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 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 collected 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 post-fire year. In contrast to the unburned plots, fungi and bacteria in the burned plots experienced rapid succession, with 5-6 compositional turnover periods. Analogous to plants, fire-adapted, or "fire-loving," pyrophilous microbes drove successional dynamics. The dominant pyrophilous bacteria and fungi experienced marked trade-offs in abundance over time, especially for fungi, with an initial peak in the Basidiomycete yeast *Geminibasidium* followed by trade-offs with the filamentous Ascomycetes *Pyronema, Aspergillus,* and *Penicillium*. For bacteria, the Proteobacteria genus *Massilia* dominated burned plots throughout the year. Yet, the following two most dominant bacteria, the Firmicute *Bacillus* and Proteobacteria *Noviherbaspirillum,* traded off in abundance over time. Our high temporal sampling allowed us to capture the dynamics of microbial secondary succession for the first time, which indicates that the trade-offs among a few dominant pyrophilous microbes control microbial succession and thus might have important impacts on ecosystem functions.

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 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), 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 drive post-fire organic matter decomposition (Semenova-Nelsen et al., 2019), nutrient cycling (Pérez-Valera et al., 2020), and plant regeneration via symbiotic mycorrhizal fungi (Dove & Hart, 2017).

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 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). Although wildfire impacts on soil microbes are understood, the lack of continuous temporal sampling of disturbed ecosystems has limited our understanding of secondary succession. However, existing studies on primary succession suggest that ecological and physiological differences (i.e., growth rate, stress tolerance, nutrient requirements) (Sun et al., 2017) between bacteria and fungi lead to distinct successional trajectories (Brown & Jumpponen, 2014; Fernández-Martínez et al., 2017), driven by environmental filtering or historical constraints (Schluter & Ricklefs, 1993). In disturbed ecosystems, indirect wildfire effects on the soil environment, including soil burn severity, increased ash deposition, soil pH, and nutrients (Köster et al., 2021; Neaxry et al., 1999), can

restructure microbial communities (Whitman et al., 2019). Moreover, differential responses and adaptations to soil moisture between bacteria and fungi (Placella et al., 2012) (Evans & Wallenstein, 2012), suggest that post-fire precipitation can affect soil microbial communities potentially resulting in distinct successional trajectories, as those observed during primary succession.

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 likely evolved under the same fire regime as the ecosystem they inhabit. The rapid fruiting of pyrophilous fungi after fires has been known for over a century (Seaver, 1909), and in recent decades next-generation sequencing has revealed that pyrophilous Ascomycota such as *Pyronema* can increase 100-fold post-fire (Reazin et al., 2016) and dominate over 60% of sequences in a burned pine forest (Bruns et al., 2020). Furthermore, recent studies provide evidence of pyrophilous bacteria, such as the Proteobacteria *Massilia* (Enright et al., 2021; Whitman et al., 2019), suggesting that fire resilience and adaptations might be widely distributed within soil microbiomes. In fact, pyrophilous fungi have a suite of traits that allow for the survival to fire (i.e., heat resistant spores, sclerotia) and the post-fire environment (i.e., xerotolerance, aromatic C degradation) (Bruns et al., 2020; Whitman et al., 2019). However, although we know that pyrophilous microbes exist, our limited understanding of their distribution in systems outside of pine forest (Pressler et al., 2019), their successional patterns and turnover rates, or the replacement of existing taxa with new species, hinders our ability to explore how pyrophilous microbes mediate the successional trajectory of vegetation in fire-disturbed ecosystems.

Secondary succession begins in a nutrient-rich environment, with low competition for nutrients and moisture (Dalling, 2019). Thus, trade-offs in colonization and resource utilization,

108 a hallmark of successional theory (Tilman 1990), allow surviving or fast-growing organisms to
109 control the initial successional stages (Turner et al., 1998). Over time, species with similar
110 resource use (i.e., overlapping niches) as initial colonizers will be excluded from the community
111 (Pacala et al., 1996), while differentiation in resource use (i.e., complementarity) will promote
112 species coexistence. Whether these patterns translate to belowground microbes remains unclear.
113 Additionally, soil microbial communities have short generation times (Hannula et al., 2019), and
114 on average, the first sampling of post-fire microbiomes occur two years post-fire (Dove & Hart,
115 2017; Pressler et al., 2019), thereby missing the fine-scale temporal succession that can occur
116 directly after a fire. To date, a couple of studies have repeatedly sampled the same post-fire
117 environment and found rapid changes in microbial composition (Ferrenberg et al., 2013; Qin &
118 Liu, 2021), suggesting that microbial communities likely experience high turnover rates.
119 Therefore, to capture the dynamics needed to develop microbial successional theory, it is integral
120 to sample at a scale relevant to soil microbial communities.
121 Chaparral is a shrubland adapted to high-severity fire and a biodiversity hotspot
122 distributed in Mediterranean climates worldwide (Barro & Conard, 1991; Rundel, 2018). The
123 secondary succession of chaparral vegetation is well understood (Keeley et al., 2005). Fire is
124 considered the main initiator of secondary succession, thus making chaparral ideal for studying
125 microbial secondary succession. Yet, although the dominant chaparral vegetation forms
126 mycorrhizal associations required for establishment and survival (Allen et al., 2005; Van der
127 Heijden et al., 1998), only13% of post-fire microbial research occurs in shrublands (Pressler et
128 al., 2019), and none discuss secondary succession. Moreover, ectomycorrhizal fungi experience
129 high mortality rates during wildfires (Dove & Hart, 2017; Pulido-Chavez et al., 2021), but the
130 ability of mycorrhizal fungi to survive a fire or the length they can survive without a host is
131 unknown. With drylands covering nearly 41% of the Earth's terrestrial surface and expanding

132 with climate change (Feng & Fu, 2013), it is critical to understand post-fire successional
133 dynamics in dryland systems such as chaparral.
134 Here, we studied the 2018 Holy Fire, which burned 94 km^2 of Southern California
135 chaparral, to determine the effects of wildfire on soil microbiomes, their successional
136 trajectories, and turnover rates. We sampled soils at 9-time points during the first post-fire year,
137 resulting in the highest resolution temporal sampling of post-fire microbes to date, which enabled
138 us to measure both immediate and temporal effects of wildfire on microbial dynamics across the
139 first post-fire year. We then tested the following hypotheses: (**H1**) wildfire will decrease
140 bacterial and fungal biomass and richness immediately following the fire, leading to a shift in the
141 community composition; (**H2**) bacterial and fungal biomass and richness will increase with time
142 since fire, but one-year will not be sufficient time for either community to return to unburned
143 levels; **(H3)** wildfire will have a distinct impact on fungal guilds with symbiotic mycorrhizal
144 fungi experiencing the largest declines; **(H4)** soil burn severity and precipitation will both affect
145 microbial succession, but post-fire precipitation will impose a larger impact on bacterial
146 communities **(H5)** bacterial, and fungal succession will be initiated by pyrophilous microbes,
147 which will trade-off in abundance over time.
148
149 **2. Methods**
150 ***2.1 Study Area, plot design, and soil collection***
151 The Holy Fire burned 94 km^2 in the Cleveland National Forest across Orange and
152 Riverside counties in Southern California from August 6 to September 13, 2018. On September
153 30, 2018, within weeks of the fire being declared contained, we established nine plots (6 burned
154 and 3 unburned) along a gradient of fire severities (**Fig. 1A**). Plots were selected for similarity in
155 aspect, slope, elevation, and pre-fire vegetation dominance by manzanita *(Arctostaphylos*

156 *glandulosa),* an ectomycorrhizal host, and chamise (*Adenostoma fasciculatum),* an arbuscular
157 and ectomycorrhizal host (Allen et al., 2005). Plots were placed on average 25 m from forest
158 access roads to avoid edge effects. Each circular plot contained four 1 m^2 subplots located at 5 m
159 from the center in each cardinal direction (**Fig. 1B**). Our study site experiences a Mediterranean-
160 type climate with warm, dry summers and cool, wet winters, with an average yearly temperature
161 of 17˚C and precipitation of 12.5 mm. Precipitation data, based on monthly summaries, was
162 gathered from the El Cariso weather station accessed from the RAWS USA Climate Archives
163 (raws.dri.edu). Additional plot information can be found in the supplements **(Table S1)**.
164 We sampled soils at 17, 25, 34, 67, 95, 131, 187, 286, and 376 days, corresponding to
165 approximately 2 and 3 weeks, and 1, 2, 3, 4, 6, 9, and 12 months post-fire. We used BAER soil
166 burn severity maps (Parson et al., 2010) to roughly locate plots at medium and high severity
167 (**Fig. 1A**), but their coarse-scale measurement (30m) does not coincide with microbial
168 communities. Since ash depth increases with soil heating (Parson et al., 2010) and fire-severity
169 (Bodí et al., 2014), we used ash depth as a proxy for burn severity, where we averaged three
170 separate measurements of ash depth (cm) per each 1m^2 subplot at day 17, before any
171 precipitation event could wash away the ash. Thus, our measure of soil burn severity refers to
172 initial ash depth. At each of the 9 time-points, we collected the top 10cm of soil beneath the ash
173 or the duff from each of the 36 subplots with a ~250 mL releasable bulb planter cleaned between
174 samples with 70% ethanol (**Fig. 1C**). High-severity wildfires consume the organic layer; thus, for
175 consistency, we removed the litter layer in the unburned plots before sampling. Soils were
176 transported to the University of California-Riverside (UCR) within hours of sampling, stored
177 overnight at 4˚C, sieved (2 mm) within 24 hours, and a subsample was frozen at -80°C for DNA
178 extraction.
179

