2022). Reburns in forests adapted to infrequent, high-severity fires provide another lens for assessing microbial resilience and understanding recovery trajectories after repeat disturbance (Barreiro and Díaz-Raviña, 2021; Shade et al., 2012). As SI fires become more

common in forest ecosystems, understanding how repeated disturbances shape microbial community recovery will be important for predicting long-term ecosystem responses under climate change.

We studied lodgepole pine (*Pinus contorta* var. *latifolia*) forests in Grand Teton National Park, WY along a chronosequence of postfire stand development (6, 22, and 34 years) following stand-replacing fire in a typical long-interval (LI) fire regime, and an area where stand-replacing fire recurred in a 16-year-old regenerating forest (SI) to answer three questions: (1) How does soil microbial community composition vary during early stand development? We expected that (a) bacterial and fungal communities would be distinct among 6-, 22-, and 34-year-old forests; and (b) the relative abundance of fire-responsive taxa would decrease as stand age increases. (2) What factors explain variation in soil microbial community composition during early stand development? We expected litter and soil nutrient properties to be most important for explaining variation in bacterial and fungal communities because these resources shape microbial interactions and drive shifts in community composition. (3) Do soil microbial communities respond differently to short-interval reburns compared to typical fire-return intervals? We expected that (a) soil bacterial and fungal community composition will be distinct between short- and long-interval burns of the same post-fire age, and (b) soil bacterial communities will have a greater relative abundance of fire-responsive bacteria such as *Blastococcus*, *Arthrobacter*, and *Massilia* following SI fire compared to long-interval burns of the same age due to larger changes in soil nutrient availability. We further expected that soil fungal communities would have a higher relative abundance of fire-responsive and saprotrophic fungi compared to a long-interval reburn of the same age, due to reductions in ectomycorrhizal fungi (EcM) associated with reduced host tree recovery.

2. Methods

2.1. Study area

This study was conducted in July 2022 along the Rockefeller Parkway portion of Grand Teton National Park (GRTE) in northwestern Wyoming, USA, including areas where postfire microbial responses (e.g., the spatial structure of microbial lipid abundances and fungi to bacteria ratios) were assessed previously (Smithwick et al., 2012). Subalpine conifer forests cover most of the vegetated portion of this region and are dominated by lodgepole pine. Summers are relatively short and dry (14.2 °C and 3.6 cm mean July temperature and precipitation, respectively) while winters are relatively long, cold, and wet (−10.4 °C and 9.9 cm for January; 1991–2020, Snake River Weather Station WY, NOAA, 2024). Most precipitation falls as snow, with an annual average of 682-cm (1991–2020, Snake River Weather Station, WY, NOAA, 2024), though snowpack has declined steadily since the 1980s (Hostetler et al., 2021). Soils are classified as Sandy- or Loamy-skeletal, mixed, Typic Humicrypts from the Moran-Gestrin-Leighcan and Matcher, stony-Moran-Tolby families (National Cooperative Soil Survey, USDA Natural Conservation Service).

Subalpine lodgepole pine forests in the GYE are adapted to high-severity (stand-replacing fires) that occurred historically at 100–300-year intervals during exceptionally warm, dry periods throughout the Holocene (Higuera et al., 2011). We studied aggrading lodgepole pine forests in areas that experienced stand-replacing burns from three fires. The 48,157-ha Huck Fire burned from August 20 to September 13, 1988 during the extensive 1988 fire season (Rothermel et al., 1994). The 1280-ha Glade Fire burned just south of Yellowstone National Park in GRTE from August 16 to September 10, 2000. Both fires burned through mature lodgepole pine forests that had established after high-severity fire in the late 1800s (Loope and Gruell, 1973). The 8750-ha Berry Fire burned from July 25th through early September 2016 in similar mature forest but also reburned areas of 16-year-old lodgepole pine regeneration recovering from the 2000 Glade Fire, thus including both long and short fire-return intervals (Fig. 1).

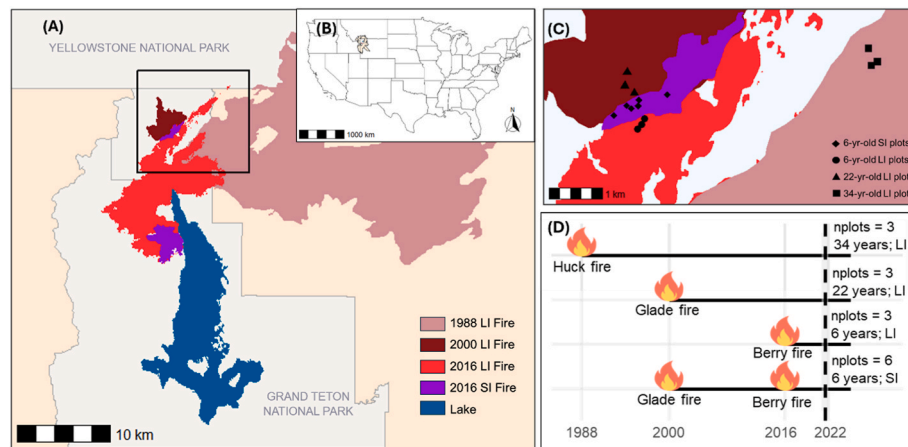


Fig. 1. Location and fire boundaries of the study area. (A) Fire perimeters of the long-interval (LI) 1988 Huck (pink), 2000 Glade (dark red), and 2016 Berry (bright red) fires. Purple areas are areas of short-interval fire (SI) where 16-year-old stands burned in 2016. Sampling area is enclosed in the black box. (B) Location of the Greater Yellowstone Ecosystem in the continental United States. (C) Zoomed section showing the location of sampled plots where color and shape indicate stand age and fire return interval. (D) Timeline of stand ages and fire return intervals in sampled lodgepole pine plots. Black horizontal lines represent each stand, labeled with the number of plots (n_{plots}), stand age, and type of fire return interval (LI or SI). Fire events are shown with flame icons, and the vertical dashed, shaded line indicates the year all sites were sampled (2022). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. Plot selection

Within each long-interval fire, we established three 0.25-ha plots (50 m $\times$ 50 m) oriented due north and separated by at least 100 m ($n = 9$; Fig. 1). All plots had burned as stand-replacing fire (100 % of prefire trees were killed). Plots were purposefully chosen to be geographically close (within 5 km), at the same elevation (~ 2150 m) on flat terrain, and with similar soils and similar climate to avoid confounding environmental effects. Within the SI fire, we sampled soil microbial communities in six plots that were burned at high severity in both fires (2000 Glade and 2016 Berry). These plots were established in 2017, one year postfire (Turner et al., 2019), and were resampled in 2021–2022 to assess effects of SI fire on N stocks and fluxes (Turner et al., 2025). Augmenting our study with samples from these reburned plots allowed us to compare soil microbial communities (a) in stands of the same age (6 yr) that shared the most recent fire (2016) but burned at long vs. short interval, and (b) in stands that all burned in the previous long-interval fire (2000) but did or did not reburn in 2016 (Fig. 1).

