Bacterial and fungal communities experience rapid succession during the first year following a wildfire in a California chaparral

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Keywords: Secondary succession, Chaparral, Wildfire, Bacteria, Fungi, Temporal turnover, pyrophilous microbes,

Abstract

The rise in wildfire frequency in the western United States has increased interest in secondary succession. However, despite the role of soil microbial communities in plant regeneration and establishment, microbial secondary succession is poorly understood owing to a lack of measurements immediately post-fire and at high temporal resolution. To fill this knowledge gap, we collected soils at 2 and 3 weeks and 1, 2, 3, 4, 6, 9, and 12 months after a chaparral wildfire in Southern California. We assessed bacterial and fungal biomass with qPCR of 16S and 18S and richness and composition with Illumina MiSeq sequencing of the 16S and ITS2 amplicons. We found that fire severely reduced bacterial biomass by 47% and richness by 46%, but the impacts were stronger for fungi, with biomass decreasing by 86% and richness by 68%. These declines persisted for the entire post-fire year, but bacterial biomass and richness oscillated in response to precipitation, whereas fungal biomass and richness did not. Fungi and bacteria experienced rapid succession, with 5-6 compositional turnover periods. As with plants, fast-growing surviving microbes drove successional dynamics. For bacteria, succession was driven by the phyla Firmicutes and Proteobacteria, with the Proteobacteria *Massilia* dominating all successional time points, and the Firmicutes (*Domibacillus* and *Paenibacillus*) dominating early- to mid-successional stages (1-4.5 months), while the Proteobacteria *Noviherbaspirillum* dominated late successional stages (4.5-1 year). For fungi, succession was driven by the phyla Ascomycota, but ectomycorrhizal basidiomycetes, and the heat-resistant yeast, *Geminibasidium* were present in the early successional stages (1 month). However, pyrophilous filamentous Ascomycetes *Pyronema*, *Penicillium*, and *Aspergillus*, dominated all post-fire time points. While wildfires vastly decrease bacterial and fungal biomass and richness, similar to plants, pyrophilous bacteria and fungi increase in abundance and experience rapid succession and compositional turnover in the first post-fire year, with potential implications for post-fire

chaparral regeneration.

1. Introduction

The rapid increase in wildfire frequency, severity, and extent in the western United States (Riley & Loehman, 2016) has encouraged a resurgence of interest in secondary succession. Secondary succession, or the trajectory along which an ecosystem develops following a disturbance, such as a wildfire, has been extensively studied for plants (Derroire et al., 2016; Donato et al., 2012; Hanes, 1971), but belowground microbial communities have been largely overlooked. Understanding how wildfires alter soil microbial succession is necessary to predict post-fire effects on ecosystem recovery and function since soil microbes affect post-fire plant community regeneration via symbiotic associations with fungi (Dove & Hart, 2017), drive organic matter decomposition (Semenova-Nelsen et al., 2019) and nutrient cycling (Pérez-Valera et al., 2020).

Microbial succession is a major process affecting the health and function of all ecosystems. However, wildfire-induced mortality (Hart et al., 2005) can reset the successional clock due to reductions in richness and biomass (Dooley & Treseder, 2012; Pérez-Valera et al., 2018; Pressler et al., 2019) and the replacement of fungal basidiomycetes with saprobic ascomycetes (Cairney & Bastias, 2007), which can affect ecosystem regeneration and function. Successional theory incorporates patterns of change and species turnover, the replacement of existing taxa with new species, due to environmental filtering or historical constraints (Schluter & Ricklefs, 1993). In the context of the secondary succession of early microbial assemblages, historical constraints, such as fire regime, may reflect microbial turnover since pyrophilous "fire-loving" microbes have evolved under the same fire regime as the ecosystem they inhabit. In fact,

pyrophilous fungi were first discovered over a century ago (Petersen, 1970; Seaver, 1909), and next-generation sequencing has revealed that pyrophilous Ascomycota such as *Pyronema* can increase 100-fold post-fire (Reazin et al., 2016), dominating over 60% of sequences in the soils of burned pine forest (Bruns et al., 2020). In addition, current studies have provided evidence of pyrophilous bacteria (Enright et al., 2021; Whitman et al., 2019), suggesting that fire resilience and adaptations might be widely distributed within the soil microbial communities. However, we lack an understanding of the fine-scale changes of pyrophilous microbes and their patterns and turnover rates during early secondary succession. Consequently, limiting our ability to predict the successional trajectory of fire-disturbed ecosystems and our understanding of the role that pyrophilous microbes might play in the successional dynamics of wildfire-affected sites.

Patterns of succession are expected to vary predictably across disturbance severity, with surviving, fast-growing organisms controlling the initial successional patterns (Turner et al., 1998). However, the successional niche hypothesis posits that during early succession, species assemble based on tradeoffs between competitive ability and growth (Pacala et al., 1996). Whereby niche exclusion leads to the removal of species due to overlapping niches. In contrast, niche complementarity allows for the coexistence of species via their ability to use different forms of a resource. Therefore, niche complementarity is suggested to be important for facilitation (Bertness & Callaway, 1994; Callaway et al., 2002) and, thus, might drive early successional patterns in post-fire environments. However, soil microbial communities have short generation times (Hannula et al., 2019), and on average, post-fire microbial research occurs two years post-fire (Dove & Hart, 2017; Pressler et al., 2019), consequently missing the fine-scale temporal succession that can occur directly after a fire and preventing microbial succession theory development. To date, only one study has sampled twice in a post-fire environment and found rapid changes in bacterial composition (Ferrenberg et al., 2013), suggesting that other

post-fire microbial communities likely experience similarly high turnover rates. Soil microbial communities and ecosystem recovery is inextricably linked. Thus, to properly understand the successional trajectories of the post-fire ecosystem, we must first understand the successional dynamics of the pyrophilous microbes that dominate early post-fire systems as they may shape available niche space and exert feedback responses onto the local habitat.

Chaparral is a fire-adapted shrubland found in drylands across the globe (Barro & Conard, 1991), which has coevolved under a high-severity fire regime. In fact, in chaparral, fire is the main initiator of secondary vegetation succession, making it ideal for studying secondary microbial succession. The dominant vegetation types in chaparral form symbiotic associations with mycorrhizal fungi (Allen & Kitajima, 2013; Kummerow et al., 1978). These symbiotic associations can mediate plant stress and increase access to nutrients, thus making them vital for plant establishment and survival (Baldrian, 2016; Van der Heijden et al., 1998). Yet, very little is understood about post-fire microbial succession in chaparral, with only 13% of research on post-fire microbiomes occurring in shrublands (Pressler et al., 2019). Since 66-86% of post-fire microbial research occurs in forests, in particular pine forests (Dove & Hart, 2017; Pressler et al., 2019), it is unclear whether the research on forest pyrophilous microbes is generalizable to drylands such as chaparral.

This study aimed to determine the effects of wildfire on soil microbiomes, their successional trajectories, and their turnover rates. We studied the 2018 Holy Fire, which burned 94 km² of chaparral in the Cleveland National Forest in Southern California. We performed unprecedented, high-resolution temporal sampling of soils for one year, at 2 and 3 weeks, and 1, 2, 3, 4, 6, 9, and 12 months post-fire, allowing us to measure the direct effects of wildfire (as measured at 17 days post-fire) and overall wildfire effects as measured for the entire sampling year. We then used Illumina MiSeq Sequencing to test the following hypotheses: (**H1**) wildfire

will decrease both bacterial and fungal biomass and richness, leading to a shift in the community composition; **(H2)** bacterial and fungal biomass and richness will increase with time since fire, but one-year post-fire will not be sufficient time for either community to return to unburn levels; **(H3)** changes in bacterial and fungal biomass and richness will be associated with post-fire precipitation events, and initial ash deposition; **(H4)** bacterial and fungal succession will be initiated by pyrophilous microbes, which will decrease in abundance over time.

2. Methods

2.1 Study Area and plot design

The Holy Fire burned 94 km² in the Cleveland National Forest across Orange and Riverside counties in Southern California from August 6 to September 13, 2018. On September 30, 2018, within approximately two weeks of the fire being declared 100% contained, we established nine plots (6 burned and 3 unburned) along a gradient of fire severities (**Fig. 1A**). Plots were selected for similarity in aspect, slope, elevation (average 1251 m and ranged from 1199 m to 1288 m), and pre-fire vegetation dominance by manzanita (*Arctostaphylos glandulosa*), an ectomycorrhizal host, and chamise (*Adenostoma fasciculatum*), a plant that associates with both arbuscular and ectomycorrhizal fungi (M. Allen et al., 2005). Plots were placed on average 25 m from access roads to avoid edge effects. Each plot consisted of a 10 m diameter circle with four 1 m² subplots, 5 m from the center in each of the cardinal directions (**Fig. 1B**) for repeated soil collection for a total of 36 subplots.

Our study site experiences a Mediterranean-type climate with warm, dry summers and cool, wet winters, with an average yearly temperature of 17°C and precipitation of 12.5 mm.

Precipitation data was gathered from RAWS USA Climate Archive and was based on the monthly summaries. Soils at the site are mapped in the Cieneba and Friant series and are classified as Typic Xerorthents and Lithic Haploxerolls. They are sandy and gravelly loams with an average pH of 6.7. Additional site-specific information, including geographical coordinates and elevation, can be found in the supplementary tables (**Table S1**).

