1 Bacterial and fungal communities experience rapid succession during the first year following a
2 wildfire in a California chaparral
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36 **Abstract**

37   The rise in wildfire frequency in the western United States has increased interest in

38   secondary succession. However, despite the role of soil microbial communities in plant

39   regeneration and establishment, microbial secondary succession is poorly understood owing to a

40   lack of measurements immediately post-fire and at high temporal resolution. To fill this

41   knowledge gap, we collected soils at 2 and 3 weeks and 1, 2, 3, 4, 6, 9, and 12 months after a

42   chaparral wildfire in Southern California. We assessed bacterial and fungal biomass with qPCR

43   of 16S and 18S and richness and composition with Illumina MiSeq sequencing of the 16S and

44   ITS2 amplicons. We found that fire severely reduced bacterial biomass by 47% and richness by

45   46%, but the impacts were stronger for fungi, with biomass decreasing by 86% and richness by

46   68%. These declines persisted for the entire post-fire year, but bacterial biomass and richness

47   oscillated in response to precipitation, whereas fungal biomass and richness did not. Fungi and

48   bacteria experienced rapid succession, with 5-6 compositional turnover periods. As with plants,

49   fast-growing surviving microbes drove successional dynamics. For bacteria, succession was

50   driven by the phyla Firmicutes and Proteobacteria, with the Proteobacteria *Massilia* dominating

51   all successional time points, and the Firmicutes (*Domibacillus* and *Paenibacillus*) dominating

52   early- to mid-successional stages (1-4.5 months), while the Proteobacteria *Noviherbaspirillum*

53   dominated late successional stages (4.5-1 year). For fungi, succession was driven by the phyla

54   Ascomycota, but ectomycorrhizal basidiomycetes, and the heat-resistant yeast, *Geminibasidium*

55   were present in the early successional stages (1 month). However, pyrophilous filamentous

56   Ascomycetes *Pyronema, Penicillium,* and *Aspergillus,* dominated all post-fire time points. While

57   wildfires vastly decrease bacterial and fungal biomass and richness, similar to plants,

58   pyrophilous bacteria and fungi increase in abundance and experience rapid succession and

59   compositional turnover in the first post-fire year, with potential implications for post-fire

60   chaparral regeneration.

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1. Introduction

64   The rapid increase in wildfire frequency, severity, and extent in the western United States

65   (Riley & Loehman, 2016) has encouraged a resurgence of interest in secondary succession.

66   Secondary succession, or the trajectory along which an ecosystem develops following a

67   disturbance, such as a wildfire, has been extensively studied for plants (Derroire et al., 2016;

68   Donato et al., 2012; Hanes, 1971), but belowground microbial communities have been largely

69   overlooked. Understanding how wildfires alter soil microbial succession is necessary to predict

70   post-fire effects on ecosystem recovery and function since soil microbes affect post-fire plant

71   community regeneration via symbiotic associations with fungi (Dove & Hart, 2017), drive

72   organic matter decomposition (Semenova-Nelsen et al., 2019) and nutrient cycling (Pérez-Valera

73   et al., 2020).

74   Microbial succession is a major process affecting the health and function of all

75   ecosystems. However, wildfire-induced mortality (Hart et al., 2005) can reset the successional

76   clock due to reductions in richness and biomass (Dooley & Treseder, 2012; Pérez-Valera et al.,

77   2018; Pressler et al., 2019) and the replacement of fungal basidiomycetes with saprobic

78   ascomycetes (Cairney & Bastias, 2007), which can affect ecosystem regeneration and function.

79   Successional theory incorporates patterns of change and species turnover, the replacement of

80   existing taxa with new species, due to environmental filtering or historical constraints (Schluter

81   & Ricklefs, 1993). In the context of the secondary succession of early microbial assemblages,

82   historical constraints, such as fire regime, may reflect microbial turnover since pyrophilous "fire-

83   loving" microbes have evolved under the same fire regime as the ecosystem they inhabit. In fact,

84   pyrophilous fungi were first discovered over a century ago (Petersen, 1970; Seaver, 1909), and

85   next-generation sequencing has revealed that pyrophilous Ascomycota such as Pyronema can

86   increase 100-fold post-fire (Reazin et al., 2016), dominating over 60% of sequences in the soils

87   of burned pine forest (Bruns et al., 2020). In addition, current studies have provided evidence of

88   pyrophilous bacteria (Enright et al., 2021; Whitman et al., 2019), suggesting that fire resilience

89   and adaptations might be widely distributed within the soil microbial communities. However, we

90   lack an understanding of the fine-scale changes of pyrophilous microbes and their patterns and

91   turnover rates during early secondary succession. Consequently, limiting our ability to predict

92   the successional trajectory of fire-disturbed ecosystems and our understanding of the role that

93   pyrophilous microbes might play in the successional dynamics of wildfire-affected sites.

94   Patterns of succession are expected to vary predictably across disturbance severity, with

95   surviving, fast-growing organisms controlling the initial successional patterns (Turner et al.,

96   1998). However, the successional niche hypothesis posits that during early succession, species

97   assemble based on tradeoffs between competitive ability and growth (Pacala et al., 1996).

98   Whereby niche exclusion leads to the removal of species due to overlapping niches. In contrast,

99   niche complementarity allows for the coexistence of species via their ability to use different

100   forms of a resource. Therefore, niche complementarity is suggested to be important for

101   facilitation (Bertness & Callaway, 1994; Callaway et al., 2002) and, thus, might drive early

102   successional patterns in post-fire environments. However, soil microbial communities have short

103   generation times (Hannula et al., 2019), and on average, post-fire microbial research occurs two

104   years post-fire (Dove & Hart, 2017; Pressler et al., 2019), consequently missing the fine-scale

105   temporal succession that can occur directly after a fire and preventing microbial succession

106   theory development. To date, only one study has sampled twice in a post-fire environment and

107   found rapid changes in bacterial composition (Ferrenberg et al., 2013), suggesting that other

108   post-fire microbial communities likely experience similarly high turnover rates. Soil microbial

109   communities and ecosystem recovery is inextricably linked. Thus, to properly understand the

110   successional trajectories of the post-fire ecosystem, we must first understand the successional

111   dynamics of the pyrophilous microbes that dominate early post-fire systems as they may shape

112   available niche space and exert feedback responses onto the local habitat.

