

# Prescribed fire selects for a pyrophilous soil sub-community in a northern California mixed conifer forest

Monika S. Fischer | Neem J. Patel | Phillip J. de Lorimier | Matthew F. Traxler 

Department of Plant and Microbial Biology,  
University of California, Berkeley, Berkeley,  
California, USA

## Correspondence

Matthew F. Traxler, University of California,  
Berkeley, 111 Koshland Hall, Berkeley, CA  
94720, USA.

Email: [mtrax@berkeley.edu](mailto:mtrax@berkeley.edu)

## Funding information

NIH Shared Instrumentation, Grant/Award  
Number: 1S10OD010786-01; DOE Office of  
Science and Office of Biological and  
Environmental Research (BER), Grant/Award  
Number: DE-SC0020351

## Abstract

Prescribed fire is a critical strategy for mitigating the effects of catastrophic wildfires. While the above-ground response to fire has been well-documented, fewer studies have addressed the effect of prescribed fire on soil microorganisms. To understand how soil microbial communities respond to prescribed fire, we sampled four plots at a high temporal resolution (two burned, two controls), for 17 months, in a mixed conifer forest in northern California, USA. Using amplicon sequencing, we found that prescribed fire significantly altered both fungal and bacterial community structure. We found that most differentially abundant fungal taxa had a positive fold-change, while differentially abundant bacterial taxa generally had a negative fold-change. We tested the null hypothesis that these communities assembled due to neutral processes (i.e., drift and/or dispersal), finding that >90% of taxa fit this neutral prediction. However, a dynamic sub-community composed of burn-associated indicator taxa that were positively differentially abundant was enriched for non-neutral amplicon sequence variants, suggesting assembly via deterministic processes. In synthesizing these results, we identified 15 pyrophilous taxa with a significant and positive response to prescribed burns. Together, these results lay the foundation for building a process-driven understanding of microbial community assembly in the context of the classical disturbance regime of fire.

## INTRODUCTION

Under the current trajectory of climate change, wildfires are expected to continue increasing in frequency and severity in western North America and other regions across the globe (Doerr & Santín, 2016; Flannigan et al., 2009; Mueller et al., 2020). Wildfires burn hundreds of millions of hectares in forests annually (Giglio et al., 2013) and contribute to the global carbon cycle both in terms of atmospheric input of CO<sub>2</sub> and terrestrial sequestration of carbon in the form of pyrogenic organic matter (Bird et al., 2015; Bowman et al., 2009; Pellegrini et al., 2018). A key strategy toward decreasing the frequency of devastating wildfires is the

implementation of lower-intensity prescribed fires and managed wildfires (Duane et al., 2019). These lower-intensity controlled burns have proven effective in reducing the fuel load and the likelihood of catastrophic fire (Agee & Skinner, 2005; North et al., 2021; Ryan et al., 2013). While the effects of prescribed fire on plant and animal communities are increasingly well-documented (Brockway & Lewis, 1997; Kramer et al., 2021; North et al., 2021; Ryan et al., 2013), our understanding of the impact of fire management strategies on microbial communities is more limited (Certini et al., 2021; Woolet & Whitman, 2020). In this study, we investigated the effects of prescribed burns on soil bacteria and fungi with the aim of understanding the ecological processes that shape these communities during the first 1.5 years following fire.

Monika S. Fischer and Neem J. Patel contributed equally to this work.

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Several key ecological processes operate together to dictate community assembly after perturbations (Hanson et al., 2012; Prach & Walker, 2019). One process by which communities assemble is the deterministic (or 'niche') process of ecological selection, which encompasses environmental filtering and biotic competition. In contrast, neutral (or stochastic) processes of community assembly include dispersal and drift (Hanson et al., 2012). Understanding the relative contributions of these processes to community assembly after disturbance is critical because; (1) they ultimately determine the successional trajectory and recovery time of these communities, and (2) possible interventions designed to enhance community recovery and long-term resilience will likely need to take these processes into account if they are to be successful. When a new habitat becomes available for microbial colonization, neutral processes typically dominate early on, with selection playing a more important role over time (Burns et al., 2016; Dove et al., 2022; Ferrenberg et al., 2013). High intensity fire can be among the most extreme types of disturbance, effectively resulting in a new habitat that is recolonized over time via secondary succession (Meiners et al., 2015). Consistent with this notion, neutral processes have been shown to play a strong role in soil bacterial communities for weeks after severe wildfire, with deterministic processes playing a more important role in shaping the soil bacterial community over months-to-years (Dove et al., 2022; Ferrenberg et al., 2013).

Work across multiple fire-affected systems is starting to paint a complex picture of the impacts of fire on microbial communities (Fox et al., 2022). A recently proposed conceptual model provides a framework for considering the thermo-chemical gradient that defines the post-fire soil habitat (Bruns et al., 2020). This model describes the insulative capacity of soil, such that the effect of fire decreases with depth. Under this model, post-fire soils can be divided into three functional zones: (1) a 'necromass zone' near the soil surface where no organism is able to survive and most organic material is pyrolyzed, (2) a mid-depth 'Goldilocks zone' where most organisms are killed, but some are induced to break dormancy, and (3) below the Goldilocks zone where there is little-to-no effect of the fire (Bruns et al., 2020). Many organisms are able to survive at depths below the surface, even during the most extreme wildfires (Certini et al., 2021). Communities present at, or in close proximity to the soil surface are generally dramatically impacted by fire (Barbour et al., 2022). The documented effects of fire on the soil microbial community include a decrease in overall biomass (Dooley & Treseder, 2012; Holden & Treseder, 2013; Pressler et al., 2018) and a significant perturbation of the community structure (Day et al., 2019; Glassman et al., 2016; Weber et al., 2014;

Whitman et al., 2019; Xiang et al., 2014). Both fungal and bacterial communities have been observed to decrease in richness after severe wildfire (Day et al., 2019; Enright et al., 2022; Glassman et al., 2016; Weber et al., 2014; Xiang et al., 2014), although there are notable exceptions (Whitman et al., 2019).

Over a hundred years of macroscopic fruiting body observations on various heat or fire treated substrates (Lisiewska, 1992; Petersen, 1970; Seaver, 1909), combined with recent community DNA sequencing studies in post-fire habitats (Fox et al., 2022), suggest that a distinct pyrophilous fungal community assembles in fire-affected soils. These pyrophilous fungi produce abundant fruiting bodies commonly seen on the surfaces of burnt soil and pyrolyzed wood, and more recently these taxa have also been identified via DNA sequencing of post-fire soils (Adamczyk et al., 2012; Ammitzball et al., 2022; Day et al., 2019; Day et al., 2020; Enright et al., 2022; Hughes et al., 2020; Li et al., 2019; Livne-Luzon et al., 2021; Mino et al., 2021; Qin & Liu, 2021; Raudabaugh et al., 2020; Reazin et al., 2016; Semenova-Nelsen et al., 2019; Su et al., 2022; Weber et al., 2014; Whitman et al., 2019; Xiang et al., 2014). Commonly observed pyrophilous fungi include Ascomycete members of the genera *Pyronema*, *Anthracobia*, *Geopyxis*, *Tricharina*, *Morchella*, and *Peziza*, along with Basidiomycete members of the genera *Pholiota*, *Lyophyllum*, and *Myxomphalia* (Fox et al., 2022; Hughes et al., 2020).

Comparatively less is known about bacterial taxa that respond positively in post-fire soils, although taxa that appear across recent studies include Pseudomonadota members of the genera *Paraburkholderia* and *Massilia*, Actinomycetota members of the genus *Arthrobacter*, and Bacteriodota members of the genus *Flavobacterium* (Enright et al., 2022; Weber et al., 2014; Whitman et al., 2019; Xiang et al., 2014; Yang et al., 2020). Only a few studies have investigated the effect of prescribed fire on both soil fungal and bacterial communities, and the time resolution of sampling in these studies has been limited. These reports examined a western North American grassland ecosystem at single time-point three-years post-fire (Qin et al., 2020), a central North American shrub-encroached prairie ecosystem at two time points; pre-fire and post-fire (Mino et al., 2021), an Australian Eucalyptus forest at three time-points following fire (Ammitzball et al., 2022), and a western North American grassland at three time-points post-fire (Glassman et al., 2023). In this study, we build on this growing body of literature with a high temporal resolution time-series following two prescribed fires in a western North American montane mixed conifer forest.