2.3. Stand characteristics

Stand characteristics in the nine LI plots were sampled in July 2022 as part of the pre-treatment measurements for an ongoing field experiment. Each 0.25 ha plot was divided into four 20-m $\times$ 20-m quadrants in the NW, NE, SW, and SE corners to sample vegetation, soil, and litter. To quantify aboveground lodgepole biomass, lodgepole pine stems in the postfire cohort were counted along two 2-m $\times$ 20-m belt transects on the inner side of each quadrant's east and west boundaries. Basal diameter was recorded for the closest tree at distance of 4, 5, 6, and 7-m radiating from the quadrant center in each cardinal and sub-cardinal direction, respectively ($n = 8$ trees per quadrant). Aboveground biomass was predicted for each tree using locally developed allometric equations (Copenhaver and Tinker, 2014; Turner et al., 2004), averaged and multiplied by stand density at the quadrant level, and then averaged by plot.

Soil samples for chemical analysis were sampled by collecting three mineral soil cores (2-cm diameter and 15-cm depth) within a 3-m radius of each quadrant center. If present, litter and organic (O) horizons (typically minimal) were removed before the cores were pooled by quadrant, sieved to 2 mm in the field, and air dried in paper bags at ambient room temperature for soil property analyses. Litter samples (O_i) were collected adjacent to soil samples within 27.5 $\times$ 27.5 cm quadrats

(~ 756.25 cm²); any woody material was removed, and samples were air dried in paper bags. Litter samples were transported back to the lab, and oven-dried at 60 °C to obtain mass per area. To obtain C and N concentrations, soil and litter were dried at 105 °C and 60 °C, respectively, ground to a powder, homogenized, and subsampled for chemical composition analysis using a Thermo Flash EA1112 (Grassland Ecology Lab, University of Wisconsin-Madison). Soil pH was determined from the supernatant of a 1:1 soil:CaCl₂ (0.1 M) solution using a micro pH electrode connected to a Thermo Scientific Orion Star A111 benchtop pH meter.

2.4. Microbial community sampling

Soil samples for microbial analysis were collected on July 29–30, 2022 from all 15 plots (i.e., the nine plots that varied in stand age and the six reburned plots established previously). Soils were sampled in the same formation as described above (total of 1 composite sample per subplot, or 4 samples per plot), and all field equipment was cleaned with ethanol between plots. Prior to collecting soil samples for DNA extraction, the weather was typical (warm, dry, sunny), and there had been no rain events for three weeks, which we expect would lessen variation between soil microbial communities introduced by differences in recent precipitation history. Microbial samples were sieved (<2 mm) in the field and pooled by subplot, then stored at -20 °C for up to one week before being transported to Madison, WI, and stored at -80 °C until DNA extraction.

2.5. DNA extraction, amplification, and sequencing

Total genomic DNA was extracted for each soil sample with one blank extraction (identical methods but using empty tubes) per 11 samples using a DNeasy PowerLyzer PowerSoil DNA extraction kit (QIAGEN, Germantown, MD) following the manufacturer's instructions. Extracted DNA was amplified in triplicate PCR reactions targeting the 16S rRNA gene v4 with 515f and 806r primers for bacteria (Walters et al., 2016) and the ITS2 region with 5.8s and ITS4-Fun primers for fungi (Taylor et al., 2016). Primers also contained barcodes and Illumina sequencing adapters (Kozich et al., 2013). Amplified DNA was confirmed via gel electrophoresis, then normalized and pooled using a SequalPrep Normalization (96) Plate Kit (ThermoFisher Scientific, Waltham, MA). Library cleanup for pooled samples (including blanks) used a Wizard SV Gel and PCR Clean-Up System A9282 (Promega,

Madison, WI). The pooled and cleaned libraries were sent to the UW-Madison Biotechnology Center for 2 x 250 paired-end (bacteria) and 2 x 300 paired-end (fungi) Illumina MiSeq sequencing.

2.6. Bioinformatics

16S rRNA gene amplicon sequences were processed using the DADA2 pipeline (Callahan et al., 2016) within the QIIME2 framework (Bolyen et al., 2019). Demultiplexed sequences were analyzed for quality with FastQC. Sequences were then dereplicated, denoised, and used to determine operational taxonomic units (OTUs, or amplicon sequencing variant). Chimeric sequences and singletons were removed, and OTUs identified as chloroplasts and mitochondria were also excluded. Primers for the 16S region targeted both bacteria and archaea, but because communities were dominated by bacteria (>99 % of total reads), we will refer to bacteria when discussing communities determined by sequencing the 16S gene. For ITS2 reads, we quality filtered and trimmed sequences using ITSxpress (Rivers et al., 2018), followed by the same DADA2 workflow described above. Taxonomy was assigned using the SILVA database taxonomy classifiers for bacteria (Quast et al., 2013) and UNITE rDNA ITS database for fungi (Abarenkov et al., 2023; Bokulich et al., 2018; Kõljalg et al., 2020). Fungal OTUs were designated into functional groups using the FUNGuild database (Nguyen et al., 2016). Only functional assignments with 'highly probable' confidence were retained.

2.7. Data analysis

We assessed differences in stand characteristics, litter mass, and soil and litter nutrient properties (% C, % N, and C: N) among the nine long-interval fire plots (6-, 22-, and 34-year-old stands) using ANOVAs and post-hoc Tukey's HSD tests ($p < 0.05$). Prior to analysis, all response variables were tested for normality and transformed accordingly. Lodgepole pine biomass and litter mass were $\log_{10}$ transformed; percent cover data and soil and litter % C and % N were arc-sine-square root transformed; and soil and litter C:N were square root transformed.

All analyses of microbial communities were conducted separately for bacterial and fungal communities. To obtain plot-level measurements and avoid pseudo-replication, observed OTUs were summed across the four samples within each plot, after which relative abundance was calculated. To assess differences in microbial community diversity and composition among long-interval postfire stand-age classes (6-, 22-, and 34-year-old stands; Question 1), we first used permutational analysis of variance (PERMANOVA) on Bray-Curtis dissimilarity matrices of relative abundance data to test if community composition was significantly different among stand ages (Okansen et al., 2013) and plotted the dissimilarities using principal coordinate analysis (PCoA). Differences in the relative abundance of taxa at the phylum level among stand ages were assessed with ANOVA followed by a post-hoc Tukey HSD test. Because an assumption of PERMANOVA is equal variance among groups, an analysis of multivariate homogeneity of group dispersions was performed. To assess if community dissimilarity decreased with increasing stand age, differences in beta diversity (calculated as the average distance of communities to group spatial mean) among age classes were evaluated (Anderson, 2006). Richness of the soil microbial community was described using the weighted linear regression model of OTU richness estimates, which weights observations based on variance (Willis et al., 2017). Normality was tested with a Shapiro test, then ANOVA was used to test the effect of stand age on mean estimated richness, followed by a post-hoc Tukey HSD test. Differences in fungal guild abundances among stand ages were assessed using Kruskal-Wallis rank-sum tests followed by pairwise Wilcoxon rank-sum tests with Benjamini-Hochberg false discovery rate (FDR) correction. To determine which specific taxa were differentially abundant in each age class, we estimated the $\log_2$ -fold change in the relative abundance of bacterial and fungal OTUs using the Wald testing procedure and a false discovery

rate cutoff of 0.05 (B. D. Martin et al., 2020).

