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

M. Fabiola Pulido-Chavez[1,*], James W. J. Randolph[2], Cassandra Zalman[3], Loralee Larios[4], Peter M. Homyak[5], and Sydney I. Glassman[6,*]

[1]Department of Microbiology and Plant Pathology, University of California-Riverside, 900 University Ave, Riverside, CA, 92521, mpuli011@ucr.edu
[2]Department of Microbiology and Plant Pathology, University of California-Riverside, 900 University Ave, Riverside, CA, 92521, jrand005@ucr.edu
[3]Schmid College of Science and Technology, Chapman University, Orange, CA, 92866, medvedef@chapman.edu
[4]Department of Botany and Plant Sciences, University of California-Riverside, 900 University Ave, Riverside, CA, 92521, loralee@ucr.edu
[5]Department of Environmental Sciences, University of California-Riverside, 900 University Ave, Riverside, CA, 92521, phomyak@ucr.edu
[6]Department of Microbiology and Plant Pathology, University of California-Riverside, 900 University Ave, Riverside, CA, 92521, sydneyg@ucr.edu

*Correspondence: Sydney I Glassman, sydneyg@ucr.edu and M. Fabiola Pulido-Chavez, mpuli011@ucr.ed Department of Microbiology and Plant Pathology, University of California-Riverside

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Abstract

The rise in wildfire frequency and severity across the globe has increased interest in secondary succession. However, despite the role of soil microbial communities in the regeneration of post-fire vegetation and biogeochemical cycling, the lack of measurements immediately post-fire and at high temporal resolution has resulted in a limited understanding of microbial secondary succession. To fill this knowledge gap, we sampled soils at 17, 25, 34, 67, 95, 131, 187, 286, and 376 days after a Southern California wildfire in fire-adapted chaparral shrublands. We assessed bacterial and fungal biomass with qPCR of 16S and 18S and richness and composition with Illumina MiSeq sequencing of 16S and ITS2 amplicons. 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%. While bacterial biomass and richness oscillated in response to precipitation, the declines in biomass and richness for both groups persisted for the entire year. In contrast to the unburned plots, burned fungal and bacterial communities experienced rapid succession, with 5-6 compositional turnover periods. Analogous to plants, "fire-loving" pyrophilous microbes increased post-fire and drove successional dynamics. Interestingly, many of the same pyrophilous taxa found in forests worldwide also dominated post-fire chaparral and traded off markedly in abundance over time. For fungi, an initial peak in the Basidiomycete yeast *Geminibasidium* traded off with the filamentous Ascomycetes *Pyronema, Aspergillus,* and *Penicillium*. For bacteria, the Proteobacteria genus *Massilia* dominated burned plots throughout the year, but the following most dominant bacteria, the Firmicute *Bacillus* and Proteobacteria *Noviherbaspirillum,* traded off in abundance over time. Our unprecedented high-resolution temporal sampling allowed us to capture post-fire microbial secondary successional dynamics and show that putative tradeoffs in thermotolerance,

colonization, and competition among dominant pyrophilous microbes control microbial succession with possible implications for ecosystem function.

1. Introduction

The rapid increase in wildfire frequency, severity, and extent in the western United States (Riley & Loehman, 2016) and around the globe (Abatzoglou et al., 2019) has renewed 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), but belowground microbial communities have been comparatively overlooked. Understanding how wildfires alter soil microbial succession may be necessary to predict post-fire effects on ecosystem recovery, and function since soil microbes drive post-fire organic matter decomposition (Semenova-Nelsen et al., 2019), nutrient cycling (Pérez-Valera et al., 2020), and plant regeneration (Dove & Hart, 2017).

Plant succession is a major process affecting the health and function of ecosystems. During succession, the dominant species may change in an orderly and predictable manner (Shugart, 2013). Early colonizers (fast-growing, short-lived species) are often replaced by long-lived stable communities . However, wildfire can reset the successional clock, shifting the course of succession away from equilibrium (Reilly & Spies, 2016) and initiating secondary succession. Because secondary succession often begins with low competition in a nutrient-rich environment (Dalling, 2008), colonization and resource use tradeoffs will often drive successional dynamics (Tilman, 1990). Indeed, the sequence of species replacement suggests that early colonizers with similar resource use (i.e., overlapping niches) will dominate open space but will inevitably be replaced by late-stage species with differentiation in resource use (i.e., complementarity),

allowing for species coexistence (Pacala et al., 1996; Turnbull et al., 2013). However, whether the patterns recognized in plant successional theory translate to belowground soil microbes remains unclear.

Research on post-fire soil microbiomes suggests that fires can reset microbial succession via fire-induced mortality (Hart et al., 2005), reductions in microbial richness and biomass (Dooley & Treseder, 2012; Pressler et al., 2019), and the replacement of fungal basidiomycetes and symbiotic mycorrhizal fungi with ascomycetes and saprobic fungi (Cairney & Bastias, 2007; Fox et al., 2022). Indeed, for over a century, pyrophilous "fire-loving" fungi have been consistently found in post-fire mushroom surveys (McMullan-Fisher et al., 2011; Seaver, 1909). More recently, next-generation sequencing indicates that the pyrophilous Ascomycete *Pyronema* can increase 100 fold after prescribed fires (Reazin et al., 2016) and dominate over 60% of the sequences in experimental pyrocosms (Bruns et al., 2020). Furthermore, there is increasing evidence of pyrophilous bacteria, such as the Proteobacteria *Massilia* (Enright et al., 2022; Whitman et al., 2019). Together, evidence suggests that pyrophilous microbes likely evolved under the same fire regime as the ecosystems they inhabit (Dove et al., 2021) and likely have fire adaptations analogous to plants (Rundel, 2018). Pyrophilous microbes have traits that allow for the survival to fire (i.e., heat resistant spores, sclerotia) (Day et al., 2020; Petersen, 1970) and the post-fire environment (i.e., xerotolerance, decomposition of nitrogen and aromatic hydrocarbons) (Fischer et al., 2021; Nelson et al., 2021; Steindorff et al., 2021). However, most research is based on single time-point sampling (Dove & Hart, 2017; Pressler et al., 2019); thus, the successional trajectory of pyrophilous microbes is nearly unknown. However, recent research suggests that bacteria and fungi experience rapid post-fire community changes (Ferrenberg et al., 2013; Qin & Liu, 2021), leading to different successional trajectories (Ammitzboll et al., 2022).

Although these studies sampled two to three times in the first post-fire year, to adequately capture the rapid growth and turnover rates of soil microbes and thus the dynamics needed to develop microbial successional theory (Hannula et al., 2019), it is integral to sample directly post-fire and at high temporal resolution.

Here, we propose that microbial ecological succession theory can be developed and tested in nature by focusing on California chaparral. Chaparral is a shrubland adapted to high-severity fire and a biodiversity hotspot distributed in Mediterranean climates worldwide (Barro & Conard, 1991; Rundel, 2018). Chaparral plant secondary succession is relatively well understood and typically initiated by fire (Keeley et al., 2005). Yet, although the dominant chaparral vegetation forms mycorrhizal associations required for their establishment and survival (Allen et al., 2005), little is known about chaparral microbial succession. Indeed, only 13% of post-fire microbiome research occurs in shrublands (Pressler et al., 2019). With drylands covering nearly 41% of Earth's terrestrial surface and expanding with climate change (Feng & Fu, 2013), it is critical to understand secondary successional dynamics in dryland systems such as chaparral. While our focus is on chaparral, which is likely to have fire-adapted microbes due to its evolutionary history, we expect that successional patterns will be broadly generalizable to other biomes since pyrophilous bacteria and fungi appear to be phylogenetically conserved (Enright et al., 2022). Indeed, some fungal taxa within the Ascomycota family Pyronemataceae and a few Basidiomycota genera appear to be globally distributed in fire-disturbed Spanish shrublands (Pérez-Valera et al., 2018) and Pinaceae (Hughes et al., 2020; Reazin et al., 2016; Whitman et al., 2019; Xiang et al., 2014), Eucalyptus (Ammitzboll et al., 2022; McMullan-Fisher et al., 2011), and Redwood-Tanoak forests (Enright et al., 2022).

However, predicting the successional trajectory of soil microbes is complicated by direct and indirect wildfire effects (Neary et al., 1999). Whereas soil burn severity drives direct fire impacts (Reazin et al., 2016; Whitman et al., 2019), changes in soil moisture, pH, and nutrients can indirectly impact post-fire microbes (Köster et al., 2014; Neary et al., 1999), potentially driving succession via environmental filtering (Schluter & Ricklefs, 1993). Indeed, research supports the role of differential responses to soil burn severity (Whitman et al., 2019) and soil moisture in structuring microbiomes (Evans & Wallenstein, 2012; Placella et al., 2012; Yang et al., 2021). Bacteria rapidly respond to soil wet-up (Barnard et al., 2013; Placella et al., 2012), whereas fungi appear to be more resilient to soil moisture changes (Barnard et al., 2013; Evans & Wallenstein, 2012). Furthermore, microbial life strategies can determine microbial response to fire. Research shows that fire decreases ectomycorrhizal fungi (EMF) (Cowan et al., 2016; Glassman et al., 2016; Pulido-Chavez et al., 2021) and arbuscular fungi (AMF) (Xiang et al., 2015) but can temporarily increase saprobic richness (Enright et al., 2022; Semenova-Nelsen et al., 2019). Yet, the limited studies on how fires affect multiple microbial guilds (Certini et al 2021) lack the resolution to identify the direct effect of wildfire and the length of time that mycorrhizal fungi can survive after plant host death, a question essential for post-fire ecosystem recovery.