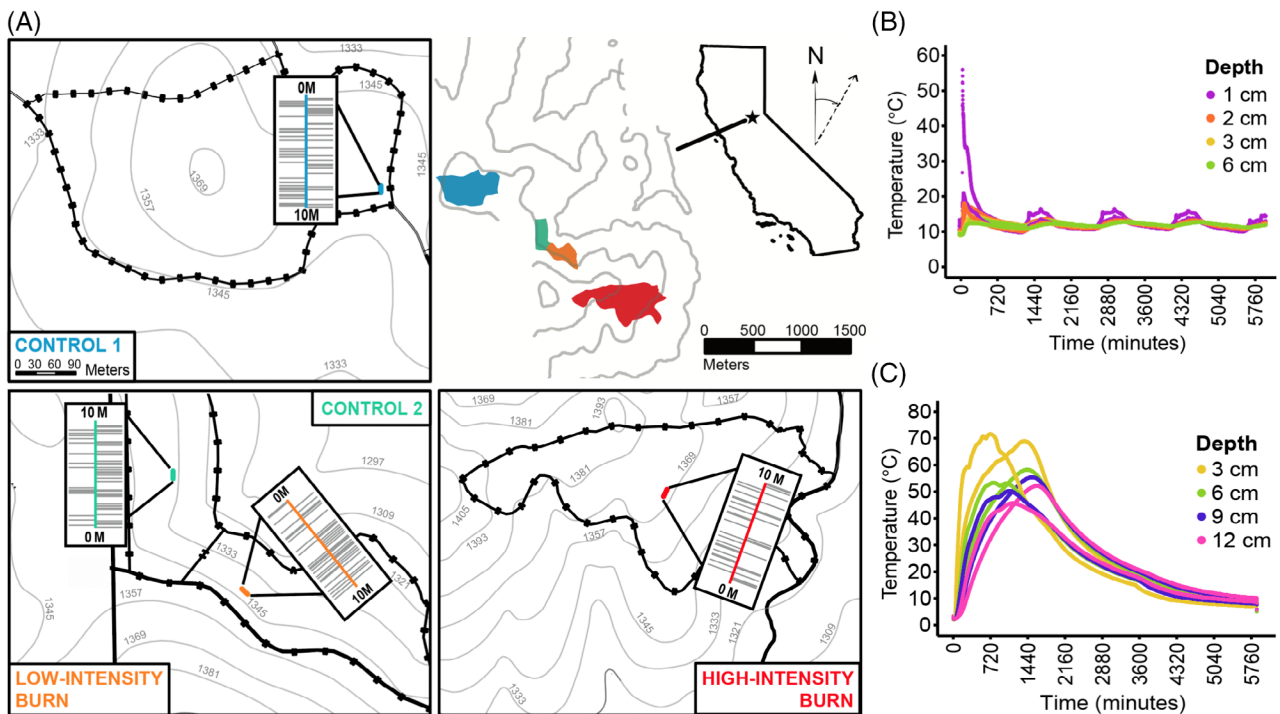
Here, we sought to address four major questions. First, how does prescribed fire affect overall richness, abundance, and community composition? Second,

what are the temporal dynamics of community changes, either at the whole-community level and/or on the level of individual taxa? Third, which taxa share similar responses to fire? And finally, what ecological processes (i.e., stochastic or deterministic) drive formation of the community after prescribed fire? To address these questions, we profiled post-fire changes in bacterial and fungal communities through sampling of two prescribed burn plots and two no-burn control plots over a 17-month time course in a mixed conifer forest in northern California, USA. With the resulting data, we undertook a series of analyses designed to answer the key questions above. Additionally, we combined the results of these independent analyses to delineate a pyrophilous community of taxa that shared the characteristics of being (1) positively differentially abundant in burned plots, (2) indicator species associated with community shifts following fire, and (3) detected in burned plots in a pattern that was likely shaped by deterministic processes. In sum, this work provides a foundation for understanding the ecological processes that shape post-fire microbial communities and identifies members of this pyrophilous community.

## EXPERIMENTAL PROCEDURES

### Site descriptions and prescribed fire treatments

Prescribed fires were conducted at the University of California's Blodgett Forest Research Station located near Georgetown, California, USA. Blodgett Forest is a mixed conifer forest (mostly *Pinus lambertiana*, *Pinus ponderosa*, and *Pseudotsuga menziesii*, with some scattered *Calocedrus decurrens*, *Sequoiadendron giganteum*, *Abies concolor*, and *Quercus kelloggii*). Soil is in the Holland series, generally characterized as fine-loamy, mixed, mesic Ultic Haploxeralfs. We established four 10 m transects (Figure 1), one within each of the four experimental plots, at roughly 1360 m elevation; Hi (38.89598, -120.64800), Lo (38.90016, -120.65648), 1c (38.90562, -120.66345), and 2c (38.90191, -120.65901). The Hi and Lo plots were treated with prescribed fire, while Plots 1c and 2c remained as untreated controls throughout a 17-month sampling time series. All prescribed burns were facilitated with fossil fuel drip torches containing a 2:1, diesel: gasoline mixture. Fossil fuel was excluded from transects.



**FIGURE 1** Site descriptions and soil temperatures during experimental burns. (A) Maps showing the location of sampling sites. On the top-right, a star indicates the general location of Blodgett Forest Research Station within the outline of the state of California. Adjacent to California is a zoomed-in topographic map of Blodgett Forest Research Station, which shows the location of our experimental plots; 'Control 1' = blue, 'Control 2' = green, 'Low-intensity burn' = orange, 'High-intensity burn' = red. Three panels show further zoomed-in detail of these four plots. Cross-hatched black lines indicate experimental plot boundaries, grey topography lines indicate elevation in meters, and small coloured line in each plot highlights the location of each 10 m transect. Random sampling locations along each transect are highlighted with a zoomed-in view in a rectangular box adjacent to each transect. (B,C) Soil temperature (°C) measured every 15 min starting a few hours prior to each experimental burn within a few meters of the Low-intensity transect (B), and High-intensity transect (C). Two thermocouples were placed at each depth, and temperature measurements continued for at least 4 days, the x-axis is divided into 12-h increments.

Ignited fossil fuel was dripped at least two meters away, and fire naturally travelled across our transects as it burned through dry plant debris. The two control Plots (1c and 2c) have not burned since the University of California acquired the property in 1933. However, prior to that, indigenous people regularly burned the area roughly every 5–10 years, up until the gold rush of 1849 and subsequent rapid European colonization displaced and decimated indigenous populations across the region (Taylor, Trouet, et al., 2016; Taylor, Walters, et al., 2016). All four study sites were harvested with narrow gauge railroads between 1900 and 1920, thus most trees were less than 100 years old at the time of our sample collection.

Prior to our study, Plot 1c experienced very little management activity except for fire suppression. The forest structure in Plot 1c was relatively dense (116 tons/ha composed of all six strata, i.e., canopy to ground fuels in fall of 2018, Figure S1; Prichard et al., 2013). The basal area of Plot 1c was 59 m<sup>2</sup>/ha, with an average canopy tree size of 53 cm dbh. The Hi plot experienced low-intensity prescribed burns in 2002, 2009, and 2017. The basal area was 54 m<sup>2</sup>/ha with an average canopy tree size of 66 cm dbh. The forest structure in the Hi plot is complex, multiage, and with a generally open understory with patches of high-density young trees (for site photos, see Figure S1). Within the Hi Plot, on 4 January 2019, we burned a small area (roughly 20 m x 10 m) including a slash pile ~1.5 m tall producing a localized high-intensity fire. The fuel load, including all six strata from canopy to ground fuels, for the entire Hi plot was 33 tons/ha (Prichard et al., 2013).

Both the Lo plot and Plot 2c were regenerated with a clearcut harvest in 1981 and then planted with all native conifer species (i.e., those listed above). These two plots are directly adjacent to each other and have been managed for a fast rate of development toward mature forest structure, with thinning of canopy occurring at stand ages 10, 27, and 39 years. The forest was generally an even-aged structure, with well-spaced canopy trees and little understory density (Figure S1). The basal area within the Lo and 2c plots was 75 m<sup>2</sup>/ha, with an average canopy tree size of 53 cm dbh. The Lo plot was treated with low-intensity prescribed fire in 2013 and then again as part of this study on 25 October 2018 (fuel load = 64 tons/ha). Plot 2c was not previously burned and had a fuel load, including all six strata from canopy to ground fuels, of 57 tons / ha in fall 2018 (Prichard et al., 2013).

To measure soil temperature during and after fire, we buried Extech SDL200 dataloggers roughly 0.5 m below the soil surface (excluding O horizon), and 2–3 m away from our sampling transect. Each datalogger was equipped with four thermocouples (platinum 100 ohm), and the dataloggers were protected inside a hard plastic shoebox with a hole cut in the side to allow

the thermocouples to exit. Thermocouples were inserted horizontally (parallel to soil surface) along the wall of the datalogger hole at 1, 2, 3, 6, 9, and 12 cm from the soil surface (excluding O horizon). Temperature was measured every minute until the batteries discharged (roughly 4 days). We selected temperature measurement depths based on previous observations and the proposed thermo-chemical gradient model (Bruns et al., 2020). During the Lo prescribed burn, thermocouples placed 1 cm below the soil surface recorded a maximum temperature of 56.0°C and returned to ambient temperature <12 h after the fire began. Temperatures 2–6 cm below the soil surface did not deviate substantially from the ambient temperature during the Lo burn. We simultaneously measured temperature in both the Lo plot (Figure 1B) and Plot 1c (Figure S1A). During the Hi prescribed burn, thermocouples placed at 3 cm below the soil surface recorded a maximum temperature of 71.7°C, and 12 cm below the surface reached a maximum temperature of 52.2°C (Figure 1C). Soil temperature after the Hi burn gradually returned to ambient temperature after 4 days. In summary, the heat from the Lo prescribed burn was relatively low, shallow, and not sustained. In contrast, the heat from the Hi prescribed burn was comparatively high, deep, and sustained.

## Experimental design and sample collection

Our general experimental design was four plots × one transect in each plot × three soil cores/time-point/transect × two depths collected from each core × at least 20 time-points. Transect sampling locations were randomly assigned without replacement for each plot for the entirety of our sampling time-series, thus no location along the 10 m transect was sampled more than once. Prior to burning, and in control plots, 10 cm soil cores were collected using an ethanol-sterilized soil sampler (JMC PN031). After burning, we collected soil core samples from 0–3 to 3–6 cm. The O horizon was omitted, only A horizon was collected. Sampling depths were initially determined based on previous work (Bruns et al., 2020) and the data from our temperature sensors (Figure 1B,C). All transects were sampled at every time point, weather permitting. Triplicate soil samples were collected at least once immediately prior to burning, once immediately after burning, and then once every month thereafter, resulting in a total of 338 samples over the course of 17 months (see File S1 for sample metadata detailing exact dates). To capture community dynamics associated with the first precipitation event, we increased our sampling frequency during the weeks following the first precipitation event and the start of the wet season in late November 2018. Multiple cores were collected per sample, per timepoint and immediately pooled in a 50 mL conical tube, to a total



volume of 25–30 mL of soil. After collection, samples were transported by car and immediately placed in a  $-80^{\circ}\text{C}$  freezer. Soil pH was measured using a soil to water ratio of 1: 2.5 within 48 h of sample collection.