To assess if soil and litter physical or chemical properties were predictors of bacterial and fungal community composition (Question 2), distance-based redundancy analysis (dbRDA) was performed to evaluate how much variation in community composition could be explained by soil and litter and physical or chemical properties. We used Spearman's rank order correlation analysis to assess relationships between predictor variables and did not include variables that were highly correlated ($r \geq 0.3$) in the same model of soil microbial community composition. Variance partitioning was used to assess the proportions of variation explained by each variable.

To test if short-interval fires alter microbial communities (Question 3), we compared microbial communities in the six returns to (a) the three 6-year old (i.e., these share the most recent 2016 fire), and (b) to the three 22-yr that burned in 2000 and did not reburn in 2016 (i.e., these share only the 2000 fire). We first used permutational analysis of variance on Bray-Curtis dissimilarity matrices of relative abundance data to test if fire return interval was a significant predictor of community composition in stands of the same age, then plotted the dissimilarities using principal coordinate analysis (PCoA). Differences in the relative abundance of taxa at the phylum level, beta diversity, richness, and differential abundance of OTUs were assessed as described in question 1, but with fire return interval as the response variable. All statistical analyses and figures were produced in R 4.4.0 (R Core Team 2024).

3. Results

3.1. Stand characteristics in aggrading lodgepole pine forests

Total lodgepole pine aboveground biomass was significantly higher in older stands, about 2.5 times greater relative to the 22-year-old stands and nine times greater in the 22-year-old stands relative to the 6-year-old stands (Table 1). Some soil and litter physical or chemical properties differed with stand age (Table 1). Soil percent N did not differ between the 6- and 22-year-old stands but increased by 33 % from the 22- to 34-year-old stands (Table 1). Soil percent C also increased with stand age, showing a 46 % increase in the 34-year-old stand relative to the 6-year-old stand, resulting in no difference in soil C:N ratios (Table 1). Soil pH was moderately acidic and did not vary with stand age (Table 1). Litter mass was significantly higher in the 34-year-old stands (0.44 Mg ha^{-1}) than in the 6-year-old stands (8.01 Mg ha^{-1} ; Table 1) and was strongly positively correlated with lodgepole pine biomass ($r = 0.9$, $p = 0.001$). Litter percent N and C:N ratio did not vary with stand age, but litter percent C was greater in the 34 vs. 6-yr-old stands (Table 1).

3.2. Question 1: soil microbial community diversity, richness, and composition during early stand development after long (>100 yr) fire return intervals

Soil bacterial and fungal community composition were distinct among 6-, 22-, and 34-year-old stands (PERMANOVA; bacteria, $r^2 = 0.47$, $p = 0.004$; fungi, $r^2 = 0.40$, $p < 0.001$; Table 2; Fig. 2). Among bacteria, Actinobacteriota ($25.2 \pm 1.08 \%$) and Proteobacteria ($23.9 \pm 1.13 \%$) comprised nearly half of the sequences detected in soils, followed by Acidobacteriota ($15.4 \pm 0.64 \%$), Verrucomicrobiota ($11.9 \pm 0.94 \%$), Chloroflexi ($8.54 \pm 1.48 \%$), and Planctomycetota ($7.37 \pm 0.55 \%$). Despite high-level similarities in bacterial community structure across stand ages, we identified 24 bacterial OTUs as being differentially abundant in at least one age class (Fig. 3). Responses varied within a phylum, with some taxa becoming enriched and others depleted as stand age increased. These differences were largely explained by an increase in Proteobacteria in the 34-year-old stands compared to younger stands ($p = 0.011$) and a decrease in Planctomycetota with increasing stand age ($p < 0.001$). Only two OTUs, both from the phylum Actinobacteria, were differentially abundant between the youngest and oldest stands.

Table 1

Biomass, productivity, mineral soil, and litter characteristics for 6-, 22- and 34-year-old postfire lodgepole pine stands ($n = 3$). Mean values are followed by one standard error in parentheses. Differences among means were assessed using an ANOVA on transformed variables (see Methods). Letters next to values denote significant differences among age classes (Tukey's test, $\alpha = 0.05$).

Variable	Berry (6-yrs)	Glade (22-yrs)	Huck (34-yrs)	<i>p</i> -value
	Mean	Mean	Mean	
Stand characteristics				
Lodgepole pine density (stems/ha)	162,229 ^b (8,279)	5,823 ^a (728)	14,115 ^a (3,129)	
Total lodgepole pine aboveground biomass (Mg ha ⁻¹)	6.21 ^c (0.7)	48.9 ^b (2.5)	120.6 ^a (21.9)	<0.001
Litter and soil characteristics				
Forest floor litter				
Litter C (%)	48.3 ^b (0.12)	50.1 ^{ab} (1.13)	51.7 ^a (0.43)	0.036
Litter N (%)	1.24 (0.10)	1.08 (0.06)	1.28 (0.02)	0.164
Litter C:N ratio	39.8 (3.02)	47.0 (1.96)	40.7 (0.85)	0.101
Litter mass (Mg ha ⁻¹)	0.50 ^c (0.11)	3.38 ^b (0.30)	8.01 ^a (0.43)	<0.001
Soil (0–15 cm)				
Soil C (%)	2.17 ^b (0.27)	2.43 ^{ab} (0.19)	3.46 ^a (0.26)	0.021
Soil N (%)	0.09 ^b (0.01)	0.10 ^{ab} (0.01)	0.14 ^a (0.01)	0.012
Soil C:N ratio	23.5 (1.10)	23.0 (0.47)	25.1 (0.93)	0.287
pH	4.26 (0.08)	4.51 (0.07)	4.65 (0.14)	0.112

Table 2

PERMANOVA results for the Bray-Curtis dissimilarities of bacterial and fungal OTU relative abundances with stand age. $n = 3$.

	df	SS	Pseudo F	R^2	P
Bacteria	2	0.547	2.616	0.47	0.004
Fungi	2	1.494	2.039	0.40	0.001

Specifically, an OTU in the family Mycobacteriaceae was enriched in the 34-year-old stands, while an OTU in the family Solirubrobacteraceae was depleted. The rest of the differentially abundant taxa were between the 22-year-old stand and the 6- or 34-year-old stands. Chloroflexi peaked in 22-year-old stands ($p < 0.001$), but its relative abundance did not differ between the 6- and 34-year-old stands. Notably, Chloroflexi was the only phylum to have OTUs that were consistently enriched in a single stand age (22-yr-old) and made up 14.7 % of the community at that age versus 6.5 % and 5.5 % in the 6- and 34-year-old communities, respectively. Additionally, other taxa shared between the 6- and 34-year-old stands were classified as *Candidatus udaeobacter* (Verrucomicrobiota), an OTU in Planctomycetota, and an OTU in Proteobacteria.