Here, we performed the highest resolution temporal sampling of post-fire microbiomes to date, sampling soil at 9-time points over one year following a chaparral wildfire, allowing us to identify immediate and temporal effects of wildfire on microbial successional dynamics. We then tested the following hypotheses: (**H1**) wildfire will decrease bacterial and fungal biomass and richness, leading to a shift in the community composition, where one year will not be sufficient time to return to unburned levels; **(H2)** wildfire will have a distinct impact on fungal

153 guilds with symbiotic mycorrhizal fungi experiencing the largest declines; **(H3)** higher soil burn
154 severity will lead to larger reductions in both bacteria and fungi while precipitation will impose a
155 larger impact on bacterial than fungal succession; **(H4)** succession will be initiated by
156 pyrophilous microbes, which like plants, will trade off in abundance over time based on their
157 traits.

158 **2. Methods**

159 ***2.1 Study Area, plot design, and soil collection***

160 The Holy Fire burned 94 km^2 in the Cleveland National Forest in Southern California
161 from August 6 to September 13, 2018. On September 30, 2018, we established nine plots (6
162 burned and 3 unburned) along a gradient of fire severities (**Fig. 1A**). Plots were selected for
163 similarity in aspect, slope, elevation, and pre-fire vegetation dominance by manzanita
164 *(Arctostaphylos glandulosa),* an ectomycorrhizal host, and chamise (*Adenostoma fasciculatum),*
165 an arbuscular and ectomycorrhizal host (Allen et al., 2005). Plots were placed on average 25 m
166 from forest access roads to avoid edge effects. Each circular plot contained four 1 m^2 subplots
167 located 5 m from the center in each cardinal direction (**Fig. 1B**). Our study site experiences a
168 Mediterranean-type climate with warm, dry summers and cool, wet winters, with an average
169 yearly temperature of 17˚C and precipitation of 12.5 mm. Precipitation data, based on monthly
170 summaries, was gathered from the El Cariso weather station (raws.dri.edu). Additional plot
171 information can be found in the supplements **(Table S1)**.

172 We sampled soils at 17, 25, 34, 67, 95, 131, 187, 286, and 376 days, corresponding to
173 approximately 2 and 3 weeks, and 1, 2, 3, 4, 6, 9, and 12 months post-fire. We used BAER soil
174 burn severity maps (Parson et al., 2010) to roughly locate plots at medium and high severity
175 (**Fig. 1A**), but their coarse-scale measurement (30m) does not coincide well with microbial

176 communities. Since ash depth increases with soil heating (Parson et al., 2010) and fire severity
177 (Bodí et al., 2014), we used ash depth as a proxy for soil burn severity, where we averaged three
178 separate measurements of ash depth (cm) per each 1 m^2 subplot at day 17, before any
179 precipitation event could wash away the ash. Thus, our measure of soil burn severity refers to
180 initial ash depth. At each of the 9 time points, we collected the top 10 cm of soil beneath the ash
181 or duff from each of the 36 subplots with a ~250 mL cleaned releasable bulb planter (**Fig. 1C**).
182 Soils were transported to the University of California-Riverside (UCR) within hours of sampling,
183 stored overnight at 4˚C, sieved (2 mm) within 24 hours, and a subsample was frozen at -80°C for
184 DNA extraction.
185
186 ***2.3 DNA extraction, amplification, and sequencing***
187 DNA was extracted from soil using Qiagen DNeasy PowerSoil Kits following the
188 manufacturer's protocol, except the centrifugation time was increased to 1.5 min after adding the
189 C3 solution due to large amounts of precipitate. DNA extracts were stored at -20˚C for
190 subsequent analysis. Extracted DNA was amplified using the primer pair ITS4-fun and 5.8s
191 (Taylor et al., 2016) to amplify the ITS2 region for fungi and the primer pair 515F-806R to
192 amplify the V4 region of the 16S rRNA gene for archaea and bacteria (Caporaso et al., 2011)
193 using the Dual-Index Sequencing Strategy (DIP) (Kozich et al., 2013). Although our 16S primers
194 amplify archaea and bacteria, for simplicity, we refer to 16S methods and results simply as
195 bacteria since archaea only contributed <1% of sequencing reads. We conducted polymerase
196 chain reaction (PCR) in two steps. The first PCR amplified gene-specific primers, and the second
197 PCR ligated the DIP barcodes and adaptors for Illumina sequencing. For bacteria, we combined
198 1 µl of 1:10 diluted DNA, 10.5 µL of Ultra-Pure Sterile Molecular Biology Grade (Genesee

199 Scientific, San Diego, CA, USA), 12.5 µL of AccuStart ToughMix (2x concentration; Quantabio,
200 Beverly, MA, USA), and 0.5 µL each of the 10 µM 515F and 806R primers. Thermocycler
201 conditions for PCR1 were: 94°C for 2 min followed by 29 cycles of 94°C for 30 s, 55°C for 30 s,
202 68°C for 1 min followed by a 2 min extension at 68°C. For fungi, we combined 5 µl of
203 undiluted fungal DNA, 6.5 µl of ultra-pure water, 12.5 µl of AccuStart ToughMix, and 0.5 µL
204 each of the 10 µM ITS4-fun and 5.8s primers. Thermocycler conditions for PCR1 were: 94 °C
205 for 2 min, followed by 30 cycles of 94 °C for 30 s, 55 °C for 30 s, 68 °C for 2 min followed by a
206 10 min extension at 68°C. PCR1 products were cleaned with AMPure XP magnetic beads
207 (Beckman Coulter Inc., Brea, CA), following the manufacturer's protocols. The DIP PCR2
208 primers containing the barcodes and adaptors for Illumina sequencing were ligated to the
209 amplicons during the second PCR step in a 25 µL reaction containing 2.5 µL of the 10 µM DIP
210 PCR2 primers, 6.5 µL of ultra-pure water, 12.5 µL of Accustart ToughMix, and 1 µL of PCR1
211 product. Thermocycler conditions for PCR2 for bacteria and fungi were: 94°C for 2 min
212 followed by 10 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 1 min. Bacterial and fungal
213 PCR products for each of the 324 samples (9 plots x 4 sub-plots x 9 time-points) were then
214 separately pooled based on gel electrophoresis band strength and cleaned with AMPure
215 following established methods (Glassman et al., 2018). Each pool was then checked for quality
216 and quantity with the Agilent Bioanalyzer 2100, pooled at a 2:3 ratio (0.4 units for bacteria to 0.6
217 units for fungi), and sequenced with Illumina MiSeq 2x300bp at the UCR Institute for
218 Integrative Genome Biology. In addition to our 324 samples sequenced in four Illumina MiSeq
219 runs, we added negative DNA extractions and PCR controls from each time point and mock
220 communities (ZymoBIOMICS microbial community standard, Zymo, Irvine, CA) to each library
221 for additional quality control and inference.

222

223 ***2.4 Bacterial and fungal biomass***

224 Bacterial and fungal biomass was quantified with quantitative (q) PCR. We used the
225 FungiQuant-F/FungiQuant-R primers to target the 18s rDNA for fungi (Liu et al., 2012) and the
226 Eub338/Eub518 primers for bacteria (Fierer et al., 2005). To estimate bacterial and fungal small-
227 subunit rDNA gene abundances, we generated standard curves using a 10-fold serial dilution of
228 the standards by cloning the 18S region of *Saccharomyces cerevisiae* or the 16S region of
229 *Escherichia coli* into puc57 plasmid vectors constructed by GENEWIZ, Inc. (NJ, USA) as
230 previously established (Averill & Hawkes, 2016). The 10 µl qPCR reactions were performed in
231 triplicate. Reactions contained 1 µL undiluted DNA, 1 µl of 0.05M Tris-HCl ph8.3, 1 µL of
232 2.5mM $MgCl_2$ (New England BioLabs (NEB); Ipswich, MA), 0.5 µL of 0.5mg/ml BSA, 0.5 µL
233 of 0.25mM dNTP (NEB), 0.4 µL of both primers at 0.4µM, 0.5 µL of 20X Evagreen Dye (VWR
234 International; Radnor, PA), 0.1 µL of Taq DNA polymerase (NEB) and 4.6 µL ultra-pure water.
235 We employed the CFX384 Touch Real-Time PCR Detection System with the following
236 conditions: 94˚C for 5 min, followed by 40 cycles of 94˚C for 20 seconds, 52˚C (for bacteria) or
237 50˚C (for fungi) for 30 seconds, followed by an extension at 72˚C for 30 seconds. Gene copy
238 numbers were generated using a regression equation using the quantification cycle (Cq),
239 calculated as the average Cq value per sample in relation to the known/calculated copies in the
240 Cq/threshold cycles (Ct). Thus, the gene copy number was determined using the following
241 equation, 10^ (Cq-b)/m), where the y-intercept and slope were generated from the standard curve.
242 All values were generated by CFX Maestro software.