113   Chaparral is a fire-adapted shrubland found in drylands across the globe (Barro &

114   Conard, 1991), which has coevolved under a high-severity fire regime. In fact, in chaparral, fire

115   is the main initiator of secondary vegetation succession, making it ideal for studying secondary

116   microbial succession. The dominant vegetation types in chaparral form symbiotic associations

117   with mycorrhizal fungi (Allen & Kitajima, 2013; Kummerow et al., 1978). These symbiotic

118   associations can mediate plant stress and increase access to nutrients, thus making them vital for

119   plant establishment and survival (Baldrian, 2016; Van der Heijden et al., 1998). Yet, very little is

120   understood about post-fire microbial succession in chaparral, with only 13% of research on post-

121   fire microbiomes occurring in shrublands (Pressler et al., 2019). Since 66-86% of post-fire

122   microbial research occurs in forests, in particular pine forests (Dove & Hart, 2017; Pressler et al.,

123   2019), it is unclear whether the research on forest pyrophilous microbes is generalizable to

124   drylands such as chaparral.

125   This study aimed to determine the effects of wildfire on soil microbiomes, their

126   successional trajectories, and their turnover rates. We studied the 2018 Holy Fire, which burned

127   94 km^2 of chaparral in the Cleveland National Forest in Southern California. We performed

128   unprecedented, high-resolution temporal sampling of soils for one year, at 2 and 3 weeks, and 1,

129   2, 3, 4, 6, 9, and 12 months post-fire, allowing us to measure the direct effects of wildfire (as

130   measured at 17 days post-fire) and overall wildfire effects as measured for the entire sampling

131   year. We then used Illumina MiSeq Sequencing to test the following hypotheses: (**H1**) wildfire

132   will decrease both bacterial and fungal biomass and richness, leading to a shift in the community

133   composition; (**H2**) bacterial and fungal biomass and richness will increase with time since fire,

134   but one-year post-fire will not be sufficient time for either community to return to unburn levels;

135   (**H3**) changes in bacterial and fungal biomass and richness will be associated with post-fire

136   precipitation events, and initial ash deposition; (**H4**) bacterial and fungal succession will be

137   initiated by pyrophilous microbes, which will decrease in abundance over time.

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140   **2. Methods**

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142   *2.1 Study Area and plot design*

143   The Holy Fire burned 94 km^2 in the Cleveland National Forest across Orange and

144   Riverside counties in Southern California from August 6 to September 13, 2018. On September

145   30, 2018, within approximately two weeks of the fire being declared 100% contained, we

146   established nine plots (6 burned and 3 unburned) along a gradient of fire severities (**Fig. 1A**).

147   Plots were selected for similarity in aspect, slope, elevation (average 1251 m and ranged from

148   1199 m to 1288 m), and pre-fire vegetation dominance by manzanita *(Arctostaphylos*

149   *glandulosa),* an ectomycorrhizal host, and chamise (*Adenostoma fasciculatum),* a plant that

150   associates with both arbuscular and ectomycorrhizal fungi (M. Allen et al., 2005). Plots were

151   placed on average 25 m from access roads to avoid edge effects. Each plot consisted of a 10 m

152   diameter circle with four 1 m^2 subplots, 5 m from the center in each of the cardinal directions

153   (**Fig. 1B**) for repeated soil collection for a total of 36 subplots.

154   Our study site experiences a Mediterranean-type climate with warm, dry summers and

155   cool, wet winters, with an average yearly temperature of 17°C and precipitation of 12.5 mm.

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156   Precipitation data was gathered from RAWS USA Climate Archive and was based on the

157   monthly summaries. Soils at the site are mapped in the Cieneba and Friant series and are

158   classified as Typic Xerorthents and Lithic Haploxerolls. They are sandy and gravelly loams with

159   an average pH of 6.7. Additional site-specific information, including geographical coordinates

160   and elevation, can be found in the supplementary tables **(Table S1)**.

161

162   *2.2 Soil collection*

163   We sampled soils 17, 25, 34, 67, 95, 131, 187, 286, 376 days post-fire. During our

164   sampling on post-fire day 17, we also assessed soil burn severity by averaging three separate

165   measurements of ash depth (cm) within each 1 m^2 subplot. At each time point, the top 10 cm of

166   mineral soil beneath the ash (A horizons) was collected from each subplot with a ~250 mL

167   resealable bulb planter **(Fig. 1C).** Due to the lack of organic layer in the burned plots, soils were

168   not separated by the organic and mineral horizon. In unburned plots, we removed the litter layer

169   before sampling A horizons. We sterilized the soil corer and gloves with 70% ethanol between

170   subplots to avoid cross-contamination, transported soils to the University of California-Riverside

171   within hours of sampling, and stored them overnight at 4˚C. Within 24 hours, soils were sieved

172   (2 mm), and a subsample was frozen at -80°C for DNA extraction.

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174   *2.3 DNA extraction, amplification, and sequencing*

175   To identify bacterial and fungal biomass, richness, and composition, DNA was extracted

176   from soil using Qiagen DNeasy PowerSoil Kits following the manufacturer's protocol, with one

177   modification. The centrifugation time was increased from 1 min to 1.5 min after adding the C3

178   solution because the sample still contained a large amount of precipitate. DNA extracts were

179   stored at -20˚C for subsequent analysis. Extracted DNA was quantified, and quality checked

180   using NanoDrop and amplified using the primer pair ITS4-fun and 5.8s (Taylor et al., 2016) to

181   amplify the ITS2 region for fungi and the primer pair 515F-806R to amplify the V4 region of the

182   16S rRNA gene for archaea and bacteria (Caporaso et al., 2011) using the Dual-Index

183   Sequencing Strategy (DIP) (Kozich et al., 2013). Although our 16S primers amplify both archaea

184   and bacteria, for simplicity, we refer to 16S methods and results simply as bacteria since archaea

185   only contributed <1% of sequencing reads. We conducted polymerase chain reaction (PCR) in

186   two steps, each with 25µl aliquots. The first PCR amplified gene-specific primers, and the

187   second PCR ligated the DIP barcodes for Illumina sequencing. For bacteria, we combined 1 µl of

188   1:10 diluted DNA, 10.5 µL of ultra-pure water, 12.5 µL of AccuStart ToughMix, and 0.5 µL

189   each of the 10 µM 515F and 806R primers. Thermocycler conditions for PCR 1 were: 94°C for 2

190   min followed by 29 cycles of 94°C for 30 s, 55°C for 30 s, 68°C for 1 min followed by an

191   extension step for 10 min at 68°C. For fungi, we combined the gene-specific primers (ITS4-fun

192   and 5.8s) at 0.5 µL each at 10 µM, 5 µl of undiluted fungal DNA, 6.5 µl of Ultra-Pure Sterile

193   Molecular Biology Grade (Genesee Scientific, San Diego, CA, USA) water, and 12.5 µl of

194   AccuStart ToughMix (2x concentration; Quantabio, Beverly, MA, USA). Thermocycler

195   conditions for PCR 1 were: 94 °C for 2 min., followed by 30 cycles of 94 °C for 30 s, 55 °C for

196   30 s, 68 °C for 2 min with an extension step for 10 min at 68 °C. PCR products were then