2.2 Soil collection

We sampled soils 17, 25, 34, 67, 95, 131, 187, 286, 376 days post-fire. During our sampling on post-fire day 17, we also assessed soil burn severity by averaging three separate measurements of ash depth (cm) within each 1 m² subplot. At each time point, the top 10 cm of mineral soil beneath the ash (A horizons) was collected from each subplot with a ~250 mL resealable bulb planter (**Fig. 1C**). Due to the lack of organic layer in the burned plots, soils were not separated by the organic and mineral horizon. In unburned plots, we removed the litter layer before sampling A horizons. We sterilized the soil corer and gloves with 70% ethanol between subplots to avoid cross-contamination, transported soils to the University of California-Riverside within hours of sampling, and stored them overnight at 4°C. Within 24 hours, soils were sieved (2 mm), and a subsample was frozen at -80°C for DNA extraction.

2.3 DNA extraction, amplification, and sequencing

To identify bacterial and fungal biomass, richness, and composition, DNA was extracted from soil using Qiagen DNeasy PowerSoil Kits following the manufacturer's protocol, with one modification. The centrifugation time was increased from 1 min to 1.5 min after adding the C3 solution because the sample still contained a large amount of precipitate. DNA extracts were stored at -20°C for subsequent analysis. Extracted DNA was quantified, and quality checked

using NanoDrop and amplified using the primer pair ITS4-fun and 5.8s (Taylor et al., 2016) to amplify the ITS2 region for fungi and the primer pair 515F-806R to amplify the V4 region of the 16S rRNA gene for archaea and bacteria (Caporaso et al., 2011) using the Dual-Index Sequencing Strategy (DIP) (Kozich et al., 2013). Although our 16S primers amplify both archaea and bacteria, for simplicity, we refer to 16S methods and results simply as bacteria since archaea only contributed <1% of sequencing reads. We conducted polymerase chain reaction (PCR) in two steps, each with 25 µl aliquots. The first PCR amplified gene-specific primers, and the second PCR ligated the DIP barcodes for Illumina sequencing. For bacteria, we combined 1 µl of 1:10 diluted DNA, 10.5 µL of ultra-pure water, 12.5 µL of AccuStart ToughMix, and 0.5 µL each of the 10 µM 515F and 806R primers. Thermocycler conditions for PCR 1 were: 94°C for 2 min followed by 29 cycles of 94°C for 30 s, 55°C for 30 s, 68°C for 1 min followed by an extension step for 10 min at 68°C. For fungi, we combined the gene-specific primers (ITS4-fun and 5.8s) at 0.5 µL each at 10 µM, 5 µl of undiluted fungal DNA, 6.5 µl of Ultra-Pure Sterile Molecular Biology Grade (Genesee Scientific, San Diego, CA, USA) water, and 12.5 µl of AccuStart ToughMix (2x concentration; Quantabio, Beverly, MA, USA). Thermocycler conditions for PCR 1 were: 94 °C for 2 min., followed by 30 cycles of 94 °C for 30 s, 55 °C for 30 s, 68 °C for 2 min with an extension step for 10 min at 68 °C. PCR products were then cleaned with AMPure XP magnetic Bead protocol (Beckman Coulter Inc., Brea, CA, USA) following manufacturers' protocols. The DIP PCR2 primers containing the barcodes and adaptors for Illumina sequencing were ligated to the amplicons during the second PCR step in a 25 µL reaction containing 2.5 µL of the 10 µM DIP PCR2 primers, 6.5 µL of ultra-pure water, 12.5 µL of Accustart ToughMix, and 1 µL of PCR 1 product. Thermocycler conditions for the second PCR were 94°C for 2 min followed by 9 cycles of 94°C for 30 s, 60°C for 30 s, 72°C for 1 min, and an extension step of 10 min at 72°C for both bacteria and fungi. Bacterial and fungal PCR

products were then separately pooled based on gel electrophoresis band strength and cleaned with AMPURE following established methods (Glassman et al., 2021). Each pool was then checked for quality and quantity with the Agilent Bioanalyzer 2100, pooled at a 2:3 ratio (0.4 units for bacteria to 0.6 units for fungi), and sequenced with Illumina MiSeq 2x300bp at the University of California-Riverside Institute for Integrative Genome Biology.

2.4 Bacterial and fungal biomass

Bacterial and fungal biomass was quantified with quantitative polymerase chain reaction (qPCR). We used the FungiQuant-F and FungiQuant-R primer set to target the 18S rDNA for fungi (Liu et al., 2012) and the Eub338/Eub518 primer pair for bacteria (Fierer et al., 2005). To estimate bacterial and fungal small-subunit rDNA gene abundances, standard curves were generated using a 10-fold serial dilution of the standards that were generated by cloning the 18S region of *Saccharomyces cerevisiae* or the 16S region of *Escherichia coli* into puc57 plasmid vectors, which were constructed by GENEWIZ, Inc. (NJ, USA) as previously established (Averill & Hawkes, 2016). The 10 µl qPCR reactions were each performed in triplicate. Reactions contained 1 µL undiluted DNA, 1 µl of 0.05M Tris-HCl pH8.3, 1 µL of 2.5mM MgCl₂ (New England Bio Sci), 0.5 µL of 0.5mg/ml BSA, 0.5 µL of 0.25mM dNTP (New England BioScience) 0.4 µL of both primers at 0.4µM, 0.5 µL of 20X Evagreen Dye (VWR), 0.1 µL of Taq DNA polymerase (New England Bio Sci) and 4.6 µL ultra-pure water. We employed the CFX384 Touch Real-Time PCR Detection System with the following conditions: 94°C for 5 min, followed by 40 cycles of 94°C for 20 seconds, 52°C (for bacteria) or 50°C (for fungi) for 30 seconds, followed by an extension at 72°C for 30 seconds. We used gel electrophoresis to confirm that the products were the correct size. Bacterial and fungal gene copy numbers were generated using a regression equation, $10^{(Cq-b)/m}$, where the y-intercept and the slope were

generated from the standard curve while the Cq value was calculated as the average Cq value per sample in relation to the known/calculated copies in the standard Cq (CT) values were generated by CFX Maestro software.

2.5 Bioinformatics

Illumina data was processed with Qiime2 (Bolyen et al., 2019). Briefly, our 324 samples (9 plots x 4 subplots x 9-time points) resulted in 763 bacterial and fungal samples and several negatives (DNA extractions and PCR samples), and positive controls (mock PCR) and were sequenced in four Illumina MiSeq runs. The demultiplexed fastQ files from the four Illumina sequencing runs were processed individually by using cutadapt (Martin, 2011) to remove the primers and ran through DADA2 to filter out and remove chimeric sequences and low-quality regions and to produce Amplicon Sequence Variants (ASVs) (Callahan et al., 2017). DADA2 outputs from each library were merged into one library for downstream processing, including the removal of singletons and taxonomic assignments. We used the SILVA reference database for bacteria (Yilmaz et al., 2014) and the UNITE reference database for fungi (Kõljalg et al., 2005) for taxonomic assignment. Any sequences assigned to mitochondria and chloroplasts for bacteria were removed from the ASV table before subsequent analysis. Raw fungal ASV tables were exported and parsed through FUNGuild (N. H. Nguyen et al., 2016) to assign functional ecological guilds to each fungal ASV. Fungal guilds include arbuscular fungi (AMF), ectomycorrhizal fungi (EMF), saprotrophs, and pathogens, including only guilds with highly probable confidence ranking for any downstream analysis.

2.6 Statistical analysis

All statistical analyses were conducted using R (1.4.17). Fungal and bacterial alpha diversity was estimated after rarefaction to account for uneven sequencing depth using BiodiversityR (Kindt & Coe, 2005) with the following metrics: observed species richness, Simpson, Shannon, Chao1, and Ace. Patterns of species richness were similar across metrics for both bacteria and fungi (**Fig. S1**); thus, we solely focused on observed ASVs as our metric for species richness for all downstream analyses. To test for treatment effects on bacterial and fungal species richness and each fungal guild (AMF, EMF, pathogens, and saprobes), we fitted thirteen statistical models with treatment (burned vs. unburned), times since fire (days), ash depth (cm), total monthly precipitation (mm), and their respective interactions as predictors. We used generalized mixed effect models (glmer) with a negative binomial distribution in the MASS package (Venables & Ripley, 2002) to account for the over-dispersion of the data and the fact that the conditional variance was higher than the conditional mean (Bliss, 1953; Ross & Preece, 1985). Moreover, time since fire and precipitation were scaled and centered, and the level of nestedness for all models was tested by running a null model with different nested levels ("plot," "subplot," "time since fire") and no predictors. Model selections were made via comparison of Akaike Information Criterion (AICc) in the MuMIN package (Barton, 2020). All species richness models, including the models for each fungal guild, contained "plot," "subplot," and "time since fire" as random effects, and all biomass models contained "plot" and "time since fire" as random effects. Pseudo R^2 , or the variance explained (marginal and conditional) for all models, was calculated using the *r.squaredGLMM* function in the MuMIn Package.

We compared beta diversity across treatments using a distance matrix generated using the "Avgdist" function within the Vegan package (Oksanen et al., 2018), allowing us to calculate the average subsampled Bray-Curtis dissimilarity per 100 iterations and then square-root transforming. Results were visualized using Non-Metric Multidimensional Scaling (NMDS)

ordinations. We used permutational multivariate analysis of variance (PERMANOVA) as implemented with the Adonis function in the vegan package. To test for the significant effects of wildfire, time since fire, and their respective interaction. In addition, PERMANOVA was also used to test the effect of fire on the bacterial and fungal communities at each independent sampling time point. Lastly, to quantify succession, we employed the codyn package (Hallett et al., 2016) to identify the total species turnover between two-time points, including the relative species appearance and disappearance, the rate of directional change using Euclidean distance, and community stability (Collins et al., 2000). To visualize spatial species turnover (Baselga, 2010), we took advantage of the fact that early successional periods display large variability (Collins, 1990; Pandolfi, 2008). Thus, we tested the homogeneity of the bacterial and fungal communities during succession using multivariate dispersion of Bray-Curtis dissimilarities with the betadisper function (vegan) and visualized the results using PCoA. To further quantify succession, we performed a Mantel test to determine the correlation between temporal distance and community composition as in (Gao et al., 2020). Succession was further visualized by characterizing the community composition patterns at the genus level using phyloseq (McMurdie & Holmes, 2013) and plotting the relative abundance profile of the ASVs composing above 3% of the total sequence abundance for each time point (time since fire). We used generalized linear mixed effect models (glmer) to determine genera with significantly different relative abundance between treatments, with plot and time since fire as a random effect.