243

244 ***2.5 Bioinformatics***

245 Illumina data was processed with Qiime2 (Bolyen et al., 2019). The demultiplexed fastQ
246 files from the four Illumina sequencing runs were processed individually using cutadapt (Martin,
247 2011) to remove the primers and ran through DADA2 to filter out and remove chimeric
248 sequences and low-quality regions and to produce Amplicon Sequence Variants (ASVs)
249 (Callahan et al., 2017). DADA2 outputs from each library were merged into one library for
250 downstream processing, including the removal of singletons and taxonomic assignments. We
251 used the SILVA reference database for bacteria (Yilmaz et al., 2014) and the UNITE reference
252 database for fungi (Kõljalg et al., 2005) for taxonomic assignment (accessed on 10/27/2020).
253 Sequences assigned to mitochondria and chloroplasts for bacteria or not assigned to the Kingdom
254 Fungi were removed from ASV tables before subsequent analysis. Fungal ASV tables were
255 exported and parsed through FUNGuild (Nguyen et al., 2016) to assign functional ecological
256 guilds. We only included high probable confidence rankings for the following guilds for
257 downstream analysis: AMF, EMF, saprotrophs, and pathogens. Moreover, negative and mock
258 controls were inspected to ensure that sequences in negative controls were negligible and that
259 mock taxonomy correlated with known communities. Sequences were submitted to the National
260 Center for Biotechnology Information Sequence Read Archive under BioProject accession
261 number PRJNA761539.
262

263 ***2.6 Statistical analysis***

264 Statistical analyses were conducted in R 4.1.1 (R Core Team, 2021), and all statistical
265 codes are available on GitHub https://github.com/pulidofabs/SecondarySuccession-Chaparral.
266 The ASV tables were rarefied to a sequences/sample depth of 7,115 for bacteria and 11,480 for
267 fungi to account for uneven sequencing depth. Fungal and bacterial alpha diversity was estimated

using BiodiversityR (Kindt & Coe, 2005) with the following metrics: observed species richness, Simpson, Shannon, Chao1, and ACE. Since patterns of species richness were similar across metrics **(Fig. S1)**, we focused on richness estimated as the number of observed ASVs after rarefaction for all downstream analyses. To test if wildfire decreased biomass and richness and if biomass and richness increased with time since fire **(H1)**, if wildfire will have a distinct impact on fungal guilds **(H2)**, and to determine if changes in biomass and richness are associated with precipitation and soil burn severity **(H3)**, for both bacteria and fungi, we fitted thirteen statistical models with treatment (burned vs. unburned), time (measured as days since fire), 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). Time since fire and precipitation were scaled and centered. The level of nestedness for all models was tested by running a null model with different nested levels (plot, subplot, and time since fire) and no predictors. Model selection was made using Akaike Information Criterion (AICc) in the MuMIN package (Barton, 2020). All richness models contained plot, subplot, and time since fire as random effects, and all biomass models included 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 by generating distance matrices with the vegan Avgdist function, calculating the square-root transformed median Bray-Curtis dissimilarity per 100 subsampled iterations. We used permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2017) as implemented with the adonis function in vegan (Oksanen et al., 2018) to test

for the significant effects of wildfire, time since fire, and their interactions, on bacterial and fungal community composition overall and at each independent time point (**H1**). Results were visualized using Non-Metric Multidimensional Scaling (NMDS) ordinations.

We employed several methods to quantify succession (**H4**). We visualized succession by characterizing community composition patterns at the genus level using phyloseq (McMurdie & Holmes, 2013) and plotting the relative abundance profile of the dominant ASVs (> 3% sequence abundance) for each time point in burned versus unburned communities with ggplot2 (Wickham H, 2016). We tested for significant changes in abundance of each taxon between burned and unburned plots and over time using glmer. Similar to a study examining Sorghum microbial succession (Gao et al., 2020), we used the vegan mantel function to determine the correlation between temporal distance and community composition to determine how turnover varies in the presence or absence of fire. 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 the vegan betadisper function to calculate the multivariate dispersion of Bray-Curtis dissimilarities and visualized the results using principal coordinates analysis (PCoA). Finally, we employed the codyn package (Hallett et al., 2016) to identify various diversity metrics to assess succession (Collins et al., 2000). To evaluate whether the community is following its normal successional trajectory, we calculated direct linear change, also known as directional change, using the Euclidian distance of each microbial community. Next, we measured species turnover to determine if species appearances or disappearances drive succession. Lastly, we measured community stability as a measure of resilience, which

incorporates synchrony, or patterns of how species abundance covary over time (Loreau & de Mazancourt, 2008).

3. Results

3.1 Sequencing data

The four Illumina MiSeq runs resulted in 9.8 M bacterial and 24.6 M fungal sequences for an average of 31,052 bacterial and 78,202 fungal sequences/sample and a total of 33,078 bacterial and 11,480 fungal ASVs. Rarefaction resulted in a total of 24,874 bacterial and 7,445 fungal ASVs. Extracting the fungal guilds from the rarefied fungal ASV table resulted in 208 EMF, 70 saprobic, 65 AMF, and 26 pathogenic fungal ASVs.

3.2 Wildfire effects on bacterial and fungal biomass and richness

Fire led to significant reductions in bacterial and fungal biomass and richness during the first post-fire year (**Tables S2; S3**). Fire had more significant impacts on biomass than richness for both bacteria and fungi and larger effects on fungi than bacteria overall (**Fig. 2**). On average, across the year, fire reduced richness by 46% for bacteria and 68% for fungi **(Fig. S1A)** and biomass by 47% for bacteria **(Fig. S2A**) and 86% for fungi **(Fig. S2B**). The direct, immediate effect of wildfire at 17 days post-fire was stronger for biomass than richness, with bacterial biomass decreasing by 84% **(Fig. 2A)** and fungal biomass by 97% **(Fig. 2B)**. In contrast, fungal richness declined by 45% **(Fig. 2D)**, but bacterial richness temporarily increased by 31% at 17 days but declined by 29% at 25 days post-fire **(Fig. 2C; Table S2)**. While the differences in biomass and richness between the burned and unburned sites lessened with time since fire, one year was insufficient for bacterial and fungal biomass or richness to recover to unburned levels

(**Fig. 2**). The effects of fire across time remained larger for fungi than for bacteria, with fungal biomass remaining 80% and richness 61% lower and bacterial biomass remaining 43% and richness 23% lower in the burned plots at 1-year post-fire (**Fig. 2, Table S2**).

3.3 Drivers of changes in richness and biomass

Negative binomial models showed that the direct impact of fire negatively affected bacterial and fungal biomass and richness, which was lessened by the positive interaction effect of soil burn severity with time since fire (**Fig. 3; Table S3**). Furthermore, fire effects on fungal richness were further attenuated by a direct and positive impact of time since fire **(Table S3)**. Soil burn severity had significant adverse direct effects on bacterial and fungal richness but no significant direct effects on biomass, meaning that biomass was equally reduced in the presence of fire regardless of severity **(Figs. 3C,3D; Table S3**). While precipitation had no significant direct effects, precipitation interacted with time since fire to negatively affect bacterial richness (**Fig. 2C**) but positively affect fungal richness **(Fig. 2D; Table S3)**. Moreover, bacterial biomass responded positively to a fire and precipitation interaction (**Fig. 2A; Table S3**).

3.4 *Wildfire effects on the richness of different fungal guilds*

Wildfire led to large and significant reductions for all fungal guilds **(Table S4, Fig. S3)**, with the largest initial declines for AMF. On average, across time points, EMF decreased by 68%, pathogens by 71%, saprobes by 86%, and AMF by 98% in burned plots compared to unburned plots **(Fig. S3)**. Moreover, one year was insufficient for any guild to return to unburned levels. In fact, at 376 days, AMF was on average 89%, pathogens 69%, and saprobes 61% lower in the burned plots (**Fig. S4**). Interestingly, EMF experienced a decrease in richness over time

359 due to a fire and time interaction, resulting in species richness being 91% lower in the burned
360 plots at 376 days post-fire (**Fig. S4; Table S4**). EMF richness further declined with soil burn
361 severity (**Table S4**). Moreover, a fire and precipitation interaction negatively affected EMF and
362 pathogen richness **(Table S4).**
363
364 ***3.5 Wildfire changes microbial community composition***
365 Fire significantly affected bacterial and fungal community structure, explaining 13% of
366 the compositional variation for bacteria and 11% for fungi. Time since fire had smaller impacts
367 on community composition, explaining 4% of the variation for bacteria and 1% for fungi.
368 Finally, the fire and time interaction explained 2% variation for bacteria and 1% for fungi **(Table**
369 **S5)**. Community composition between burned and unburned plots significantly varied at all 9-
370 time points for both bacteria **(Fig. S5)** and fungi **(Fig. S6)**, with differences increasing over time
371 from 12% to 21% for bacteria (**Fig. S5)** and 9% to 13% for fungi **(Fig. S6**) from day 17 to 376
372 post-fire. The changes in burned bacterial **(Fig. 4A)** and fungal composition **(Fig. 4C)** were
373 driven by the dominance of previously rare taxa, which traded off in abundance over time **(Figs.**
374 **4B, 4D**). Burned bacterial communities experienced less discernable tradeoffs than fungi due to
375 the consistent dominance of the Proteobacteria *Massilia*, which composed on average 57% of the
376 sequences throughout the year **(Fig. 4B)**. However, three Firmicutes quickly dominated, with
377 *Bacillus* (13%), an uncultured Clostridiales (26%), and *Paenibacillus* (4%) dominating at 34-
378 and 67-days post-fire. The Firmicutes rapidly declined and traded off with the Proteobacteria
379 *Noviherbaspirillum,* which increased in abundance over time, from 1% at 34 days to 24% by the
380 end of the year **(Fig. 4B)**. For burned fungi, two Basidiomycetes that dominated at 17 days post-
381 fire, the yeast *Geminibasidium* (45%) and the EMF *Inocybe* (16%), rapidly declined and traded