180 ***2.3 DNA extraction, amplification, and sequencing***

181 DNA was extracted from soil using Qiagen DNeasy PowerSoil Kits following the
182 manufacturer's protocol, except the centrifugation time was increased to 1.5 min after adding the
183 C3 solution due to a large amount of precipitate. DNA extracts were stored at -20˚C for
184 subsequent analysis. Extracted DNA was amplified using the primer pair ITS4-fun and 5.8s
185 (Taylor et al., 2016) to amplify the ITS2 region for fungi and the primer pair 515F-806R to
186 amplify the V4 region of the 16S rRNA gene for archaea and bacteria (Caporaso et al., 2011)
187 using the Dual-Index Sequencing Strategy (DIP) (Kozich et al., 2013). Although our 16S primers
188 amplify archaea and bacteria, for simplicity, we refer to 16S methods and results simply as
189 bacteria since archaea only contributed <1% of sequencing reads. We conducted polymerase
190 chain reaction (PCR) in two steps. The first PCR amplified gene-specific primers, and the second
191 PCR ligated the DIP barcodes for Illumina sequencing. For bacteria, we combined 1 µl of 1:10
192 diluted DNA, 10.5 µL of Ultra-Pure Sterile Molecular Biology Grade (Genesee Scientific, San
193 Diego, CA, USA), 12.5 µL of AccuStart ToughMix (2x concentration; Quantabio, Beverly, MA,
194 USA), and 0.5 µL each of the 10 µM 515F and 806R primers. Thermocycler conditions for
195 PCR1 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
196 min. For fungi, we combined 5 µl of undiluted fungal DNA, 6.5 µl of ultra-pure water, 12.5 µl
197 of AccuStart ToughMix, and 0.5 µL each of the 10 µM ITS4-fun and 5.8s primers. Thermocycler
198 conditions for PCR1 were: 94 °C for 2 min, followed by 30 cycles of 94 °C for 30 s, 55 °C for 30
199 s, 68 °C for 2 min. PCR1 products were then cleaned with AMPure XP magnetic beads
200 (Beckman Coulter Inc., Brea, CA, USA) following manufacturers' protocols. The DIP PCR2
201 primers containing the barcodes and adaptors for Illumina sequencing were ligated to the
202 amplicons during the second PCR step in a 25 µL reaction containing 2.5 µL of the 10 µM DIP

203 PCR2 primers, 6.5 µL of ultra-pure water, 12.5 µL of Accustart ToughMix, and 1 µL of PCR1
204 product. Thermocycler conditions for the second PCR for bacteria and fungi were: 94°C for 2
205 min followed by 9 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 1 min. Bacterial and
206 fungal PCR products for each of the 324 samples (9 plots x 4 sub-plots x 9 time-points) were
207 then separately pooled based on gel electrophoresis band strength and cleaned with AMPure
208 following established methods (Glassman et al., 2018). Each pool was then checked for quality
209 and quantity with the Agilent Bioanalyzer 2100, pooled at a 2:3 ratio (0.4 units for bacteria to 0.6
210 units for fungi), and sequenced with Illumina MiSeq 2x300bp at the UCR Institute for
211 Integrative Genome Biology. In addition to our 324 samples sequenced in four Illumina MiSeq
212 runs, we added negative DNA extractions and negative PCR controls from each time point and
213 mock communities (ZymoBIOMICS microbial community standard, Zymo, Irvine, CA) to each
214 library for additional quality control and inference.
215
216 ***2.4 Bacterial and fungal biomass***
217 Bacterial and fungal biomass was quantified with quantitative (q) PCR. We used the
218 FungiQuant-F and FungiQuant-R primers to target the 18s rDNA for fungi (Liu et al., 2012) and
219 the Eub338/Eub518 primers for bacteria (Fierer et al., 2005). To estimate bacterial and fungal
220 small-subunit rDNA gene abundances, standard curves were generated using a 10-fold serial
221 dilution of the standards that were generated by cloning the 18S region of *Saccharomyces*
222 *cerevisiae* or the 16S region of *Escherichia coli* into puc57 plasmid vectors, which were
223 constructed by GENEWIZ, Inc. (NJ, USA) as previously established (Averill & Hawkes, 2016).
224 The 10 µl qPCR reactions were performed in triplicate. Reactions contained 1 µL undiluted
225 DNA, 1 µl of 0.05M Tris-HCl ph8.3, 1 µL of 2.5mM $MgCl_2$ (New England BioLabs (NEB);
226 Ipswich, MA), 0.5 µL of 0.5mg/ml BSA, 0.5 µL of 0.25mM dNTP (NEB), 0.4 µL of both

227 primers at 0.4µM, 0.5 µL of 20X Evagreen Dye (VWR), 0.1 µL of Taq DNA polymerase (NEB)
228 and 4.6 µL ultra-pure water. We employed the CFX384 Touch Real-Time PCR Detection
229 System with the following conditions: 94˚C for 5 min, followed by 40 cycles of 94˚C for 20
230 seconds, 52˚C (for bacteria) or 50˚C (for fungi) for 30 seconds, followed by an extension at 72˚C
231 for 30 seconds. Gene copy numbers were generated using a regression equation, 10^ (Cq-b)/m,
232 where the y-intercept and slope were generated from the standard curve. The Cq value was
233 calculated as the average Cq value per sample in relation to the known/calculated copies in the
234 standard Cq (CT); values were generated by CFX Maestro software.
235
236 ***2.5 Bioinformatics***
237 Illumina data was processed with Qiime2 (Bolyen et al., 2019). The demultiplexed fastQ
238 files from the four Illumina sequencing runs were processed individually using cutadapt (Martin,
239 2011) to remove the primers and ran through DADA2 to filter out and remove chimeric
240 sequences and low-quality regions and to produce Amplicon Sequence Variants (ASVs)
241 (Callahan et al., 2017). DADA2 outputs from each library were merged into one library for
242 downstream processing, including the removal of singletons and taxonomic assignments. We
243 used the SILVA reference database for bacteria (Yilmaz et al., 2014) and the UNITE reference
244 database for fungi (Kõljalg et al., 2005) for taxonomic assignment (accessed on 10/27/2020).
245 Sequences assigned to mitochondria and chloroplasts for bacteria or not assigned to the Kingdom
246 Fungi were removed from ASV tables before subsequent analysis. Raw fungal ASV tables were
247 exported and parsed through FUNGuild (Nguyen et al., 2016) to assign functional ecological
248 guilds to each fungal ASV. We identified the following fungal guilds and included only high
249 probable confidence rankings for downstream analysis: arbuscular fungi (AMF), ectomycorrhizal
250 fungi (EMF), saprotrophs, and pathogens. Moreover, negative and mock controls were inspected

251 to ensure that sequences in negative controls were negligible and that mock taxonomy correlated
252 with known communities. Sequences were submitted to the National Center for Biotechnology
253 Information Sequence Read Archive under BioProject accession number PRJNA761539.
254
255 ***2.6 Statistical analysis***
256 Statistical analyses were conducted in R, 4.1.1 (R Core Team, 2021), and all statistical
257 codes are available on GitHub https://github.com/pulidofabs/SecondarySuccession-Chaparral.
258 To account for uneven sequencing depth, ASV tables were rarefied to a
259 sequences/sample depth of 7,115 for bacteria and 11,480 for fungi. Fungal and bacterial alpha
260 diversity was estimated using BiodiversityR (Kindt & Coe, 2005) with the following metrics:
261 observed species richness, Simpson, Shannon, Chao1, and ACE. Since patterns of species
262 richness were similar across metrics **(Fig. S1)**, we focused on richness estimated as the number
263 of observed ASVs after rarefaction for all downstream analyses. To test if wildfire decreased
264 biomass and richness (**H1**), if biomass and richness increased with time since fire **(H2),** if
265 wildfire will have distinct impact on fungal guilds **(H3)**, and to determine if changes in biomass
266 and richness were associated with precipitation and soil burn severity **(H4),** for both bacteria and
267 fungi, we fitted thirteen statistical models with treatment (burned vs. unburned), time (measured
268 as days since fire), ash depth (cm), total monthly precipitation (mm), and their respective
269 interactions as predictors. We used generalized mixed effect models (glmer) with a negative
270 binomial distribution in the MASS package (Venables & Ripley, 2002) to account for the over-
271 dispersion of the data and the fact that the conditional variance was higher than the conditional
272 mean (Bliss, 1953; Ross & Preece, 1985). Moreover, time since fire and precipitation were
273 scaled and centered, and the level of nestedness for all models was tested by running a null
274 model with different nested levels ("plot," "subplot," "time since fire") and no predictors. Model

275 selections were made via comparison of Akaike Information Criterion (AICc) in the MuMIN
276 package (Barton, 2020). All richness models contained "plot," "subplot," and "time since fire" as
277 random effects, and all biomass models contained "plot" and "time since fire" as random effects.
278 Pseudo $R^{2,}$ or the variance explained (marginal and conditional) for all models, was calculated
279 using the r.squaredGLMM function in the MuMIn Package.