Fungal communities were dominated by Basidiomycota (54.21 $\pm$ 0.05 %) and Ascomycota (40.78 $\pm$ 0.05 %), comprising ~95 % of ITS2 sequences detected in soils. The most abundant genera detected were *Inocybe* (phylum Basidiomycota) and *Wilcoxina* (phylum Ascomycota), making up over 22.4 % of all sequences. Fungal compositional changes were largely explained by an increase in the relative abundance of Basidiomycota (34.49 $\pm$ 4.7 % to 65.9 $\pm$ 4.8 %) and decrease in the relative abundance of Ascomycota (57.2 $\pm$ 4.26 % to 30.4 $\pm$ 4.25 %) as stand age increased. The relative abundance of fungal functional groups

supported this trend. Ectomycorrhizal relative abundance increased between the 6- and 22-year-old stands ($p < 0.001$) and 6- and 34-year-old stands ($p = 0.022$). Ectomycorrhizal genera *Cortinarius*, *Piloderma*, *Rhizopogon*, and *Amphinema* (phylum Basidiomycota) became more enriched in the 34-year-old stands compared to the 22- and 6-year-old stands (Fig. 4). By contrast, *Wilcoxina* (phylum Ascomycota) were more depleted in the 34-year-old stands than the 22- or 6-year-old stands. Ericoid mycorrhizal genera *Leohumicola* and *Calypotryma* (phylum Ascomycota) were also more enriched in the 6-year-old stands compared to the 22- and 34-year-old stands (Fig. 4). The EcM genus and known symbiont of lodgepole pine *Suillus* had a mixed response, with *Suillus brevipes* decreasing with stand age and *Suillus tomentosus* increasing with stand age (Fig. 4).

Beta diversity did not differ among age classes indicating that differences in microbial community composition were not explained by within-group variability, and within-age class dissimilarity did not decrease with stand age (Fig. 2). Despite differences in community composition, there were no detectable differences in mean estimated species richness among age classes for bacteria ($p = 0.096$) or fungi ($p = 0.62$).

3.2.1. Fire responsive microbial taxa

Several of the taxa that were differentially abundant across stand ages belong to known fire-adapted or responsive groups. Among bacteria, an OTU in the *Micrococcaceae* family was depleted in the 22-year-old stands compared to the 6-year-old stands, and OTUs from the phylum Actinobacteria (genera *Actinomadura*, *Conexibacter*) were depleted in the 34-year-old stands relative to the 22-year-old stands. Among fungi, OTUs in the family *Pyronemataceae* and genus

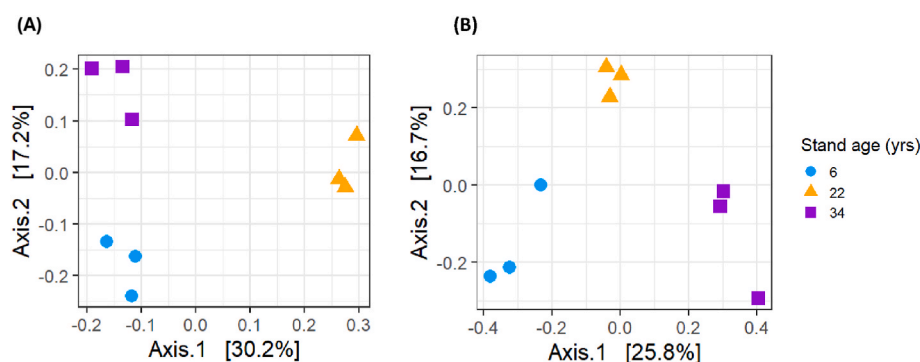


Fig. 2. PCoA ordination of Bray-Curtis dissimilarities of bacterial (A) and fungal (B) community composition for all samples ($n = 3$). Both color and shape indicate stand age. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

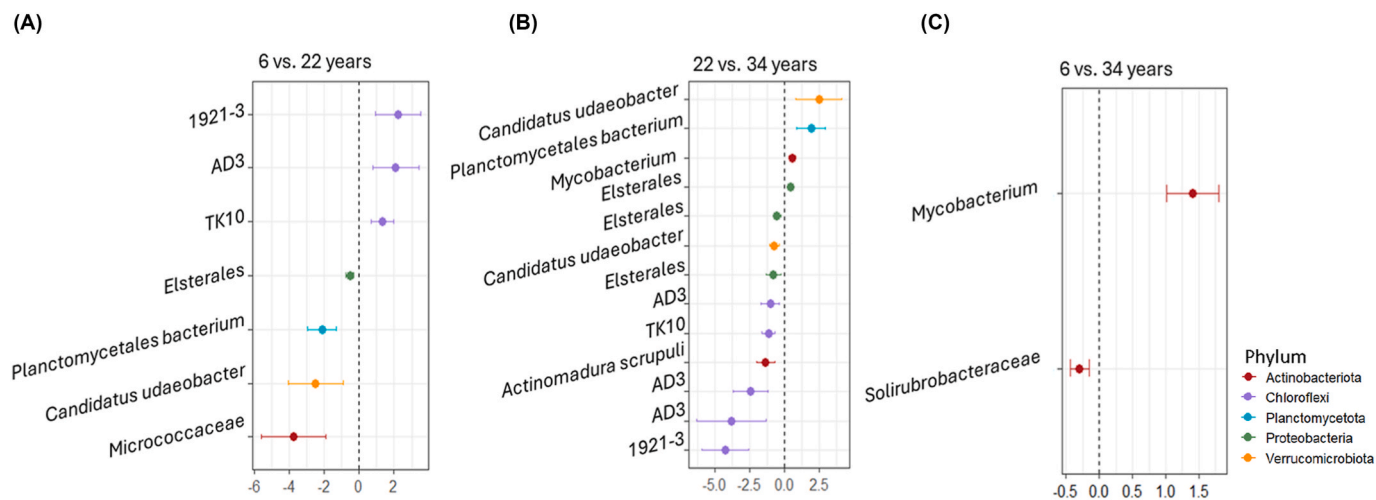


Fig. 3. Differentially abundant bacterial OTUs among stand ages. Each point represents a single bacterial OTU, and colored horizontal lines indicate a 95 % confidence interval. Points are colored by phylum and indicate significantly depleted (negative) or enriched (positive) taxa in the older stand. Panels show differentially abundant taxa between the a) 6- and 22-year-old stands, b) 22- and 34-year-old stands, c) 6- and 34-year-old stands.