3. Results

3.1 Sequencing data

The four Illumina MiSeq runs resulted in 9,812,505 bacterial and 24,555,739 fungal sequences for an average of 31,052 bacterial and 78,202 fungal sequences/sample and a total of 33,078 bacterial ASVs and 11,480 fungal ASVs. To account for uneven sequencing depths, the raw ASV tables were rarefied to a depth of 7,115 sequences/sample for bacteria and 11,480 sequences/sample for fungi, resulting in a total of 24,874 bacterial ASVs and 7,445 fungal ASVs. To eliminate the effect of differences in fungal read numbers while retaining the variation in abundance between the different fungal ecological guilds, we extracted the fungal guilds from the previously rarefied fungal ASV table resulting in 208 EMF, 70 saprobic, 65 AMF, and 26 pathogens ASVs.

3.2 Wildfire effects on bacterial and fungal biomass and richness

Fire led to large and significant reductions in bacterial and fungal biomass and richness during the first post-fire year. Overall, bacterial biomass was reduced by 47% ($p < 0.0001$; **Fig. 2A, S2**) and fungal biomass by 86% ($p < 0.0001$; **Fig. 2B, S2**), whereas bacterial richness decreased by 46% ($p < 0.0001$; **Fig. 2C, S1A**) and fungal richness by 68% ($p < 0.0001$; **Fig. 2D, S1A**) in the burned sites. The direct effect of wildfire was stronger for biomass than species richness, with bacterial biomass decreasing by 84% (**Fig. 2A**) at 17 days post-fire and fungal biomass by 97% (**Fig. 2B**). In contrast, bacterial species richness temporarily increased by 31% at 17 days (**Fig. 2C; Table S2**), and fungal richness declined by 45% (**Fig 2D; Table S2**). However, the difference in biomass and richness between the burned and unburned sites lessened with time since fire, to a greater degree for bacteria than fungi (**Fig2; Table S2**). One year was insufficient time for either biomass or richness to recover to unburned levels, with bacterial (**Fig. 2A**) and fungal (**Fig. 2B**) biomass remaining 43% and 80% lower (**Table S2**) and bacterial (**Fig. 2C**) and fungal richness (**Fig. 2D**) remaining 23% and 61% lower in burned sites (**Table S2**).

3.3 Drivers of changes in richness and biomass

The declines in bacterial and fungal biomass ($p < 0.0001$; **Fig. 2A, 2B**) and richness ($p < 0.01$; **Fig. 2C, 2D; Table S3**) were associated with wildfire. However, precipitation interacted with wildfire to positively affect bacterial biomass ($p = 0.002$) but not fungal biomass nor bacterial or fungal richness (**Table S3**). Furthermore, time since fire positively influenced fungal richness ($p = 0.03$), and the effect was stronger when it interacted with precipitation ($p = 0.001$; **Figure 2D; Table S3**). In contrast, the time since fire and precipitation interaction negatively affected bacterial richness ($p < 0.0001$), but no effects were observed for bacterial or fungal biomass ($p > 0.05$; **Table S3**). In addition, there was a negative effect of ash depth on bacterial ($p = 0.0001$, **Fig. 3C**) and fungal richness ($p = 0.0005$, **Fig. 3D**). However, there was a weak but significant positive interaction between ash depth and time since fire, on bacterial ($p = 0.001$) and fungal biomass ($p = 0.003$; **Table S3**) and bacterial ($p = 0.02$; **Fig 3C**) and fungal richness ($p = 0.0001$; **Fig. 3D; Table S3**).

3.4 Wildfire effects on the richness of the different fungal guilds

Wildfire led to selective mortality of fungal guilds, with the largest declines for arbuscular mycorrhizal fungi (AMF). On average, AMF decreased by 98% ($p < 0.0001$; **Table S4**) and became nearly undetectable in burned plots. Ectomycorrhizal fungi (EMF) decreased by 68% ($p = 0.03$), pathogens by 71% ($p = 0.0003$), and saprobes by 86% ($p < 0.0001$; **Table S4**) in burned plots compared to unburned plots (**Fig. S3; Table S4**). Overall, richness for all fungal groups remained lower in the burned plots than the unburned plots for the entire year (**Fig. S4**). Moreover, treatment and precipitation interacted to impose a negative effect on EMF ($p < 0.0001$) and pathogenic fungi ($p = 0.03$); however, no treatment and precipitation effect was observed for AMF and saprobic fungi (**Table S4**). Furthermore, there was a significant

interaction between treatment and time since fire for ectomycorrhizal and saprobic fungi. This interaction had a negative effect on EMF richness ($p < 0.0001$), but it had a positive effect on saprobic species richness ($p = 0.001$; **Table S4**). Lastly, ash depth negatively affected EMF richness ($p = 0.01$; **Table S4**).

3.5 Wildfire changes microbial community composition

Bacterial (**Fig. 4A**) and fungal (**Fig. 4C**) community composition differed between burned and unburned soil communities. Community differences were explained by treatment (burned vs. unburned), which explained 13% of the variation for bacteria and 11% for fungi ($p < 0.0001$; **Table S5**), followed by time since fire, which explained 4% of the variation for bacteria and 2% for fungi ($p < 0.0001$; **Table S5**). Moreover, there were significant interaction effects with treatment and time since fire which explained 2% of the variation for bacteria and 1% for fungi (**Table S5**). The differences between the burned and unburned communities remained constant for the entire year for both the bacterial (**Fig. S5**) and fungal communities (**Fig. S6**), and these differences increased over time (**Fig. S5, S6**). For example, at 17 days, fire explained 12% of the variation in the composition of bacteria and 9% for fungi compared to 1-year post-fire, where fire explained 21% of the variation for bacteria and 13% for fungi (**Fig. S5, S6**).

3.6 Wildfire led to the dominance of previously rare taxa

Wildfires increased community dominance of previously absent or rare taxa (**Fig. S7; Table S6**). Whereas the unburned bacterial communities lacked dominance (**Fig. S7A; Table S6**), two Proteobacteria, *Massilia* (16.2%), and *Noviherbaspirillum* (3.3%) and 3 Firmicutes, *Paenibacillus* (5%) and *Domibacillus* (2.7%), *Bacillus* (2.9%) dominated the burned communities (**Fig. S7A; Table S6**). However, the dominance of the bacteria genera was phylum

specific, where the Firmicutes (*Domibacillus* and *Paenibacillus*) decreased, and the Proteobacteria (*Noviherbaspirillum* and *Massilia*) increased with time since fire (**Fig. 4B**). In contrast, fungal dominance shifted from Basidiomycota and EMF, particularly in the genera *Inocybe* which composed (13%) of the relative abundance, *Thelephora* (2.5%), *Tomentella* (2.6%), *Cenococcum* (3.3%), and *Cortinarius* (6%), to domination by saprobes in the Ascomycota. These ascomycetes include *Pyronema* (34.1%; *P. omphalodes* and *P. domesticum*), followed by *Penicillium* (16%; *P. decumbens*, *P. riverlandense*, and *Penicillium* sp.) and *Aspergillus* (8%; *A. udagawae*, *A. elsenburgensis*, and *A. fumigatus*; **Fig. S7B**; **Table S6**). Similarly, post-fire dominance of the fungal genera over time also shifted dominance with phyla specific response where Basidiomycota (*Geminibasidium* and *Inocybe*) decreased, and Ascomycota (*Pyronema*, *Aspergillus*, and *Penicillium*) increased with time since fire (**Fig. 4D**).

3.7 Microbial successional dynamics

Both bacterial (**Fig. 5A**) and fungal (**Fig. 5B**) community composition experienced rapid and distinct successional trajectories in the burned plots, with bacteria experiencing more significant successional changes (**Fig. 5C**, **Mantel R = 0.33, p = 0.001**) than fungi (**Fig. 5D**, **Mantel R = 0.16, p = 0.001**), which appear to be driven by six major compositional turnover points for bacteria (**Fig. 5E**) and five for fungi (**Fig. 5F**). In contrast, the unburned bacterial (**Fig. 6A**) and fungal (**Fig. 6B**) communities remained stable over time. There were no successional changes in bacterial (**Fig. 6A, 6C**, **Mantel R = 0.046, P = 0.122**) or fungal (**Fig. 6B, 6D**, **Mantel R = 0.046, P = 0.061**) communities, and no significant compositional turnover at any time points for bacteria (**Fig. 6E**) or fungi (**Fig. 6F**). Moreover, early successional turnover in the burned sites was driven by the disappearance of taxa, more so for bacteria (from 25-131 days), than fungi (25-34 days; **Table S7**), while later bacterial turnover time points were driven by species

appearance (187-376 days; **Tables S7**). In contrast, appearance dominated mid-successional turnover periods in the fungal communities (**67-187 days; Table S7**), and late-successional turnover was again driven by species disappearance (**286-376; Table S7**). Moreover, bacterial rates of change and stability were higher in the burned communities, but synchrony was lower (**Table S7**). However, while the rate of change in the fungal-burned communities was higher, stability (**Table S7**) and synchrony were lower (**Table S7**).