382 off with filamentous Ascomycetes **(Fig. 4D)**, including *Pyronema,* which increased as
383 *Geminibasidium* decreased. Indeed, *Pyronema* dominated from days 25 to 95 post-fire, peaking
384 at 67 days post-fire with 67% sequence abundance. In addition, the Ascomycetes *Aspergillus*
385 increased from 2% to 22% and *Penicillium* from 36% to 49% from 17 to 376 days post-fire **(Fig.**
386 **4D)**.
387
388 ***3.6 Microbial successional dynamics***
389 Directional change was higher in burned than unburned bacterial and fungal
390 communities, suggesting that succession is occurring in burned plots **(Table S6)**. Moreover,
391 bacterial and fungal burned communities experienced low synchrony **(Table S6),** indicating
392 community stability due to the dominance of a few genera. Indeed, community stability was
393 higher in burned than unburned plots and for bacteria than fungi **(Tables S6**), suggesting that
394 bacterial succession is proceeding to potential equilibrium due to increasing bacterial richness
395 and resilience. In contrast, fungal communities were more susceptible to change. Visual
396 confirmation of these trends established that burned bacterial **(Fig. 5A)** and fungal **(Fig. 5B)**
397 communities experienced rapid and distinct successional trajectories, with bacteria **(Fig. 5C)**
398 experiencing successional changes at roughly double the rate of fungi **(Fig. 5D)**. These
399 successional changes in burned plots were driven by six major compositional turnover points for
400 bacteria at 25, 34, 95, 131, 187, and 376 days **(Fig. 5E)** and five for fungi at 25, 34, 67, 95, and
401 131 days post-fire **(Fig. 5F)**. In contrast, the unburned bacterial **(Fig. 6A)** and fungal **(Fig. 6B)**
402 communities experienced low dominance and remained stable over time with no succession
403 **(Figs. 6C, 6D)** or compositional turnover (**Figs. 6E, 6F).**
404

405 ***3.7 Taxa driving microbial succession***

406 Early turnover events for bacteria **(Fig. 5A)** and fungi **(Fig. 5B)** in burned plots were
407 driven by the disappearance of taxa, more so for bacteria (days 17-95) than fungi (days 17-25;
408 **Table S6**). Indeed, increased dominance by a few taxa, including the Firmicutes *Bacillus* at 25
409 days post-fire, *Paenibacillus* and *Domibacillus* (34-67 days), and the Proteobacteria
410 *Noviherbaspirillum* (95 days), and the constant dominance of *Massilia* (34-286 days post-fire)
411 resulted in the disappearance of early surviving bacterial species, including *RB41*, *Conexibacter*,
412 *Candidatus Udaeobacter,* and *Bacillus* over time **(Fig. 5A; Table S6)**. In contrast, fungal
413 succession was initiated by the rapid dominance of *Geminibasidium* and EMF genera that
414 dominated the unburned communities, including *Inocybe, Cortinarius*, and *Tomentella* in the
415 Basidiomycota and *Balsamia* in the Ascomycota and one previously rare Basidiomycete EMF
416 genus *Mallocybe,* a subgenus of *Inocybe* **(Fig. 5B, 6B)**. Interestingly, all species of EMF rapidly
417 disappeared from the community at 25 days post-fire and were replaced by the constant
418 dominance of *Pyronema*, *Penicillium,* and *Aspergillus* **(Fig. 5B)**. However, as succession ensued,
419 species appearance drove late-year successional stages for bacteria (187-376 days; **Fig. 5A**) and
420 mid-year successional stages for fungi (67-187 days; **Fig. 5B; Table S6)**. For bacteria, the
421 appearance of two Bacteroidetes, *Pedobacter* and *Adhaeribacter*, and the Actinobacteria
422 *Blastococcus* shaped late-year (days 187-376) bacterial succession (**Fig. 5A)**. For fungi, mid-year
423 succession (days 95-187) was driven by the appearance of filamentous fungal Ascomycetes in
424 the Pyronemataceae and in the Sordariaceae genus *Gelasinospora*, and Basidiomycota
425 mushroom-forming taxa. For example, the previously dominant EMF genus *Inocybe* returned,
426 and the pyrophilous Basidiomycete saprobes *Coprinellus* and *Tephrocybe,* which were rare in the
427 unburned communities (<0.01% sequence abundance), also appeared. Late-year fungal

succession (days 286-376) was driven by the increased dominance of *Tephrocybe* and *Aspergillus,* the disappearance of *Inocybe* and the Ascomycota *Rasamsonia,* and the decreased abundance of *Pyronema* **(Fig. 5B)**.

4. Discussion

Here, we present the highest resolution temporal sampling of post-fire microbiomes to date, enabling us to show for the first time that bacteria and fungi experience rapid succession driven by the dominance of pyrophilous taxa that trade off in abundance over time **(H4)**. Although our study was in California chaparral, many of the dominant pyrophilous taxa identified here also dominate other burned environments, including Spanish shrublands (Pérez-Valera et al., 2018) and pine (Bruns et al., 2020; Reazin et al., 2016), spruce (Whitman et al., 2019), Eucalyptus (Ammitzboll et al., 2022; McMullan-Fisher et al., 2011), and redwood-tanoak forests (Enright et al., 2022), indicating the generality of our results to wildfire-affected ecosystems. We found that wildfire decreased bacterial and fungal biomass and richness, leading to community composition shifts that persisted the entire year (**H1**). Fungal guilds were differentially affected by fire and time, with AMF and saprobes experiencing the largest immediate fire impacts, but over time, EMF experienced the largest declines (**H2)**. Interestingly, AMF rapidly succumbed to the death of their host while EMF survived for 1-2 months, answering the question of how long it takes mycorrhizal fungi to die after their host. Moreover, microbial richness and biomass changes were driven by multiple abiotic interactions, including interactions between time since fire, precipitation, and soil burn severity (**H3**).

4.1 Wildfire decreased bacterial and fungal biomass and richness

Fire decreased soil bacterial and fungal biomass and richness, corroborating previous post-fire studies in Mediterranean shrublands (Pérez-Valera et al., 2018) and forests (Dooley & Treseder, 2012). We noted a larger fire effect on fungal biomass and richness relative to bacteria, consistent with previous research showing that bacteria are more resistant to fire than fungi (Certini et al., 2021; Glassman et al., 2021; Pourreza et al., 2014; Pressler et al., 2019). Although richness and biomass increased over time for both microbial groups, one year was insufficient for either group to recover to unburned levels, consistent with previous studies that indicate that microbial biomass and richness recovery could take decades (Pérez-Valera et al., 2018; Treseder et al., 2004). Interestingly, we observed a transient increase in bacterial richness directly post-fire, which may result from taxa such as the Actinobacteria genera *Soliribrobacter* and *Conexibacter* (Albuquerque & da Costa, 2014) that may be favored by the increase in soil pH observed here **(Table S1)** and in other studies (Neary et al., 1999) or by post-fire increases in nitrogen and phosphorus availability (Certini et al., 2021). While several species of EMF survived for the first months, fire-induced mortality was rapid for AMF and saprobes. Yet, EMF was most impacted by fire over time, corroborating studies across ecosystems that point to the negative impact of fire on mycorrhizal richness, primarily driven by host mortality (Dove & Hart, 2017; Pulido-Chavez et al., 2021).

4.2 Pyrophilous fungi dominate the burned communities

Previously detected pyrophilous fungi from globally burned ecosystems also dominated California chaparral, indicating that pyrophilous microbes are not biome-specific. Instead, these fungi may be activated by temperature thresholds reached during high severity fires, which are common in chaparral and some Pinaceae forests (Agee, 1993; Keeley & Zedler, 2009; Neary et

al., 1999). Specifically, our burned communities were dominated by Ascomycota in the genera *Pyronema, Penicillium*, and *Aspergillus,* similar to dominant fungal species post-fire in Mediterranean shrublands (Livne-Luzon et al., 2021), boreal spruce (Whitman et al., 2019), and montane pine forests (Bruns et al., 2020; Fujimura et al., 2005; Pulido-Chavez et al., 2021). Both *Pyronema (P. omphalodes)* and *Aspergillus* (*A. fumigatus*) are known pyrophilous fungi of California chaparral (Dunn et al., 1982), and we identified additional species including *P. domesticum*, *A. udagawae*, and *A. elsenburgensis*. These fungi are adapted to wildfire and produce fire-resistant structures, including dormant spores, sclerotia, and conidia, which are heat-activated (Gottlieb, 1950; Moore, 1962; Rhodes, 2006; Warcup & Baker, 1963). The rapid and efficient germination of *Aspergillus* (in the subgenus *Fumigati*, including *A. udagawae*) induced by high temperatures (Rhodes, 2006) and its ability to use various carbon and nitrogen sources, including ammonium and nitrate (Krappmann & Braus, 2005), may position *Aspergillus* to rapidly dominate post- fire. Furthermore, *Pyronema domesticum*, a relatively well-studied pyrophilous fungus, can mineralize pyrogenic organic matter, PyOM (Fischer et al., 2021), allowing it to take advantage of an abundant post-fire substrate. Moreover, *Geminibasidium,* a recently described thermotolerant Basidiomycete yeast (Nguyen et al., 2013), dominated at 17 days post-fire. While not typically described as pyrophilous, presumably because most pyrophilous fungi are described from mushrooms (McMullan-Fisher et al., 2011), two other studies have found *Geminibasidium* to increase post-fire in pine forests (Pulido-Chavez et al., 2021; Yang et al., 2020), suggesting that it is pyrophilous. Together, these results indicate that dominant pyrophilous fungi are more widespread than expected and that their response to fire is likely due to fire adaptive traits and temperature thresholds.