280 We compared beta diversity by generating distance matrices with the Vegan Avgdist
281 function, calculating the square-root transformed median Bray-Curtis dissimilarity per 100
282 subsampled iterations. We used permutational multivariate analysis of variance (PERMANOVA)
283 (Anderson, 2017) as implemented with the Adonis function in the vegan package (Oksanen et
284 al., 2018) to test for the significant effects of wildfire, time since fire, and their interactions, on
285 bacterial and fungal community composition overall and at each independent time point (**H1**).
286 Results were visualized using Non-Metric Multidimensional Scaling (NMDS) ordinations.

287 We visualized succession by characterizing the community composition patterns at the
288 genus level using phyloseq (McMurdie & Holmes, 2013) and plotting the relative abundance
289 profile of the dominant ASVs (greater than 3% sequence abundance) for each time point in
290 burned and unburned communities independently with ggplot2. We tested for significant changes
291 in abundance of each taxa between burned and unburned plots and over time using glmer.
292 Moreover, we employed several methods to quantify succession (**H5**). Similar to a study
293 examining microbial turnover in Sorghum plants (Gao et al., 2020), we used the mantel function
294 in vegan to determine the correlation between temporal distance and community composition to
295 determine how turnover varies in the presence or absence of fire. To visualize spatial species
296 turnover (Baselga, 2010), we took advantage of the fact that early successional periods display
297 large variability (Collins, 1990; Pandolfi, 2008). Thus, we tested the homogeneity of the
298 bacterial and fungal communities during succession using the vegan betadisper function to

299 calculate the multivariate dispersion of Bray-Curtis dissimilarities and visualized the results
300 using PCoA. Finally, we employed the codyn package (Hallett et al., 2016) to identify various
301 factors of diversity metrics to assess succession (Collins et al., 2000). First, to identify whether
302 the community is experiencing its normal successional trajectory, per the ecological successional
303 theory, we calculated direct linear change, also known as directional change, using the Euclidian
304 distance of each microbial community. Moreover, we measured total species turnover or the rate
305 of species change between two-time points to determine if species appearances or disappearances
306 drive succession. Lastly, we measured community stability as a measure of resilience, or rate of
307 return to the original state, which is product synchrony or patterns of how species abundance
308 covary over time (Loreau & de Mazancourt, 2008)
309

310 **3. Results**

311 ***3.1 Sequencing data***

312 The four Illumina MiSeq runs resulted in 9.8 M bacterial and 24.6 M fungal sequences
313 for an average of 31,052 bacterial and 78,202 fungal sequences/sample and a total of 33,078
314 bacterial and 11,480 fungal ASVs. Rarefaction resulted in a total of 24,874 bacterial and 7,445
315 fungal ASVs. Extracting the fungal guilds from the rarefied fungal ASV table resulted in 208
316 EMF, 70 saprobic, 65 AMF, and 26 pathogenic fungal ASVs.
317

318 ***3.2 Wildfire effects on bacterial and fungal biomass and richness***

319 Fire led to large and significant reductions in bacterial and fungal biomass and richness
320 during the first post-fire year (**Tables S2; S3)**. Fire had larger impacts on biomass than richness
321 for both bacteria and fungi and larger impacts on fungi than bacteria overall (**Fig. 2**). On average
322 across the year, fire reduced richness by 46% for bacteria (**Fig. S1A**) and 68% for fungi **(Fig.**

323 **S1A)** and biomass by 47% for bacteria **(Fig. S2A**), and 86% for fungi **(Fig. S2B**). The direct,
324 immediate effect of wildfire at 17 days post-fire was stronger for biomass than richness, with
325 bacterial biomass decreasing by 84% **(Fig. 2A)** and fungal biomass by 97% **(Fig. 2B).** In
326 contrast, fungal richness declined by 45% **(Fig. 2D)**, but bacterial richness temporarily increased
327 by 31% but declined by 29% at 25 days post-fire **(Fig. 2C; Table S2)**. While the differences in
328 biomass and richness between the burned and unburned sites lessened with time since fire, one
329 year was insufficient for bacterial and fungal biomass or richness to recover to unburned levels
330 (**Fig. 2)**. The effects of fire across time remained larger for fungi than for bacteria, with fungal
331 biomass remaining 80% and richness 61% lower and bacterial biomass remaining 43% and
332 richness 23% lower in the burned plots at 1-year post-fire (**Fig. 2, Table S2).**
333
334 ***3.3 Drivers of changes in richness and biomass***
335 Negative binomial models showed that the direct impact of fire negatively affected
336 bacterial and fungal biomass and richness **(Table S3)**, which was lessened by the positive
337 interaction effect of time since fire and soil burn severity **(Fig. 3; Table S3).** While time since
338 fire only directly affected fungal richness (**Table S3)**. Soil burn severity had significant adverse
339 direct effects on bacterial and fungal richness but no significant effects on biomass, meaning that
340 biomass was equally reduced in the presence of fire regardless of severity **(Fig. 3; Table S3**).
341 Precipitation did not directly affect bacterial or fungal biomass or richness, but it interacted with
342 time since fire affected bacterial negatively (**Fig. 2C)** and positively affected fungal richness
343 **(Fig. 2D; Table S3).** However, bacterial biomass responded positively to a fire and precipitation
344 interaction (**Fig. 2A; Table S3).**
345
346 **3.4** ***Wildfire effects on the richness of the different fungal guilds***

347 Wildfire led to large and significant reductions for all fungal guilds **(Table S4, Fig. S3),**
348 with the largest declines for AMF. On average across time points, EMF decreased by 68%,
349 pathogens by 71%, saprobes by 86%, and AMF by 98% in burned plots compared to unburned
350 plots **(Fig. S3).** Moreover, one year was insufficient for any guild to return to unburned levels. In
351 fact, at 376 days, AMF was on average 89%, pathogens 69%, saprobes 61% lower in the burned
352 plots (Fig. S4). Interestingly, EMF experienced a decrease in richness over time, resulting in
353 species richness being 91% lower in the burned plots at 376 days post-fire. (**Fig. S4)**. Although
354 EMF richness did not significantly differ from the unburned plots at 25 days, fire interacted with
355 time since fire caused EMF to decrease in the burned plots (**Fig. S4; Table S4**). EMF richness
356 further declined with soil burn severity (**Table S4).** Moreover, a fire and precipitation interaction
357 negatively affected EMF and pathogen richness **(Table S4).** In the unburned plots, mycorrhizal
358 and pathogen richness remained unchanged over time (**Fig. S4)**, but an interaction between fire
359 and time resulted in a sharp dip in saprobic richness in the unburned plots at 286 days post-fire,
360 causing a brief overlap between the burned and unburned plots (**Fig. S4, Table S4).**
361
362 ***3.5 Wildfire changes microbial community composition***
363 Fire significantly affected the community structure of bacteria and fungi, explaining 13%
364 of the compositional variation for bacteria and 11% for fungi **(Table S5).** Time since fire had
365 smaller impacts on community composition, explaining 4% of the variation for bacteria and 1%
366 for fungi. In comparison, a fire and time interaction explained 2% of the variation for bacteria
367 and 1% for fungi **(Table S5).** Community composition between burned and unburned plots
368 significantly varied at all 9-time points for both bacteria **(Fig. S5)** and fungi **(Fig. S6),** with
369 differences increasing over time from 12% to 21% for bacteria (**Fig. S5)** and 9% to 13% for
370 fungi from day 17 to day 376 post-fire **(Fig. S6)**. The changes in bacterial **(Fig. 4B)** and fungal

371 composition **(Fig. 4D)** were driven by the dominance of previously rare taxa, which traded off in
372 abundance over time in the burned plots. Bacterial communities experienced less discernable
373 trade-offs than fungi due to the consistent dominance of the Proteobacteria *Massilia*, which
374 composed on average 57% of the sequences throughout the year in the burned plots **(Fig. 4B)**.
375 However, three Firmicutes quickly dominated, with *Bacillus* (13%), an uncultured Clostridiales
376 (26%), and *Paenibacillus* (4%) dominating at 34 and 67 days post-fire. The Firmicutes rapidly
377 declined and traded abundances with the Proteobacteria *Noviherbaspirillum,* which increased in
378 abundance over time, from 1% at 34 days to 24% by the end of the year **(Fig. 4B).** For fungi, two
379 Basidiomycetes that dominated at 17 days post-fire, the yeast *Geminibasidium* (45%) and the
380 EMF *Inocybe* (16%), rapidly declined and traded abundance with filamentous Ascomycetes **(Fig.**
381 **4D)**. While the Ascomycete *Penicillium* quickly established dominance and constantly occupied
382 an average sequence abundance of 38% over the year **(Figs. 4D)**, *Pyronema* rapidly dominated,
383 peaking at 67 days with 67% of the total sequences post-fire. *Pyronema* slowly declined
384 thereafter as *Aspergillus* slowly increased in abundance over time, from 2% at17 days to 22%
385 376 days post-fire **(Fig. 4D)**.
386
387 ***3.6 Microbial successional dynamics***
388 Directional change in the community was higher in the burned bacterial and fungal
389 communities, confirming that succession is occurring **(Table S6).** Moreover, the low synchrony
390 observed in bacterial and fungal burned communities (Table S6) indicates community stability
391 due to the dominance of a few genera. Analysis of the community stability collaborated these
392 results and was higher for bacteria than fungi, and it was higher in the burned than unburned
393 bacterial communities **(Tables S6).** Indicating that bacterial succession is rapidly proceeding to
394 the point of potential equilibrium due to increasing bacterial richness and resilience. In contrast,