After conducting the main study described in this manuscript, we burned our Control No. 2 plot ('2c') on 13 February 2020 to conduct an additional exploratory experiment to test if sampling depth affected the resulting observed microbial community. For this exploratory experiment, six replicate soil samples were collected from the following depths at two time points pre- and post-fire (a moderate-intensity broadcast burn 13 February 2020); 0–1, 1–2, 2–3, 3–4, 4–5, 5–10, and 10–20 cm. In addition, we later pooled equivalent amounts of soil from 0 to 3 and from 0 to 10 cm prior to DNA extraction. Figure S1B shows varying soil temperature data during and after this burn, and Figures S2 and S3 illustrate that there were no significant differences in the composition or diversity of the microbial communities observed at the scale of 0–20 cm in Blodgett soil (PERMANOVA  $p > 0.05$ , and ANOVA  $p > 0.1$ ,  $n = 6$ , File S2 for specific  $F$ -statistics and  $p$ -values).

## DNA extraction, PCR amplification, and sequencing

We generally followed the methodology described in Simmons et al., 2018. To isolate total gDNA from soil, 1.2–1.5 g of soil (optimized to maximize gDNA yield) was transferred to a 2 mL eppendorf tube and then we followed the Qiagen PowerSoil DNA extraction kit protocol. We eluted the gDNA on 100  $\mu\text{L}$  of DEPC water (i.e., treated with 0.1% diethylpyrocarbonate for molecular biology work). 5 ng/ $\mu\text{L}$  of DNA was used for simultaneous PCR amplification and Illumina library preparation with dual 12 bp barcodes exactly as described by Simmons et al. (2018). Primer sequences for ITS2 and the V3/V4 region of 16S are in File S3 (Gao et al., 2019; Simmons et al., 2018; Taylor, Trouet, et al., 2016; Taylor, Walters, et al., 2016). A total of 649 samples (including kit controls and blanks) were randomly assigned barcodes, and randomly distributed spatially across 96-well PCR plates (excluding corners) and sequencing libraries. 100 ng of DNA from each sample was pooled to form a library. Libraries were sequenced via a PE300 strategy on Illumina MiSeq, and the resulting data were demultiplexed at the UC Davis Genome Center, Davis, California.

## Raw sequence processing

For the ITS2 sequences, we used AMPtk v1.5.1 (which used VSEARCH v2.15.0) to quality filter reads, trim off primer sequences, and merge forward and reverse reads together (Palmer et al., 2018). Merged reads <100 bp were filtered out, and remaining reads were

trimmed to 300 bp. We then used DADA2 v1.14 (via R v4.0.3) to dereplicate the sequences, infer amplicon sequence variants (ASVs), remove chimeras, assign taxonomy, and ultimately build the tables used in downstream analyses: ASV table, taxonomy table, and sequence table (Callahan et al., 2016, p. 2; R Core Team, 2020). The UNITE v.8.3 database was used to assign fungal taxonomy, and FUNGuild added functional guild information for many taxa (Nguyen et al., 2016; Nilsson et al., 2019). We allowed both 'probable' and 'highly probable' FUNGuild assignments.

For 16S sequences, we used QIIME2 v2021.8 for all our read processing steps (Bolyen et al., 2019; Estaki et al., 2020). We used built-in tools to quality filter reads and to trim reads where the quality score was <25. QIIME2 incorporates cutadapt (Martin, 2011) to remove primer sequences and merge reads using the default parameters. In the DADA2 (Callahan et al., 2016) step of the QIIME2 pipeline, merged 16S reads were trimmed to 400 bp, followed by dereplication, ASV inference, and chimera removal. The output ASV table was then used to assign taxonomy using a SILVA 138 SSU database (Quast et al., 2012; Yilmaz et al., 2014). The QIIME2 pipeline outputs a fasta file containing all ASVs with their associated sequences, an ASV table, and a taxonomy table, which are used for downstream analyses. We then removed suspected contaminant ASVs (i.e., those present in sequencing blanks) from both ITS and 16S datasets via the decontam v.1.8.0 package in R v.4.0.3 (Davis et al., 2018; R Core Team, 2020). Finally, we filtered both 16S and ITS2 datasets for samples with >10,000 reads, based on our negative controls, for downstream analyses.

## Statistics and other analyses

All downstream data operations were performed in R v4.0.3–v4.2.2, unless otherwise noted (R Core Team, 2020). Plot visualizations were performed via ggplot2 v.3.3.5 (Wickham, 2009), and general data-wrangling via tidyverse v.1.3.0 (Wickham et al., 2019). To confirm that sequencing depth was sufficient, we plotted rarefaction curves with the *rarecurve* function from phyloseq v1.36.0 (McMurdie & Holmes, 2013; Figure S4). To test for community differences by treatment, and explore the influence of other environmental variables, we conducted a principal component analysis (PCA, via the *rda* function) on Hellinger transformed ASV tables (*decostand* function; Borcard et al., 2018; Oksanen et al., 2020). PCA results were plotted using the phyloseq v1.36.0 function, *plot\_ordination* (McMurdie & Holmes, 2013). We used the *adonis* function from vegan v.2.5–7 (Oksanen et al., 2020) to test fire treatment effects via PERMANOVA on Hellinger transformed ASV tables. Vegan v.2.5–7 was also used to calculate diversity metrics. Richness was calculated

using base R v4.0.3. We identified chronologically significant time points and associated indicator taxa via TITAN2 v.2.4.1 run on concatenated ITS2 and 16S ASV tables (Baker & King, 2010, 2013; King & Richardson, 2003). To test for burn treatment effects on the abundance of each ASV, we performed a differential abundance analysis via metagenomeSeq v.1.40.0 (Paulson et al., 2013) with data format support from biomformat v.1.26.0 (McDonald et al., 2012). The initial correlation network was calculated on concatenated ITS2 and 16S ASV tables using the C++ program FastSpar v.1.0.0, which is based on Pearson correlation, and we implemented a  $p$ -value threshold of  $p < 0.01$  for significant correlations (Watts et al., 2019). To identify correlated cohorts of ASVs, we did a network modularity test and node connectivity analysis based on the code from Whitman et al. using igraph v.1.2.6 (Csardi & Nepusz, 2006; Guimerà & Nunes Amaral, 2005; Whitman et al., 2019; Figure S11). Correlation networks were visualized with the graphic program Cytoscape v.3.9.1 (Shannon et al., 2003).

We evaluated ecological mechanisms of community assembly by testing the null hypothesis that community assembly was a random, or neutral process. Specifically, we used Burns et al.'s implementation of Sloan's Community Neutral Model (Burns et al., 2016; Sloan et al., 2006) to fit a neutral model to concatenated 16S and ITS2 ASV table for each plot. A 95% confidence interval around the neutral model fit separated taxa into two groups: (1) ASVs that fell within the 95% confidence interval are inferred to be present in the communities due to neutral processes, or (2) ASVs that fell outside the 95% confidence interval are inferred to be present in the community due to non-neutral (i.e., deterministic) processes. To investigate how neutral model fit changed over time, we divided our samples as equally as possible along the time-series, and then rarefied samples to 6651 ASVs total between the ITS2 and 16S data prior to fitting the neutral model. The fit of the neutral model did not differ substantially over time (Figure S5).

## RESULTS

### Prescribed fire alters soil microbial community composition

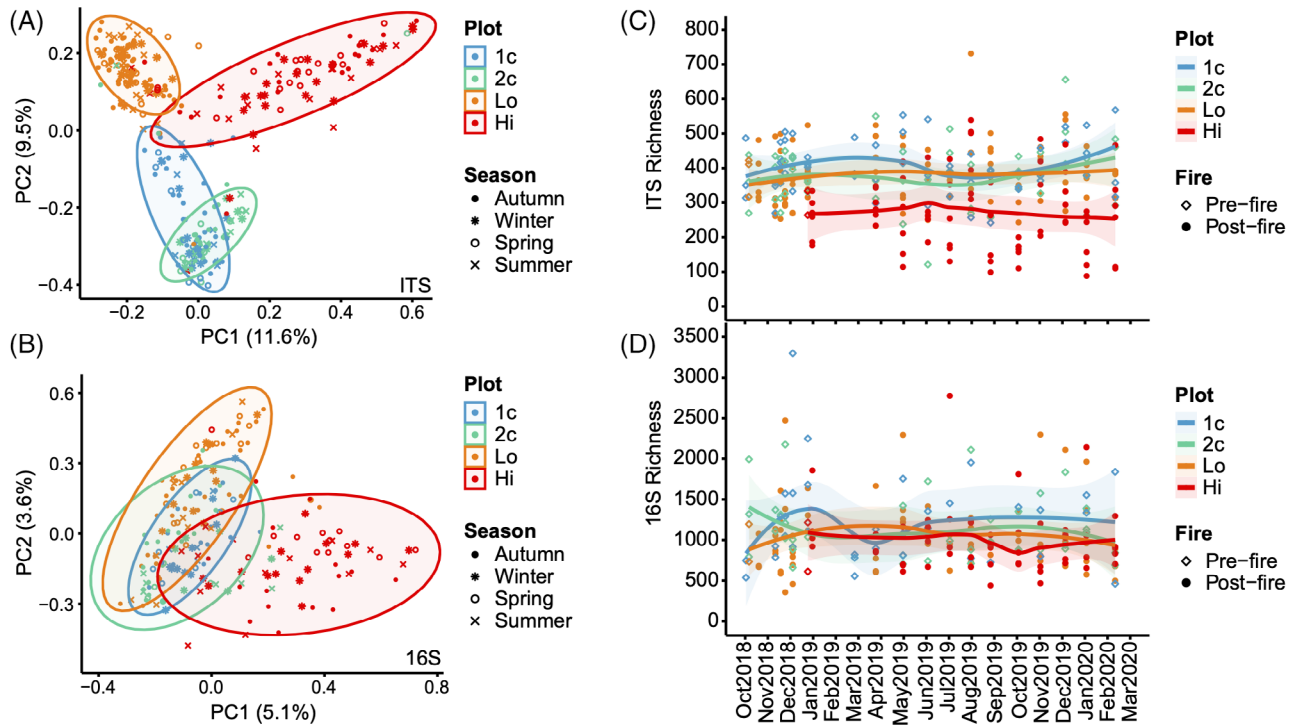
To assess the impact of prescribed fire on soil communities, we sampled two prescribed burn plots and two no-burn control plots over a 17-month time course in a mixed conifer forest in the Sierra Nevada mountains of northern California, USA (Figure 1). This included 338 samples collected over 22 timepoints, yielding a high-resolution time course for community profiling via 16S and ITS2 amplicon sequencing. Rarefaction curves for each of our samples reached clear asymptotes, demonstrating that our sequencing depth was