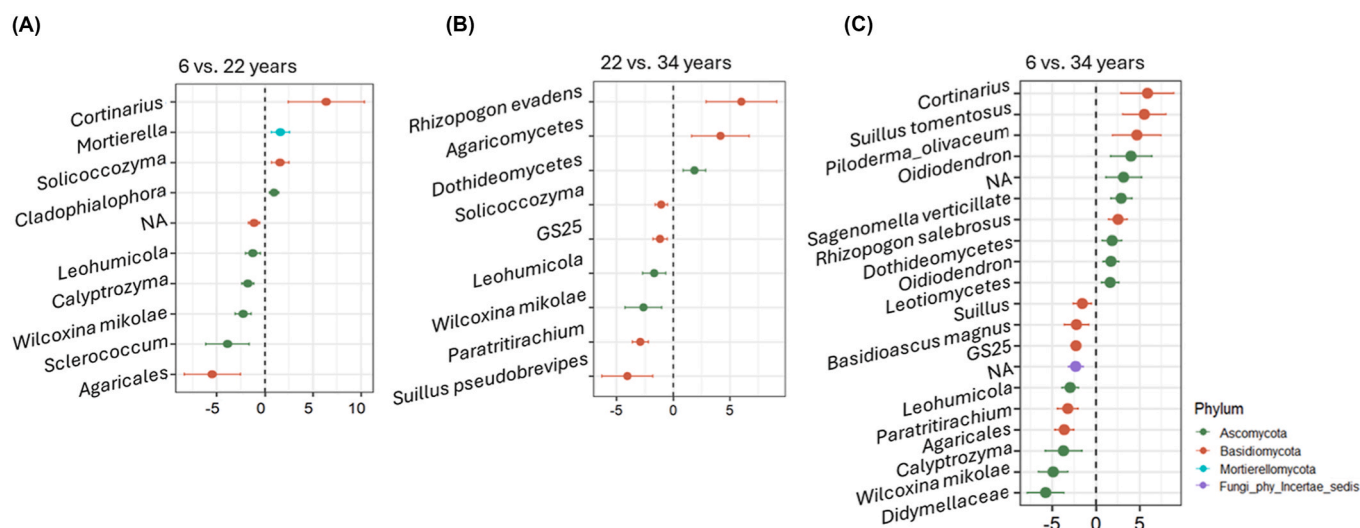


Fig. 4. Differentially abundant fungal OTUs among stand ages. Each point represents a single bacterial OTU, and colored horizontal lines indicate a 95 % confidence interval. Points are colored by phylum and indicate significantly depleted (negative) or enriched (positive) taxa in the older stand. Panels show differentially abundant taxa between the a) 6- and 22-year-old stands, b) 22- and 34-year-old stands, c) 6- and 34-year-old stands.

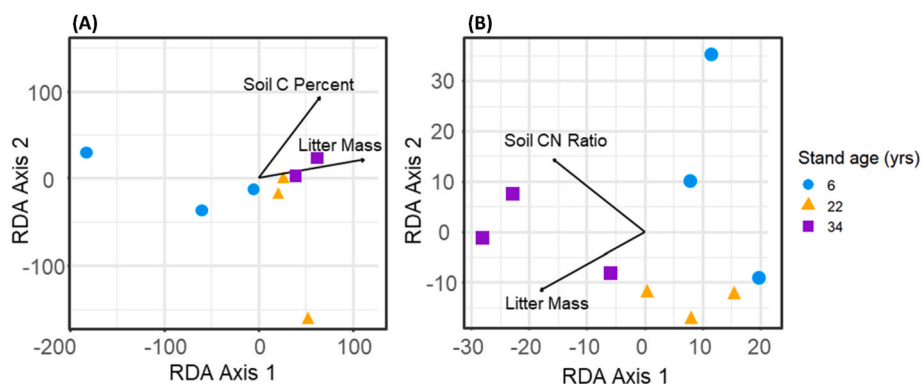


Fig. 5. Distance-based redundancy analysis (dbRDA) of bacterial (A) and fungal (B) soil microbial community composition and environmental variables across postfire stand age classes. Points represent plots colored and shaped by stand age, and black arrows indicate the direction and strength of correlations with environmental variables.

Calypotrozima were enriched in the 6-year-old stands compared to the 22- and 34-year-old stands. Other taxa that were enriched in the 6-year-old stand compared to the 34-year-old stand included OTUs in the genera *Paratritirachium* and *Basidioascus*. Taxa that were depleted in the youngest stands compared to the older stands included OTUs from the genera *Rhizopogon*, *Oidiodendron*, *Piloderma*, and *Cortinarius*.

3.3. Question 2: Explanatory factors of soil microbial community composition

Distance-based redundancy analysis indicated that litter mass and soil C: N were the most important factors affecting bacterial community composition across stand ages. Together they explained 28.6 % of the variation in bacterial community composition (Fig. 5a). Variance partitioning showed that soil C: N uniquely explained 12.7 % of variation, while litter mass uniquely explained 14.5 %, with the remaining explained variation shared between variables. For fungal community composition, soil C % and litter mass were the most explanatory variables, together explaining 23.9 % of variation (Fig. 5b). Variance partitioning further revealed that litter mass uniquely explained 13.9 % of variation and soil C % explained 8.8 %.

3.4. Question 3: Effects of SI fire on soil microbial community composition

Bacterial and fungal community composition were distinct between SI and LI burns of the same age (PERMANOVA; bacteria, $r^2 = 0.33$, $p = 0.002$; fungi, $r^2 = 0.35$, $p < 0.001$; Fig. 6). However, despite compositional differences, richness of both bacterial and fungal communities did not differ between 6-year-old stands recovering after SI and LI fires. Differences in bacterial community composition at the phylum level were primarily driven by a decrease in Proteobacteria ($p = 0.04$) and increase in Chloroflexi ($p < 0.001$) in the stands recovering from SI fire. Fungal communities in stands recovering from SI fire were similarly dominated by Ascomycota ($46.9 \pm 3.69\%$) and Basidiomycota ($35.7 \pm 4.3\%$), but unclassified taxa accounted for over 10 % of sequences compared to 2.5 % in the 6-year-old stands recovering from LI fire.

Two bacterial taxa identified as known fire responders were OTUs in the order Gaiellales were enriched in the 6-year-old stands recovering from LI fire. Among taxa enriched in stands recovering from SI vs. LI fire of the same age, two belonged to the phylum Chloroflexi and one to the phylum Myxococcota (genus *Anaeromyxobacter*), a diazotrophic taxon. Overall, the bacterial community of 6-year-old stands recovering from SI fire was more similar to the 22-year-old stands recovering from LI fire (which have the same stand history until 2016, when part of the 16-year-old regrowth burned again) than the 6-year-old stands recovering from LI fire (which shared the most recent fire). Only two bacterial OTUs were

differentially abundant between 6-year-old stands recovering from SI fire and 22-year-old stands recovering from LI fire, including *Micrococcaceae* (genus *Arthrobacter*), which was enriched in stands recovering from fire SI stands.

By contrast, known fire-responsive fungi were more evident in stands recovering from SI fire compared to stands recovering from LI fire of the same age. Taxa that were enriched include the ascomycete *Rhodotarzettia rosea* (family *Pyronemataceae*) and the basidiomycete *Geminibasidium*. Compared to 22-year-old stands recovering from LI fire, EcM genera including *Suillus*, *Cortinarius*, *Hebeloma*, and *Inocybe* were depleted in SI stands (Fig. 7d).

4. Discussion

This study showed that differences in soil microbial communities among lodgepole pine stands recovering from LI fires were primarily driven by community composition rather than richness or beta diversity (i.e., how similar self-replicates are from the same treatment). The strong role of soil nutrient properties and litter mass in explaining variation in community composition suggests that differences in microbial communities reflect changing environmental conditions as forests recover rather than direct and more immediate effects of fire, such as high soil temperatures and increased pH (Barreiro and Díaz-Raviña, 2021). This is supported by the inconsistent enrichment of known pyrophilous taxa in 6-year-old compared to 22- and 34-yr old stands. We also found that novel SI fire altered soil microbial community composition compared to LI fires of the same age, with fire return interval explaining 33 % and 35 % of the variation in bacterial and fungal community composition respectively. Further, pyrophilous bacterial taxa were depleted after the SI fire while pyrophilous fungi were enriched compared to LI fire of the same age. Reductions in postfire conifer regeneration resulting from SI fire may have stronger effects on soil fungal communities than on bacterial communities.