395 fungal communities are less stable more susceptible to change. Visual confirmation of these
396 trends established that both bacterial **(Fig. 5A)** and fungal **(Fig. 5B)** communities experienced
397 rapid and distinct successional trajectories in the burned plots, with bacteria **(Fig. 5C)**
398 experiencing successional changes at double the rate of fungi **(Fig. 5D)**. These successional
399 changes in the burned plots were driven by six major compositional turnover points for bacteria
400 at 25, 34, 95, 131, 187, and 376 days post-fire **(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 lower 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)** were driven by
407 the disappearance of taxa, more so for bacteria (days 17-95) than fungi (17-25; **Table S6**).
408 Whereas high diversity and the lack of dominance drove early bacterial succession **(Fig. 5A)**, as
409 succession proceeded, dominance by a few taxa, including the Firmicutes *Bacillus* at 25 days
410 post-fire, *Paenibacillus* and *Domibacillus* (34-67 days), and the Proteobacteria
411 *Noviherbaspirillum* (95 days), and the constant dominance of *Massilia* (34-286 days post-fire)
412 resulted in the disappearance of bacterial species over time **(Fig. 5A; Table S6)**. In contrast,
413 fungal 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-stage bacterial (187-376 days; **Fig. 5A**) and mid-stage fungal (67-
420 187 days) succession **(Fig. 5B; Table S6).** For bacteria, the appearance of two Bacteroidetes,
421 *Pedobacter* and *Adhaeribacter*, and the Actinobacteria *Blastococcus* shaped mid-stage bacterial
422 succession (**Fig. 5A)**. For fungi, mid-stage succession was driven by the appearance of
423 Basidiomycota mushroom-forming taxa, including the return of the previously dominant EMF
424 genus *Inocybe*, and the appearance of the saprobes, *Coprinellus,* and *Tephrocybe,* which were
425 rare in the unburned communities (<0.01% sequence abundance). The appearance of unknown
426 filamentous Ascomycota in the Sordariaceae and Pyronemataceae also drove mid-stage fungal
427 succession. In contrast, late-stage succession was driven by the increased dominance of
428 *Tephrocybe* and *Aspergillus* and the disappearance of *Inocybe* and *Rasamsonia,* and the
429 decreased abundance of *Pyronema* from 286-376 days post-fire **(Fig. 5B).**
430

431 **4. Discussion**

432 Here, we present the highest resolution temporal sampling of post-fire microbiomes to
433 date, enabling us to show for the first time that bacteria and fungi experience rapid succession
434 driven by the dominance of previously rare "fire-loving" pyrophilous taxa that increase post-fire
435 but experience marked trade-offs in abundance over time. Although our study was in California
436 chaparral, many of the dominant pyrophilous taxa identified here also dominate other burned
437 environments, including pine (Bruns et al., 2020; Reazin et al., 2016), spruce forests (Whitman et
438 al., 2019), redwood tanoak forests (Enright et al., 2021), and Spanish shrublands (Pérez-Valera et
439 al., 2018), indicating the generality of our results to wildfire-affected ecosystems. We found that
440 wildfire decreased bacterial and fungal biomass and richness, shifting community composition
441 (**H1)** and persisting for the entire year for both bacteria and fungi (**H2**). Fungal guilds were
442 differentially affected by fire and time, with AMF and saprobes experiencing larger direct fire

443 impacts than pathogens or EMF. However, over time, mycorrhizal fungi experience larger
444 declines than pathogens and saprobes (**H3).** Interestingly, AMF immediately succumbed to the
445 death of their host while EMF survived for 1-2 months, answering the question of how long it
446 takes mycorrhizal fungi to die after the death of their host. Moreover, soil severity negatively
447 affected bacterial and fungal richness, while bacterial biomass and fungal richness were
448 positively influenced by precipitation's interaction with time and fire (**H4).** Finally, we found
449 strong evidence that fire causes bacteria and fungi to undergo rapid secondary succession
450 dominated by pyrophilous microbes that trade-off in abundance over time (**H5),** likely driving
451 post-fire ecosystem recovery.
452
453 ***4.1 Wildfire decreased bacterial and fungal biomass and richness***
454 Soil bacterial and fungal biomass and richness declined in the burned sites, corroborating
455 previous post-fire studies in Mediterranean shrublands (Pérez-Valera et al., 2018) and forests
456 (Dooley & Treseder, 2012). We noted a more significant fire effect on fungal biomass and
457 richness relative to bacteria, consistent with previous research (Certini et al., 2021; Glassman et
458 al., 2021; Pourreza et al., 2014; Pressler et al., 2019), showing that bacteria are more resistant to
459 fire than fungi (Certini et al., 2021; Dunn et al., 1982). Although richness and biomass increased
460 over time for both microbial groups, one year was insufficient for either group to recover to
461 unburned levels, consistent with previous studies (Pérez-Valera et al., 2018; Treseder et al.,
462 2004), indicating that microbial biomass and richness could take decades to recover. Moreover,
463 we observed a transient increase in bacterial richness directly post-fire. This transient increase
464 may result from taxa such as bacteria in the Actinobacteria genera *Soliribrobacter* and
465 *Conexibacter* (Albuquerque & da Costa, 2014) that may be favored by the increase in soil pH
466 observed here **(Table S1)** and in other studies (Neary et al., 1999; Rousk et al., 2010) or by post-

467 fire pulses of nitrogen and phosphorus (Certini et al., 2021). We observed a larger direct fire
468 impact on AMF and pathogens than EMF and saprobes; however, EMF was more impacted over
469 time. Although studies have noted the decrease in EMF and saprobic richness (Dove & Hart,
470 2017; Enright et al., 2021; Pulido-Chavez et al., 2021) and AMF richness or colonization (Dove
471 & Hart, 2017; Enright et al., 2021), generalization of our observations are difficult as the vast
472 majority of studies focus on 1-2 guilds (Dove & Hart, 2017). Although EMF did not experience
473 the largest immediate effect of wildfire compared to the other guilds, we speculate that EMF
474 persisted for a few weeks post-fire because their host roots remained alive. Thus, the increase in
475 EMF mortality with time is dependent on host mortality, providing evidence for the importance
476 of surviving host for EMF survival.
477
478 ***4.2 Precipitation and soil burn severity affected soil bacterial and fungal communities***
479 Due to our high-resolution temporal sampling and fine-scale measurement of soil burn
480 severity, we detected the effect of precipitation and fire severity on microbial recovery.
481 Precipitation did not affect fungal biomass, interacted with time to negatively affect bacterial but
482 positively affected fungal richness, and bacterial biomass in the burned plots. These results are
483 consistent with previous studies (Barnard et al., 2013), which showed that bacterial biomass can
484 bloom in response to rewetting. This distinct response in richness could be due to mortality and
485 survival characteristics and physiological and morphological differences between these microbial
486 groups (Blazewicz et al., 2014; Placella et al., 2012; Selbmann et al., 2013) and their potential
487 adaptation to normal water conditions in chaparral. For example, fungi can prime themselves for
488 stressful situations by activating or enhancing resistance to drought (Evans & Wallenstein, 2012;
489 Guhr & Kircher, 2020), allowing them to maintain a constant reproduction rate regardless of the
490 external environmental conditions. Moreover, the high morphological plasticity of fungi,

including their ability to alternate growth forms based on environmental conditions, such as hyphal growth in low nutrient conditions or meristematic growth in stressful conditions (Selbmann et al., 2013), may allow fungi to survive small changes in moisture content, while forcing certain bacterial groups to enter a dormant state, inhibiting growth (Schimel, 2018). Thus, to be evolutionarily successful, bacteria may 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), thus potentially explaining the peaks in biomass and richness observed after high rain events (day 131).

Our results show that initial ash depth, measured before the first rains, can serve as an index of soil burn severity measured on a scale relevant to the soil microbiome, which can aid in understanding the initial and long-lasting impacts of fire severity on soil microbiomes. Similar to studies in boreal (Whitman et al., 2019) and oak forests (Pourreza et al., 2014), bacterial and fungal richness strongly responded to soil burn severity. However, contrary to a meta-analysis (Dooley & Treseder, 2012), neither bacterial nor fungal biomass was directly impacted by soil burn severity. Due to the frequent high-severity fires in this system, we speculate that biomass might depend on a temperature threshold (fire intensity) rather than fire severity. However, since we observed an interaction effect of time since fire and severity on biomass, we speculate that previously observed severity effects, which results from studies that on average sample two years post-fire (Dove & Hart, 2017; Pressler et al., 2019), may represent an interaction effect of time and severity and not a direct effect of severity.

.