197   cleaned with AMPure XP magnetic Bead protocol (Beckman Coulter Inc., Brea, CA, USA)

198   following manufacturers' protocols. The DIP PCR2 primers containing the barcodes and adaptors

199   for Illumina sequencing were ligated to the amplicons during the second PCR step in a 25 µL

200   reaction containing 2.5 µL of the 10 µM DIP PCR2 primers, 6.5 µL of ultra-pure water, 12.5 µL

201   of Accustart ToughMix, and 1 µL of PCR 1 product. Thermocycler conditions for the second

202   PCR were 94°C for 2 min followed by 9 cycles of 94°C for 30 s, 60°C for 30 s, 72°C for 1 min,

203   and an extension step of 10 min at 72°C for both bacteria and fungi. Bacterial and fungal PCR

204   products were then separately pooled based on gel electrophoresis band strength and cleaned

205   with AMPURE following established methods (Glassman et al., 2021). Each pool was then

206   checked for quality and quantity with the Agilent Bioanalyzer 2100, pooled at a 2:3 ratio (0.4

207   units for bacteria to 0.6 units for fungi), and sequenced with Illumina MiSeq 2x300bp at the

208   University of California-Riverside Institute for Integrative Genome Biology.

209

210   *2.4 Bacterial and fungal biomass*

211   Bacterial and fungal biomass was quantified with quantitative polymerase chain reaction

212   (qPCR). We used the FungiQuant-F and FungiQuant-R primer set to target the 18s rDNA for

213   fungi (Liu et al., 2012) and the Eub338/Eub518 primer pair for bacteria (Fierer et al., 2005). To

214   estimate bacterial and fungal small-subunit rDNA gene abundances, standard curves were

215   generated using a 10-fold serial dilution of the standards that were generated by cloning the 18S

216   region of *Saccharomyces cerevisiae* or the 16S region of *Escherichia coli* into puc57 plasmid

217   vectors, which were constructed by GENEWIZ, Inc. (NJ, USA) as previously established

218   (Averill & Hawkes, 2016). The 10 µl qPCR reactions were each performed in triplicate.

219   Reactions contained 1 µL undiluted DNA, 1 µl of 0.05M Tris-HCl ph8.3, 1 µL of 2.5mM $MgCl_2$

220   (New England Bio Sci), 0.5 µL of 0.5mg/ml BSA, 0.5 µL of 0.25mM dNTP (New England

221   BioScience) 0.4 µL of both primers at 0.4µM, 0.5 µL of 20X Evagreen Dye (VWR), 0.1 µL of

222   Taq DNA polymerase (New England Bio Sci) and 4.6 µL ultra-pure water. We employed the

223   CFX384 Touch Real-Time PCR Detection System with the following conditions: 94˚C for 5

224   min, followed by 40 cycles of 94˚C for 20 seconds, 52˚C (for bacteria) or 50˚C (for fungi) for 30

225   seconds, followed by an extension at 72˚C for 30 seconds. We used gel electrophoresis to

226   confirm that the products were the correct size. Bacterial and fungal gene copy numbers were

227   generated using a regression equation, $10^{(Cq-b)/m}$, where the y-intercept and the slope were

228   generated from the standard curve while the Cq value was calculated as the average Cq value per

229   sample in relation to the known/calculated copies in the standard Cq (CT) values were generated

230   by CFX Maestro software.

231

232   *2.5 Bioinformatics*

233   Illumina data was processed with Qiime2 (Bolyen et al., 2019). Briefly, our 324 samples

234   (9 plots x 4 subplots x 9-time points) resulted in 763 bacterial and fungal samples and several

235   negatives (DNA extractions and PCR samples), and positive controls (mock PCR) and were

236   sequenced in four Illumina MiSeq runs. The demultiplexed fastQ files from the four Illumina

237   sequencing runs were processed individually by using cutadapt (Martin, 2011) to remove the

238   primers and ran through DADA2 to filter out and remove chimeric sequences and low-quality

239   regions and to produce Amplicon Sequence Variants (ASVs) (Callahan et al., 2017). DADA2

240   outputs from each library were merged into one library for downstream processing, including the

241   removal of singletons and taxonomic assignments. We used the SILVA reference database for

242   bacteria (Yilmaz et al., 2014) and the UNITE reference database for fungi (Kõljalg et al., 2005)

243   for taxonomic assignment. Any sequences assigned to mitochondria and chloroplasts for bacteria

244   were removed from the ASV table before subsequent analysis. Raw fungal ASV tables were

245   exported and parsed through FUNGuild (N. H. Nguyen et al., 2016) to assign functional

246   ecological guilds to each fungal ASV. Fungal guilds include arbuscular fungi (AMF),

247   ectomycorrhizal fungi (EMF), saprotrophs, and pathogens, including only guilds with highly

248   probable confidence ranking for any downstream analysis.

249

250   *2.6 Statistical analysis*

251   All statistical analyses were conducted using R (1.4.17). Fungal and bacterial alpha

252   diversity was estimated after rarefaction to account for uneven sequencing depth using

253   BiodiversityR (Kindt & Coe, 2005) with the following metrics: observed species richness,

254   Simpson, Shannon, Chao1, and Ace. Patterns of species richness were similar across metrics for

255   both bacteria and fungi **(Fig. S1)**; thus, we solely focused on observed ASVs as our metric for

256   species richness for all downstream analyses. To test for treatment effects on bacterial and fungal

257   species richness and each fungal guild (AMF, EMF, pathogens, and saprobes), we fitted thirteen

258   statistical models with treatment (burned vs. unburned), times since fire (days), ash depth (cm),

259   total monthly precipitation (mm), and their respective interactions as predictors. We used

260   generalized mixed effect models (glmer) with a negative binomial distribution in the MASS

261   package (Venables & Ripley, 2002) to account for the over-dispersion of the data and the fact

262   that the conditional variance was higher than the conditional mean (Bliss, 1953; Ross & Preece,

263   1985). Moreover, time since fire and precipitation were scaled and centered, and the level of

264   nestedness for all models was tested by running a null model with different nested levels ("plot,"

265   "subplot," "time since fire") and no predictors. Model selections were made via comparison of

266   Akaike Information Criterion (AICc) in the MuMIN package (Barton, 2020). All species

267   richness models, including the models for each fungal guild, contained "plot," "subplot," and

268   "time since fire" as random effects, and all biomass models contained "plot" and "time since fire"

269   as random effects. Pseudo R^2, or the variance explained (marginal and conditional) for all

270   models, was calculated using the *r.squaredGLMM* function in the MuMIn Package.