more than sufficient to capture the diversity of taxa in each of our samples (Figure S4). We first asked if prescribed fire affected the community composition and/or richness in our burned plots. We found that there was a modest but significant difference in the composition of both fungal and bacterial communities when testing the treatment effect of prescribed fire versus no-burn controls (PERMANOVA, 16S:  $R^2 = 0.0238$ ,  $p = 0.00099$ ; and ITS:  $R^2 = 0.0795$ ,  $p = 0.00099$ ). Consistent with the PERMANOVA results, a scatterplot of fungal principal component (PC) 1 and PC2 shows three distinct clusters associated with either high-intensity prescribed burn ('Hi'), low-intensity prescribed burn ('Lo'), or the non-burn controls ('1c' and '2c'; Figure 2A). In contrast, a scatterplot of bacterial PC1 and PC2 shows control samples nested within an overlapping region of distinct Hi burn and Lo burn clusters (Figure 2B). For fungal communities, PC1 correlated with soil pH, whereas PC2 correlated with experimental treatments (Figure S6). For bacterial communities, PC1 also correlated with soil pH, however none of our measured environmental or experimental variables clearly explained the variation across PC2 (Figure S7). Soil pH increased following the Hi prescribed burn, but not the Lo prescribed burn (Figures S6 and S7). Season, time since burn, average daily air temperature, and precipitation did not explain the variation between our samples (Figures S6 and S7).

Prescribed fire generally did not affect diversity or richness over time, with one exception (Figures 2C and S8). In the Hi burn plot, fungal Shannon diversity, richness, and to a lesser extent, evenness, were all reduced post-fire, and remained lower than in the Lo burn, and unburned control plots throughout the sampling time series. To test this, we used ANOVA to ask if richness differed significantly between our plots at each timepoint (File S2). There was no significant difference in richness between our plots prior to burning the high plot ( $p > 0.1$ ). In contrast, there was a significant difference in richness at the timepoint immediately after burning the Hi plot, which was sustained for the majority of the timeseries. ( $p < 0.05$ ). Taken together, these results demonstrate that prescribed fire had a significant effect on soil microbial community composition, those effects persisted for 17 months post-fire, and higher intensity prescribed fire had a stronger effect on fungi than bacteria.

### Fungal and bacterial differential abundance trend in opposite directions after fire

We next asked if fire led to shifts in relative abundance of fungal and bacterial taxa when comparing burned to control treatments. To do so, we conducted a differential abundance analysis. Overall, the majority of bacterial (81.4%) and fungal (82.3%) ASVs had roughly



**FIGURE 2** Fire alters soil microbial community structure. (A,B) Scatterplots depicting the first two principal components (PC) from a principal component analysis (PCA) on Hellinger-transformed ITS (A) and 16S (B) amplicon community sequencing data. PC1 and PC2 explained the most variation in both datasets (% variation noted on each axis). Ellipses = 95% confidence interval. PERMANOVA testing the treatment effects of burned versus unburned; 16S:  $R^2 = 0.0238$ ,  $p = 0.00099$ ; and ITS:  $R^2 = 0.0795$ ,  $p = 0.00099$ . (C,D) Community richness over time for ITS (C) and 16S (D) data. Points are individual samples, and the data for each plot are summarized by fitting a local polynomial regression line. The shaded area around each line indicates a 95% confidence interval.

equivalent abundances across treatments, and thus did not meet our threshold for significant differential abundance ( $\text{Log}_2$  Fold Change  $>|2|$ ,  $p_{\text{adj}} < 0.01$ ; Figure 3). Of the ASVs that did meet this threshold (which we refer to as ‘differentially abundant’ throughout the rest of this report), 15.7% of fungal ASVs and 7.1% of bacterial ASVs were significantly higher in abundance in burned plots, as compared to controls ( $\text{Log}_2$  Fold Change  $>2$ ,  $p_{\text{adj}} < 0.01$ ; Figure 3). In contrast, 1.9% of fungal ASVs and 11.5% of bacterial ASVs were significantly lower in abundance in the burned plots, as compared to control plots ( $\text{Log}_2$  Fold Change  $< -2$ ,  $p_{\text{adj}} < 0.01$ ; Figure 3). These data illustrated a clear trend in which more fungal taxa responded positively to prescribed fire, while more bacterial taxa responded negatively. This analysis yielded lists of differentially abundant taxa (File S4) for cross-comparisons to the outputs of the analyses in the following sections.

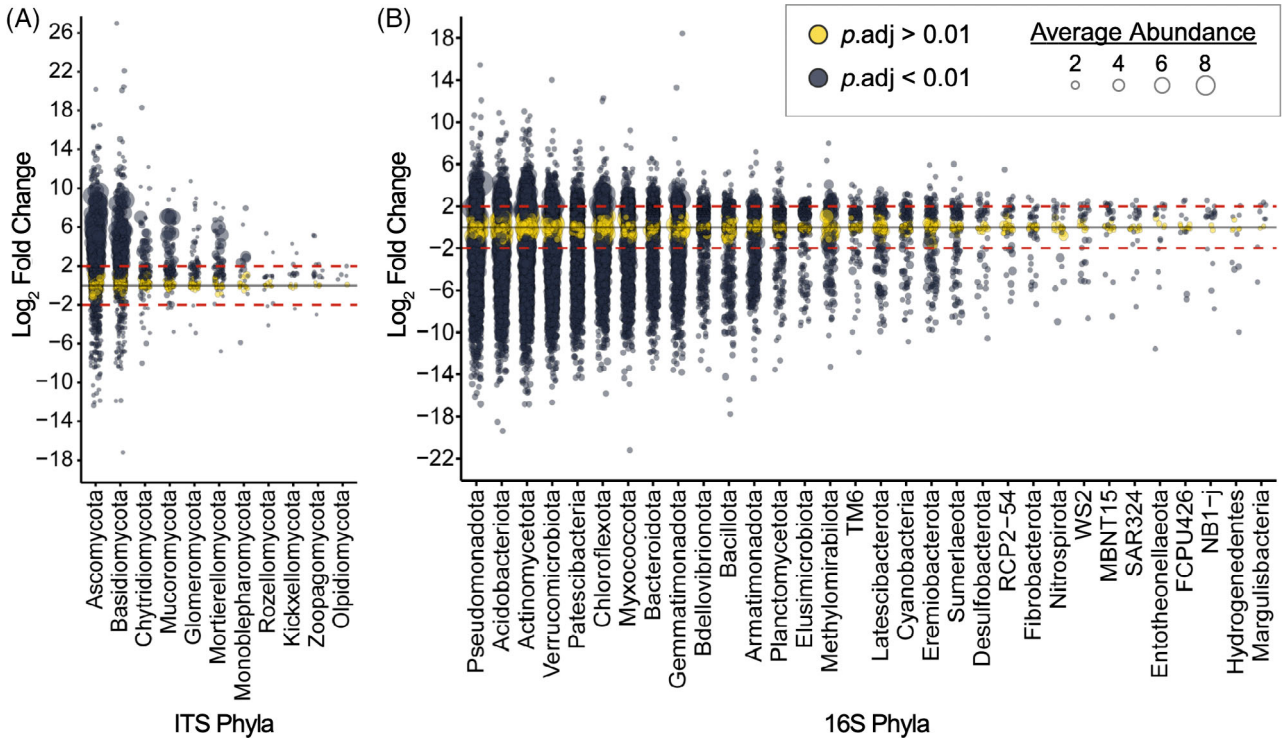
### Indicator taxa are associated with changes in community composition following prescribed fire

We next sought to examine when the soil communities changed during our sampling time-series and to identify