4.3 Pyrophilous bacteria dominate burned communities and drive succession

Wildfire led to a complete turnover of the chaparral soil bacterial communities favoring putative pyrophilous bacteria that have been detected after fires in temperate and boreal forests,

515 such as taxa belonging to the phyla Actinobacteria, Acidobacteria, Firmicutes, and
516 Proteobacteria (Enright et al., 2021; Whitman et al., 2019; Xiang et al., 2014). In particular, the
517 dominance of the genera *Massilia, Noviherbaspirillium,* and *Paenibacillus* may be attributed to
518 their ability to survive the wildfire and exploit transient niches in the early post-fire environment.
519 For example, *Paenibacillus xerothermodurans* is an endospore-forming bacterium that has been
520 shown to contain heat-inducible transcriptional proteins, which can protect heat-induced protein
521 denaturation (Kaur et al., 2018). However, *Massilia* does not form endospores but was
522 nonetheless the most dominant genus post-fire. *Massilia* is a known fast reproducing (Enright et
523 al., 2021; Whitman et al., 2019) rhizospheric bacteria (Li et al., 2014), capable of colonizing the
524 roots of various plants (Ofek et al., 2012) and forming associations with arbuscular fungi (Iffis et
525 al., 2014). Thus, we speculate that a fast reproduction rate and arbuscular association allow
526 *Massilia* to promote its ability to dominate post-fire systems by increasing its proliferation within
527 the soil (Toljander et al., 2005). Lastly, an uncultured Firmicute Clostridiales dominated early
528 succession. Previous studies suggest that Clostridiales produce resistant spores that can survive
529 harsh conditions and lack of nutrients by triggering sporulation (Paredes-Sabja et al., 2011). This
530 suggests that Clostridiales survived the wildfire and quickly sporulated, resulting in early post-
531 fire dominance. Together these results suggest that post-fire dominant bacteria in wildfire-
532 adapted systems have coevolved and developed mechanisms to survive the fire resulting in niche
533 exclusion and dominance in recently burned ecosystems.
534 Our high temporal resolution sampling enabled us to demonstrate the secondary
535 succession of bacterial communities and contextualize these dynamics in broader successional
536 theory. Moreover, we were able to show that putative pyrophilous bacteria experience rapid
537 turnover, resulting in a marked trade-off in abundance over time, information currently lacking
538 in soil bacterial communities and post-fire disturbed ecosystems. In bacterial communities,

539 succession and community turnover occurred rapidly and was initiated by aerobic, heterotrophic
540 bacteria that form endospores and produce antibiotics, which may improve their competitive
541 abilities.

542 Like plant successional patterns (Capitanio & Carcaillet, 2008; Egler, 1954), early
543 successional stages were characterized by high bacterial diversity and a lack of dominance,
544 mimicking the distributions observed in unburned communities. Previous studies suggest that in
545 complex resource environments, such as those created by wildfire, niche complementarity
546 becomes more important than competition because diverse communities can better exploit
547 resources (Eisenhauer et al., 2013). Our results support this idea, as the dominant taxa in our
548 study have been shown to use different forms and types of resources. For example,
549 *Paenibacillu*s can fix nitrogen (Monciardini et al., 2003; Slepecky & Hemphill, 2006), *Bacillus*
550 and *Conexibacter* can reduce nitrogen, and *Bacillus* can further solubilize phosphate (J. et al.,
551 2001; Kalayu, 2019), suggesting that niche partitioning may promote positive interactions
552 between bacteria in the early successional stages (<25 days). However, as succession progressed,
553 the bacterial community converged on one dominant functional strategy, where all three genera
554 that dominated most successional stages (*Massilia, Paenibacillus,* and *Noviherbaspirillum)* have
555 similar functional roles, including phosphorus solubilization (*Paenibacillus, Massilia*), nitrogen
556 fixation (*Paenibacillus*), and reduction (*Massilia, Paenibacillus*) (Bailey et al., 2014; Baldani et
557 al., 2014; Grady et al., 2016; Gu et al., 2016; Wan et al., 2020; Woolet & Whitman, 2020).
558 Moreover, *Massilia* and *Noviherbaspirillium* are putative polycyclic aromatic hydrocarbon
559 degraders, a component of pyrogenic organic matter, an abundant post-fire carbon resource
560 (Baldani et al., 2014; Grady et al., 2016), which may enable them to thrive in the post-fire
561 environment; suggesting that the diverse functional potential of the dominant taxa may allow
562 these bacteria to survive in a changing environment.

563 ***4.3 Pyrophilous fungi dominate the burned communities and drive succession***

564 Interestingly, previously detected pyrophilous fungi from globally burned ecosystems
565 also dominate California chaparral. Although our experiment did not study mechanisms
566 controlling pyrophilous microbial dominance, it is clear that pyrophilous microbes are not
567 biome-specific. Instead, these fungi may be activated by temperature thresholds, such as
568 temperatures reached during high severity fire, which are common in chaparral and some
569 Pinaceae forests (Agee, 1993; Keeley & Zedler, 2009; Neary et al., 1999). Specifically, our
570 communities were dominated by Ascomycota in the genera *Pyronema, Penicillium*, and
571 *Aspergillus,* similar to dominant fungal species in wildfire affected boreal spruce forest
572 (Whitman et al., 2019), montane pine forests (Fujimura et al., 2005; Pulido-Chavez et al., 2021),
573 Mediterranean shrublands (Livne-Luzon et al., 2021) and controlled pyrocosm studies (Bruns et
574 al., 2020) Both *Pyronema (P. omphalodes)* and *Aspergillus* (*A. fumigatus*) are known
575 pyrophilous fungi of California chaparral (Dunn et al., 1982). We identified additional species
576 that responded positively to wildfire, including *P. domesticum*, *A. udagawae*, and *A.*
577 *elsenburgensis.* These pyrophilous fungi are adapted to wildfire (Moore, 1962; Rhodes, 2006)
578 and produce fire-resistant structures such as dormant spores, sclerotia, and conidia (Smith et al.,
579 2015; Warcup & Baker, 1963), which are heat activated (Gottlieb, 1950; Warcup & Baker,
580 1963). The rapid and efficient germination of *Aspergillus* (in the subgenus *Fumigati*, including
581 *A. udagawae*) induced by high temperatures (Rhodes, 2006) and its ability to use various carbon
582 and nitrogen sources, including ammonium and nitrate (Krappmann & Braus, 2005), may
583 position *Aspergillus* to rapidly dominate after chaparral fires. Furthermore, *Pyronema*
584 *domesticum*, a relatively well-studied pyrophilous fungus, can mineralize pyrogenic organic
585 matter, a dominant substrate in burned environments (Fischer et al., 2021), thus potentially
586 allowing it to take advantage of the abundant food source in this system. Finally,

587 *Geminibasidum,* a recently described thermotolerant Basidiomycete yeast (H. D. T. Nguyen et
588 al., 2013), dominated 45% of our sequences at 17 days post-fire. While not typically described as
589 pyrophilous, presumably because most pyrophilous fungi are described from sporocarps
590 (McMullan-Fisher et al., 2011), recent studies using next-generation sequencing have found
591 *Geminibasidium* to increase post-fire in pine forests (Pulido-Chavez et al., 2021; Yang et al.,
592 2020). Thus, it is likely that *Geminibasidium* is an underrepresented pyrophilous fungus that
593 appears after high severity fires in multiple ecosystems. Together, these results suggest that
594 dominant pyrophilous fungi are more widespread than expected and that their response to fire
595 might be due to fire adaptations and requirements.

596 Although knowledge of pyrophilous fungi is growing, we lacked an understanding of
597 how soon these pyrophilous fungi appear, how they trade in abundance over time, and their
598 turnover rates (Fox et al., 2022). We show that pyrophilous fungi experience rapid turnover,
599 trading in abundance over time, and by establishing their dominance in early successional stages
600 (<25 days), they maintain control of the system for the entire year. Early fungal successional
601 stages (3 weeks post-fire) were dominated by surviving ectomycorrhizal Basidiomycetes, such as
602 *Cortinarius, Inocybe,* and *Tomentella,* which dominated the unburned fungal communities and
603 that have been previously found in burned pine forests (Gassibe et al., 2011; Glassman et al.,
604 2016; Owen et al., 2019; Pulido-Chavez et al., 2021) and pine-dominated Mediterranean systems
605 (Gassibe et al., 2011; Hernández-Rodríguez et al., 2013). However, fast-growing saprobic and
606 pyrophilous fungi in the genera *Pyronema, Penicillium*, and *Aspergillus* quickly dominated all
607 successional time points, beginning at 25 days. The results for *Pyronema* are consistent with
608 pyrocosm studies (Bruns et al., 2020). Although it is possible that the EMF signal detected could
609 be due to relic DNA (Carini et al., 2016), high UV conditions, such as those in post-fire systems
610 (Neary et al., 1999), rapidly degrade relic DNA (Torti et al., 2015), suggesting that these EMF

611 survived the fire and clung to a dying host for at least 2 months, as in the case of *Inocybe*. Thus,
612 we suggest that this is not relic DNA but a true signal of how long it takes EMF to die once their
613 host dies. Ectomycorrhizal survival may be attributable to their exploration type and specificity
614 for current vs. stored photosynthates (Gray & Kernaghan, 2020; Pena et al., 2010). For example,
615 long/medium exploration types, such as *Cortinarius,* require more carbon for maintenance and
616 only remain in the community for 17 days post-fire. Whereas *Inocybe*, a short-contact type
617 (Agerer, 2001; Koide et al., 2014), survived for up to 67 days post-fire. Thus, we speculate that
618 early EMF could have survived on their hosts' stored photosynthates. However, not all EMF
619 hosts died, as sprouting was observed as early as 286 days post-fire, suggesting that the EMF that
620 survived the fire could have survived on the lower resources provided by the resprouting
621 manzanita and chamise shrubs.