271   We compared beta diversity across treatments using a distance matrix generated using the

272   "Avgdist" function within the Vegan package (Oksanen et al., 2018), allowing us to calculate the

273   average subsampled Bray-Curtis dissimilarity per 100 iterations and then square-root

274   transforming. Results were visualized using Non-Metric Multidimensional Scaling (NMDS)

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275 ordinations. We used permutational multivariate analysis of variance (PERMANOVA) as

276 implemented with the Adonis function in the vegan package. To test for the significant effects of

277 wildfire, time since fire, and their respective interaction. In addition, PERMANOVA was also

278 used to test the effect of fire on the bacterial and fungal communities at each independent

279 sampling time point. Lastly, to quantify succession, we employed the codyn package (Hallett et

280 al., 2016) to identify the total species turnover between two-time points, including the relative

281 species appearance and disappearance, the rate of directional change using Euclidean distance,

282 and community stability (Collins et al., 2000). To visualize spatial species turnover (Baselga,

283 2010), we took advantage of the fact that early successional periods display large variability

284 (Collins, 1990; Pandolfi, 2008). Thus, we tested the homogeneity of the bacterial and fungal

285 communities during succession using multivariate dispersion of Bray-Curtis dissimilarities with

286 the betadisper function (vegan) and visualized the results using PCoA. To further quantify

287 succession, we performed a Mantel test to determine the correlation between temporal distance

288 and community composition as in (Gao et al., 2020). Succession was further visualized by

289 characterizing the community composition patterns at the genus level using phyloseq (McMurdie

290 & Holmes, 2013) and plotting the relative abundance profile of the ASVs composing above 3%

291 of the total sequence abundance for each time point (time since fire). We used generalized linear

292 mixed effect models (glmer) to determine genera with significantly different relative abundance

293 between treatments, with plot and time since fire as a random effect.

294

295

296 **3. Results**

297

298 *3.1 Sequencing data*

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299   The four Illumina MiSeq runs resulted in 9,812,505 bacterial and 24,555,739 fungal

300   sequences for an average of 31,052 bacterial and 78,202 fungal sequences/sample and a total of

301   33,078 bacterial ASVs and 11,480 fungal ASVs. To account for uneven sequencing depths, the

302   raw ASV tables were rarefied to a depth of 7,115 sequences/sample for bacteria and 11,480

303   sequences/sample for fungi, resulting in a total of 24,874 bacterial ASVs and 7,445 fungal ASVs.

304   To eliminate the effect of differences in fungal read numbers while retaining the variation in

305   abundance between the different fungal ecological guilds, we extracted the fungal guilds from

306   the previously rarefied fungal ASV table resulting in 208 EMF, 70 saprobic, 65 AMF, and 26

307   pathogens ASVs.

308

309   *3.2 Wildfire effects on bacterial and fungal biomass and richness*

310   Fire led to large and significant reductions in bacterial and fungal biomass and richness

311   during the first post-fire year. Overall, bacterial biomass was reduced by 47% (p<0.0001; **Fig.**

312   **2A, S2**) and fungal biomass by 86% (p<0.0001; **Fig. 2B, S2**), whereas bacterial richness

313   decreased by 46% (p<0.0001; **Fig. 2C, S1A**) and fungal richness by 68% (p<0.0001; **Fig. 2D,**

314   **S1A**) in the burned sites. The direct effect of wildfire was stronger for biomass than species

315   richness, with bacterial biomass decreasing by 84% **(Fig. 2A)** at 17 days post-fire and fungal

316   biomass by 97% **(Fig. 2B).** In contrast, bacterial species richness temporarily increased by 31%

317   at 17 days **(Fig. 2C; Table S2),** and fungal richness declined by 45% **(Fig 2D; Table S2).**

318   However, the difference in biomass and richness between the burned and unburned sites lessened

319   with time since fire, to a greater degree for bacteria than fungi **(Fig2; Table S2).** One year was

320   insufficient time for either biomass or richness to recover to unburned levels, with bacterial (**Fig.**

321   **2A**) and fungal (**Fig. 2B**) biomass remaining 43% and 80% lower (**Table S2**) and bacterial (**Fig.**

322   **2C**) and fungal richness (**Fig. 2D**) remaining 23% and 61% lower in burned sites **(Table S2).**

323   *3.3 Drivers of changes in richness and biomass*

324   The declines in bacterial and fungal biomass ($p<0.0001$; **Fig. 2A, 2B**) and richness

325   **($p<0.01$; Fig. 2C, 2D; Table S3)** were associated with wildfire. However, precipitation

326   interacted with wildfire to positively affect bacterial biomass ($p = 0.002$) but not fungal biomass

327   nor bacterial or fungal richness **(Table S3)**. Furthermore, time since fire positively influenced

328   fungal richness ($p=0.03$), and the effect was stronger when it interacted with precipitation

329   **($p=0.001$; Figure 2D; Table S3).** In contrast, the time since fire and precipitation interaction

330   negatively affected bacterial richness **($p < 0.0001$),** but no effects were observed for bacterial or

331   fungal biomass **($p>0.05$; Table S3).** In addition, there was a negative effect of ash depth on

332   bacterial **($p = 0.0001$, Fig. 3C)** and fungal richness **($p = 0.0005$, Fig. 3D)**. However, there was a

333   weak but significant positive interaction between ash depth and time since fire, on bacterial **($p =$**

334   **0.001**) and fungal biomass **($p = 0.003$; Table S3) and** bacterial **($p = 0.02$; Fig 3C)** and fungal

335   richness **($p = 0.0001$; Fig. 3D; Table S3)**.

336

337   **3.4 *Wildfire effects on the richness of the different fungal guilds***

338   Wildfire led to selective mortality of fungal guilds, with the largest declines for

339   arbuscular mycorrhizal fungi (AMF). On average, AMF decreased by 98% **($p < 0.0001$; Table**

340   **S4**) and became nearly undetectable in burned plots. Ectomycorrhizal fungi (EMF) decreased by

341   68% ($p = 0.03$), pathogens by 71% ($p = 0.0003$), and saprobes by 86% **($p < 0.0001$; Table S4)** in

342   burned plots compared to unburned plots **(Fig. S3; Table S4)**. Overall, richness for all fungal

343   groups remained lower in the burned plots than the unburned plots for the entire year **(Fig. S4).**

344   Moreover, treatment and precipitation interacted to impose a negative effect on EMF **(p**

345   **<0.0001)** and pathogenic fungi ($p = 0.03$); however, no treatment and precipitation effect was

346   observed for AMF and saprobic fungi **(Table S4).** Furthermore, there was a significant

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347   interaction between treatment and time since fire for ectomycorrhizal and saprobic fungi. This

348   interaction had a negative effect on EMF richness (p < 0.0001), but it had a positive effect on

349   saprobic species richness **(p = 0.001; Table S4)**. Lastly, ash depth negatively affected EMF

350   richness **(p = 0.01; Table S4).**

351

352   *3.5 Wildfire changes microbial community composition*

353   Bacterial (**Fig. 4A)** and fungal (**Fig. 4C)** community composition differed between

354   burned and unburned soil communities. Community differences were explained by treatment

355   (burned vs. unburned), which explained 13% of the variation for bacteria and 11% for fungi **(p <**

356   **0.0001; Table S5),** followed by time since fire, which explained 4% of the variation for bacteria

357   and 2% for fungi **(p < 0.0001; Table S5).** Moreover, there were significant interaction effects

358   with treatment and time since fire which explained 2% of the variation for bacteria and 1% for

359   fungi **(Table S5)**. The differences between the burned and unburned communities remained

360   constant for the entire year for both the bacterial (**Fig. S5**) and fungal communities (**Fig. S6**), and

361   these differences increased over time (**Fig. S5, S6**). For example, at 17 days, fire explained 12%

362   of the variation in the composition of bacteria and 9% for fungi compared to 1-year post-fire,

363   where fire explained 21% of the variation for bacteria and 13% for fungi (**Fig. S5, S6**).