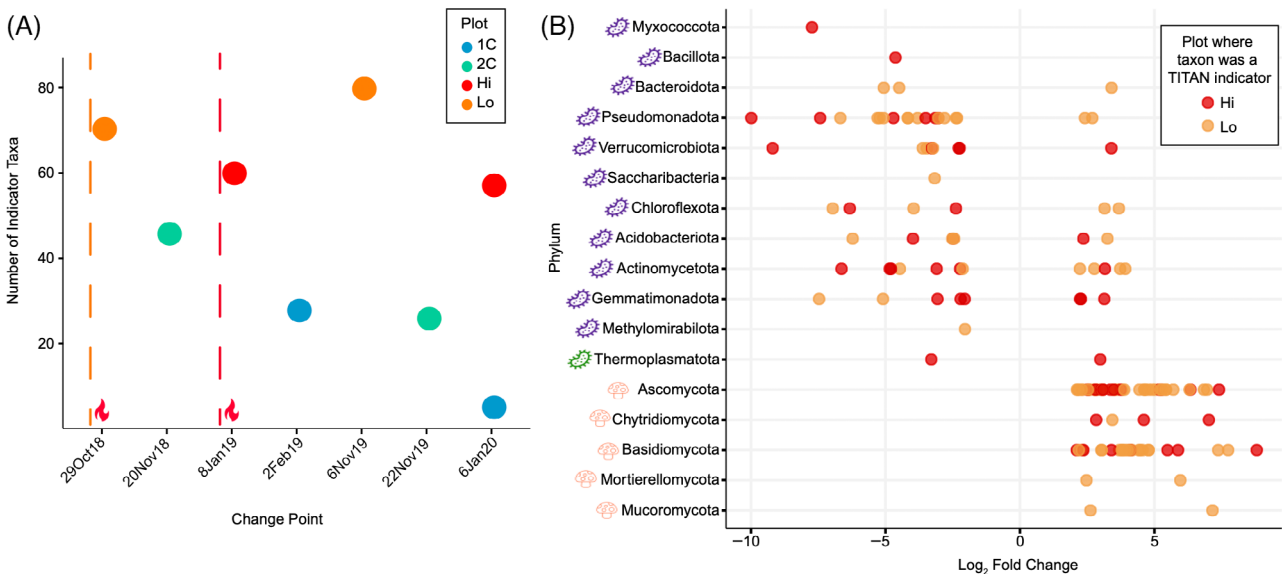
individual taxa that were indicative of whole community change. To that end, we merged our ITS and 16S datasets and applied a change point analysis combined with indicator taxa analysis (via Threshold Indicator Taxa Analysis, or TITAN), which identified two chronologically significant shifts in community composition in each of our four plots (Figures 4A and S9 and File S5). The first change point for both burned plots occurred immediately following prescribed fire, and then roughly 1 year later. In contrast, change points in our control plots occurred at varying times during winter months (Figure 4A). For example, Plot 1c experienced community shifts that coincided with minimum mid-winter temperatures, whereas Plot 2c experienced community shifts that coincided with the first precipitation event of the winter-wet season (Figure S10). Around the change points, we identified substantially more indicator taxa in burned plots; Lo = 156, Hi = 121, than in control plots; 1c = 32, 2c = 73 (Figure 4A).

We next defined a ‘dynamic sub-community’ comprised of ASVs that were indicators in the burned plots (but not in control plots) and that were differentially abundant, as defined in the previous section. This dynamic sub-community included representatives of 17 phyla, including 11 bacterial phyla, 5 fungal phyla, and 1 archaeal phylum (Figure 4B). Differential





**FIGURE 3** Differential abundance of taxa in burned plots as compared to control plots. Scatterplots illustrating the Log<sub>2</sub> Fold Change differential abundance (y-axis) of fungi (A), bacteria, and archaea (B) in burned versus control plots. Each point represents one amplicon sequence variant (ASV), coloured by adjusted  $p$ -value;  $p_{adj} < 0.01$  (navy),  $p_{adj} > 0.01$  (yellow). The size of each point is scaled to represent the average abundance of each ASV across all samples, and ASVs were binned by phylum (x-axis). Red dashed lines denote Log<sub>2</sub> Fold Change  $> |2|$ , which, along with an adjusted  $p$ -value  $< 0.01$ , was used as a cut-off to determine significant differential abundance.



**FIGURE 4** A dynamic sub-community emerges after fire composed of TITAN indicators with significant differential abundances. (A) Total number of amplicon sequence variants (ASVs) identified by TITAN as indicators of whole-community change in the control plots (1C and 2C) and in the treatment plots (Hi and Lo). The y-axis is the number of ASV indicators, and the x-axis is the date on which there was a significant shift in the whole community ('change point'). Dashed vertical lines and flame symbol denote the time-point at which treatment plots were burned. (B) Plot illustrating the differential abundance of the dynamic sub-community. This dynamic sub-community was defined by TITAN indicators of the burned plots which were significantly differentially abundant (Log<sub>2</sub> Fold Change  $> |2|$ ,  $p < 0.01$ ). The y-axis shows these ASVs binned by phylum and is composed of 11 bacterial phyla (purple microbe symbol), five fungal phyla (orange fungi symbol) and one archaeal phylum (green microbe symbol). Each point is one ASV that is coloured the by plot (Lo or Hi) in which it was an indicator.



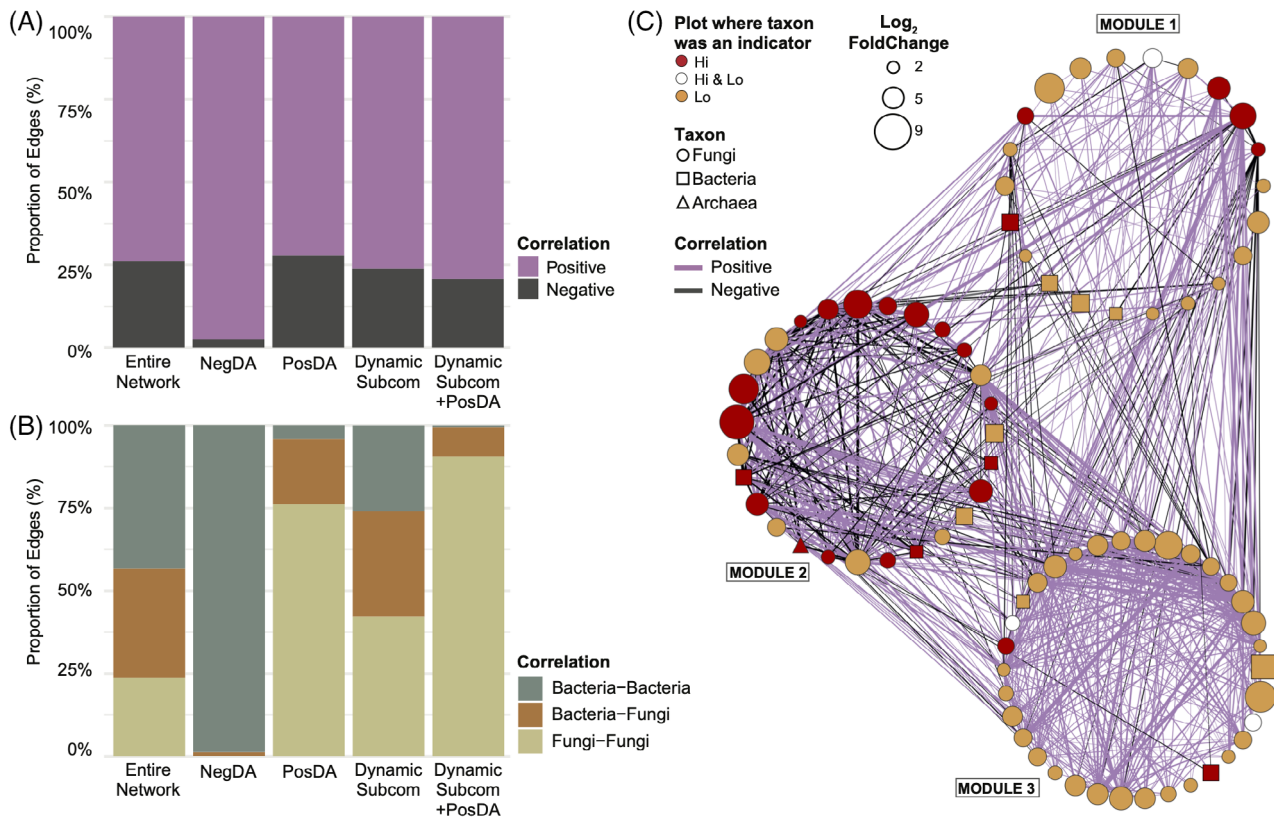
abundances for each indicator ASV in these phyla are shown in Figure 4B. Fungal members of the dynamic sub-community had a positive change in relative abundance, whereas bacterial members of the dynamic sub-community were much more variable, but commonly exhibited negative changes in relative abundance.

### Prescribed fire drives microbial community substructure

To identify ecologically related cohorts of soil microbes, we calculated a correlation network from the combined ITS2 and 16S dataset. The entire network contained 5812 ASVs ('nodes') and 411,689 correlations ('edges'), of which 74% of correlations were positive and 26% were negative (Figure 5A and File S6). Correlations between two bacterial taxa made up 42.3% of the entire network, while 23.1% of correlations were between two fungi, and 32.3% of correlations

were between one bacterial ASV and one fungal ASV (Figure 5B). Correlations involving archaea were rare, constituting 2.3% of the whole network. To further illuminate meaningful correlations, we subset the entire network for different groups of taxa that were highlighted by the previous analyses including: differentially abundant ASVs, indicator ASVs identified by TITAN, and the dynamic sub-community identified in the previous section. In all cases, positive correlations dominated within these categories (Figure 5A). ASVs with a positive differential abundance were mostly comprised of fungal–fungal correlations (76.2%; Figure 5B), while ASVs with a negative differential abundance were enriched for correlations between bacteria (98.8%, Figure 5B). Furthermore, ASVs with a positive differential abundance had a higher degree of network connectivity (70,315 correlations) than ASVs with a negative differential abundance (20,931 correlations).