3.8 *Pyrophilous taxa drive post-fire succession*

Bacterial succession was initiated by the same genera present in the unburned sites (**Fig. 5A, 6A**), specifically genera in the phyla Actinobacteria and Acidobacteria, with no strong dominance by any single taxa (**Fig. 5A**). However, bacterial turnover at 25 days post-fire resulted in the dominance of the Firmicute *Bacillus*. A secondary turnover at 34 days post-fire resulted in the dominance of the Firmicutes *Domibacillus* and *Paenibacillus* and the Proteobacteria *Massilia*, followed by continuous domination by the Proteobacteria *Massilia*, *Noviherbaspirillum*, and Firmicute *Paenibacillus* until day 187, after which Firmicutes gave way to domination by Actinobacteria and Acidobacteria (**Fig. 5A**). At 286 days post-fire, bacterial communities became less dominated by a few taxa, and diversity increased similar to unburned communities (**Fig. 5A, 6A**); however, the community composition differed (**Table S8**).

Fungal succession was initiated by a Basidiomycetous yeast, *Geminibasidium* (21%) and EMF, present in the unburned community (38%, **Fig. 5B, 6B**), specifically the phyla Basidiomycota *Cortinarius*, *Inocybe*, *Mallocybe*, and *Tomentella*, and two Ascomycota, *Balsamia* and *Cenococcum* (**Fig. 5B, 6B**). However, fungal turnover at 25 days post-fire resulted in the dominance of saprobic Ascomycetes (44%) in the genera *Aspergillus*, *Penicillium*, and *Pyronema* (**Fig. 5B**). Unlike bacteria, the subsequent turnovers at 34, 67, and 95 days post-fire

resulted in the decrease of *Inocybe* and *Geminibasidium* to the point of being undetected in the community (**Fig. 5B**) and the total dominance of *Aspergillus*, *Penicillium*, and *Pyronema* (**Fig. 5B**). After 131 days post-fire (5th turnover, **Fig. 5B, 5F**), turnover in the fungal community stalled. Mushroom-forming taxa, including the ectomycorrhizal fungi *Inocybe*, and the saprobes, *Coprinellus* and *Tephrocybe*, returned to the community (> 3% relative abundance, **Fig. 5B**) and increased in abundance with time since fire (**Fig. 5B, Table S8**).

4. Discussion

This study presents the first evidence of a fine-scale temporal succession of bacteria and fungi after a wildfire. Consistent with our first hypothesis, wildfire decreased bacterial and fungal biomass and richness while altering community composition. As predicted by our second hypothesis, species biomass and richness increased with time since fire. Still, one year was insufficient for biomass, richness, or the community to return to unburned levels. In support of the 3rd hypothesis, precipitation and ash depth were associated with changes in bacterial and fungal biomass and richness. However, these effects were treatment and time since fire dependent. Finally, consistent with our fourth hypothesis, pyrophilous bacteria and fungi detected in pine forests also initiated succession in chaparral shrublands and experienced rapid post-fire succession.

4.1 Wildfire decreased bacterial and fungal biomass and richness

Soil bacterial and fungal biomass and richness declined in the burned sites, corroborating previous post-fire studies in Mediterranean shrublands (Pérez-Valera et al., 2018) and boreal and temperate forests (Dooley & Treseder, 2012). We noted a more significant fire effect on fungal

biomass and richness than bacteria, consistent with previous research (Certini et al., 2021; Pressler et al., 2019), showing that bacteria are more resistant to fire than fungi (Certini et al., 2021; Dunn et al., 1982). Moreover, we observed a transient increase in bacterial richness directly post-fire. This transient increase may result from bacteria being favored by the increase in soil pH that is frequently observed after wildfires (Neary et al., 1999; Rousk et al., 2010) or by post-fire increases in nutrient and C availability (Pourreza et al., 2014). Furthermore, we show that fungi experienced a larger decrease in biomass than bacteria, concurrent with previous studies (Pressler et al., 2019).

Precipitation had adverse effects on bacterial richness in the burned communities but positive effects on the burned bacterial and fungal biomass and richness over time, supporting previous studies (Barnard et al., 2013). This distinct response could be due to physiological differences between these microbial groups (Placella et al., 2012) and their potential adaptation to the normal water conditions in chaparral. For example, fungi can prime themselves for stressful situations by efficiently activating and enhancing resistance to stressful conditions, such as drought (Evans & Wallenstein, 2012; Guhr & Kircher, 2020). This priming ability may allow fungi to maintain constant reproduction rates regardless of the external environmental conditions. However, in unfavorable conditions, bacteria enter a dormant state that inhibits growth to survive (Schimel, 2018). Thus, to be evolutionarily successful, bacteria respond rapidly to favorable conditions, e.g., rain, and rapidly replicate to outcompete other microbes for the pulse of nutrients released during the rain event (Homyak et al., 2014). Additionally, we show that initial ash depth, in this case, measured before the first rains (17 days post-fire), can serve as an index of soil burn severity. In our study, this severity index had a long-lasting impact on bacterial and fungal biomass and richness, suggesting that the burned sites might be under the indirect effects caused by the wildfire and that burn severity can help predict biomass and richness.

4.2 *Pyrophilous bacteria dominate burned communities and drive succession*

Wildfire led to a complete turnover of the chaparral soil bacterial and fungal communities favoring pyrophilous bacteria and fungi that have been detected after fires in temperate and boreal forests, such as taxa belonging to the phyla Actinobacteria, Acidobacteria, Firmicutes, and Proteobacteria (Enright et al., 2021; Whitman et al., 2019; Xiang et al., 2014). In particular, the dominance of the genera *Massilia*, *Noviherbaspirillum*, and *Paenibacillus* may be attributed to their ability to survive the wildfire and exploit transient niches in the early post-fire environment. For example, *Paenibacillus xerothermodurans* is an endospore-forming bacterium that has been shown to contain heat-inducible transcriptional proteins, which can protect heat-induced protein denaturation (Kaur et al., 2018). However, *Massilia* does not form endospores but was nonetheless the most dominant genera post-fire. *Massilia* is a fast colonizing bacteria, which has been speculated to promote its ability to rapidly colonize the post-fire environment (Enright et al., 2021; Whitman et al., 2019). Together these results suggest that post-fire dominant bacteria in wildfire-adapted systems have coevolved and developed mechanisms to survive the fire resulting in niche exclusion and dominance in recently burned ecosystems.

For the first time, we were able to show the secondary succession of bacterial communities in a disturbed environment, providing an in-depth understanding of how these communities change over time. In bacterial communities, succession and community turnover occurred rapidly and was initiated by aerobic, heterotrophic bacteria that form endospores and produce antibiotics. Consistent with previous studies, these genera belong to the phyla Acidobacteria, Actinobacteria, and Firmicutes (Enright et al., 2021; Whitman et al., 2019). Like plant successional patterns (Capitanio & Carcaillet, 2008; Egler, 1954), early successional stages were characterized by high bacterial diversity and a lack of dominance, mimicking the distributions observed in unburned communities. Previous studies suggest that in complex

resource environments, niche complementarity becomes more important than competition because diverse communities can better exploit resources (Eisenhauer et al., 2013). Our results support this idea, as the dominant taxa in our study have been previously shown to use different forms and types of resources. For example, *Paenibacillus* can fix nitrogen (Monciardini et al., 2003; Slepecky & Hemphill, 2006), *Bacillus* and *Conexibacter* can reduce nitrogen, and *Bacillus* can further solubilize phosphate (J. et al., 2001; Kalayu, 2019), suggesting that niche partitioning favors positive interactions between bacteria in the early successional stages (<25 days). However, as succession progressed, functional redundancy replaced niche complementary as recognized by the bacteria that dominated most successional stages (*Massilia*, *Paenibacillus*, and *Noviherbaspirillum*). All three genera have been shown to have multiple functional roles, including phosphorus solubilization (*Paenibacillus*, *Massilia*), nitrogen fixation (*Paenibacillus*), and reduction (*Massilia*, *Paenibacillus*), and are putative polycyclic aromatic hydrocarbon degraders, a component of pyrogenic organic matter (*Noviherbaspirillum*, *Massilia*; (Bailey et al., 2014; Baldani et al., 2014; Grady et al., 2016; Gu et al., 2016; Wan et al., 2020; Woollet & Whitman, 2020). The diverse functional potential of the dominant taxa may allow these bacteria to survive in a changing environment. Additionally, *Massilia* is known to be a dominant rhizospheric bacteria (Li et al., 2014), capable of colonizing the roots of various plants (Ofek et al., 2012) and of forming associations with arbuscular fungi (Iffis et al., 2014). This association can allow for the proliferation of *Massilia* while increasing the formation of mycorrhizal roots (Toljander et al., 2005). These results suggest that *Massilia* and *Paenibacillus* (arbuscular associates) may be well-linked to the secondary succession of chaparral vegetation.