622 Successional theory states that early successional stages are dominated by fast-growing
623 species that quickly dominate the open space (Kinzig & Pacala, 2013). Our data suggest that this
624 trait in the ecological theory applies to fungal succession. The fungal community was dominated
625 by fast-growing, thermotolerant fungi, *Penicillium*, *Aspergillus,* and *Pyronema* (Dix & Webster,
626 1995; McGee et al., 2006). It is well known that both *Penicillium* and *Aspergillus* can readily
627 reproduce via asexual means, thus in their asexual states, they can readily reproduce without
628 needing a comparable mate (Crow, 1992), allowing rapid colonization of the open niche.
629 Although stress selection is suggested to dominate sexual reproduction (Grishkan et al., 2003),
630 our results suggest that in chaparral, a fire-adapted ecosystem, stress adaptations such as the
631 melanized conidia and thick cell walls of *Aspergillus* and *Penicillium* (Cordero & Casadevall,
632 2017; Lagashetti et al., 2019), and the formation of dormant spores or conidia might be
633 characteristic of the historical fire regime of the system, thus allowing these fungi to rapidly
634 dominate all successional time points during the first post-fire year. Lastly, we noted the

emergence of fungal decomposers, such as *Coprinellus* and *Tephrocybe,* at later successional stages, supporting previous research (McMullan-Fisher et al., 2011). The onset of fruiting body development of well-known decomposers, such as *Coprinellus*, suggest that the potential mortality of early successional forbs and the increased dead woody material in the system might be providing the organic C required for saprobic communities.

5 Conclusion

Due to our unprecedented high-resolution temporal sampling, we show that bacterial and fungal communities experience rapid secondary succession and trade-offs in abundance. 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 the lack of repeated post-fire sampling. We found that microbial communities were dominated by post-fire microbes that were rare or absent pre-fire and which trade-off in abundance over time, in a manner that may affect post-fire biogeochemical cycling and vegetation regeneration due to their abilities to transform post-fire nutrients or associate with regenerating vegetation. Additionally, post-fire dominant bacteria and fungi in wildfire-adapted systems appear to have many traits analogous to plants, such as fire adaptations and the ability to grow fast and rapidly exploit post-fire niches, making it easier to adapt successional theory developed in plants to microbes. We conclude that although wildfire leads to drastic reductions in microbial species richness, biomass, and community composition, post-fire bacteria and fungi experience rapid successional changes that align with plant successional theory. Understanding these dynamics can increase our ability to predict if and how

659 ecosystems will recover after fire, a disturbance that is increasingly widespread with climate
660 change.
661
662 **Acknowledgments**
663 We thank the Cleveland National Forest and the Trabuco Ranger District, including District
664 Ranger Darrel Vance and Officers Jeffrey Heys, Emily Fudge, Victoria Stempniewicz, and Jacob
665 F. Rodriguez, for their guidance, help with the permitting and site selection process. We thank
666 Judy A. Chung for help with fieldwork and molecular work and Aral C. Greene, Dylan Enright,
667 and Sameer S. Saroa for fieldwork assistance. We thank Amelia Nelson, Elizah Stephens, and
668 Kaleigh A. Russell, and our anonymous reviewers for their helpful comments on the manuscript.
669 This work was supported by UC Riverside, the BLM JFSP Award #012641-002, and Shipley
670 Skinner Award to MFPC and SIG, and the USDA-NIFA Award 2022-67014-36675 to SIG and
671 PMH.
672
673 **Conflict of interest**
674 Authors do not declare any conflict of interest or relationship that might influence the author's
675 objectivity.
676
677 **Author's contribution:** SIG conceived of the study and acquired permits; LL, SIG, and PMH
678 came up with the experimental design; SIG, LL, PMH, MFPC, and JWJR performed fieldwork;
679 MFPC and JWJR performed all molecular work; MFPC performed all bioinformatics, statistical
680 analysis, made all of the figures, and wrote the first draft; all authors contributed to writing and
681 editing of the manuscript.
682

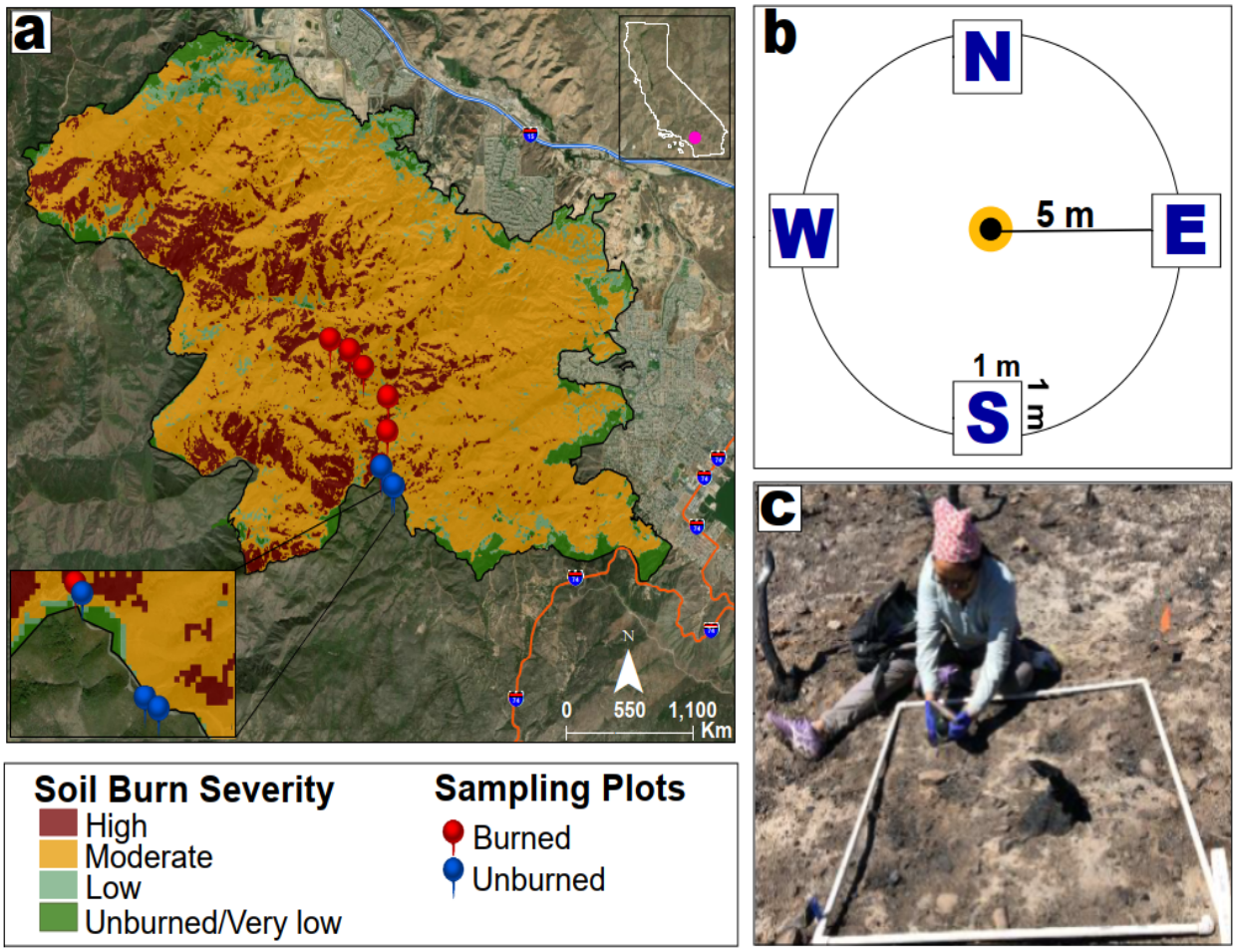

Figure 1. A) Location of the study area and plots (6 burned; 3 unburned) within the Holy Fire burn scar in the Cleveland National Forest in Southern California. Soil burn severity is based on the USDA BAER classifications. B) Plot experimental design, each with four 1m^2 subplots placed 5m from the center 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.