To examine the structure of our network, we used a fast, greedy, hierarchical agglomeration algorithm



**FIGURE 5** A correlation network clusters the positively responsive dynamic sub-community by fire treatment. Stacked bar plots summarizing the proportion of (A) positive and negative correlations ('edges'), and (B) taxon interactions for the entire, unfiltered network, in addition to the network subset for taxa which were negatively differentially abundant ('NegDA'), positively differentially abundant ('PosDA'), the dynamic sub-community ('Dynamic Subcom'), and the positively responsive dynamic sub-community ('Dynamic Subcom + PosDA'). (C) Correlation network of the positively responsive dynamic sub-community (members of the dynamic sub-community that showed positive changes in relative abundance after fire,  $p < 0.01$ ,  $\text{Log}_2$  Fold Change  $> 2$ ). Nodes are amplicon sequence variants (ASVs), taxonomy is represented by shape, and lines represent a significant correlation between taxa ( $p < 0.01$ , FastSpar). Purple line = positive correlation, black line = negative correlation, and line width is proportional to the correlation value. Greedy clustering identified meaningful substructure to the network and assigned each ASV to one of three modules. Node colours indicate the burn plot(s) in which the ASV was an indicator of community change and node size is proportional to the  $\text{Log}_2$  fold change for each ASV.

(Clauset et al., 2004; Newman, 2006). This algorithm calculates a single Q-value that describes how clearly the network can be divided into sub-networks, or modules, as compared to random chance;  $Q > 3$  is indicative of significant modularity. With this test, we detected a significant community substructure in our network, composed of 19 modules ( $Q = 0.33$ ). A high percentage (98.6%) of all taxa fell within the first three modules (File S7). Figure 5C illustrates the structure of the correlation network after filtering for members in the ‘positively responsive dynamic sub-community’ (i.e., only the members of the dynamic sub-community that showed positive changes in relative abundance after fire). This network contains 84 ASVs and 1576 correlations, of which 79.2% were positive and 20.8% were negative (Figure 5). We noted that in this filtered network, Module 2 was mostly composed of ASVs from the Hi burn plot (66.7%) and was characterized by a relatively high proportion of negative correlations (37.7%). In contrast, Module 3 was dominated by ASVs from Lo burn plot (88.6%) and had a very high proportion of positive correlations (92.2%). Module 1 was enriched for ASVs from the Lo burn plot (72.7%) that had relatively low connectivity (3.0 mean edges per node,  $SD = 1.72$ ) versus ASVs from Module 2 (10.4 mean edges per node,  $SD = 8.06$ ) and Module 3 (6.8 mean edges per node,  $SD = 5.65$ ). Overall, this analysis highlighted several notable patterns: (1) positive correlations dominated in the Lo burn plot, while negative correlations, possibly indicating competition, were more common in the Hi burn plot, (2) each burned plot largely contained its own cohort of dynamically responding ASVs, and (3) the positively responsive dynamic sub-community was mostly composed of fungi.

## Both neutral and deterministic processes drive soil community assembly patterns

We next sought to evaluate which ecological processes might underlie the assembly of the entire soil microbial community, including our identified positively responsive dynamic sub-community. Using Sloan’s neutral community model (Burns et al., 2016; Sloan et al., 2006), we identified bacterial and fungal ASVs whose presence could be accounted for by either neutral processes (e.g., dispersal or drift) or non-neutral processes (e.g., selection through environmental filtering or biotic interactions; File S8 and Figure S12). ASVs that fall within the 95% confidence interval around the neutral model prediction are understood to be driven by stochastic, or neutral processes (grey, ‘neutral’ in Figure 6). In contrast, ASVs that fall outside the 95% confidence interval are likely driven by non-neutral or deterministic processes. Specifically, these non-neutral ASVs were either observed more frequently than expected given their average relative abundance in the

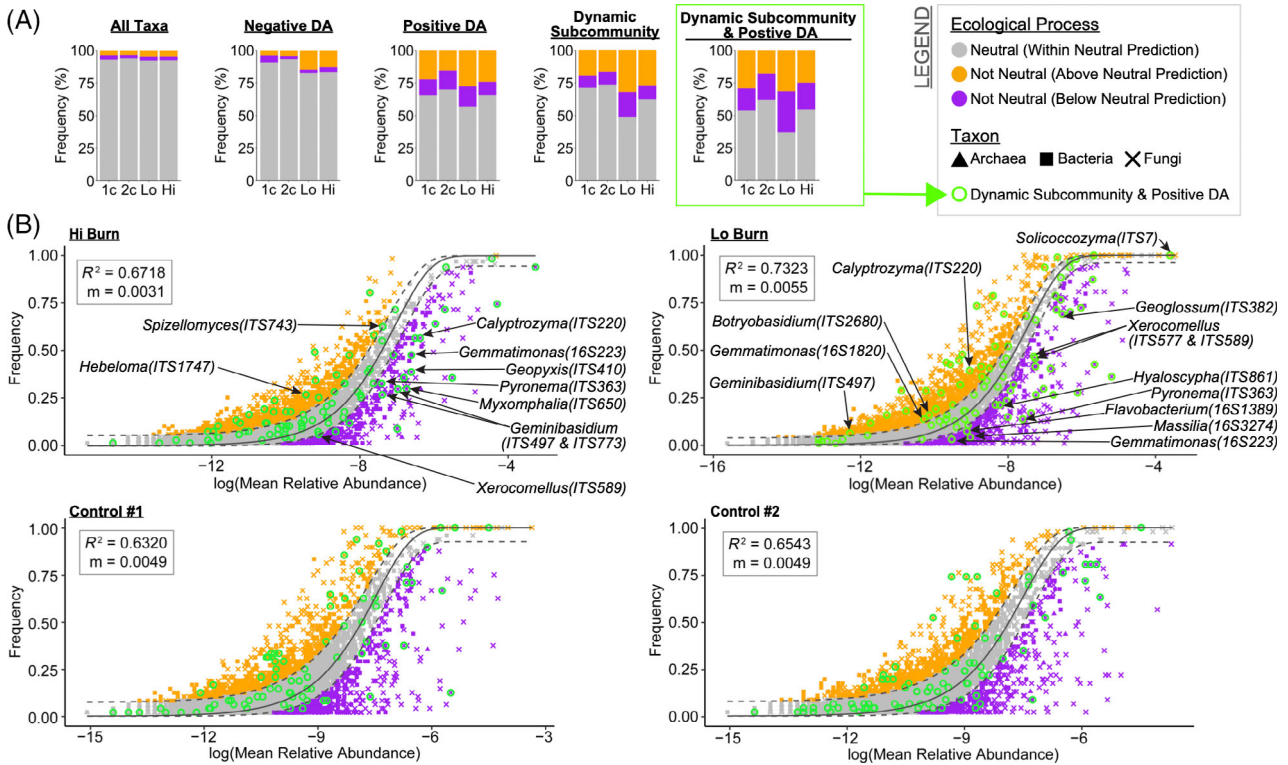
entire dataset (orange, ‘above’ in Figure 6) or less frequently but at higher average relative abundance than expected (purple, ‘below’ in Figure 6). Sloan’s neutral community model also estimates the rate of dispersal, or migration ( $m$ ) into the community. This migration value in all plots was close to zero ( $m < 0.01$ ), indicating that dispersal likely had a very limited influence on community structure in either the control or burned plots.

On average 92.8% ( $\pm 0.7\%$ ) of ASVs in each of our four plots fit the neutral prediction (Figure 6A), and the fit of the neutral model was roughly equivalent across all plots;  $R^2 = 0.63\text{--}0.73$  (Figure 6B). Importantly, the positively responsive dynamic sub-community was enriched for taxa that fell outside the neutral prediction (‘Dynamic Sub-community and Positive DA’, in Figure 6A). Specifically, 63.0% (58/92) of Lo burn ASVs and 45.7% (42/92) of Hi burn plot ASVs were non-neutral. Both of these positively responsive dynamic sub-communities make up 0.2% of the total community in the Hi plot or the Lo plot.

We next sought to identify the members of the positively responsive dynamic sub-community that were non-neutral in either burned plot but were also neutral or absent in control plots. Twenty-nine ASVs fit this stringent set of criteria. Eighteen of these 29 ASVs were classified to the genus level, representing 15 unique genera, which we highlight within Figure 6 B (see also File S9 and Figure 7). Taken together, these analyses suggest that most ASVs in our samples are present due to stochastic, or neutral processes. However, the presence of a substantial portion of the positively responsive dynamic sub-community could not be explained by the neutral model, implying that their presence was likely the result of deterministic processes, such as ecological selection.

## Pyrophilous taxa respond dynamically within the first year following fire

As noted in the previous section, 18 ASVs were identified to the genus level that passed our stringent filter for deterministically driven fire-responsive taxa. Passing this filter required that these ASVs showed patterns of positive differential abundance, dynamic response to fire, and non-neutrality that together we take as indicative of a pyrophilous lifestyle. These ASVs represented 12 genera of fungi: *Pyronema*, *Calyptrozoma*, *Geoglossum*, *Geopyxis*, and *Hyaloscypha* (Ascomycota); *Botryobasidium*, *Geminibasidium*, *Solicoccozyma*, *Hebeloma*, *Myxomphalia*, and *Xerocomellus* (Basidiomycota); and *Spizellomyces* (Chytridiomycota). Bacterial genera that were represented included *Mas-silia* (Pseudomonadota), *Flavobacterium* (Bacteriota), and *Gemmatimonas* (Gemmatimonadota). To further examine and compare the temporal dynamics of ASVs in these genera, we normalized abundances of each



**FIGURE 6** A combination of neutral and deterministic processes drive assembly of the positively responsive dynamic sub-community. (A) Stacked bar-plots illustrating the number of taxa that fell within, above, or below the neutral model for all taxa and then subset for taxa which were either negatively or positively differentially abundant, the dynamic subcommunity, and the positively responsive dynamic subcommunity. (B) Scatterplots for each experimental plot showing ITS (fungi) and 16S (bacteria and archaea) amplicon sequence variants (ASVs) by their mean relative abundance per sample and the proportion of samples in which each ASV is present ('frequency'). Sloan's Neutral Community Model was fit to the data in each plot. This model prediction is depicted as a solid black line, with a 95% confidence interval (dashed black lines). ASVs that fell within this 95% confidence interval are coloured grey. ASVs that fell outside this neutral predicted are coloured either orange (above model) or purple (below model). ASVs that are members of the positively responsive dynamic sub-community are circled in lime-green, and of these, those that are only found in our burn plots are labelled with genus name and ASV number (in parentheses). ' $R^2$ ' quantifies how well the neutral model fit the data, and 'm' is the estimated migration rate.