4.3 Pyrophilous fungi drive fungal secondary succession

Although it is clear that pyrophilous fungi exist and are widespread, we lacked an understanding of how soon these pyrophilous fungi appear, their turnover rates, and if they trade off in abundance over time (Fox et al., 2022). Here, we show that surviving ectomycorrhizal Basidiomycetes *Cortinarius, Inocybe,* and *Tomentella,* previously found in burned temperate pine forests (Owen et al., 2019; Pulido-Chavez et al., 2021) and pine-dominated Mediterranean systems (Gassibe et al., 2011; Hernández-Rodríguez et al., 2013) also dominate early chaparral fungal succession. Although it is possible that the EMF signal detected could be relic DNA (Carini et al., 2016), high UV conditions, common in post-fire systems (Neary et al., 1999), are likely to have degraded relic DNA (Torti et al., 2015), suggesting that these EMF could have survived the fire and clung to a dying host for at least two months. The survival of these EMF may be attributable to their exploration type and specificity for current versus stored photosynthates (Gray & Kernaghan, 2020; Pena et al., 2010). For example, *Cortinarius,* a long/medium exploration type, which requires more carbon for maintenance, only survived for 17 days post-fire. In contrast, *Inocybe*, a short-contact type (Agerer, 2001; Koide et al., 2014), survived for up to 67 days post-fire, suggesting that it may be less carbon demanding or adapted to warming (Fernandez et al., 2017). Our results indicate that early EMF could have survived on their hosts' stored photosynthates or the lower resources provided by the surviving and resprouting manzanita and chamise shrubs.

Successional theory states that early successional stages are dominated by fast-growing or ruderal (R) organisms (Kinzig & Pacala, 2013) that tradeoff between stress tolerance (S) and competitive (C) life-history strategies over time (Grime, 1977; Zhang et al., 2018). Recent adaptations of Grime's C-S-R to microbiomes suggest that pyrophilous microbes survive and

thrive post-fire with traits analogous to plants, including post-fire resource acquisition (C), thermotolerant structures (S), and fast growth (R) (Enright et al., 2022; Whitman et al., 2019). Our data suggest that pyrophilous microbes fit into these trait categories and that tradeoffs among these traits might drive microbial succession, such that surviving thermotolerant fungi (i.e., *Geminibasidium* and *Pyronema*) colonize first, followed by fast-colonizers (i.e., *Penicillium* and *Aspergillus*), which were overtaken by competitive fungi capable of exploiting post-fire resources. (i.e., *Coprinellus* and *Tephrocybe)*. Whereas *Geminibasidium* is thermo- and xero-tolerant (Nguyen et al., 2013), *Pyronema* produces thermotolerant sclerotia (Moore, 1962), enabling wildfire survival. Although both species are thermotolerant, differences in the morphological growth characteristics between the yeast *Geminibasidium* and the filamentous *Pyronema* may explain the tradeoff in dominance. For example, unicellular proliferation allowed *Geminibasidium* to dominate instantly, but the ability to forage for nutrients and rapidly increase surface colonization may allow the filamentous *Pyronema* to better dominate the open space. Interestingly, *Gelasinospora heterospora,* a fungus closely related to heat-activated *Neurospora crassa* (Dettman et al., 2001; Emerson, 1948), that produces pigmented mycelia, and is known to require heat or chemical treatment for germination (Alexopoulous & Mims, 1952), was highly abundant at 25, 34, and 95 days post-fire, suggesting it is also pyrophilous. The decline of thermotolerators coincided with the dominance of fast-growing Ascomycete fungi in the genera *Penicillium* and *Aspergillus* (Dix & Webster, 1995; McGee et al., 2006), which both produce copious asexual conidia (Crow, 1992), allowing for rapid colonization of the open niche, analogous to early dominant post-fire plants, which are also often asexual (James, 1984). Lastly, like plants, competition appears to drive later successional dynamics (Tilman, 1990; Zhang et al., 2018), as suggested by the emergence of pyrophilous fungal decomposers, such as *Coprinellus*

and *Tephrocybe* at 9-12 months, corroborating findings from Eucalyptus forests (Ammitzboll et al., 2022; McMullan-Fisher et al., 2011). Evidence suggests that *Coprinellus* can degrade aromatic hydrocarbons (Steindorff et al., 2021), supporting the idea that it is outcompeting earlier fungal taxa for this abundant and complex carbon source. In conclusion, our results indicate that tradeoffs among fire-adapted traits analogous to those in plants might drive post-fire microbial succession.

4.4 Pyrophilous bacteria dominate and initiate bacterial secondary succession

Our high temporal sampling enabled us to demonstrate that bacteria experience rapid succession and community turnover initiated by aerobic, heterotrophic bacteria that form endospores and produce antibiotics, which may improve their competitive abilities in the post-fire environment. Moreover, we show that previously detected putative pyrophilous bacteria from Canadian (Whitman et al., 2019) and Chinese boreal (Xiang et al., 2014), and California redwood-tanoak forests (Enright et al., 2022) also dominated California chaparral, suggesting that these pyrophilous bacteria might be widely distributed. Specifically, our burned communities favored taxa in the phyla Actinobacteria, Acidobacteria, Firmicutes, and Proteobacteria, similar to previous studies (Ammitzboll et al., 2022; Enright et al., 2022; Whitman et al., 2019; Xiang et al., 2014).

Bacterial successional dynamics were slightly different from fungi. The first few weeks of bacterial succession were characterized by high diversity and a lack of dominance, mimicking the distributions observed in the unburned communities. In complex resource environments, such as those created by wildfire, niche complementarity is 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 shown to use different resources. For example, *Paenibacillu*s 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). However, at 25 days, bacteria experienced a large compositional turnover, which allowed for the dominance of pyrophilous bacteria with fire-adapted traits. While tradeoffs in abundance were not as stark for bacteria as for fungi, as indicated by the constant dominance of the Proteobacteria *Massilia*, the next most abundant bacteria did experience tradeoffs from thermotolerant Firmicutes (i.e., *Bacillus, Paenibacillus,* and Clostridiales) to fast-colonizing Proteobacteria that are also capable of exploiting post-fire substrates such *Novihersparillium* and *Massilia*. Thermotolerance and heat-stress adaptation dominated survival traits, allowing Firmicutes to dominate as early as 25 days post-fire. Firmicutes contain some of the most resistant, thermotolerant endospore producing bacteria (Grady et al., 2016; Kaur et al., 2018; Mandic-Mulec et al., 2015), as well as the species *Paenibacillus xerothermodurans,* which contains heat-inducible transcriptional proteins that protect against protein denaturation (Paredes-Sabja et al., 2011). Moreover, Clostridiales can trigger sporulation in response to stress (Paredes-Sabja et al., 2011), allowing for increased proliferation post-fire. While thermotolerance is crucial for fire survival, rapidly dominating the open niche and using post-fire resources may ensure post-fire growth. *Massilia* is a fast reproducing bacteria that associates with the rhizosphere (Li et al., 2014) and colonizes AMF hyphae (Iffis et al., 2014) and the roots of various plants (Ofek et al., 2012). Thus, the dominance of *Massilia* in our study and other post-fire environments (Enright et al., 2022; Whitman et al., 2019) suggests that its diverse ecology and rapid reproduction rate promote its proliferation within the soil (Toljander et al., 2005). Moreover, our results, coupled with current knowledge in

the field, show that the continued dominance of *Massilia* and *Noviherbaspirillium* might be due to their ability to exploit post-fire resources. For example, *Bacillus* fix and reduce nitrogen (Bailey et al., 2014), while *Noviherbaspirillium,* a mid-to late-year dominant bacterial genus, may degrade polycyclic aromatic hydrocarbon (Baldani et al., 2014; Grady et al., 2016; Woolet & Whitman, 2020). We conclude that although tradeoffs are not as distinctive for bacteria as they are fungi, potentially due to interaction among traits such as fast growth under high resources and resource acquisition under low resources, our results provide evidence that pyrophilous bacteria have mechanisms to survive the fire that may drive them to tradeoff in abundance over time.

4.5 Precipitation and soil burn severity differentially affected bacteria and fungi

Although fire was the most significant driver of microbial change, we found that interactions between time and precipitation also drove successional dynamics by differentially affecting microbial biomass and richness. Precipitation interacted with time since the fire and negatively affected bacterial but positively affected fungal richness, with bacterial richness declining but fungal richness increasing after rain events. At least one study that performed a three-year precipitation manipulation experiment showed that increased precipitation decreased bacterial richness (Yang et al., 2021). In contrast to richness, precipitation interacted with fire to positively affect bacterial biomass, while fungal biomass remained unaffected by rainfall. The distinct responses to precipitation could be due to microbial physiological and morphological differences (Blazewicz et al., 2014; Placella et al., 2012; Selbmann et al., 2013). For example, fungi have high morphological plasticity, including the ability to alternate growth forms based on environmental conditions, such as hyphal growth in low nutrient conditions versus unicellular

form in rich nutrient conditions (Selbmann et al., 2013), which may allow fungi to survive small changes in moisture content, allowing for continued growth over time. Moreover, fungi can also activate or enhance resistance to drought (Evans & Wallenstein, 2012; Guhr & Kircher, 2020), allowing them to maintain a constant reproduction rate regardless of the external environmental conditions, thus explaining the positive impact on fungal richness. In contrast, bacteria can experience cell death due to rapid wet-up, while other bacterial groups enter a dormant state, inhibiting growth (Schimel, 2018). Thus, to be evolutionarily successful, bacteria may respond rapidly to favorable conditions (e.g., rain) (Leizeaga et al., 2022) and rapidly replicate to outcompete other microbes for the pulse of nutrients released during the rain event (Homyak et al., 2014), thus potentially explaining the peaks in richness observed after significant rainfall at day 131.