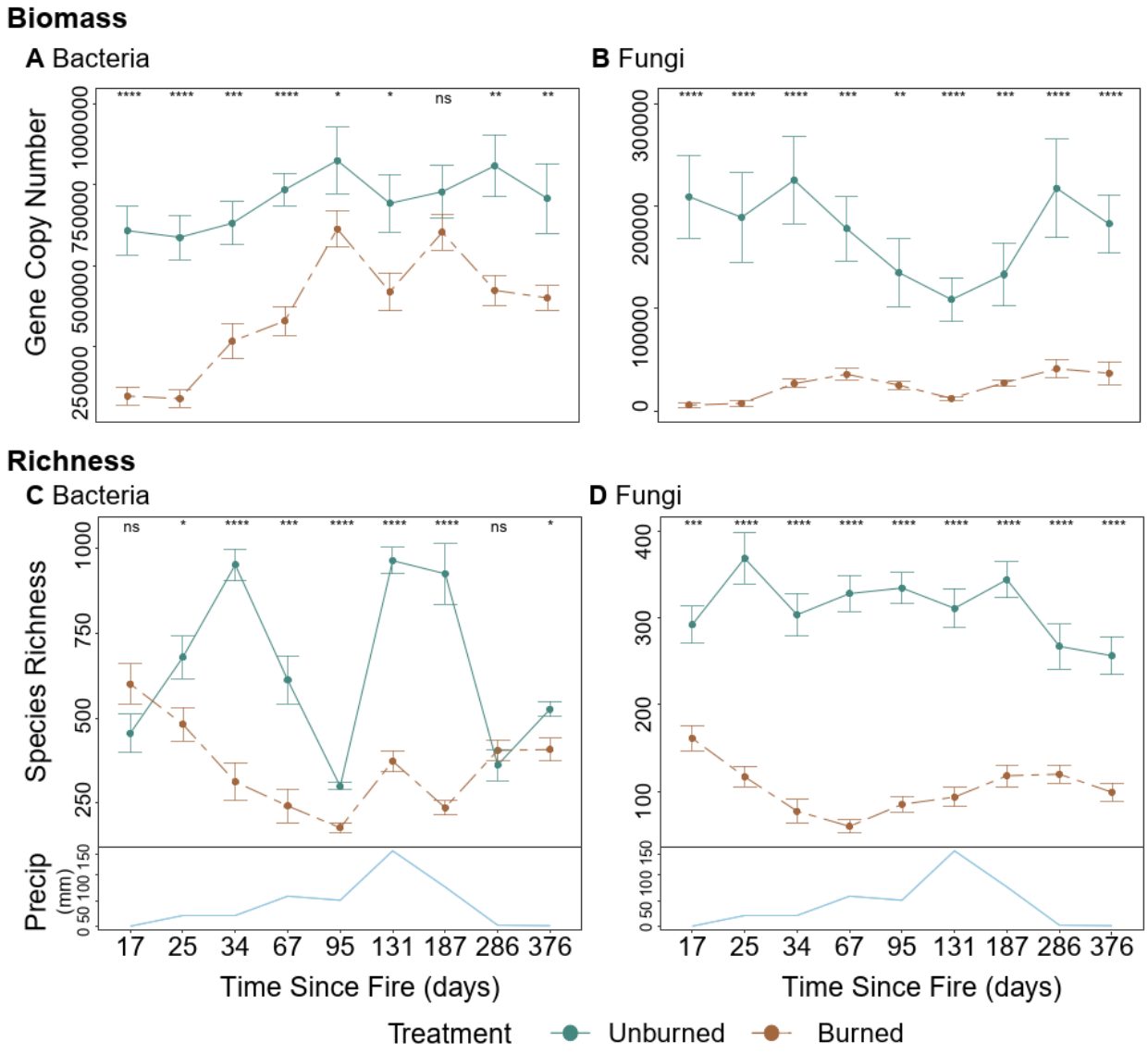

Figure 2. Change in biomass for A) bacteria and B) fungi and change in richness for C) bacteria and D) fungi at each of the 9 time-points in the first year post-fire in burned and unburned plots. Points represent mean differences averaged across burned and unburned plots, and bars represent the standard 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.

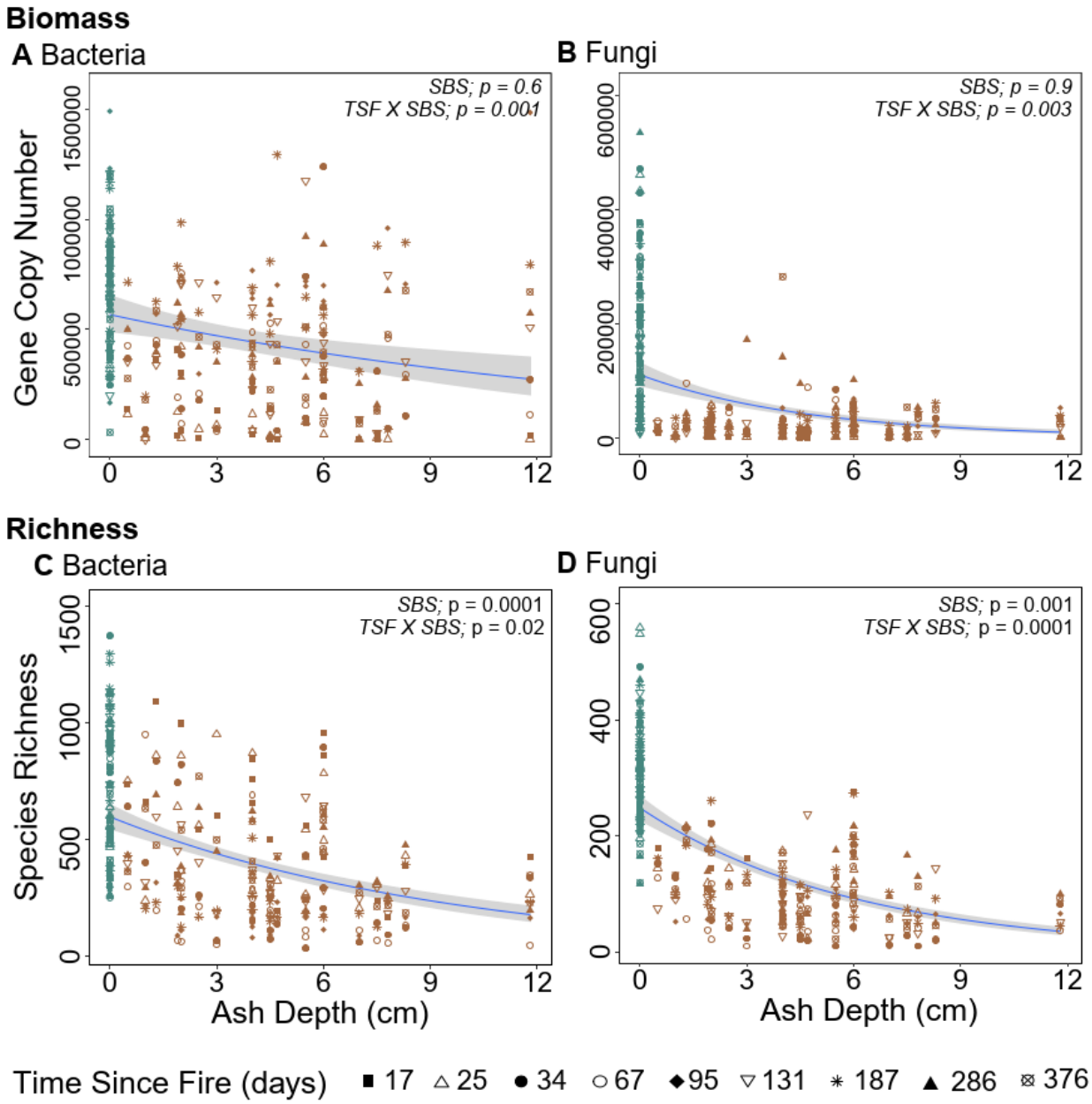

Figure 3. Change in A) bacterial and B) fungal biomass and C) bacterial and D) fungal richness in relation to soil burn severity measured as ash depth at 17 days post-fire. The significance of biomass and species richness against soil burn severity (SBS) and its interaction with time since (TSF) fire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

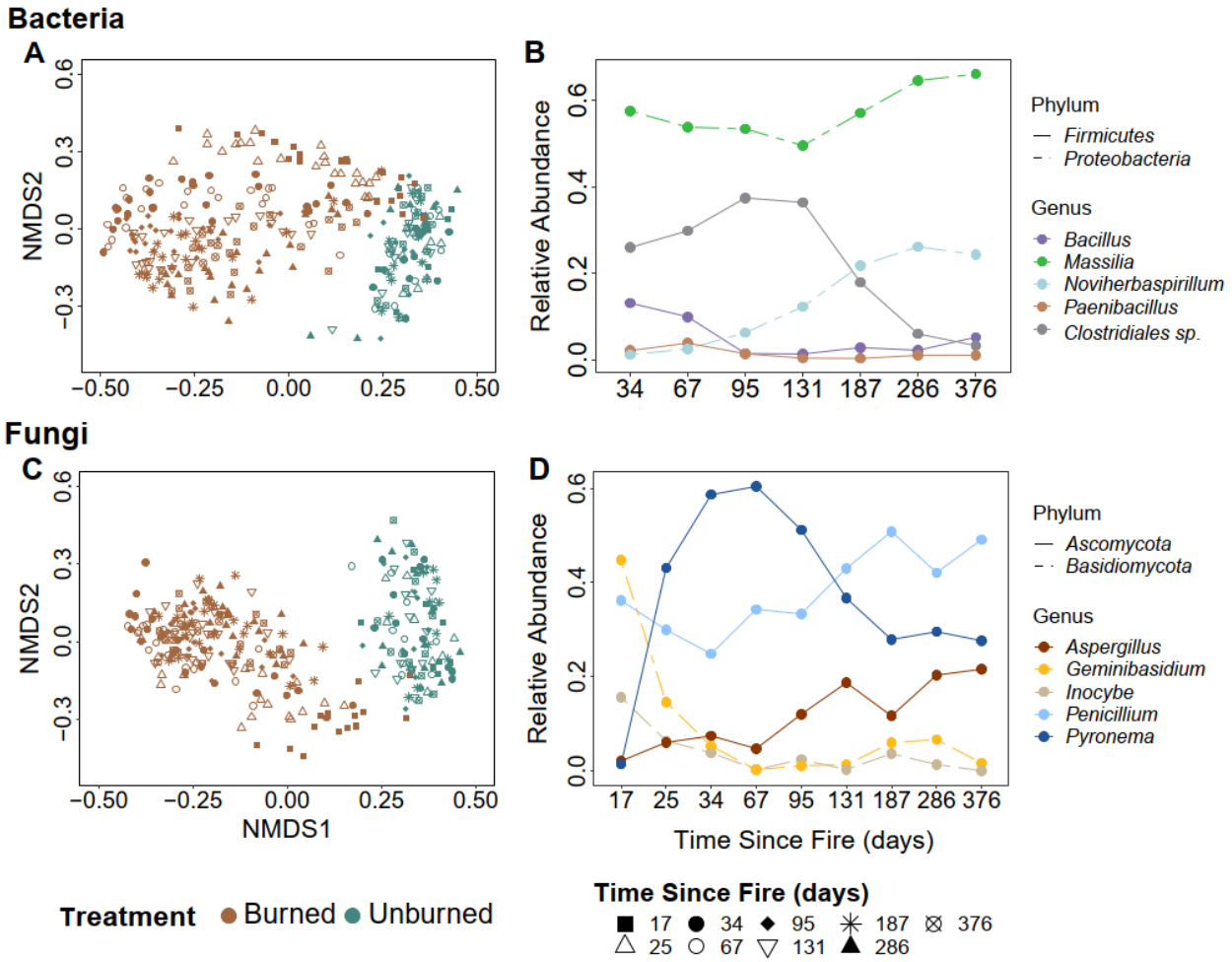

Figure 4. NMDS plot of A) bacterial and C) fungal community composition with colors denoting treatment and shape indicating time since fire. The NMDS is based on 3-dimensions and has a stress value of 0.11 for bacteria and 0.12 for fungi. Change in relative sequence abundance of the five most abundant B) bacterial and D) fungal genera in the burned plots over time. Note, the dominance of the top 5 bacterial genera began at 34 days post-fire since there wasn't clear dominance at days 17 and 25 due to the lag in post-fire bacterial declines.