364

365   *3.6 Wildfire led to the dominance of previously rare taxa*

366   Wildfires increased community dominance of previously absent or rare taxa **(Fig. S7;**

367   **Table S6).** Whereas the unburned bacterial communities lacked dominance **(Fig. S7A; Table**

368   **S6),** two Proteobacteria, *Massilia* (16.2%), and *Noviherbaspirillum* (3.3%) and 3 Firmicutes,

369   *Paenibacillus* (5%) and *Domibacillus* (2.7%), *Bacillus* (2.9%) dominated the burned

370   communities **(Fig. S7A; Table S6).** However, the dominance of the bacteria genera was phylum

15

371   specific, where the Firmicutes (*Domibacillus* and *Paenibacillus*) decreased, and the

372   Proteobacteria (*Noviherbaspirillum* and *Massilia*) increased with time since fire **(Fig. 4B).** In

373   contrast, fungal dominance shifted from Basidiomycota and EMF, particularly in the genera

374   *Inocybe* which composed (13%) of the relative abundance, *Thelephora* (2.5%), *Tomentella*

375   (2.6%), *Cenococcum* (3.3%), and *Cortinarius* (6%), to domination by saprobes in the

376   Ascomycota. These ascomycetes include *Pyronema* (34.1%; *P. omphalodes* and *P. domesticum*),

377   followed by *Penicillium (16%; P. decumbens, P. riverlandense,* and *Penicillium sp.)* and

378   *Aspergillus (8%; A. udagawae, A.elsenburgensis,* and *A. fumigatus*; **Fig. S7B; Table S6**).

379   Similarly, post-fire dominance of the fungal genera over time also shifted dominance with phyla

380   specific response where Basidiomycota (*Geminibasidium* and *Inocybe*) decreased, and

381   Ascomycota (*Pyronema, Aspergillus,* and *Penicillium)* increased with time since fire (**Fig. 4D**).

382

383   ***3.7 Microbial successional dynamics***

384   Both bacterial (**Fig. 5A**) and fungal (**Fig. 5B**) community composition experienced rapid

385   and distinct successional trajectories in the burned plots, with bacteria experiencing more

386   significant successional changes **(Fig. 5C, Mantel R = 0.33, p = 0.001)** than fungi **(Fig. 5D,**

387   **Mantel R = 0.16, p = 0.001),** which appear to be driven by six major compositional turnover

388   points for bacteria (**Fig. 5E**) and five for fungi (**Fig. 5F).** In contrast, the unburned bacterial (**Fig.**

389   **6A**) and fungal (**Fig. 6B**) communities remained stable over time. There were no successional

390   changes in bacterial (**Fig. 6A, 6C, Mantel R = 0.046, P = 0.122**) or fungal (**Fig.6B, 6D, Mantel**

391   **R= 0.046, P = 0.061**) communities, and no significant compositional turnover at any time points

392   for bacteria (**Fig. 6E)** or fungi (**Fig. 6F).** Moreover, early successional turnover in the burned

393   sites was driven by the disappearance of taxa, more so for bacteria (from 25-131 days), than

394   fungi (25-34 days; **Table S7**), while later bacterial turnover time points were driven by species

16

395   appearance (187-376 days; **Tables S7).** In contrast, appearance dominated mid-successional

396   turnover periods in the fungal communities **(67-187 days; Table S7**), and late-successional

397   turnover was again driven by species disappearance **(286-376; Table S7).** Moreover, bacterial

398   rates of change and stability were higher in the burned communities, but synchrony was lower

399   **(Table S7).** However, while the rate of change in the fungal-burned communities was higher,

400   stability **(Table S7)** and synchrony were lower **(Table S7).**

401

402   *3.8 Pyrophilous taxa drive post-fire succession*

403   Bacterial succession was initiated by the same genera present in the unburned sites **(Fig.**

404   **5A, 6A),** specifically genera in the phyla Actinobacteria and Acidobacteria, with no strong

405   dominance by any single taxa (**Fig. 5A**). However, bacterial turnover at 25 days post-fire

406   resulted in the dominance of the Firmicute *Bacillus.* A secondary turnover at 34 days post-fire

407   resulted in the dominance of the Firmicutes *Domibacillus* and *Paenibacillus* and the

408   Proteobacteria *Massilia,* followed by continuous domination by the Proteobacteria *Massilia,*

409   *Noviherbaspirillum,* and Firmicute *Paenibacillus* until day 187, after which Firmicutes gave way

410   to domination by Actinobacteria and Acidobacteria (**Fig. 5A**). At 286 days post-fire, bacterial

411   communities became less dominated by a few taxa, and diversity increased similar to unburned

412   communities (**Fig. 5A, 6A**); however, the community composition differed (**Table S8).**

413   Fungal succession was initiated by a Basidiomycetous yeast, *Geminibasidium* (21%) and

414   EMF, present in the unburned community **(**38%, **Fig. 5B, 6B),** specifically the phyla

415   Basidiomycota *Cortinarius, Inocybe, Mallocybe,* and *Tomentella,* and two Ascomycota,

416   *Balsamia* and *Cenoccocum* **(Fig. 5B, 6B).** However, fungal turnover at 25 days post-fire resulted

417   in the dominance of saprobic Ascomycetes (44%) in the genera *Aspergillus, Penicillium,* and

418   *Pyronema* **(Fig. 5B).** Unlike bacteria, the subsequent turnovers at 34, 67, and 95 days post-fire

17

419   resulted in the decrease of *Inocybe* and *Geminibasidium* to the point of being undetected in the

420   community **(Fig. 5B)** and the total dominance of *Aspergillus, Penicillium,* and *Pyronema* **(Fig.**

421   **5B).** After 131 days post-fire (5th turnover, **Fig. 5B, 5F),** turnover in the fungal community

422   stalled. Mushroom-forming taxa, including the ectomycorrhizal fungi *Inocybe*, and the saprobes,

423   *Coprinellus* and *Tephrocybe,* returned to the community (> 3% relative abundance, **Fig. 5B**) and

424   increased in abundance with time since fire **(Fig. 5B, Table S8).**

425

426

427   **4. Discussion**

428   This study presents the first evidence of a fine-scale temporal succession of bacteria and

429   fungi after a wildfire. Consistent with our first hypothesis, wildfire decreased bacterial and

430   fungal biomass and richness while altering community composition. As predicted by our second

431   hypothesis, species biomass and richness increased with time since fire. Still, one year was

432   insufficient for biomass, richness, or the community to return to unburned levels. In support of

433   the 3rd hypothesis, precipitation and ash depth were associated with changes in bacterial and

434   fungal biomass and richness. However, these effects were treatment and time since fire

435   dependent. Finally, consistent with our fourth hypothesis, pyrophilous bacteria and fungi

436   detected in pine forests also initiated succession in chaparral shrublands and experienced rapid

437   post-fire succession.