4.3 Pyrophilous fungi dominate the burned communities and drive succession

Surprisingly, we found that pyrophilous fungi that dominate burned Pinaceae forests also dominated California chaparral. While our experiment was not designed to understand the mechanisms controlling pyrophilous microbial dominance, it is clear pyrophilous microbes are not biome-specific. Instead, these fungi may be activated by temperature thresholds since this fire burned at high severity with ash depths up to 12cm, similar to fires in Pinaceae forests. Specifically, we found that our communities were dominated by Ascomycota in the genera *Pyronema*, *Penicillium*, and *Aspergillus*, which have been shown to dominate post-fire boreal spruce forests (Whitman et al., 2019), montane pine forests (Bruns et al., 2020), and Mediterranean ecosystems (Fujimura et al., 2005; Livne-Luzon et al., 2021; Whitman et al., 2019). Both *Pyronema* (*P. omphalodes*) and *Aspergillus* (*A. fumigatus*) are known as fire-responsive species in California chaparral (Dunn et al., 1982). We also identify additional *Pyronema* and *Aspergillus* species that respond positively to wildfire, including *P. domesticum*, *A. udagawae*, and *A. elsenburgensis*. These pyrophilous fungi are adapted to wildfire (Moore, 1962; Rhodes, 2006) and produce fire-resistant structures such as dormant spores, sclerotia, and conidia (Smith et al., 2015; Warcup & Baker, 1963) which are heat activated (Bruns et al., 2020; Gottlieb, 1950). The rapid and efficient germination of *Aspergillus* (in the section Fumigati) induced by high temperatures (Rhodes, 2006) and its ability to utilize various carbon and nitrogen sources, including ammonium and nitrate (Krappmann & Braus, 2005), may position *Aspergillus* to rapidly dominate after chaparral fires. Furthermore, *Pyronema domesticum*, a relatively well-studied pyrophilous fungus, can mineralize PyOM, a dominant substrate in burned environments (Fischer et al., 2021), thus potentially allowing it to take advantage of the abundant food source in this system. Together, these results suggest that dominant pyrophilous fungi are more widespread than expected and that their response to fire might be due to fire adaptations and requirements.

Early fungal succession stages were dominated by surviving ectomycorrhizal Basidiomycetes, *Mallocybe*, *Cortinarius*, and *Inocybe* that had been previously found in burned pine forests (Gassibe et al., 2011; Glassman et al., 2016; Owen et al., 2019; Pulido-Chavez et al., 2021) and early Mediterranean successional time points (Gassibe et al., 2011; Hernández-Rodríguez et al., 2013). However, fast-growing saprobic fungi in the genera *Pyronema*, *Penicillium*, and *Aspergillus* quickly dominated all successional time points, beginning at 25 days post-fire, consistent with pyrocism studies on *Pyronema* (Bruns et al., 2020). Although it is possible that the EMF signal detected could be due to relic DNA, high UV conditions, such as those in post-fire systems (Neary et al., 1999), rapidly degrade relic DNA (Torti et al., 2015), suggesting that these EMF survived the fire and the death of their host for up to 67 days, as in the case of *Inocybe*. These ectomycorrhizal fungi could have survived by displaying specificity for photosynthates, current vs. stored (Gray & Kernaghan, 2020; Pena et al., 2010), an aspect of exploration type. Whereas long/medium exploration types, *Cortinarius*, require more carbon for maintenance than short-contact types such as *Inocybe* (Agerer, 2001; Koide et al., 2014). Thus, we speculate that early EMF could have survived on their hosts' stored photosynthates. However, not all EMF hosts died; thus, the EMF that survived the fire could have survived on the lower resources provided by these resprouters.

Successional theory states that early successional stages are dominated by fast-growing species that quickly dominate the open space (Kinzig & Pacala, 2013). Our results suggest that this theory applies to fungal succession. The fungal community was dominated by fast-growing, asexual thermotolerant fungi, *Penicillium*, *Aspergillus*, and *Pyronema* (Dix & Webster, 1995; McGee et al., 2006). Asexual fungi can readily reproduce without needing a comparable mate (Crow, 1992), allowing rapid colonization of the open niche. Although stress selection is suggested to dominate sexual reproduction (Grishkan et al., 2003), our results suggest that in

chaparral, a fire-adapted ecosystem, stress adaptations such as the melanized conidia and thick cell walls of *Aspergillus* and *Penicillium* (Cordero & Casadevall, 2017; Lagashetti et al., 2019), and the formation of dormant spores or conidia might be characteristic of the historical fire regime of the system, thus allowing asexual fungi to rapidly colonize and dominate all successional time points during the first post-fire year. Lastly, we noted the emergence of fungal decomposers, *Coprinellus* and *Tephrocybe*, at later successional stages, supporting previous research (McMullan-Fisher et al., 2011). The onset of fruiting body development correlates with soil nutritional exhaustion (Kües & Liu, 2000). In our system, phosphate was significantly lower in the burned sites (data not shown), thus potentially explaining the fruiting of *Coprinellus* at later successional stages. Moreover, in support of recent studies in pine forests (Carey et al., 2020; Enright et al., 2021; Pulido-Chavez et al., 2021), we found *Geminibasidium* in our burned soils. *Geminibasidium* is a recently described thermotolerant saprobe (H. D. T. Nguyen et al., 2013) that was not present in the unburned sites but dominated early successional stages. Thus we suggest that *Geminibasidium* is underrepresented pyrophilous fungi.

5 Conclusion

We present the first fine-scale record of the temporal succession of bacterial and fungal communities in a wildfire-affected chaparral ecosystem in southern California. We found that the same pyrophilous bacteria and fungi that respond to fires in temperate pine forests and Spanish drylands also dominate in California chaparral, suggesting that post-fire microbes are heat activated and rapidly exploit post-fire niches. Our results demonstrate rapid bacterial and fungal community turnover and succession initiated as soon as 25 days post-fire for fungi and 34 days for bacteria. These results suggest that surviving bacteria and fungi control the initial

successional dynamics of the ecosystem. Additionally, post-fire dominant bacteria and fungi in wildfire-adapted systems are fast-growing, which could have developed mechanisms to efficiently utilize post-fire resources, resulting in niche exclusion and dominance in recently burned ecosystems, presenting similar successional patterns as those presented in successional theory. Moreover, the longevity of plant-associated microbes in the burned environment, including EMF and the dominance of the bacteria *Massilia*, suggests that these microbes could potentially contribute to post-fire restoration management. We conclude although wildfire leads to drastic reductions in species richness, biomass, and community composition, post-fire bacteria and fungi experience rapid successional changes that align with plant successional theory.

Acknowledgments

We thank the Cleveland National Forest and the Trabuco Ranger District, including District Ranger Darrel Vance and Officers Jeffrey Heys, Emily Fudge, Victoria Stempniewicz, and Jacob F. Rodriguez, for their guidance, help with the permitting and site selection process. We thank Judy A. Chung for help with fieldwork and molecular work and Aral C. Greene, Dylan Enright, and Sunny Saroa for fieldwork assistance. We thank Amelia Nelson, Elizah Stephens, and Kaleigh A. Russell, and our anonymous reviewers for their helpful comments on the manuscript. This work was supported by UC Riverside and the BLM JFSP Award #012641-002 and Shipley Skinner Award to MFPC and SIG.

Conflict of interest

Authors do not declare any conflict of interest or relationship that might influence the author's objectivity.

Figure 1. A) Location of the study area and plots(6 burned; 3 unburned) within the Holy Fire burn scar in the Cleveland National Forest in Southern California. Soil burn severity is based on the BAER classifications. B) Experimental design of each of the 9 plots and four 1m² subplots placed in each cardinal direction. C) Collection of the top 10 cm of soil with a releasable bulb planter within the 1 m² subplots at 17 days post-fire.

Biomass

A Bacteria

B Fungi

Richness

C Bacteria

D Fungi

Treatment —●— Unburned —●— Burned

Figure 2. Change in mean biomass A) archaea/bacteria and B) Fungi and change in mean richness for C) archaea/bacteria and D) fungi in relation to time since fire in days between burned and unburned plots. Precipitation is based on total monthly precipitation (mm) ranging from 0-148mm. The significance of each treatment (burned and unburned) per time point is denoted with an asterisk.

Figure 3. Change in A) archaeal/bacterial and B) fungal biomass and C) archaeal/bacterial and D) fungal species richness in relation to initial ash depth and its interaction time since fire. The significance of biomass and species richness is based on a negative binomial regression.

Figure 4. NMDS plot of A) bacterial and C) fungal community composition with colors denoting treatment and shape indicating time since fire (days). The NMDS is based on 3-dimensions and has a stress value of 0.11 for bacteria and 0.12 for fungi. The shift in the dominant B) bacterial and D) fungal genera over time, the color denoting the genera and line shape denoting the phyla.

Figure 5. Burned communities relative abundance at the genus level for A) archaea/bacteria and B) fungi based on taxa more than 3% sequence abundant at each time point. An asterisk next to the genera denotes the ectomycorrhizal fungal guild. The succession of the burned communities of C) archaea/bacteria and D) fungi is based on Mantel testing of the correlation between Bray-Curtis community dissimilarity and Euclidean temporal distances. Turnover of E) archaea/bacterial and F) fungal burned community composition per Bray-Curtis community dissimilarity between sampling time points (days) represented as the mean and standard error. Note time points farther apart indicate a community turnover, and closer together represent a lack of change for the given time periods. In general, bacteria experience turnover starting at 25 days post-fire and cease at 286 days post-fire, and fungi from 25 days post-fire up to 131 days post-fire where turnover ceased.

Figure 6. Unburned communities relative abundance at the genus level for A) archaea/bacteria and B) fungi based on taxa more than 3% sequence abundant at each time point. An asterisk next to general denotes ectomycorrhizal fungal guild. The succession of the unburned communities of C) archaea/bacteria and D) fungi is based on Mantel testing of the correlation between Bray-Curtis community dissimilarity and Euclidean temporal distances. Turnover of E) archaea/bacterial and F) fungal unburned community composition per Bray-Curtis community dissimilarity between sampling time points (days) represented as the mean and standard error. Note the lack of community turnover as represented by the overlapping time points.