Here, we measured ash depth before the first rains could wash away ash from the site, showing that ash depth can serve as an index of soil burn severity on a scale relevant to soil microbes and that severity negatively affected bacterial and fungal richness but not biomass. Similar to studies in boreal (Whitman et al., 2019) and oak forests (Pourreza et al., 2014), bacterial and fungal richness decreased with soil burn severity. However, contrary to a meta-analysis (Dooley & Treseder, 2012), neither bacterial nor fungal biomass was directly impacted by soil burn severity, probably due to microbial adaptations to the natural high severity fire regime of chaparral. However, since we observed an interaction effect of time since fire and severity on microbial biomass, it is possible that previously observed severity effects, derived from chronosequence studies where space is substituted for time and which, on average, occur two years post-fire (Pressler et al., 2019), may represent an interaction effect of time and severity and not a direct effect of soil burn severity.

5 Conclusion

Our unprecedented high-resolution temporal sampling allowed us to detect rapid secondary succession in bacterial and fungal communities and marked tradeoffs in abundance among pyrophilous microbes over time. We found that the same pyrophilous bacteria and fungi that respond to fires in temperate and boreal forests and Mediterranean shrublands also dominate in California chaparral, allowing us to generalize knowledge of post-fire microbiomes to dryland habitats that are rapidly increasing with climate change (Feng & Fu, 2013). While pyrophilous microbes have been described in other systems, their turnover rates were unknown due to limited post-fire sampling (Fox et al., 2022). We suggest that tradeoffs among fire-adapted traits, with thermotolerators dominating first, followed by fast colonizers, and finally by competitors capable of capitalizing on post-fire resource acquisition, drive post-fire microbial successional dynamics. It seems that pyrophilous microbes share many analogous traits to plants, enabling us to adapt successional theory developed in plants to microbes while acknowledging that bacteria and fungi do have differences in how they respond to fire due to their physiology. We conclude that post-fire bacteria and fungi experience rapid successional changes after fire and believe that understanding these dynamics can increase our ability to predict if and how ecosystems will recover after fire, an increasingly widespread disturbance with climate change.

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Conflict of interest

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

Author's contribution:

SIG conceived of the study and acquired permits; LL, SIG, and PMH came up with the experimental design; SIG, LL, PMH, MFPC, and JWJR performed fieldwork; MFPC and JWJR performed all molecular work; MFPC performed all bioinformatics, statistical analysis, made all of the figures, and wrote the first draft; all authors contributed to writing and editing of the manuscript.

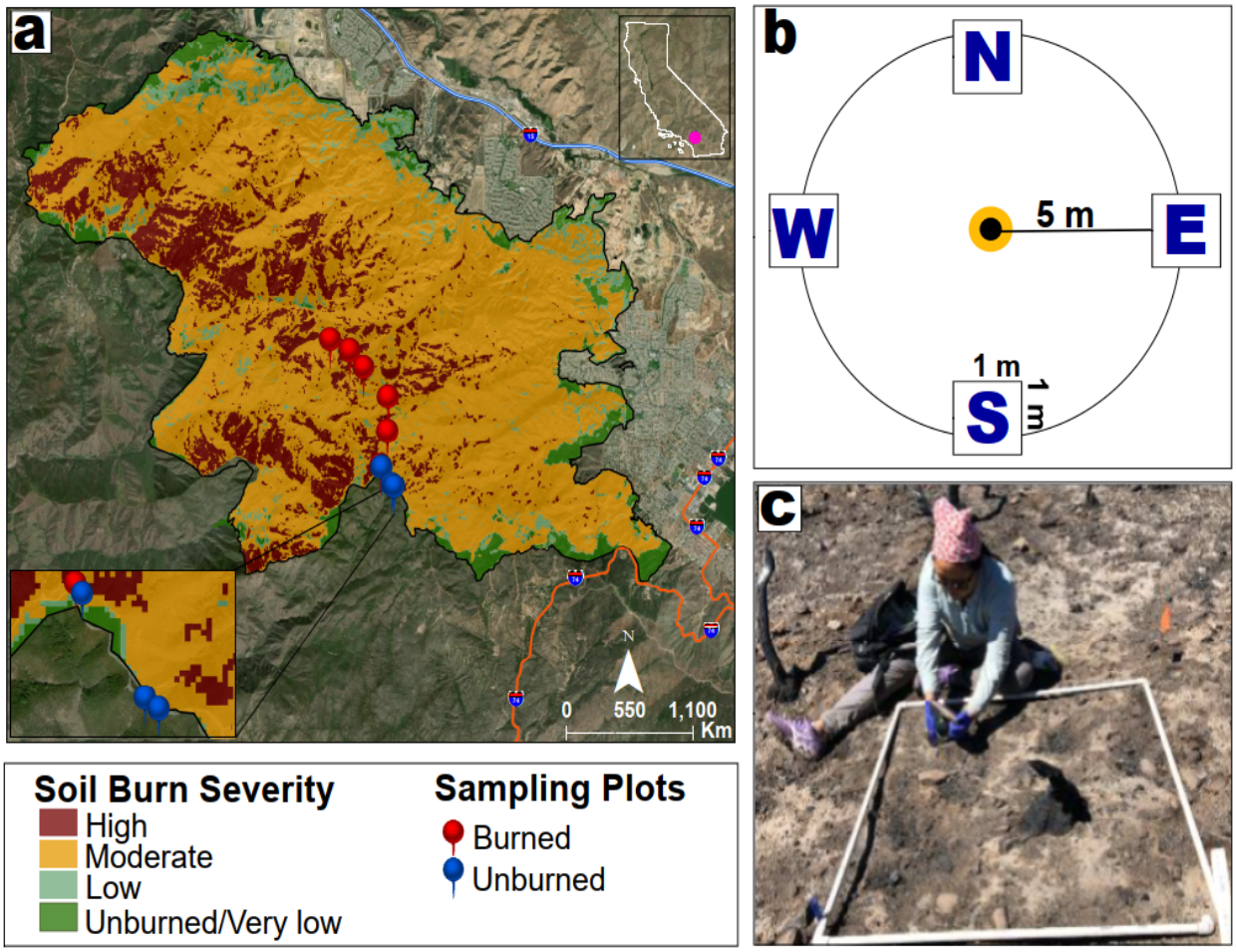

Figure 1. A) Location of the study area and plots (6 burned; 3 unburned) within the Holy Fire burn scar in the Cleveland National Forest in Southern California. Soil burn severity is based on the USDA BAER classifications. B) Plot experimental design, each with four 1m^2 subplots placed 5m from the center in each cardinal direction. C) Collection of the top 10 cm of soil beneath the ash with a releasable bulb planter within the 1 m^2 subplots at 17 days post-fire.