ASV to its maximum, averaged ASV abundances by genus, and plotted these normalized average abundances across time (Figure 7). These pyrophilous taxa were highly dynamic across time and had distinctly higher normalized relative abundances in the burned plots compared with control plots.

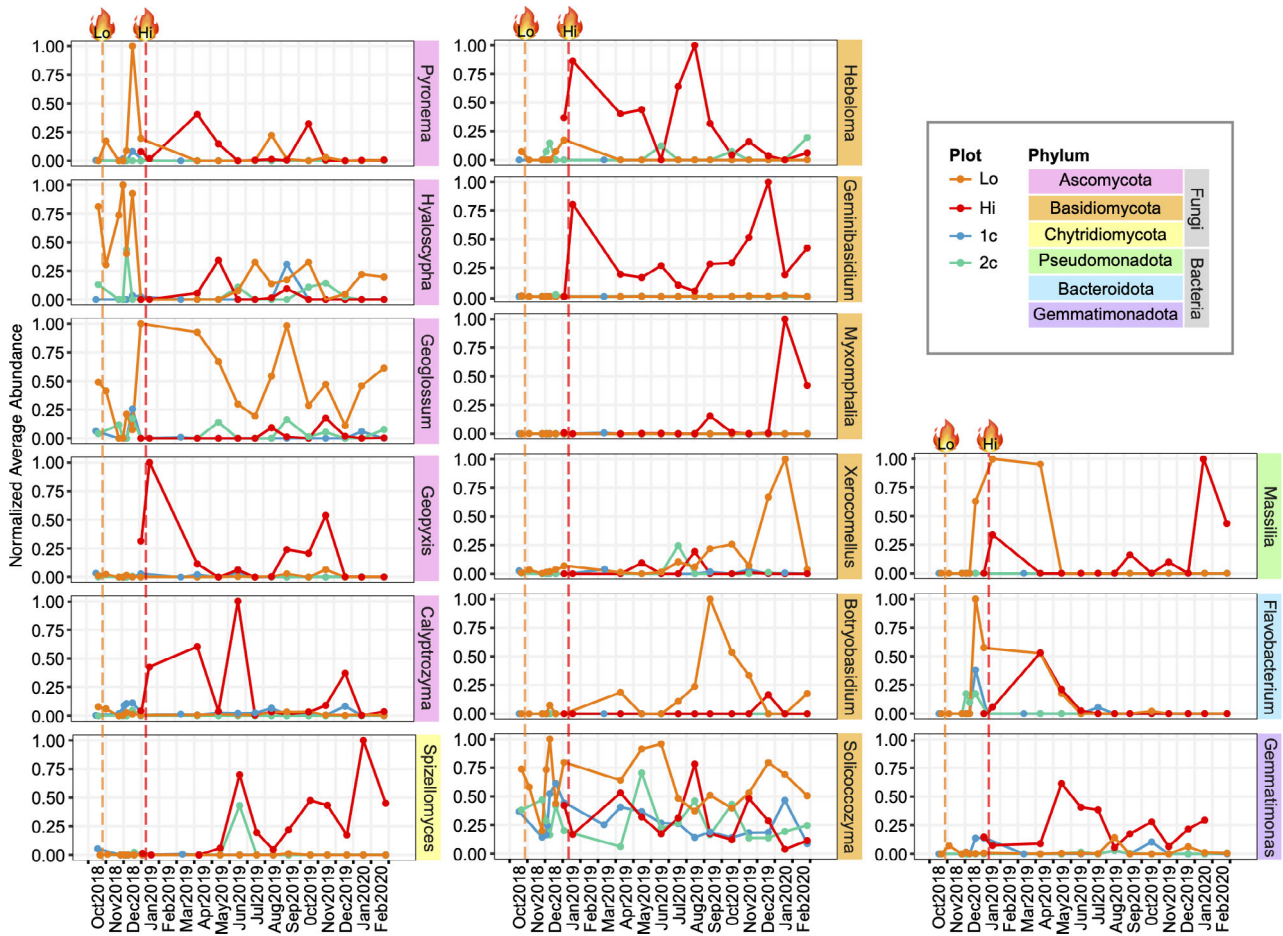
The dynamics of these pyrophilous taxa were variable across the two burned plots (Figure 7). *Pyronema* and *Gemmatimonas* both increased in abundance immediately after the Lo prescribed burn prior to any precipitation (the Lo plot was burned on 16 October 2018 and the first rain was on 20 November 2018). Following the start of the rainy season, members of the genera *Pyronema*, *Hyaloscypha*, *Geoglossum*, *Solicoccozyma*, *Flavobacterium*, and *Massilia* peaked in abundance in the Lo plot (Figure 7). In contrast, *Pyronema* slightly decreased in abundance immediately following the Hi burn, and then peaked in relative abundance 3 months later with *Calyptrozyma*, *Solicoccozyma*, and *Flavobacterium*. Immediately following the Hi burn, *Geopyxis*, *Calyptrozyma*, *Hebeloma*, *Geminibasidium*, and *Massilia* exhibited dramatic increases in relative abundance. Most taxa in all plots showed an increase

in relative abundance during the rainy season from 20 November 2018 to 31 December 2018. Fungi that form relatively large fruiting bodies in the genera *Geoglossum*, *Myxomphalia*, *Xerocomellus*, and *Botryobasidium* responded ~1 year following fire, in addition to the Chytrid, *Spizellomyces*. While these taxa showed high and dynamic relative abundances in the burned plots, the majority of these genera were barely detectable in the control plots, with the exception of *Solicoccozyma*. The ASV of *Solicoccozyma* that we identify here as pyrophilous was more abundant in the burned plots (especially the Lo plot), but it was also consistently present in both control plots. In conclusion, the series of analyses we employed here delineated a pyrophilous sub-community of microbial taxa that was uniquely responsive after prescribed fire.

## DISCUSSION

As the incidence of wildfire increases with ongoing climate change, strategies for mitigating their impact, including prescribed burns, are becoming increasingly





**FIGURE 7** Abundance of pyrophilous amplicon sequence variants (ASVs) in the positively responsive dynamic sub-community over time. Each graph depicts the normalized average abundance (y-axis) for each genus of pyrophilous ASVs over time (x-axis) in each plot (red = Hi, orange = Lo, blue = 1c, green = 2c). Dashed vertical lines and flame symbols denote the time-point at which the Hi and Lo plots were burned. Each point represents the normalized average abundance of the ASV(s) for each genus at each timepoint, and average abundances were normalized to the maximum average abundance for each genus. Each graph is labelled with the genus associated with the depicted data, and genus names are highlighted in a colour according to their Phylum.

relevant. Here, we sought to understand the impact of prescribed fire on soil fungal and bacterial communities, and the ecological processes that influence post-fire microbial community assembly. Additionally, we endeavoured to identify pyrophilous microbial taxa that responded dynamically to prescribed fire. We undertook a months-long time-course sampling of two prescribed burn plots ( $n = 1$  for low-intensity burn, and  $n = 1$  for high-intensity burn) and two unburned control plots. We found that fire altered a sub-community of both the fungal and bacterial communities in the burned plots, as compared to the unburned control plots. Using a series of downstream analyses, we conclude that, while the vast majority of the post-burn community is likely assembled via neutral processes, a sub-community that includes pyrophilous organisms likely arises through deterministic processes. A number of other studies have begun to paint a picture of post-fire microbial community structure (Certini et al., 2021; Cutler et al., 2017; Day et al., 2019; Dooley &

Treseder, 2012; Dove et al., 2021; Fox et al., 2022; Mino et al., 2021; Pérez-Valera et al., 2018; Semenova-Nelsen et al., 2019; Whitman et al., 2019), and this work further builds on those by identifying members of the sub-community that deterministically respond to fire. In doing so, this work lays the foundation for building a process-driven understanding of microbial community assembly in the context of the classical disturbance regime of fire.

Neutral processes such as passive dispersal and ecological drift have been shown to be important during the colonization of unoccupied environments (Hubbell, 2001; Prach & Walker, 2019). A recently burned landscape may seem, superficially, like such an environment. However, many organisms survive below the soil surface even during intense wildfires (Certini et al., 2021), and organismal survival becomes more likely with decreasing fire intensity (Adkins et al., 2020, 2022; Bruns et al., 2020). While neither of our prescribed fires were on par with extreme wildfire, this



notion is consistent with our data showing that the lower-intensity prescribed fire had a minimal impact on richness (Figure 2). We also found that the majority (~93%) of the soil microbial community in our plots could be accounted for by a model of neutral assembly (regardless of fire occurrence, Certini et al., 2021). Thus the community structure in our burned plots likely reflects a combination of; (1) the legacy of neutrality in the soil microbial communities that was present prior to fire, (2) de novo community assembly through neutral processes, and (3) selection of a sub-community of microbes adapted to post-fire environments.