Reference

- Agerer, R. (2001). Exploration types of ectomycorrhizae. *Mycorrhiza*, 11(2), 107–114.
<https://doi.org/10.1007/s005720100108>
- Allen, M. F., & Kitajima, K. (2013). In situ high-frequency observations of mycorrhizas. *New Phytologist*, 200(1), 222–228. <https://doi.org/10.1111/nph.12363>
- Averill, C., & Hawkes, C. V. (2016). Ectomycorrhizal fungi slow soil carbon cycling. *Ecology Letters*, 19(8), 937–947. <https://doi.org/10.1111/ele.12631>
- Bailey, A. C., Kellom, M., Poret-Peterson, A. T., Noonan, K., Hartnett, H. E., & Raymond, J. (2014). Draft Genome Sequence of *Massilia* sp. Strain BSC265, Isolated from Biological Soil Crust of Moab, Utah. *Genome Announcements*, 2(6), e01199-14, 2/6/e01199-14.
<https://doi.org/10.1128/genomeA.01199-14>
- Baldani, J. I., Rouws, L., Cruz, L. M., Olivares, F. L., Schmid, M., & Hartmann, A. (2014). The Family Oxalobacteraceae. In E. Rosenberg, E. F. DeLong, S. Lory, E. Stackebrandt, & F. Thompson (Eds.), *The Prokaryotes* (pp. 919–974). Springer Berlin Heidelberg.
https://doi.org/10.1007/978-3-642-30197-1_291
- Baldrian, P. (2016). Forest microbiome: Diversity, complexity and dynamics. *FEMS Microbiology Reviews*, fuw040. <https://doi.org/10.1093/femsre/fuw040>
- Barnard, R. L., Osborne, C. A., & Firestone, M. K. (2013). Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *The ISME Journal*, 7(11), 2229–2241.
<https://doi.org/10.1038/ismej.2013.104>
- Barro, S. C., & Conard, S. G. (1991). Fire effects on California chaparral systems: An overview. *Environment International*, 17(2–3), 135–149. [https://doi.org/10.1016/0160-4120\(91\)90096-9](https://doi.org/10.1016/0160-4120(91)90096-9)
- Barton, K. (2020). *MuMIn: Multi-Model Inference* (R package version 1.43.17.) [Computer software]. <https://CRAN.R-project.org/package=MumIn>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology and Evolution*, 9, 191–193.
- Bliss, C. I. (1953). *Fitting the negative binomial distribution to biological data (with “Note on the efficient fitting of the negative binomial” by R. A. Fisher)*, *Biometrics*, 9, (9th ed.). Biometrics.
- Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J., ... Caporaso, J. G. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, 37(8), 852–857. <https://doi.org/10.1038/s41587-019-0209-9>
- Bruns, T. D., Chung, J. A., Carver, A. A., & Glassman, S. I. (2020). A simple pyrococsm for studying soil microbial response to fire reveals a rapid, massive response by *Pyronema* species. *PLOS ONE*, 15(3), e0222691. <https://doi.org/10.1371/journal.pone.0222691>
- Cairney, J. W. G., & Bastias, B. A. (2007). Influences of fire on forest soil fungal communities

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- Function. *Canadian Journal of Forest Research*, 37(2), 207–215.
<https://doi.org/10.1139/x06-190>
- Callahan, B. J., McMurdie, P. J., & Holmes, S. P. (2017). Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *The ISME Journal*, 11(12), 2639–2643. <https://doi.org/10.1038/ismej.2017.119>
- Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844–848. <https://doi.org/10.1038/nature00812>
- Capitaino, R., & Carcaillet, C. (2008). Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. *Forest Ecology and Management*, 255(3), 431–439. <https://doi.org/10.1016/j.foreco.2007.09.010>
- Caporaso, J. G., Lauber, C. L., Walters, W. A., Berg-Lyons, D., Lozupone, C. A., Turnbaugh, P. J., Fierer, N., & Knight, R. (2011). Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *Proceedings of the National Academy of Sciences*, 108(Supplement_1), 4516–4522. <https://doi.org/10.1073/pnas.1000080107>
- Carey, C. J., Glassman, S. I., Bruns, T. D., Aronson, E. L., & Hart, S. C. (2020). Soil microbial communities associated with giant sequoia: How does the world’s largest tree affect some of the world’s smallest organisms? *Ecology and Evolution*, 10(13), 6593–6609. <https://doi.org/10.1002/ece3.6392>
- Certini, G., Moya, D., Lucas-Borja, M. E., & Mastrolonardo, G. (2021). The impact of fire on soil-dwelling biota: A review. *Forest Ecology and Management*, 488, 118989. <https://doi.org/10.1016/j.foreco.2021.118989>
- Collins, S. L. (1990). Patterns of Community Structure During Succession in Tallgrass Prairie. *Bulletin of the Torrey Botanical Club*, 117(4), 397–408. <https://doi.org/10.2307/2996837>
- Collins, S. L., Micheli, F., & Hartt, L. (2000). A method to determine rates and patterns of variability in ecological communities. *Oikos*, 91(2), 285–293. <https://doi.org/10.1034/j.1600-0706.2000.910209.x>
- Cordero, R. J., & Casadevall, A. (2017). Functions of fungal melanin beyond virulence. *Fungal Biology Reviews*, 31(2), 99–112. <https://doi.org/10.1016/j.fbr.2016.12.003>
- Crow, J. F. (1992). An advantage of sexual reproduction in a rapidly changing environment. *The Journal of Heredity*, 83(3), 169–173. <https://doi.org/10.1093/oxfordjournals.jhered.a111187>
- Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D. K., Lebrija-Trejos, E., Leiva, J. A., Odén, P.-C., Powers, J. S., Rico-Gray, V., Tigabu, M., & Healey, J. R. (2016). Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, 125(10), 1386–1397. <https://doi.org/10.1111/oik.03229>
- Dix, N. J., & Webster, J. (1995). *Fungal Ecology*. Chapman & Hall.
- Donato, D. C., Campbell, J. L., & Franklin, J. F. (2012). Multiple successional pathways and precocity in forest development: Can some forests be born complex? *Journal of Vegetation Science*, 23(3), 576–584. <https://doi.org/10.1111/j.1654-1103.2011.01362.x>
- Dooley, S. R., & Treseder, K. K. (2012). The effect of fire on microbial biomass: A meta-analysis of field studies. *Biogeochemistry*, 109(1/3), 49–61.
- Dove, N. C., & Hart, S. C. (2017). Fire Reduces Fungal Species Richness and In Situ Mycorrhizal Colonization: A Meta-Analysis. *Fire Ecology*, 13(2), 37–65. <https://doi.org/10.4996/fireecology.130237746>

- Dunn, P. H., Wells, W. G. I., Dickey, J., & Wohlgemuth, M. (1982). *Role of Fungi in Postfire Stabilization of Chaparral Ash Beds* (PSW-58, pp. 378–381) [Gen. Tech. Rep]. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S.U.S. Department of Agriculture.
- Egler, F. E. (1954). Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development with 2 figs. *Vegetatio*, 4(6), 412–417. <https://doi.org/10.1007/BF00275587>
- Eisenhauer, N., Schulz, W., Scheu, S., & Jousset, A. (2013). Niche dimensionality links biodiversity and invasibility of microbial communities. *Functional Ecology*, 27(1), 282–288. <https://doi.org/10.1111/j.1365-2435.2012.02060.x>
- Enright, D. J., Frangioso, K. M., Isobe, K., Rizzo, D. M., & Glassman, S. I. (2021). Mega-fire in Redwood Tanoak Forest Reduces Bacterial and Fungal Richness and Selects for Pyrophilous Taxa and Traits that are Phylogenetically Conserved. *BioRxiv*, 2021.06.30.450634. <https://doi.org/10.1101/2021.06.30.450634>
- Evans, S. E., & Wallenstein, M. D. (2012). Soil microbial community response to drying and rewetting stress: Does historical precipitation regime matter? *Biogeochemistry*, 109(1/3), 101–116.
- Fierer, N., Jackson, J. A., Vilgalys, R., & Jackson, R. B. (2005). Assessment of Soil Microbial Community Structure by Use of Taxon-Specific Quantitative PCR Assays. *Applied and Environmental Microbiology*, 71(7), 4117–4120. <https://doi.org/10.1128/AEM.71.7.4117-4120.2005>
- Fischer, M. S., Stark, F. G., Berry, T. D., Zeba, N., Whitman, T., & Traxler, M. F. (2021). *Pyrolyzed substrates induce aromatic compound metabolism in the post-fire fungus, Pyronema domesticum* [Preprint]. Microbiology. <https://doi.org/10.1101/2021.03.15.435558>
- Fujimura, K. E., Smith, J. E., Horton, T. R., Weber, N. S., & Spatafora, J. W. (2005). Pezizalean mycorrhizas and sporocarps in ponderosa pine (*Pinus ponderosa*) after prescribed fires in eastern Oregon, USA. *Mycorrhiza*, 15(2), 79–86. <https://doi.org/10.1007/s00572-004-0303-8>
- Gao, C., Montoya, L., Xu, L., Madera, M., Hollingsworth, J., Purdom, E., Singan, V., Vogel, J., Hutmacher, R. B., Dahlberg, J. A., Coleman-Derr, D., Lemaux, P. G., & Taylor, J. W. (2020). Fungal community assembly in drought-stressed sorghum shows stochasticity, selection, and universal ecological dynamics. *Nature Communications*, 11(1), 34. <https://doi.org/10.1038/s41467-019-13913-9>
- Gassibe, P. V., Fabero, R. F., Hernández-Rodríguez, M., Oria-de-Rueda, J. A., & Martín-Pinto, P. (2011). Fungal community succession following wildfire in a Mediterranean vegetation type dominated by *Pinus pinaster* in Northwest Spain. *Forest Ecology and Management*, 262(4), 655–662. <https://doi.org/10.1016/j.foreco.2011.04.036>
- Glassman, S. I., Levine, C. R., DiRocco, A. M., Battles, J. J., & Bruns, T. D. (2016). Ectomycorrhizal fungal spore bank recovery after a severe forest fire: Some like it hot. *The ISME Journal*, 10(5), 1228–1239. <https://doi.org/10.1038/ismej.2015.182>
- Glassman, S. I., Randolph, J. W., Saroa, S. S., Capocchi, J. K., Walters, K. E., Pulido-Chavez, M. F., & Larios, L. (2021). *Prescribed versus wildfire impacts on exotic plants and soil microbes in California grasslands* [Preprint]. Ecology. <https://doi.org/10.1101/2021.09.22.461426>
- Gottlieb, D. (1950). The physiology of spore germination in fungi. *The Botanical Review*, 16(5), 229–257. <https://doi.org/10.1007/BF02873609>