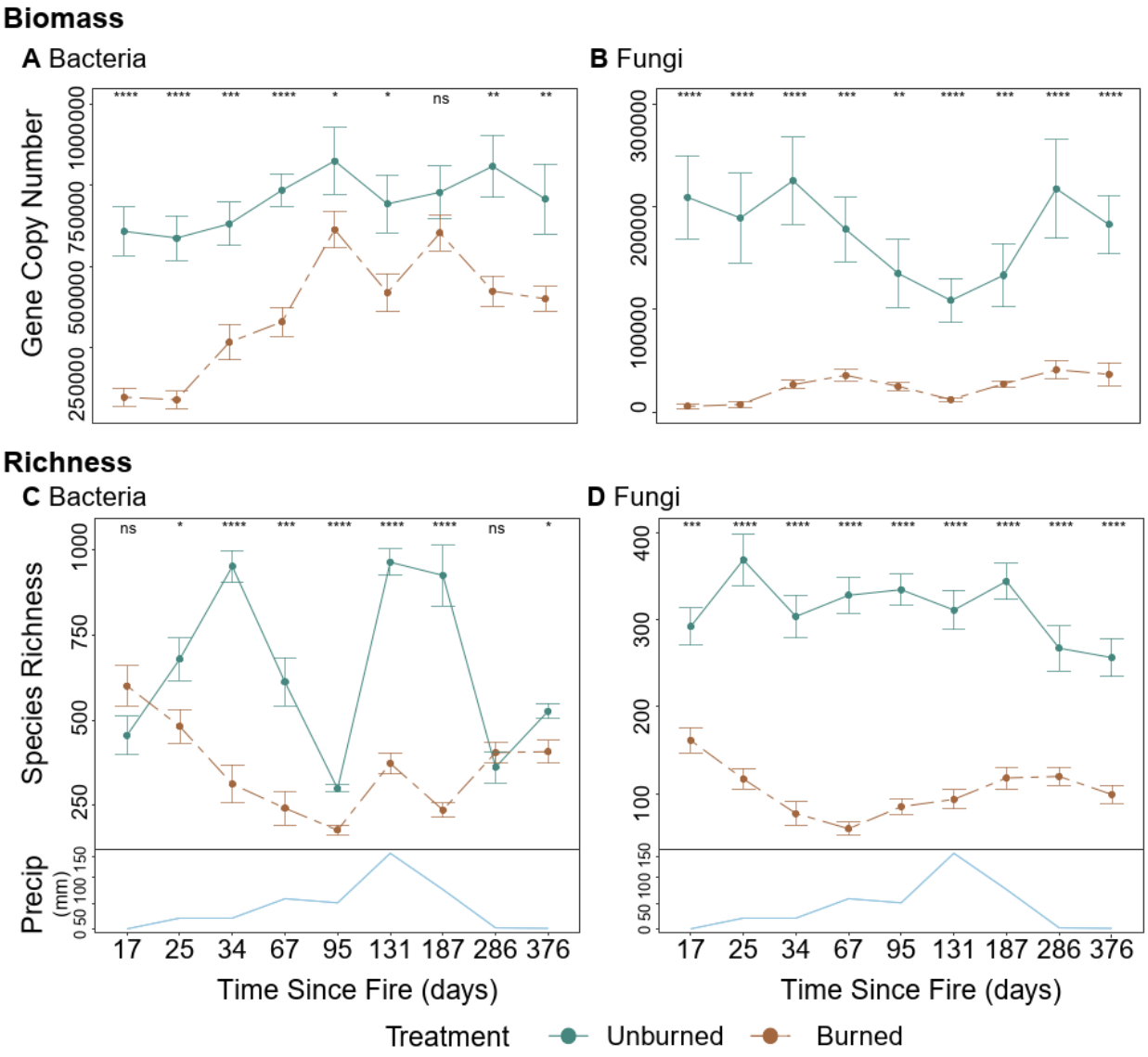

Figure 2. Change in biomass for A) bacteria and B) fungi and change in richness for C) bacteria and D) fungi at each of the 9 time-points in the first year post-fire in burned and unburned plots. Points represent mean differences averaged across burned and unburned plots, and bars represent the standard error of the mean. Precipitation is based on total monthly precipitation (mm). The significance of burned versus unburned plots per time point is denoted with an asterisk and is based on a negative binomial regression.

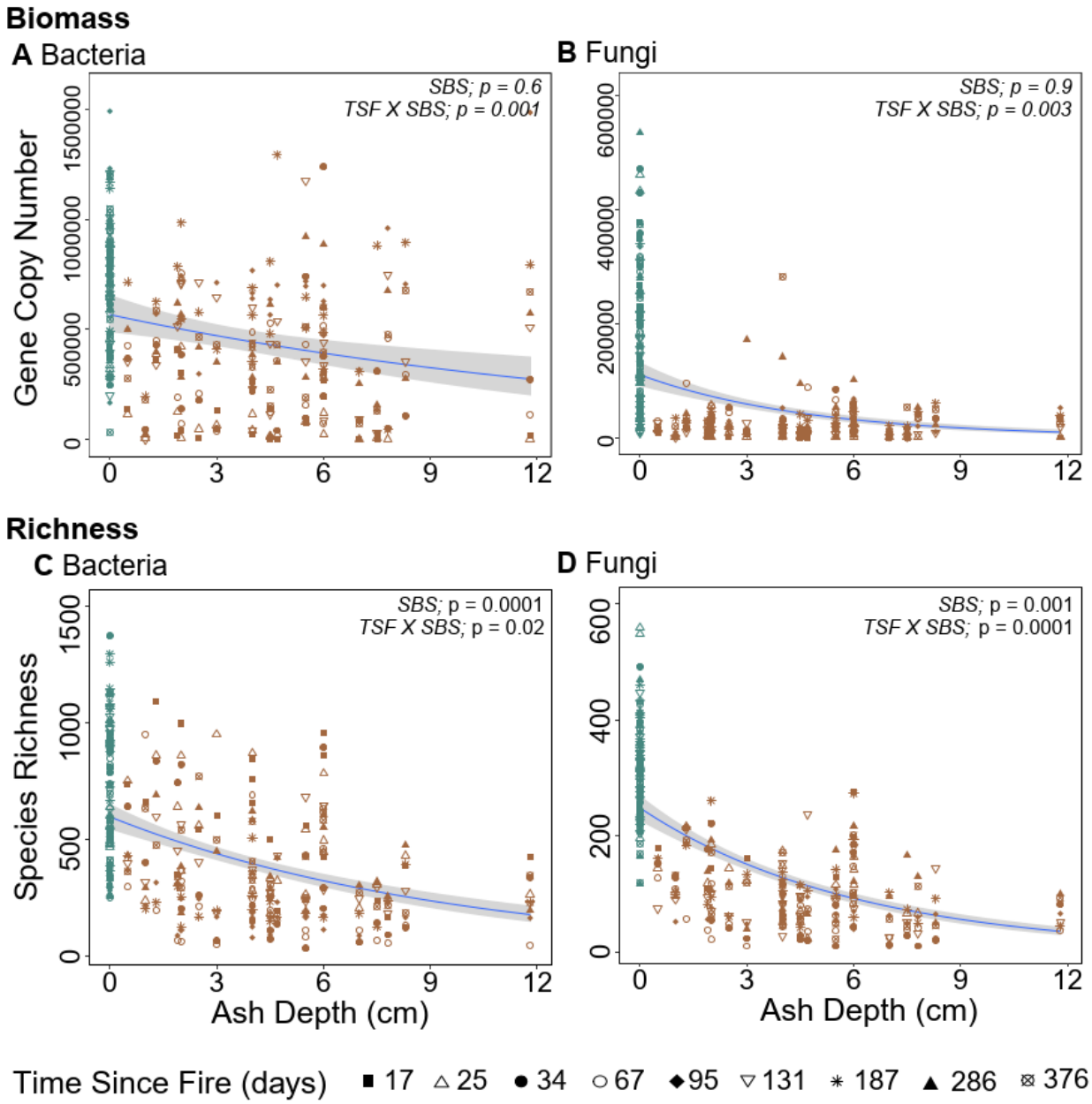

Figure 3. Change in A) bacterial and B) fungal biomass and C) bacterial and D) fungal richness in relation to soil burn severity measured as ash depth at 17 days post-fire. The significance of biomass and species richness against soil burn severity (SBS) and its interaction with time since (TSF) fire is based on a negative binomial regression, where the unburned plots are represented in blue-green and burned in brown.

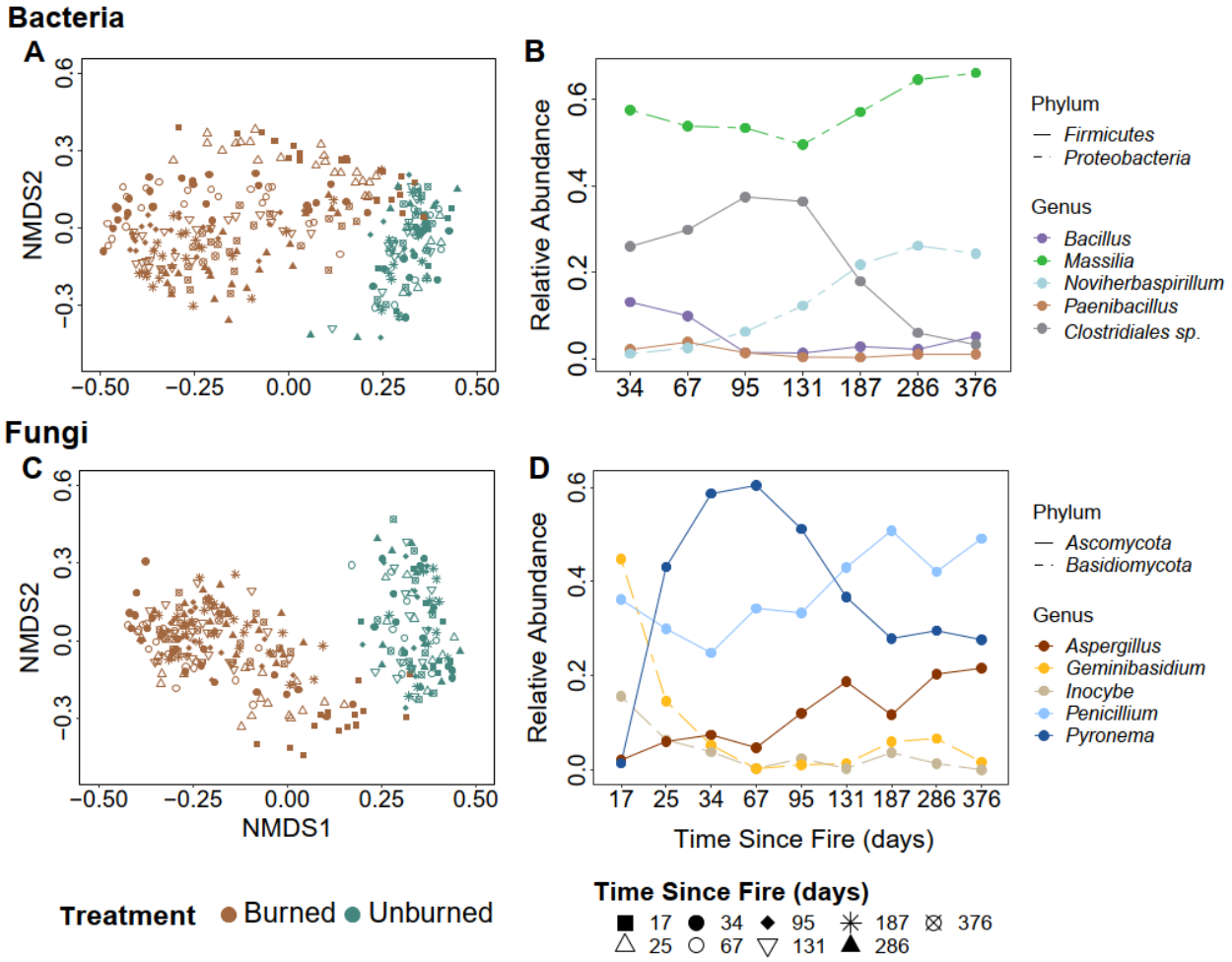

Figure 4. NMDS plot of A) bacterial and C) fungal community composition with colors denoting treatment and shape indicating time since fire. The NMDS is based on 3-dimensions and has a stress value of 0.11 for bacteria and 0.12 for fungi. Change in relative sequence abundance of the five most abundant B) bacterial and D) fungal genera in the burned plots over time. Note, the dominance of the top 5 bacterial genera began 34 days post-fire since there was no clear dominance at days 17 and 25 due to the lag in post-fire bacterial declines.