Fire is a dramatic selective force that has a myriad of effects on soil, such as direct heating during the fire event, and enduring post-fire effects including increased pH, increased hydrophobicity, decreased bioavailability of nutrients, and the deposition of a layer of pyrolyzed organic material and mineral ash. Our data do not allow us to directly distinguish between these possible selective pressures associated with fire. However, it is notable that in our Lo burned plot we did not observe any significant changes in pH, and there was little-to-no effect of heat below the soil surface (Figure 1C, S6, and S7), yet we still observed a significant effect on community composition. Thus, we hypothesize that factors beyond temperature and pH, such as deposition of pyrolyzed organic material, may underlie assembly of the pyrophilous sub-community following low-intensity fire. Further investigation will be required to test this hypothesis in situ.

Sloan's neutral community model provides a method for broadly identifying the ecological processes that drive community assembly (Sloan et al., 2006). Taxa that fell above Sloan's neutral prediction were found more frequently than their predicted abundance in the metacommunity. Conversely, taxa that fell below were highly abundant in fewer samples than would be expected, resulting from a patchy distribution across samples. Burns et al suggested that taxa above the neutral prediction are being selected for, whereas taxa below may be seen as 'invasive', or are dispersal limited, or are selected against. It is notable that most taxa that we identify as pyrophilous fell below the neutral partition in our burned plots (Figure 6B), indicating that they were highly abundant, but were detected in fewer samples than would be expected. Such a patchy distribution may be explained by how fire moves across a landscape, resulting in a spatially heterogeneous mosaic (Krawchuk et al., 2020; Meddens et al., 2018). For example, individual soil patches experience varied levels of perturbation from irregular heating, as well as non-uniform deposition of pyrolyzed organic material and changes in pH. Alternatively, patchy distributions of locally abundant taxa can arise as a result of interference competition that leads to spatial segregation of competing organisms (Abrudan et al., 2015; Rendueles et al., 2015), although more studies will be required to

link this possibility to taxa that fall below neutral model predictions.

The term 'pyrophilous' is used broadly to describe organisms that thrive following fire. In the broadest sense, pyrophilous organisms may include all those that increase in abundance after fire as compared to pre-fire, regardless of mechanism (Fox et al., 2022). Here, we identified members of the fire-responsive sub-community that were uniquely and meaningfully responsive to fire according to a series of independent analyses. Specifically, we used a differential abundance analysis to identify ASVs with significantly higher abundance in burned vs. control plots, and TITAN to identify individual taxa whose dynamics across time were indicative of whole-community shifts. Importantly, the subsets of ASVs identified by each of these analyses were also enriched for non-neutral taxa (Figure 5A), indicating that deterministic processes likely played an important role in the assembly of this fire-responsive sub-community. To directly define the pyrophilous sub-community, we included taxa that met the following conditions in our burned plots and, importantly, did not meet any of these conditions in any of our control plots; (1) they were positively differentially abundant, (2) they were indicative of community change, and (3) they were non-neutral (Figure 6).

A total of 29 ASVs passed through this stringent filter, including members of 15 different genera (Figure 7). Two of these genera currently have no precedent for being fire-responsive: *Geoglossum* (Ascomycota) and *Spizellomyces* (Chytridiomycota). Our method confirmed members of three well-known pyrophilous fungal genera; *Pyronema*, *Geopyxis*, and *Myxomphalia* (Fox et al., 2022; Salo et al., 2019; Siegel & Schwarz, 2016; Steindorff et al., 2022), plus to two bacterial genera that are increasingly associated with post-fire environments; *Massilia* and *Flavobacterium* (Enright et al., 2022; Mino et al., 2021; Su et al., 2022; Weber et al., 2014; Whitman et al., 2019; Xiang et al., 2014). Additionally, members of the bacterial genus *Gemmatimonas* were recently found to respond positively to a high severity chaparral fire (Pulido-Chavez et al., 2023). Interestingly, members of both *Massilia* and *Flavobacterium* genera have been documented to utilize and degrade phenanthrene, a polycyclic aromatic hydrocarbon found in pyrolyzed organic material, and have the potential to utilize other complex carbon compounds found in post-fire environments (Guo et al., 2023; Wang et al., 2016).

Three of the fungal taxa we identified as pyrophilous belong to genera that form beneficial mycorrhizal relationships with trees. Members of the genus *Hebeloma* have been implicated in the earliest stages of post-fire succession and pine seedling establishment (Baar et al., 1999; Hernández-Rodríguez et al., 2013; Hughes et al., 2020). Similarly, mycorrhizal members of the genera *Xerocomellus* (Basidiomycota) and

*Hyaloscypha* (Ascomycota) have been found on the roots of living trees that survived recent fire (Olchowik et al., 2021; Torres & Honrubia, 1997). One member of the pyrophilous sub-community belongs to the genus *Botryobasidium* (Basidiomycota), which are resupinate white-rot fungi that have occasionally been observed to increase in abundance following fire (Olsson & Jonsson, 2010; Penttilä & Kotiranta, 1996). White rot fungi are unique in their ability to degrade the polyaromatic polymer lignin, which has a chemical structure that is extremely similar to the pyrolyzed organic material component of a recently burned environment. Thus, white rot fungi may be able to access this pyrolyzed carbon, like *Pyronema* and *Streptomyces* (Fischer et al., 2021; Steindorff et al., 2022; Zeba et al., 2022).

Last, we identified members of three different yeast genera as pyrophilous. The genus *Calyptrozyma* is a pleomorphic Ascomycete yeast (Boekhout et al., 1995), and members of this genus often show up as highly abundant and fire-responsive in DNA sequencing datasets from soil (Day et al., 2019; Pérez-Izquierdo et al., 2021; Pulido-Chavez et al., 2021; Whitman et al., 2019), but they are also broadly prevalent in the environment (Neubert et al., 2006; Semenov et al., 2022). Members of the Basidiomycete yeast genus *Geminibasidium* are also frequently found in soils following fire, and two species have been described as specifically heat resistant (Bruns et al., 2020; Day et al., 2019; Enright et al., 2022; Hopkins et al., 2021; Nguyen et al., 2013). *Solicoccozyma* is a genus of dimorphic Basidiomycete yeasts that are generally abundant in forest soils and leaf litter (Mašínová et al., 2017), but has also been noted as fire responsive (Bruns et al., 2020; Hopkins et al., 2021). These observations are consistent with our data showing that *Solicoccozyma* was also broadly abundant in our soil samples regardless of fire (Figure 7), but fire clearly enriched for one ASV of *Solicoccozyma*, which may represent a fire-adapted subspecies.

Microbial communities are assembled through some combination of the deterministic process of ecological selection (encompassing environmental filtering and biotic interactions) and the stochastic processes of passive dispersal, ecological drift, and mutation/speciation. Here, we used parallel analyses to identify taxa that were positively responsive, temporally dynamic, and whose presence was likely attributable to deterministic processes. In delineating this pyrophilous sub-community, this work lays the foundation for future investigations into the mechanisms that drive pyrophilous community assembly in post-fire environments. Furthermore, we speculate that interactions among members of this sub-community may impact the degradation and reintegration of pyrolyzed organic matter in areas under pressure from increasingly frequent wildfires. Finally, this work sets the stage for understanding the role of this sub-community in stimulating the

recovery of the broader community of micro- and macro-organisms, while also providing a starting point for future studies aimed at harnessing deterministic interventions to enhance community resilience to fire.

## AUTHOR CONTRIBUTIONS

**Monika S. Fischer:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); validation (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Neem J. Patel:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); validation (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Phillip J. de Lorimier:** Conceptualization (supporting); investigation (supporting); methodology (supporting); writing—review and editing (supporting). **Matthew F. Traxler:** Conceptualization (equal); funding acquisition (lead); project administration (lead); resources (lead); supervision (lead); writing—original draft (equal); writing—review and editing (equal).

## ACKNOWLEDGEMENTS

This research would not have been possible without the incredible support of Ariel Roughton, Robert York, Amy Mason, and everyone at University of California, Berkeley, Center for Forestry, Blodgett Forest Research Station. Special thanks to Ariel Roughton for providing the Blodgett Forest topographic maps used in Figure 1, and to Robert York for providing the metrics of forest structure, fuel load, and so forth. We are also grateful for Peter Wyrsh, Thea Whitman, and Luis Cantu Morin for many fruitful conversations. This research used the Savio computational cluster resource provided by the Berkeley Research Computing program at the University of California, Berkeley (supported by the UC Berkeley Chancellor, Vice Chancellor for Research, and Chief Information Officer). The sequencing was carried out at the DNA Technologies and Expression Analysis Cores at the UC Davis Genome Center, supported by NIH Shared Instrumentation Grant 1S10OD010786-01. This research was supported by the DOE Office of Science and Office of Biological and Environmental Research (BER); grant no. DE-SC0020351 to Matthew F. Traxler.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Raw sequencing reads have been submitted to the SRA under accession PRJNA835883 for the ITS2 dataset and accession PRJNA835896 for the 16S dataset. Complete OTU, taxonomy, and metadata tables are available via figshare at <https://doi.org/10.6084/m9>.

[figshare.22647466](https://figshare.22647466). Full results of all statistics and other analyses can be found in the supplemental materials. All code that was used to process and analyse the data are publicly available here: <https://github.com/TraxlerLab/BlodgettProject>.

## ORCID

Matthew F. Traxler  <https://orcid.org/0000-0001-8430-595X>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Fischer, M.S., Patel, N.J., de Lorimier, P.J. & Traxler, M.F. (2023) Prescribed fire selects for a pyrophilous soil sub-community in a northern California mixed conifer forest. *Environmental Microbiology*, 1–18. Available from: <https://doi.org/10.1111/1462-2920.16475>