- Grady, E. N., MacDonald, J., Liu, L., Richman, A., & Yuan, Z.-C. (2016). Current knowledge and perspectives of Paenibacillus: A review. *Microbial Cell Factories*, 15(1), 203. <https://doi.org/10.1186/s12934-016-0603-7>
- Gray, L., & Kernaghan, G. (2020). Fungal Succession During the Decomposition of Ectomycorrhizal Fine Roots. *Microbial Ecology*, 79(2), 271–284. <https://doi.org/10.1007/s00248-019-01418-3>
- Grishkan, I., Korol, A. B., Nevo, E., & Wasser, S. P. (2003). Ecological stress and sex evolution in soil microfungi. *Proceedings of the Royal Society B: Biological Sciences*, 270(1510), 13–18. <https://doi.org/10.1098/rspb.2002.2194>
- Gu, H., Lou, J., Wang, H., Yang, Y., Wu, L., Wu, J., & Xu, J. (2016). Biodegradation, Biosorption of Phenanthrene and Its Trans-Membrane Transport by Massilia sp. WF1 and Phanerochaete chrysosporium. *Frontiers in Microbiology*, 7. <https://doi.org/10.3389/fmicb.2016.00038>
- Guhr, A., & Kircher, S. (2020). Drought-Induced Stress Priming in Two Distinct Filamentous Saprotrophic Fungi. *Microbial Ecology*, 80(1), 27–33. <https://doi.org/10.1007/s00248-019-01481-w>
- Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F. B., Ripplinger, J., Slaughter, P., Gries, C., & Collins, S. L. (2016). codyn: An r package of community dynamics metrics. *Methods in Ecology and Evolution*, 7(10), 1146–1151. <https://doi.org/10.1111/2041-210X.12569>
- Hanes, T. L. (1971). *Succession after Fire in the Chaparral of Southern California*. 41(1), 27–52. <https://doi.org/doi:10.2307/1942434>
- Hart, S. C., DeLuca, T. H., Newman, G. S., MacKenzie, M. D., & Boyle, S. I. (2005). Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management*, 220(1–3), 166–184. <https://doi.org/10.1016/j.foreco.2005.08.012>
- Hernández-Rodríguez, M., Oria-de-Rueda, J. A., & Martín-Pinto, P. (2013). Post-fire fungal succession in a Mediterranean ecosystem dominated by Cistus ladanifer L. *Forest Ecology and Management*, 289, 48–57. <https://doi.org/10.1016/j.foreco.2012.10.009>
- Homyak, P. M., Sickman, J. O., Miller, A. E., Melack, J. M., Meixner, T., & Schimel, J. P. (2014). Assessing Nitrogen-Saturation in a Seasonally Dry Chaparral Watershed: Limitations of Traditional Indicators of N-Saturation. *Ecosystems*, 17(7), 1286–1305. <https://doi.org/10.1007/s10021-014-9792-2>
- Iffis, B., St-Arnaud, M., & Hijri, M. (2014). Bacteria associated with arbuscular mycorrhizal fungi within roots of plants growing in a soil highly contaminated with aliphatic and aromatic petroleum hydrocarbons. *FEMS Microbiology Letters*, 358(1), 44–54. <https://doi.org/10.1111/1574-6968.12533>
- J., E. de los M., A., M., & F., V. (2001). Metabolic profiles and aprE expression in anaerobic cultures of Bacillus subtilis using nitrate as terminal electron acceptor. *Applied Microbiology and Biotechnology*, 57(3), 379–384. <https://doi.org/10.1007/s002530100749>
- Kalayu, G. (2019). Phosphate Solubilizing Microorganisms: Promising Approach as Biofertilizers. *International Journal of Agronomy*, 2019, 1–7. <https://doi.org/10.1155/2019/4917256>
- Kaur, N., Seuylemezian, A., Patil, P. P., Patil, P., Krishnamurti, S., Varelas, J., Smith, D. J., Mayilraj, S., & Vaishampayan, P. (2018). Paenibacillus xerothermodurans sp. Nov., an extremely dry heat resistant spore forming bacterium isolated from the soil of Cape

- Canaveral, Florida. *International Journal of Systematic and Evolutionary Microbiology*, 68(10), 3190–3196. <https://doi.org/10.1099/ijsem.0.002967>
- Kindt, R., & Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF).
- Kinzig, A. P., & Pacala, S. (2013). 9. Successional Biodiversity and Ecosystem Functioning. In *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions (MPB-33)* (pp. 175–212). Princeton University Press. <https://doi.org/10.1515/9781400847303.175>
- Koide, R. T., Fernandez, C., & Malcolm, G. (2014). Determining place and process: Functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytologist*, 201(2), 433–439. <https://doi.org/10.1111/nph.12538>
- Köljal, U., Larsson, K.-H., Abarenkov, K., Nilsson, R. H., Alexander, I. J., Eberhardt, U., Erland, S., Høiland, K., Kjoller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A. F. S., Tedersoo, L., & Vrålstad, T. (2005). UNITE: A database providing web-based methods for the molecular identification of ectomycorrhizal fungi. *New Phytologist*, 166(3), 1063–1068. <https://doi.org/10.1111/j.1469-8137.2005.01376.x>
- Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K., & Schloss, P. D. (2013). Development of a Dual-Index Sequencing Strategy and Curation Pipeline for Analyzing Amplicon Sequence Data on the MiSeq Illumina Sequencing Platform. *Applied and Environmental Microbiology*, 79(17), 5112–5120. <https://doi.org/10.1128/AEM.01043-13>
- Krappmann, S., & Braus, G. H. (2005). Nitrogen metabolism of *Aspergillus* and its role in pathogenicity. *Medical Mycology*, 43(s1), 31–40. <https://doi.org/10.1080/13693780400024271>
- Kües, U., & Liu, Y. (2000). Fruiting body production in basidiomycetes. *Applied Microbiology and Biotechnology*, 54(2), 141–152. <https://doi.org/10.1007/s002530000396>
- Kummerow, J., Alexander, J. V., Neel, J. W., & Fishbeck, K. (1978). Symbiotic Nitrogen Fixation in Ceanothus Roots. *American Journal of Botany*, 65(1), 63–69. <https://doi.org/10.2307/2442555>
- Lagashetti, A. C., Dufossé, L., Singh, S. K., & Singh, P. N. (2019). Fungal Pigments and Their Prospects in Different Industries. *Microorganisms*, 7(12), 604. <https://doi.org/10.3390/microorganisms7120604>
- Li, X., Rui, J., Mao, Y., Yannarell, A., & Mackie, R. (2014). Dynamics of the bacterial community structure in the rhizosphere of a maize cultivar. *Soil Biology and Biochemistry*, 68, 392–401. <https://doi.org/10.1016/j.soilbio.2013.10.017>
- Liu, C. M., Kachur, S., Dwan, M. G., Abraham, A. G., Aziz, M., Hsueh, P.-R., Huang, Y.-T., Busch, J. D., Lamit, L. J., Gehring, C. A., Keim, P., & Price, L. B. (2012). FungiQuant: A broad-coverage fungal quantitative real-time PCR assay. *BMC Microbiology*, 12(1), 255. <https://doi.org/10.1186/1471-2180-12-255>
- Livne-Luzon, S., Shemesh, H., Osem, Y., Carmel, Y., Migael, H., Avidan, Y., Tsafrir, A., Glassman, S. I., Bruns, T. D., & Ovadia, O. (2021). High resilience of the mycorrhizal community to prescribed seasonal burnings in eastern Mediterranean woodlands. *Mycorrhiza*, 31(2), 203–216. <https://doi.org/10.1007/s00572-020-01010-5>
- Martin, M. (2011). *Cutadapt removes adapter sequences from high-throughput sequencing reads*. <https://journal.embnet.org/index.php/embnetjournal/article/view/200/458>