438

439   *4.1 Wildfire decreased bacterial and fungal biomass and richness*

440   Soil bacterial and fungal biomass and richness declined in the burned sites, corroborating

441   previous post-fire studies in Mediterranean shrublands (Pérez-Valera et al., 2018) and boreal and

442   temperate forests (Dooley & Treseder, 2012). We noted a more significant fire effect on fungal

443   biomass and richness than bacteria, consistent with previous research (Certini et al., 2021;

444   Pressler et al., 2019), showing that bacteria are more resistant to fire than fungi (Certini et al.,

445   2021; Dunn et al., 1982). Moreover, we observed a transient increase in bacterial richness

446   directly post-fire. This transient increase may result from bacteria being favored by the increase

447   in soil pH that is frequently observed after wildfires (Neary et al., 1999; Rousk et al., 2010) or by

448   post-fire increases in nutrient and C availability (Pourreza et al., 2014). Furthermore, we show

449   that fungi experienced a larger decrease in biomass than bacteria, concurrent with previous

450   studies (Pressler et al., 2019).

451   Precipitation had adverse effects on bacterial richness in the burned communities but

452   positive effects on the burned bacterial and fungal biomass and richness over time, supporting

453   previous studies (Barnard et al., 2013). This distinct response could be due to physiological

454   differences between these microbial groups (Placella et al., 2012) and their potential adaptation

455   to the normal water conditions in chaparral. For example, fungi can prime themselves for

456   stressful situations by efficiently activating and enhancing resistance to stressful conditions, such

457   as drought (Evans & Wallenstein, 2012; Guhr & Kircher, 2020). This priming ability may allow

458   fungi to maintain constant reproduction rates regardless of the external environmental conditions.

459   However, in unfavorable conditions, bacteria enter a dormant state that inhibits growth to survive

460   (Schimel, 2018). Thus, to be evolutionarily successful, bacteria respond rapidly to favorable

461   conditions, e.g., rain, and rapidly replicate to outcompete other microbes for the pulse of

462   nutrients released during the rain event (Homyak et al., 2014). Additionally, we show that initial

463   ash depth, in this case, measured before the first rains (17 days post-fire), can serve as an index

464   of soil burn severity. In our study, this severity index had a long-lasting impact on bacterial and

465   fungal biomass and richness, suggesting that the burned sites might be under the indirect effects

466   caused by the wildfire and that burn severity can help predict biomass and richness.

19

467   ***4.2 Pyrophilous bacteria dominate burned communities and drive succession***

468   Wildfire led to a complete turnover of the chaparral soil bacterial and fungal communities

469   favoring pyrophilous bacteria and fungi that have been detected after fires in temperate and

470   boreal forests, such as taxa belonging to the phyla Actinobacteria, Acidobacteria, Firmicutes, and

471   Proteobacteria (Enright et al., 2021; Whitman et al., 2019; Xiang et al., 2014). In particular, the

472   dominance of the genera *Massilia, Noviherbaspirillium,* and *Paenibacillus* may be attributed to

473   their ability to survive the wildfire and exploit transient niches in the early post-fire environment.

474   For example, *Paenibacillus xerothermodurans* is an endospore-forming bacterium that has been

475   shown to contain heat-inducible transcriptional proteins, which can protect heat-induced protein

476   denaturation (Kaur et al., 2018). However, *Massilia* does not form endospores but was

477   nonetheless the most dominant genera post-fire. *Massilia* is a fast colonizing bacteria, which has

478   been speculated to promote its ability to rapidly colonize the post-fire environment (Enright et

479   al., 2021; Whitman et al., 2019). Together these results suggest that post-fire dominant bacteria

480   in wildfire-adapted systems have coevolved and developed mechanisms to survive the fire

481   resulting in niche exclusion and dominance in recently burned ecosystems.

482   For the first time, we were able to show the secondary succession of bacterial

483   communities in a disturbed environment, providing an in-depth understanding of how these

484   communities change over time. In bacterial communities, succession and community turnover

485   occurred rapidly and was initiated by aerobic, heterotrophic bacteria that form endospores and

486   produce antibiotics. Consistent with previous studies, these genera belong to the phyla

487   Acidobacteria, Actinobacteria, and Firmicutes (Enright et al., 2021; Whitman et al., 2019). Like

488   plant successional patterns (Capitanio & Carcaillet, 2008; Egler, 1954), early successional stages

489   were characterized by high bacterial diversity and a lack of dominance, mimicking the

490   distributions observed in unburned communities. Previous studies suggest that in complex

491 resource environments, niche complementarity becomes more important than competition

492 because diverse communities can better exploit resources (Eisenhauer et al., 2013). Our results

493 support this idea, as the dominant taxa in our study have been previously shown to use different

494 forms and types of resources. For example, *Paenibacillu*s can fix nitrogen (Monciardini et al.,

495 2003; Slepecky & Hemphill, 2006), *Bacillus* and *Conexibacter* can reduce nitrogen, and *Bacillus*

496 can further solubilize phosphate (J. et al., 2001; Kalayu, 2019), suggesting that niche partitioning

497 favors positive interactions between bacteria in the early successional stages (<25 days).

498 However, as succession progressed, functional redundancy replaced niche complementary as

499 recognized by the bacteria that dominated most successional stages (*Massilia, Paenibacillus,* and

500 *Noviherbaspirillum).* All three genera have been shown to have multiple functional roles,

501 including phosphorus solubilization (*Paenibacillus, Massilia*), nitrogen fixation (*Paenibacillus*),

502 and reduction (*Massilia, Paenibacillus*), and are putative polycyclic aromatic hydrocarbon

503 degraders, a component of pyrogenic organic matter (*Noviherbaspirillium, Massilia;* (Bailey et

504 al., 2014; Baldani et al., 2014; Grady et al., 2016; Gu et al., 2016; Wan et al., 2020; Woolet &

505 Whitman, 2020). The diverse functional potential of the dominant taxa may allow these bacteria

506 to survive in a changing environment. Additionally, *Massilia* is known to be a dominant

507 rhizospheric bacteria (Li et al., 2014), capable of colonizing the roots of various plants (Ofek et

508 al., 2012) and of forming associations with arbuscular fungi (Iffis et al., 2014). This association

509 can allow for the proliferation of *Massilia* while increasing the formation of mycorrhizal roots

510 (Toljander et al., 2005). These results suggest that *Massilia* and *Paenibacillus* (arbuscular

511 associates) may be well-linked to the secondary succession of chaparral vegetation.