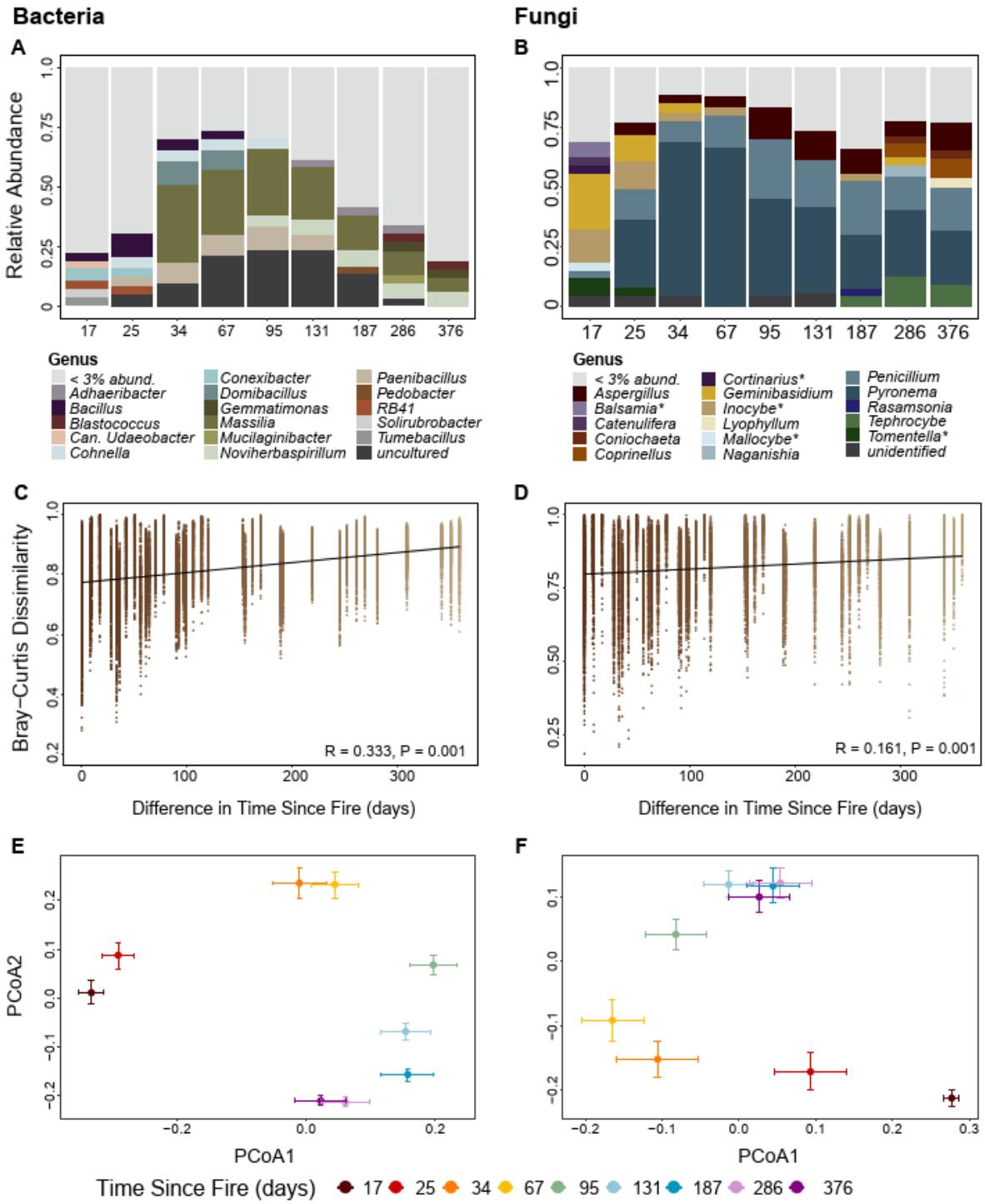

Figure 5. Relative sequence abundance of A) bacterial and B) fungal genera (ectomycorrhizal fungi denoted with an asterisk) in burned plots at all 9-time points. Mantel correlation between Bray-Curtis dissimilarity and Euclidean temporal distances in C) bacterial and D) fungal community composition in 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 time points farther apart indicate a community turnover, and overlapping points with standard errors represent a lack of compositional turnover.

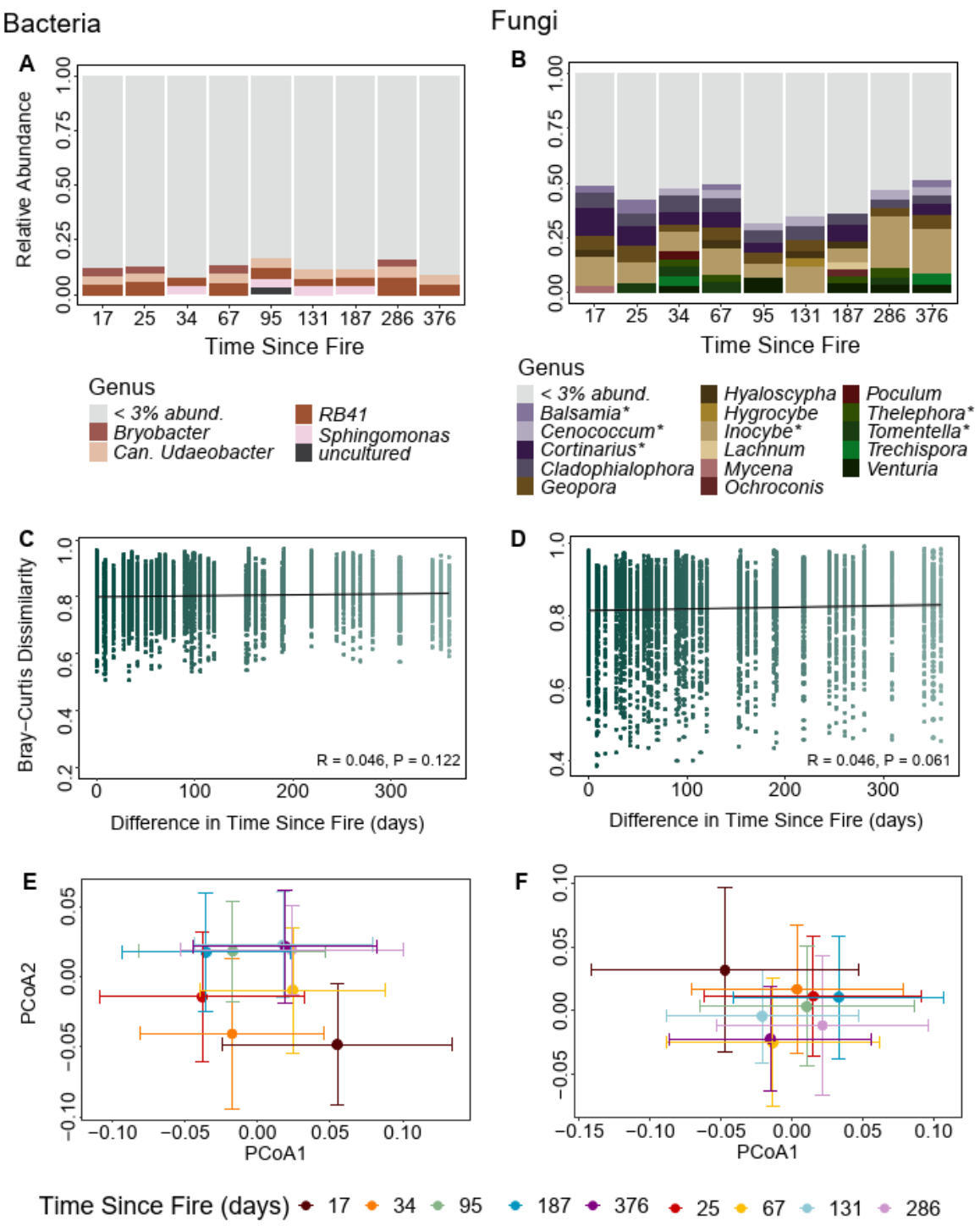

Figure 6. Relative sequence abundance of A) bacterial and B) fungal genera (ectomycorrhizal fungi denoted with an asterisk) in unburned plots at all 9-time points. Mantel correlation between Bray-Curtis dissimilarity and Euclidean temporal distances in C) bacterial and D) fungal community composition 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 overlapping standard error bars indicate no community turnover across time in unburned plots.

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