4.1. Question 1: How does soil microbial community composition change throughout early stand development?

4.1.1. LI soil microbial community diversity, richness, and composition

Our expectation that bacterial and fungal soil community composition would be distinct throughout early stand development was supported. Importantly, all plots had similar environmental conditions (all fires were high-severity and stand-replacing in subalpine forests with similar soil type and elevation), allowing us to more confidently evaluate the effects of postfire stand development on soil microbial communities at different stand ages, rather than just site-specific differences. However, since same-age plots were clustered together within the same fire, it is unclear whether these differences reflect true successional

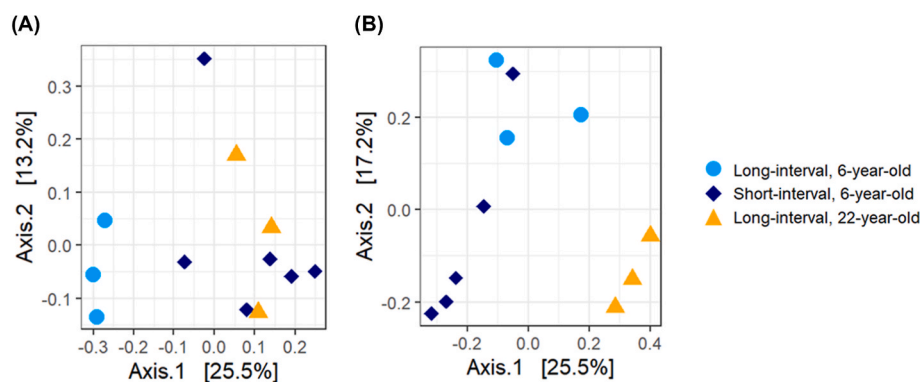


Fig. 6. PCoA ordination of Bray-Curtis dissimilarities between bacterial (A) and fungal (B) community composition for all samples ($n = 3$ for LI; $n = 6$ for SI). Color and shape indicate stand age and fire return interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

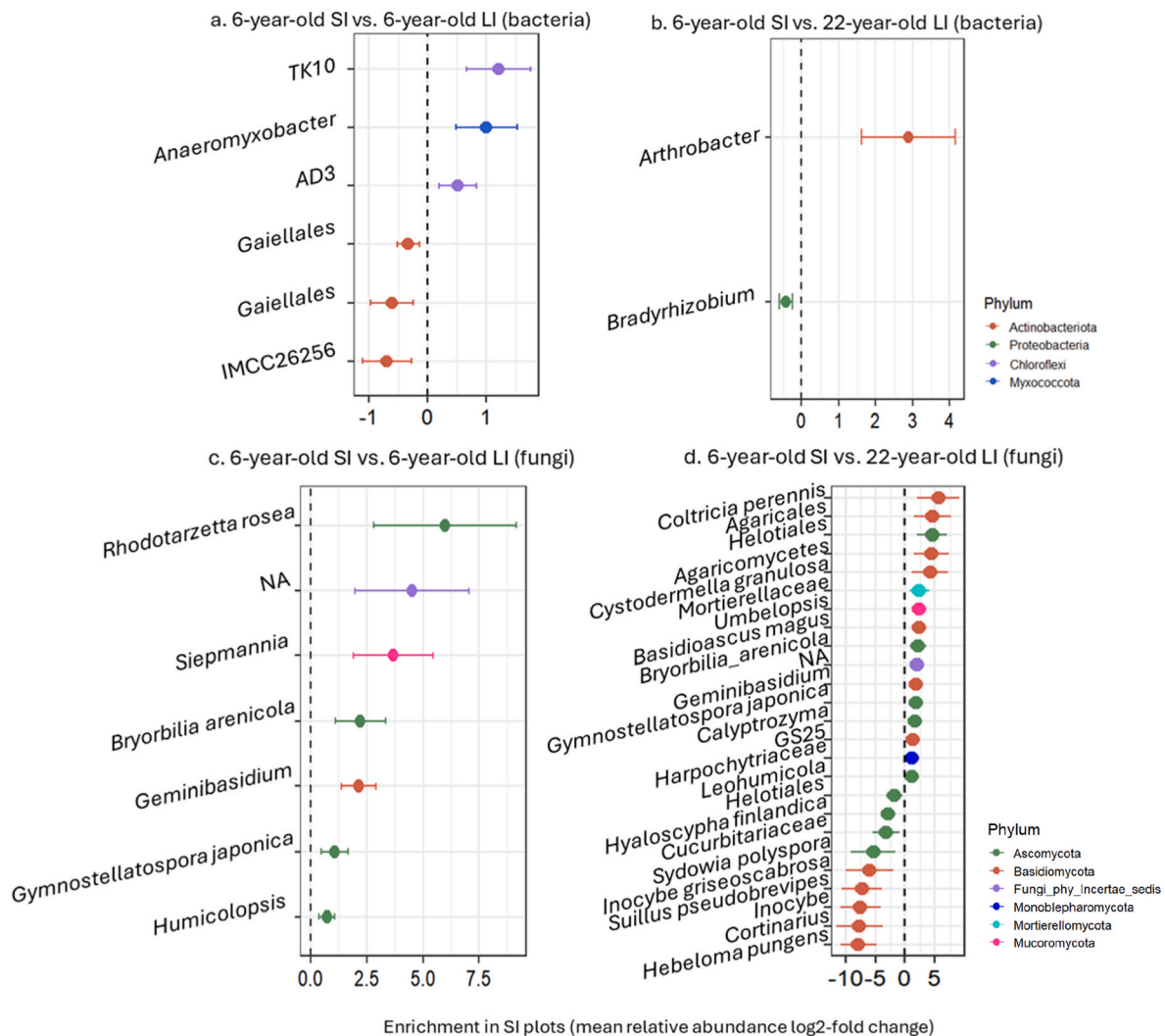


Fig. 7. Differentially abundant bacterial and fungal between stand types. The top panel shows bacterial OTUs in a) 6-year-old SI vs. 6-year-old LI stands and b) 6-year-old SI vs. 22-year-old LI stands, and the bottom panel shows fungal OTUs in c) 6-year-old SI vs. 6-year-old LI stands and d) 6-year-old SI vs. 22-year-old LI stands. Each point represents a single OTU, with colors indicating phylum and family on the y-axis. Horizontal lines show 95 % confidence intervals. Positive values indicate OTUs enriched in the SI stands, while negative values indicate depletion. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

changes in microbial communities over time or differences among fire events (Jiang et al., 2021; Knelman et al., 2015). Although direct causal relationships cannot be established, these shifts with stand development suggest microbial responses no longer reflect a direct response of high-severity fire (Adkins et al., 2020).

Stand development was associated with large compositional shifts in both bacterial and fungal communities. Changes in community dominance can be important indicators of how microbial communities assemble as stands recover from fire, as has been documented in plant communities (Abella and Fornwalt, 2015; Turner et al., 1997). For bacteria, these changes with stand age were primarily characterized by an increase in Proteobacteria, a phylum with many copiotrophic taxa that thrive in soils with greater organic inputs (Fierer et al., 2007; Wang et al., 2022). Interestingly, Chloroflexi were only enriched in the 22-year-old stands and had a higher relative abundance compared to the younger and older stands. Chloroflexi is a widely distributed forest soil phylum, and its taxa often increase in abundance after disturbances including fire (Zhou et al., 2020), drought (Maisnam et al., 2023) and forest conversion (Lan et al., 2021). Other studies have found positive correlations with Chloroflexi and total N (Li et al., 2019), which we did not observe. Chloroflexi is also generally considered to be a phylum with

many oligotrophic taxa (which dominate in soils with lower C availability) (Dragone et al., 2024), though this cannot explain the increase as the 22-year-old stands had a slightly lower soil C:N ratio.