- McGee, P. A., Markovina, A.-L., Jeong, G. C. E., & Cooper, E. D. (2006). Trichocomaceae in bark survive high temperatures and fire: Trichocomaceae in bark survive high temperatures and fire. *FEMS Microbiology Ecology*, 56(3), 365–371. <https://doi.org/10.1111/j.1574-6941.2006.00079.x>
- McMullan-Fisher, S. J. M., Tom W. May, Richard M. Robinson, Tina L. Bell, Teresa Lebel, Pam Catcheside, & Alan York. (2011). *Fungi and fire in Australian ecosystems: A review of current knowledge, management implications and future directions*. 59, 70–90.
- McMurdie, P. J., & Holmes, S. (2013). phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLOS ONE*, 8(4), e61217. <https://doi.org/10.1371/journal.pone.0061217>
- Monciardini, P., Cavaletti, L., Schumann, P., Rohde, M., & Donadio, S. (2003). Conexibacter woesei gen. Nov., sp. Nov., a novel representative of a deep evolutionary line of descent within the class Actinobacteria. *International Journal of Systematic and Evolutionary Microbiology*, 53(2), 569–576. <https://doi.org/10.1099/ijs.0.02400-0>
- Moore, E. J. (1962). The Ontogeny of the Sclerotia of Pyronema Domesticum. *Mycologia*, 54(3), 312–316. <https://doi.org/10.1080/00275514.1962.12025004>
- Neary, D. G., Klopatek, C. C., DeBano, L. F., & Ffolliott, P. F. (1999). Fire effects on belowground sustainability: A review and synthesis. *Forest Ecology and Management*, 122(1–2), 51–71. [https://doi.org/10.1016/S0378-1127\(99\)00032-8](https://doi.org/10.1016/S0378-1127(99)00032-8)
- Nguyen, H. D. T., Nickerson, N. L., & Seifert, K. A. (2013). Basidioascus and Geminibasidium: A new lineage of heat-resistant and xerotolerant basidiomycetes. *Mycologia*, 105(5), 1231–1250. JSTOR.
- Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S., & Kennedy, P. G. (2016). FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology*, 20, 241–248. <https://doi.org/10.1016/j.funeco.2015.06.006>
- Ofek, M., Hadar, Y., & Minz, D. (2012). Ecology of Root Colonizing Massilia (Oxalobacteraceae). *PLOS ONE*, 7(7), e40117. <https://doi.org/10.1371/journal.pone.0040117>
- Oksanen, J., Blanchet, G. F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2018). *Vegan: Community Ecology Package-Version 2.5.2. Ordination Methods, Diversity Analysis, and Other Functions for Community and Vegetation Ecologist*.
- Owen, S. M., Patterson, A. M., Gehring, C. A., Sieg, C. H., Baggett, L. S., & Fulé, P. Z. (2019). Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a ponderosa pine forest. *Soil Biology and Biochemistry*, 139, 107616. <https://doi.org/10.1016/j.soilbio.2019.107616>
- Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., & Ribbens, E. (1996). Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics. *Ecological Monographs*, 66(1), 1–43. <https://doi.org/10.2307/2963479>
- Pandolfi, J. M. (2008). Succession. In S. E. Jørgensen & B. D. Fath (Eds.), *Encyclopedia of Ecology* (pp. 3416–3424). Academic Press. <https://doi.org/10.1016/B978-008045405-4.00547-4>
- Pena, R., Offermann, C., Simon, J., Naumann, P. S., Geßler, A., Holst, J., Dannenmann, M., Mayer, H., Kögel-Knabner, I., Rennenberg, H., & Polle, A. (2010). Girdling Affects Ectomycorrhizal Fungal (EMF) Diversity and Reveals Functional Differences in EMF

Community Composition in a Beech Forest. *Applied and Environmental Microbiology*, 76(6), 1831–1841. <https://doi.org/10.1128/AEM.01703-09>

Pérez-Valera, E., Verdú, M., Navarro-Cano, J. A., & Goberna, M. (2018). Resilience to fire of phylogenetic diversity across biological domains. *Molecular Ecology*, 27(13), 2896–2908. <https://doi.org/10.1111/mec.14729>

Pérez-Valera, E., Verdú, M., Navarro-Cano, J. A., & Goberna, M. (2020). Soil microbiome drives the recovery of ecosystem functions after fire. *Soil Biology and Biochemistry*, 149, 107948. <https://doi.org/10.1016/j.soilbio.2020.107948>

Placella, S. A., Brodie, E. L., & Firestone, M. K. (2012). Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. *Proceedings of the National Academy of Sciences*, 109(27), 10931–10936. <https://doi.org/10.1073/pnas.1204306109>

Pourreza, M., Hosseini, S. M., Safari Sinegani, A. A., Matiniazadeh, M., & Dick, W. A. (2014). Soil microbial activity in response to fire severity in Zagros oak (*Quercus brantii* Lindl.) forests, Iran, after one year. *Geoderma*, 213, 95–102. <https://doi.org/10.1016/j.geoderma.2013.07.024>

Pressler, Y., Moore, J. C., & Cotrufo, M. F. (2019). Belowground community responses to fire: Meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos*, 128(3), 309–327. <https://doi.org/10.1111/oik.05738>

Pulido-Chavez, M. F., Alvarado, E. C., DeLuca, T. H., Edmonds, R. L., & Glassman, S. I. (2021). High-severity wildfire reduces richness and alters composition of ectomycorrhizal fungi in low-severity adapted ponderosa pine forests. *Forest Ecology and Management*, 485, 118923. <https://doi.org/10.1016/j.foreco.2021.118923>

Rhodes, J. C. (2006). *Aspergillus fumigatus*: Growth and virulence. *Medical Mycology*, 44(s1), 77–81. <https://doi.org/10.1080/13693780600779419>

Riley, K. L., & Loehman, R. A. (2016). Mid-21st-century climate changes increase predicted fire occurrence and fire season length, Northern Rocky Mountains, United States. *Ecosphere*, 7(11), e01543. <https://doi.org/10.1002/ecs2.1543>

Ross, G. J. S., & Preece, D. A. (1985). The Negative Binomial Distribution. *Journal of the Royal Statistical Society. Series D (The Statistician)*, 34(3), 323–335. JSTOR. <https://doi.org/10.2307/2987659>

Rousk, J., Brookes, P. C., & Bååth, E. (2010). Investigating the mechanisms for the opposing pH relationships of fungal and bacterial growth in soil. *Soil Biology and Biochemistry*, 42(6), 926–934. <https://doi.org/10.1016/j.soilbio.2010.02.009>

Schimel, J. P. (2018). Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 409–432. <https://doi.org/10.1146/annurev-ecolsys-110617-062614>

Schluter, D., & Ricklefs, R. E. (1993). *Species diversity: An introduction to the problem. Species diversity in ecological communities*. Chicago University Press.

Semenova-Nelsen, T. A., Platt, W. J., Patterson, T. R., Huffman, J., & Sikes, B. A. (2019). Frequent fire reorganizes fungal communities and slows decomposition across a heterogeneous pine savanna landscape. *New Phytologist*, 224(2), 916–927. <https://doi.org/10.1111/nph.16096>

Slepecky, R. A., & Hemphill, H. E. (2006). The Genus *Bacillus*—Nonmedical. In M. Dworkin, S. Falkow, E. Rosenberg, K.-H. Schleifer, & E. Stackebrandt (Eds.), *The Prokaryotes: Volume 4: Bacteria: Firmicutes, Cyanobacteria* (pp. 530–562). Springer US. https://doi.org/10.1007/0-387-30744-3_16

- Smith, M. E., Henkel, T. W., & Rollins, J. A. (2015). How many fungi make sclerotia? *Fungal Ecology*, 13, 211–220. <https://doi.org/10.1016/j.funeco.2014.08.010>
- Taylor, D. L., Walters, W. A., Lennon, N. J., Bochicchio, J., Krohn, A., Caporaso, J. G., & Pennanen, T. (2016). Accurate Estimation of Fungal Diversity and Abundance through Improved Lineage-Specific Primers Optimized for Illumina Amplicon Sequencing. *Applied and Environmental Microbiology*, 82(24), 7217–7226. <https://doi.org/10.1128/AEM.02576-16>
- Toljander, J. F., Artursson, V., Paul, L. R., Jansson, J. K., & Finlay, R. D. (2005). Attachment of different soil bacteria to arbuscular mycorrhizal fungal extraradical hyphae is determined by hyphal vitality and fungal species. *FEMS Microbiol Lett*, 7.
- Torti, A., Lever, M. A., & Jørgensen, B. B. (2015). Origin, dynamics, and implications of extracellular DNA pools in marine sediments. *Marine Genomics*, 24, 185–196. <https://doi.org/10.1016/j.margen.2015.08.007>
- Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems*, 1(6), 511–523. <https://doi.org/10.1007/s100219900047>
- Van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., & Sanders, I. R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396(6706), 69–72. <https://doi.org/10.1038/23932>
- Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (Fourth edition). Springer. <https://www.stats.ox.ac.uk/pub/MASS4/>.
- Wan, W., Qin, Y., Wu, H., Zuo, W., He, H., Tan, J., Wang, Y., & He, D. (2020). Isolation and Characterization of Phosphorus Solubilizing Bacteria With Multiple Phosphorus Sources Utilizing Capability and Their Potential for Lead Immobilization in Soil. *Frontiers in Microbiology*, 0. <https://doi.org/10.3389/fmicb.2020.00752>
- Warcup, J. H., & Baker, K. F. (1963). Occurrence of Dormant Ascospores in Soil. *Nature*, 197(4874), 1317–1318. <https://doi.org/10.1038/1971317a0>
- Whitman, T., Whitman, E., Woollet, J., Flannigan, M. D., Thompson, D. K., & Parisien, M.-A. (2019). Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. *Soil Biology and Biochemistry*, 138, 107571. <https://doi.org/10.1016/j.soilbio.2019.107571>
- Woollet, J., & Whitman, T. (2020). Pyrogenic organic matter effects on soil bacterial community composition. *Soil Biology and Biochemistry*, 141, 107678. <https://doi.org/10.1016/j.soilbio.2019.107678>
- Xiang, X., Shi, Y., Yang, J., Kong, J., Lin, X., Zhang, H., Zeng, J., & Chu, H. (2014). Rapid recovery of soil bacterial communities after wildfire in a Chinese boreal forest. *Scientific Reports*, 4. <https://doi.org/10.1038/srep03829>
- Yilmaz, P., Parfrey, L. W., Yarza, P., Gerken, J., Pruesse, E., Quast, C., Schweer, T., Peplies, J., Ludwig, W., & Glöckner, F. O. (2014). The SILVA and “All-species Living Tree Project (LTP)” taxonomic frameworks. *Nucleic Acids Research*, 42(D1), D643–D648. <https://doi.org/10.1093/nar/gkt1209>