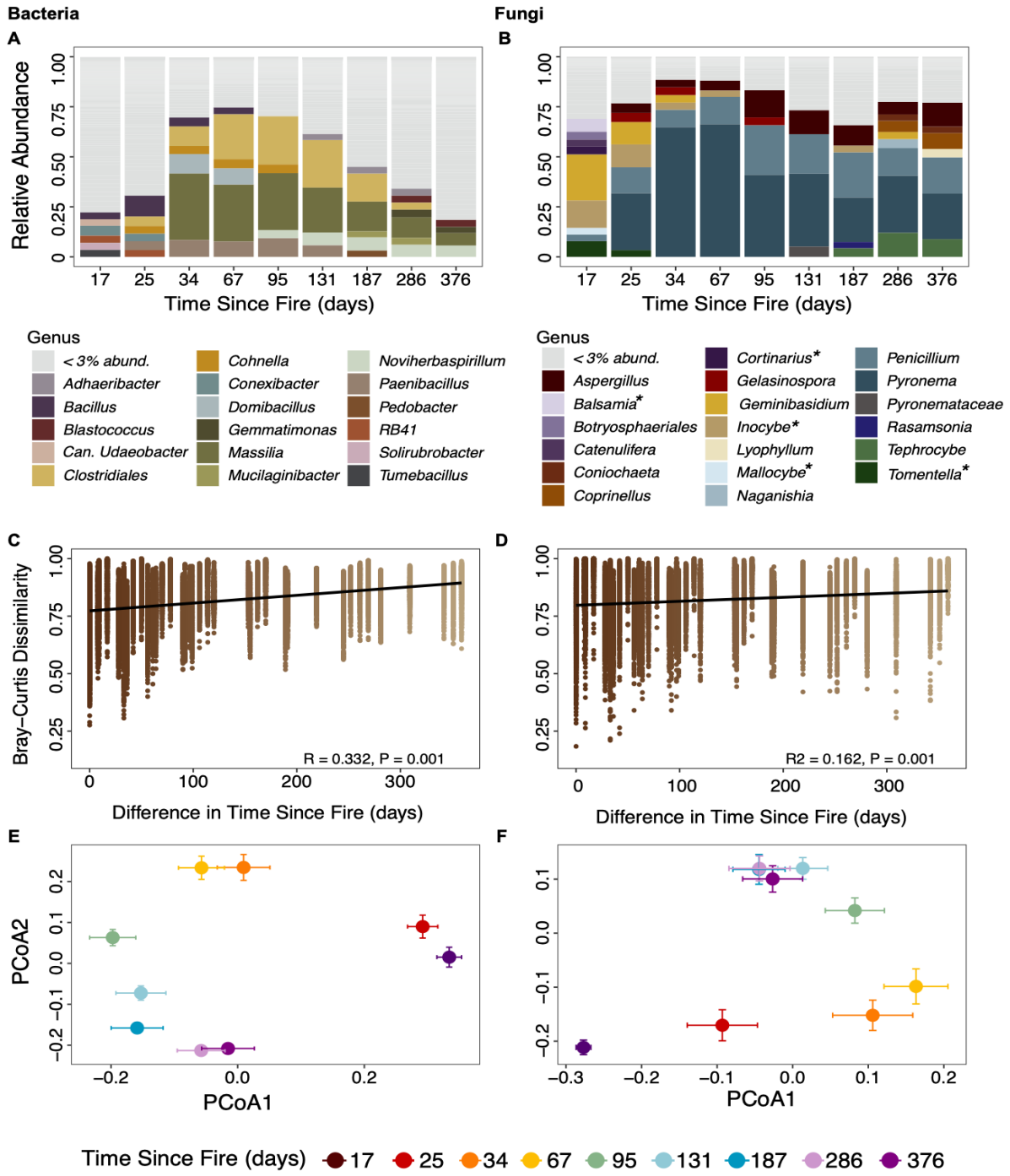

Figure 5. Relative sequence abundance of A) bacterial and B) fungal genera (ectomycorrhizal fungi denoted with an asterisk) in burned plots at all 9 time points. Mantel correlation between Bray-Curtis dissimilarity and Euclidean temporal distances in C) bacterial and D) fungal community composition in burned plots. Principal components analysis (PCoA) of the mean and standard error Bray-Curtis community dissimilarity at each time point for the burned E) bacterial and F) fungal communities. Note that time points farther apart indicate a community turnover, whereas overlapping points with standard errors represent a lack of compositional turnover. Note, 17 days represents the base level and the first turnover thus initiated at 25 days.

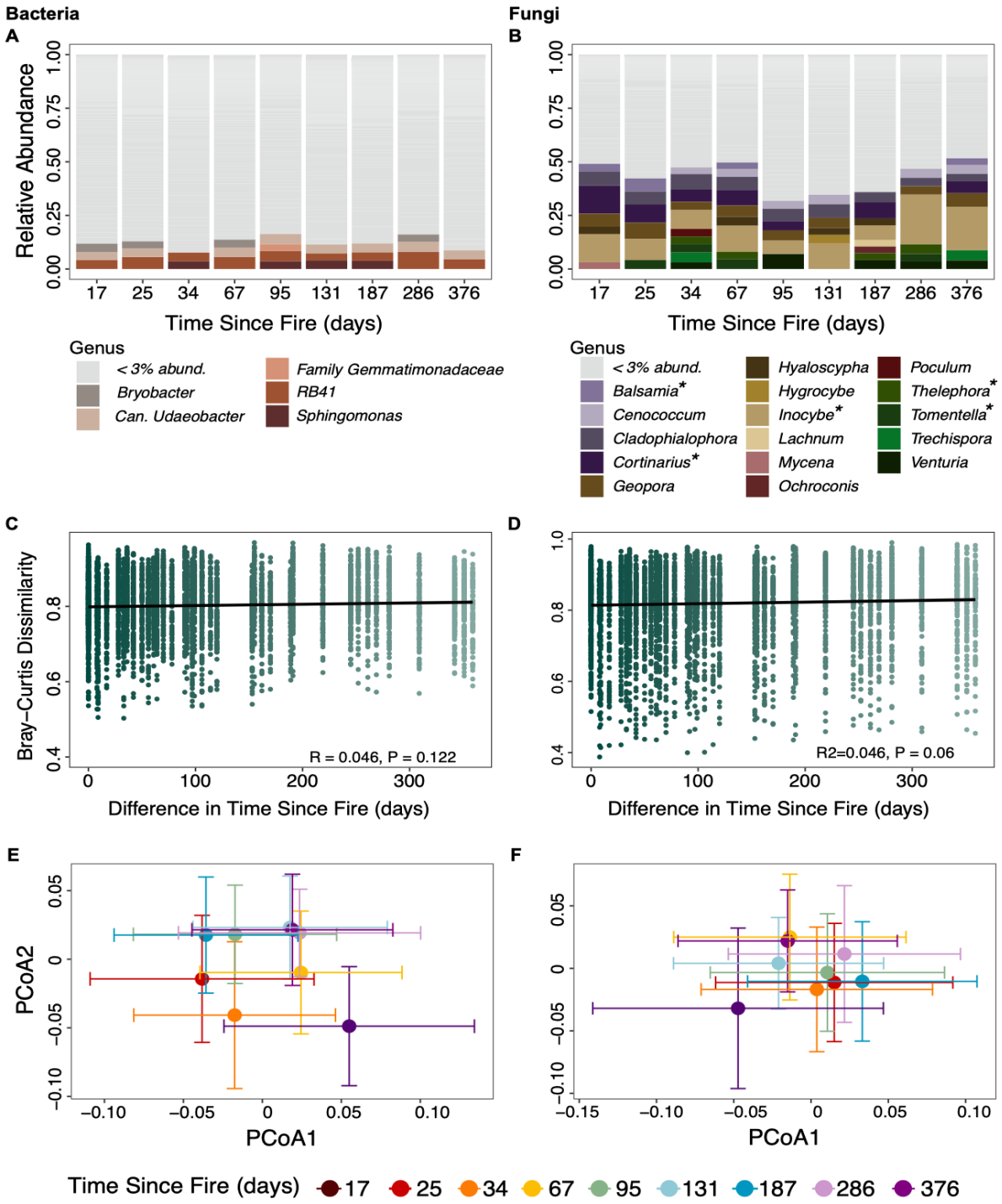

Figure 6. Relative sequence abundance of A) bacterial and B) fungal genera (ectomycorrhizal fungi denoted with an asterisk) in unburned plots at all 9-time points. Mantel correlation between Bray-Curtis dissimilarity and Euclidean temporal distances in C) bacterial and D) fungal community composition in unburned plots displaying no significant succession. Principal components analysis (PCoA) of the mean and standard error Bray-Curtis community dissimilarity at each time point for E) bacteria and F) fungi in the unburned plots. Note that overlapping standard error bars indicate no community turnover across time in unburned plots.

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