Our finding that Ascomycetes decreased while Basidiomycetes increased with stands age is consistent with patterns of postfire fungal community assembly in many ecosystems (Fox et al., 2022; Pulido-Chavez et al., 2023). Ascomycetes typically dominate immediately after fire, driven by loss of EcM due to host mortality and increases in abundance of pyrophilous fungi (Ammittzoll et al., 2021; Day et al., 2019; Holden et al., 2013; Ondik et al., 2022; Orumaa et al., 2022; Pérez-Izquierdo et al., 2021). Notably, several common post-fire EcM fungi including *Wilcoxina*, *Geopyxis*, and *Sphaerospora* are ascomycetes, suggesting a potential shift in post-fire EcM communities towards ascomycetes as stands develop (Tederloo et al., 2006; Pulido-Chavez et al., 2021). Like some previous studies, we found low relative abundance of EcM in more recently burned (younger) stands (Caiafa et al., 2023; Enright et al., 2022; Pulido-Chavez et al., 2021). We also found that EcM community composition differed and EcM relative abundance increased with stand age, similar to other forest chronosequences (Hagenbo et al., 2018; Odriozola et al., 2020). This shift likely reflects changes in nutrient availability and carbon supplied from host trees as

competitive dynamics are altered and may select for taxa with different functional traits, as EcM rely on plant-derived carbon (Treseder et al., 2004).

Within the EcM community, taxa in the genus *Suillus* have high host specificity and are known common symbionts of lodgepole pine (Bradbury et al., 1998; Lofgren et al., 2024). *Suillus brevipes*, which became depleted as stand age increased, is a rapid colonizer of young, postfire stands, may tolerate a wider range of soil conditions, and can disperse and grow quickly after disturbance (Bradbury et al., 1998). As the canopy begins to close and competition with other EcM species increases, the relative abundance, presence of fruiting bodies, and root tip colonization of *Suillus brevipes* decreases (Visser, 1995). For example, a study on the degradation of proteins by EcM fungi showed that all tested species preferentially inhabiting mature forests were characterized by high secreted protease activity. However, the protease activity of *Suillus brevipes* was cell-wall bound (Rineau et al., 2016), meaning that most of the enzymes they may use to break down proteins stay attached to the cell wall rather than being released into the soil, which would help take advantage of a more organic N rich environment (Koide et al., 2014). While often still present immediately after fire, *Suillus tomentosus* is common in older and later successional stands (Douglas et al., 2005; Kranabetter et al., 2006). The *Suillus* genus has been used as a model system for studying EcM associations but less is known about the ecological differences among *Suillus* species, which is important for understanding within-species competition and elucidating the impacts of fungal trait variation (Lofgren et al., 2024).

Differences in microbial communities among stand ages were explained by changes in composition, and our expectation that within-stand community dissimilarity would decline with stand age was not supported. Rather, beta-diversity and richness remained stable, suggesting that changes in microbial communities as stand age increases were driven by species turnover rather than an overall change in diversity. This aligns with findings from other postfire ecosystems, where microbial richness shifted rapidly after fire but stabilized within decades (Caiafa et al., 2023), suggesting the direct effect of fire on microbial richness is short-lived. Many studies report an initial postfire decline in microbial richness and diversity (Enright et al., 2022; Nelson et al., 2022; Pulido-Chavez et al., 2023), possibly due to the rapid proliferation of a few microbial groups adapted to postfire conditions (e.g., fast growth strategies that allow them to survive in harsh conditions over short periods of time; Pressler et al., 2019). However, both laboratory and field studies have shown that richness recovers quickly (<1 yr) after high-severity fire (Pérez-Valera et al., 2017; Pulido-Chavez et al., 2023; Sáenz de Miera et al., 2020). Even in boreal forests, where cold temperatures and acidic soils slow soil recovery after high-severity fire compared to temperate forests (Treseder et al., 2004), fungal species richness remained stable over a chronosequence that spanned 10–181 years (Orumaa et al., 2022). Soil microbial communities can exhibit high levels of functional redundancy (Allison and Martiny, 2008), which may contribute to their relatively rapid stabilization.

4.1.2. Fire responsive microbial taxa

Our expectation that fire-responsive bacterial taxa would be greater in relative abundance in younger stands was partially supported. Among individual OTUs, an OTU in the family *Micrococcaceae* was enriched in the 6-year-old stands compared to the 22-year-old stands, and had a 100 % match (using the NCBI BLAST database) to several taxa in the genus *Arthrobacter* that have been shown to increase in relative abundance after fire (Whitman et al., 2019). Such taxa were also enriched in a study that amended the soil with pyrogenic organic matter, suggesting they may degrade recalcitrant carbon sources and have an advantage in postfire soils (Fernández-González et al., 2017; Zeba et al., 2024). A study of lodgepole pine forests in Colorado also found that multiple pyrophilous taxa persisted for at least five years (Caiafa et al., 2023). However, besides this one OTU, previously identified fire-responsive taxa were not enriched in the youngest (6-year-old) stands, consistent

with the short-lived proliferation of certain taxa after fire (Caiafa et al., 2023). The lack of earlier data on fire-responsive taxa in the GYE prevents us from assessing how abundance may have changed in the immediate years following fire. In the older stands (34 yrs), an OTU in the family *Xanthobacteraceae* (100 % NCBI BLAST match to *Bradyrhizobium lupini*) was enriched. This species has been isolated from nodules of species of *Lupinus*, a genus present at low abundance in our plots and associated with symbiotic nitrogen fixation. Members of *Bradyrhizobia* genera are often associated with symbiotic nitrogen fixation (Young and Haukka, 1996).

Counter to our expectations, pyrophilous fungal taxa were not consistently enriched in the youngest stands. Pyrophilous Ascomycetes, including members of family *Pyronemataceae* and the genus *Calypotrozyma*, were enriched in the 6-year-old stand, consistent with their ability to inhabit oligotrophic and stressful environments (Day et al., 2019; Pérez-Izquierdo et al., 2021; Whitman et al., 2019). However, there were also several taxa enriched in the 34-year-old stands that are known common fire responders. The presence and enrichment of pyrophilous fungi at all stand ages may indicate that the conditions associated with postfire proliferation of these taxa are no longer strong drivers of community composition. For example, taxa in *Pyronemataceae* thrive in C-limited environments, supported by genome sequencing that showed enrichment in enzymes that degrade pyrolyzed organic matter (Fischer et al., 2021; Steindorff et al., 2022). As soil C and aboveground vegetation recover, communities adapted to these postfire conditions are replaced and may more closely resemble pre-fire communities (Adkins et al., 2020).