512

513 ***4.3 Pyrophilous fungi dominate the burned communities and drive succession***

514   Surprisingly, we found that pyrophilous fungi that dominate burned Pinaceae forests also

515   dominated California chaparral. While our experiment was not designed to understand the

516   mechanisms controlling pyrophilous microbial dominance, it is clear pyrophilous microbes are

517   not biome-specific. Instead, these fungi may be activated by temperature thresholds since this

518   fire burned at high severity with ash depths up to 12cm, similar to fires in Pinaceae forests.

519   Specifically, we found that our communities were dominated by Ascomycota in the genera

520   *Pyronema, Penicillium*, and *Aspergillus,* which have been shown to dominate post-fire boreal

521   spruce forests (Whitman et al., 2019), montane pine forests (Bruns et al., 2020), and

522   Mediterranean ecosystems (Fujimura et al., 2005; Livne-Luzon et al., 2021; Whitman et al.,

523   2019)*.* Both *Pyronema (P. omphalodes)* and *Aspergillus* (*A. fumigatus*) are known as fire-

524   responsive species in California chaparral (Dunn et al., 1982). We also identify additional

525   *Pyronema* and *Aspergillus* species that respond positively to wildfire, including *P. domesticum*,

526   *A. udagawae*, and *A. elsenburgensis.* These pyrophilous fungi are adapted to wildfire (Moore,

527   1962; Rhodes, 2006) and produce fire-resistant structures such as dormant spores, sclerotia, and

528   conidia (Smith et al., 2015; Warcup & Baker, 1963) which are heat activated (Bruns et al., 2020;

529   Gottlieb, 1950). The rapid and efficient germination of *Aspergillus* (in the section Fumigati)

530   induced by high temperatures (Rhodes, 2006) and its ability to utilize various carbon and

531   nitrogen sources, including ammonium and nitrate (Krappmann & Braus, 2005), may position

532   *Aspergillus* to rapidly dominate after chaparral fires. Furthermore, *Pyronema domesticum*, a

533   relatively well-studied pyrophilous fungus, can mineralize PyOM, a dominant substrate in

534   burned environments (Fischer et al., 2021), thus potentially allowing it to take advantage of the

535   abundant food source in this system. Together, these results suggest that dominant pyrophilous

536   fungi are more widespread than expected and that their response to fire might be due to fire

537   adaptations and requirements.

538   Early fungal succession stages were dominated by surviving ectomycorrhizal

539   Basidiomycetes, *Mallocybe, Cortinarius,* and *Inocybe* that had been previously found in burned

540   pine forests (Gassibe et al., 2011; Glassman et al., 2016; Owen et al., 2019; Pulido-Chavez et al.,

541   2021) and early Mediterranean successional time points (Gassibe et al., 2011; Hernández-

542   Rodríguez et al., 2013). However, fast-growing saprobic fungi in the genera *Pyronema,*

543   *Penicillium*, and *Aspergillus* quickly dominated all successional time points, beginning at 25

544   days post-fire, consistent with pyrocosm studies on *Pyronema* (Bruns et al., 2020). Although it is

545   possible that the EMF signal detected could be due to relic DNA, high UV conditions, such as

546   those in post-fire systems (Neary et al., 1999), rapidly degrade relic DNA (Torti et al., 2015),

547   suggesting that these EMF survived the fire and the death of their host for up to 67 days, as in the

548   case of *Inocybe*. These ectomycorrhizal fungi could have survived by displaying specificity for

549   photosynthates, current vs. stored (Gray & Kernaghan, 2020; Pena et al., 2010), an aspect of

550   exploration type. Whereas long/medium exploration types, *Cortinarius,* require more carbon for

551   maintenance than short-contact types such as *Inocybe* (Agerer, 2001; Koide et al., 2014). Thus,

552   we speculate that early EMF could have survived on their hosts' stored photosynthates. However,

553   not all EMF hosts died; thus, the EMF that survived the fire could have survived on the lower

554   resources provided by these resprouters.

555   Successional theory states that early successional stages are dominated by fast-growing

556   species that quickly dominate the open space (Kinzig & Pacala, 2013). Our results suggest that

557   this theory applies to fungal succession. The fungal community was dominated by fast-growing,

558   asexual thermotolerant fungi, *Penicillium*, *Aspergillus,* and *Pyronema* (Dix & Webster, 1995;

559   McGee et al., 2006). Asexual fungi can readily reproduce without needing a comparable mate

560   (Crow, 1992), allowing rapid colonization of the open niche. Although stress selection is

561   suggested to dominate sexual reproduction (Grishkan et al., 2003), our results suggest that in

562   chaparral, a fire-adapted ecosystem, stress adaptations such as the melanized conidia and thick

563   cell walls of *Aspergillus* and *Penicillium* (Cordero & Casadevall, 2017; Lagashetti et al., 2019),

564   and the formation of dormant spores or conidia might be characteristic of the historical fire

565   regime of the system, thus allowing asexual fungi to rapidly colonize and dominate all

566   successional time points during the first post-fire year. Lastly, we noted the emergence of fungal

567   decomposers, *Coprinellus* and *Tephrocybe,* at later successional stages, supporting previous

568   research (McMullan-Fisher et al., 2011). The onset of fruiting body development correlates with

569   soil nutritional exhaustion (Kües & Liu, 2000). In our system, phosphate was significantly lower

570   in the burned sites (data not shown), thus potentially explaining the fruiting of *Coprinellus* at

571   later successional stages. Moreover, in support of recent studies in pine forests (Carey et al.,

572   2020; Enright et al., 2021; Pulido-Chavez et al., 2021), we found *Geminibasidium* in our burned

573   soils. *Geminibasidium* is a recently described thermotolerant saprobe (H. D. T. Nguyen et al.,

574   2013) that was not present in the unburned sites but dominated early successional stages. Thus

575   we suggest that *Geminibasidium* is underrepresented pyrophilous fungi.