4.2. Question 2: What explains soil microbial community composition

Our expectation that soil and litter nutrient properties would be strong drivers of soil microbial community composition during early stand development was partially supported. Although soil C: N did not vary with stand age, it emerged as a key explanatory variable for bacterial community composition, underscoring the role of local (within-stand) variability in soil quality and organic matter accumulation in regulating microbial communities (Štursová et al., 2016). In a study done two years after fire in this same region, microbial and ecological variables showed congruence at spatial scales of 10–14 m, suggesting that there is a coupling between pattern (microbial communities) and process (here, N-mineralization; Smithwick et al., 2012). By contrast, a study done in 15-year-old lodgepole pine forests did not find effects of within-stand structure created by coarse wood and pine saplings on soil microbial community composition (Metzger et al., 2008). However, community composition differed among stands, suggesting that processes that occur at broader scales may have a strong influence over local scales (Metzger et al., 2008).

Litter mass, which increased with stand age, was more important for explaining variation in community composition than litter nutrient properties. Litter additions have been shown to increase soil C and microbial biomass, with rates of litter input serving as a critical control of belowground processes (Feng et al., 2022). Exclusion of plant litter inputs at forest sites in Oregon reduced soil organic carbon pools and their availability to the soil microbial community, concomitantly affecting microbial biomass, community composition, and function (Dove et al., 2019). Litter provides a relatively accessible source of nutrients to microbes, while soil C:N is processed by different microbial guilds over time (Schimel and Schaeffer, 2012).

4.3. Question 3: Effects of SI fire on soil microbial community composition

Our results showed that in forests adapted to long-interval fire, soil microbial community composition would differ in stands that experienced an anomalous short-interval fire (Fig. 6). Some prior studies have focused on microbial community responses to increased fire frequency

or successive fires, but those have mainly focused on ecosystems adapted to short- or intermediate-interval fire regimes (Albert-Belda et al., 2023; Bowd et al., 2022; Greenwood et al., 2023; Shen et al., 2016), or only focused on bacteria (Woolet et al., 2022). Examining the responses of bacterial and fungal communities together revealed distinct responses that could have implications for future ecosystem response to disturbance.

Differences in microbial community composition among stands of the same age but recovering from LI vs. SI fire may be explained by several factors. First, there might be insufficient time for full recovery of microbial communities between fires before burning recurs. Short-interval stands showed a drastic reduction in postfire tree regeneration and productivity (Turner et al., 2019), reducing litter inputs and changing the composition of the vegetative understory community (Turner et al., 2025). Short-interval fires were also associated with increased soil temperature and decreased moisture availability at one-year postfire, due to the lack of standing dead snags providing shade (Hoecker et al., 2020). These factors likely altered microbial habitat and microclimate, affecting the recovery trajectory. Second, burn severity often has strong correlations with soil microbial community composition (Fernández-García et al., 2019; Whitman et al., 2019). Stands burned at short-interval fire experienced greater combustion of above-ground biomass compared to long-interval stands (Turner et al., 2019), potentially increasing the amount of time needed for communities to recover to pre-fire levels, and decreasing microbial resilience to future disturbances (Jansson and Hofmockel, 2020; Whitman et al., 2022). Altered environmental conditions after SI fire may also limit niches for pyrophilous bacteria, preventing their enrichment in the 6-year-old SI fire compared to the LI fire of the same age. However, pyrophilous fungi may be able to exploit these postfire conditions, allowing them to thrive and proliferate even when fire responsive bacteria cannot.

Fungal communities in stands recovering from SI fire more closely resemble those in same-aged stands recovering from LI fire than do bacterial communities. Although postfire tree recovery was reduced following SI fire, aboveground lodgepole pine biomass still more closely resembles that of the 6-year-old LI forest (Turner et al., 2025). As lodgepole pine productivity increases, trees typically allocate more C to their belowground symbionts in exchange for N to support rapid productivity and biomass accumulation (Smith and Read, 2008), which is potentially reflected in the similar community composition. Conversely, 6-year-old bacterial communities in stands recovering from SI fire more closely resemble those in the 22-year-old stand recovering from LI fire. These stands share a longer fire history as they both burned in 2000 and followed the same recovery trajectory until part of the stand recovering from LI fire reburned in 2016. This similarity is largely driven by an enrichment of *Chloroflexi*, which is present in both the 6-year-old stands SI fire stands and 22-year-old LI fire stands, but not in the 6- or 34-year-old LI fire stands.

Effects of SI fire we observed are similar to those of other compound disturbances. Fire after logging increased divergence of bacterial and fungal communities from nearby forests that were logged but not burnt, and effects were more pronounced as burn severity increased (Ammitzboll et al., 2021). Ectomycorrhizal species richness and relative abundance were already greatly reduced in ponderosa pine (*Pinus ponderosa*) forests in Colorado that had experienced a mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak compared to sites not infested with MPB (Caiafa et al., 2023). A subsequent fire further reduced richness and abundance. While we did not see an overall reduction in EcM richness among stands recovering from SI and LI fire of the same age, the range of fungal OTU richness was somewhat high (178–631 for SI and 128–629 for LI) which could be a result of within-stand heterogeneity. Another study investigating the interaction between drought and recent fire found that the recovery of burned soil microbial community composition and functional enzyme profiles to pre-fire levels was slower for microbial communities that had experienced drought, with recovery delayed for at least two years after disturbance (Hinojosa et al., 2021).

4.4. Limitations

Several limitations should be considered when interpreting results of this study. We sampled at only one time period during mid-summer, and communities could vary seasonally or at shorter time scales. We report relative abundance data, which does not capture absolute population shifts in microbial taxa; thus, we cannot detect true gains or losses in specific taxa. Additionally, our study could not fully capture how the spatial arrangement of the fires across the landscape may affect microbial community patterns. Lastly, although we controlled for measurable environmental characteristics in our chronosequence (e.g., climate, elevation, aspect, and slope) there may be unmeasured differences affecting microbial communities that we could not account for. Microbial communities are highly dynamic and can change quickly over short distances in response to differing environmental conditions, which can result in significant variability even within sites of the same age class.

5. Conclusion

Our findings reveal that soil microbial communities in postfire lodgepole pine stands shift with stand development and are strongly correlated with soil C:N and litter mass. Under typical fire return intervals, this indicates that differences in soil microbial communities as stands age may be driven more by changing nutrient and microclimate conditions than by the direct effects of fire, such as soil heating or increased pH. Anomalous SI fire perturbed recovery trajectories for bacterial and fungal communities, but in different ways. Bacterial communities in stands that experienced SI fire resembled those of 22-year-old stands that burned in LI fire rather than same-aged stands that experienced LI fire. This pattern may reflect legacy effects of the previous fire, greater burn severity, or distinct soil conditions after repeat burns. Fungal communities, however, tracked more closely with stand age, suggesting a tighter link to vegetation recovery and litter inputs. By comparing these recovery trajectories across stand age and fire return interval, we show that changes in microbial communities continue throughout early stand development and are sensitive to changes in disturbance regimes. This becomes increasingly important as short-interval fires increase in frequency under climate change, potentially slowing forest recovery and altering long-term ecosystem processes if microbial recovery pathways are altered after repeat disturbance.

CRediT authorship contribution statement

Arielle C. Link: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thea Whitman:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Monica G. Turner:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Arielle Link reports financial support was provided by National Science Foundation. Monica G. Turner reports financial support was provided by National Science Foundation. Thea Whitman reports financial support was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Raw sequence reads and associated metadata have been deposited in the NCBI SRA database under BioProject PRJNA1419301.

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