576

577

578   **5 Conclusion**

579   We present the first fine-scale record of the temporal succession of bacterial and fungal

580   communities in a wildfire-affected chaparral ecosystem in southern California. We found that the

581   same pyrophilous bacteria and fungi that respond to fires in temperate pine forests and Spanish

582   drylands also dominate in California chaparral, suggesting that post-fire microbes are heat

583   activated and rapidly exploit post-fire niches. Our results demonstrate rapid bacterial and fungal

584   community turnover and succession initiated as soon as 25 days post-fire for fungi and 34 days

585   for bacteria. These results suggest that surviving bacteria and fungi control the initial

586   successional dynamics of the ecosystem. Additionally, post-fire dominant bacteria and fungi in

587   wildfire-adapted systems are fast-growing, which could have developed mechanisms to

588   efficiently utilize post-fire resources, resulting in niche exclusion and dominance in recently

589   burned ecosystems, presenting similar successional patterns as those presented in successional

590   theory. Moreover, the longevity of plant-associated microbes in the burned environment,

591   including EMF and the dominance of the bacteria *Massilia,* suggests that these microbes could

592   potentially contribute to post-fire restoration management. We conclude although wildfire leads

593   to drastic reductions in species richness, biomass, and community composition, post-fire bacteria

594   and fungi experience rapid successional changes that align with plant successional theory.

595

605

Conflict of interest

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

608   objectivity.
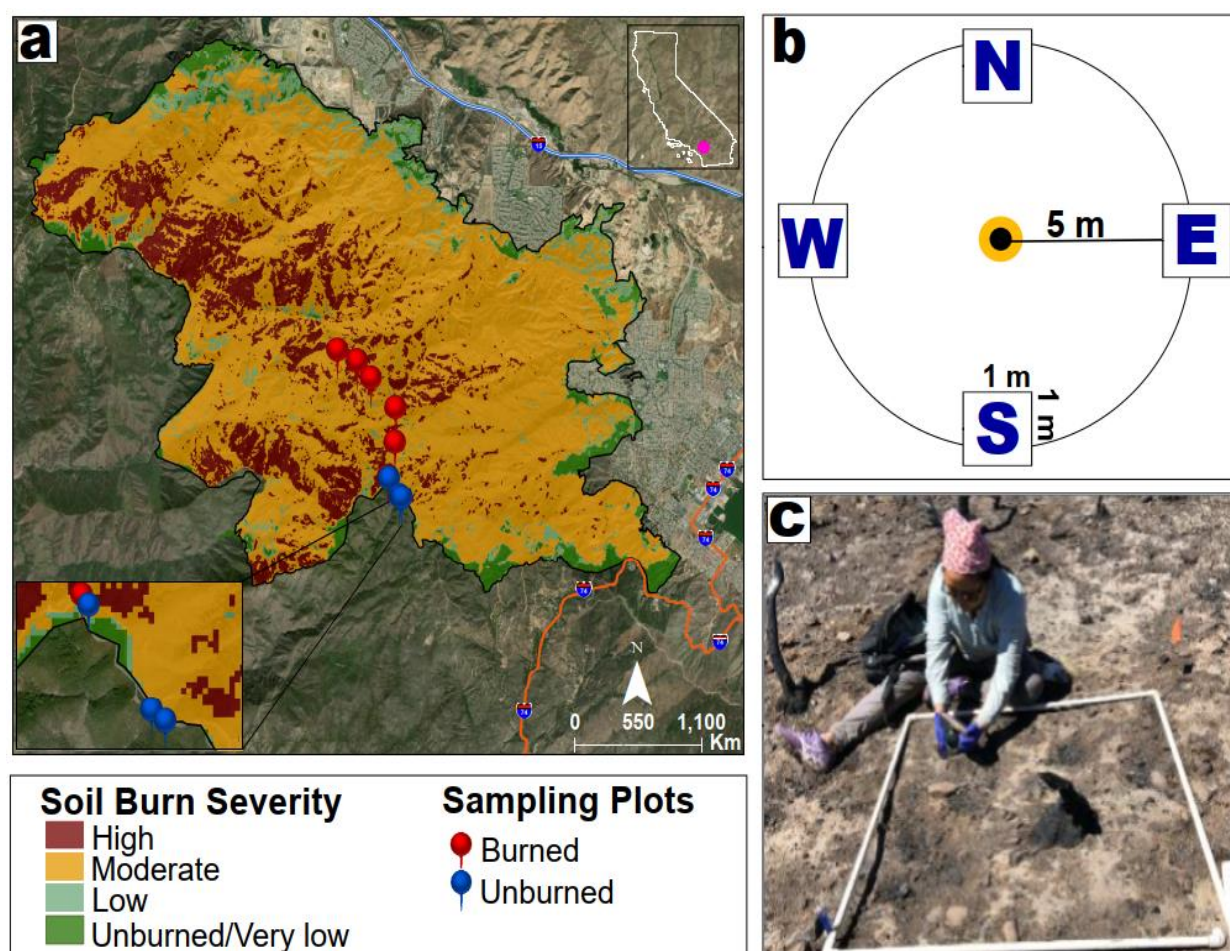
Figure 1. A) Location of the study area and plots(6 burned; 3 unburned) within the Holy Fire burn scar in the Cleveland National Forest in Southern California. Soil burn severity is based on the BAER classifications. B) Experimental design of each of the 9 plots and four $1m^2$ subplots placed in each cardinal direction. C) Collection of the top 10 cm of soil with a releasable bulb planter within the $1 \ m^2$ subplots at 17 days post-fire.
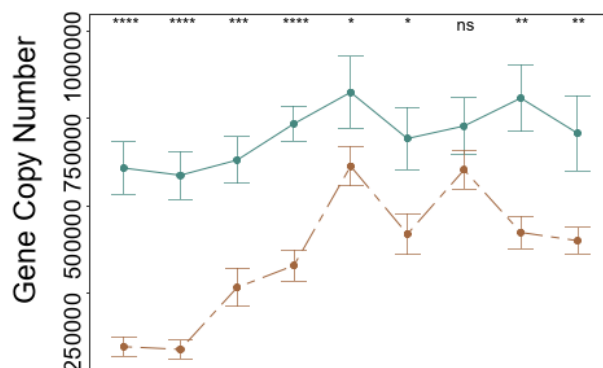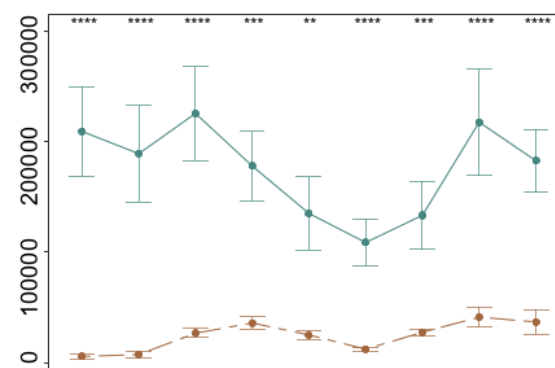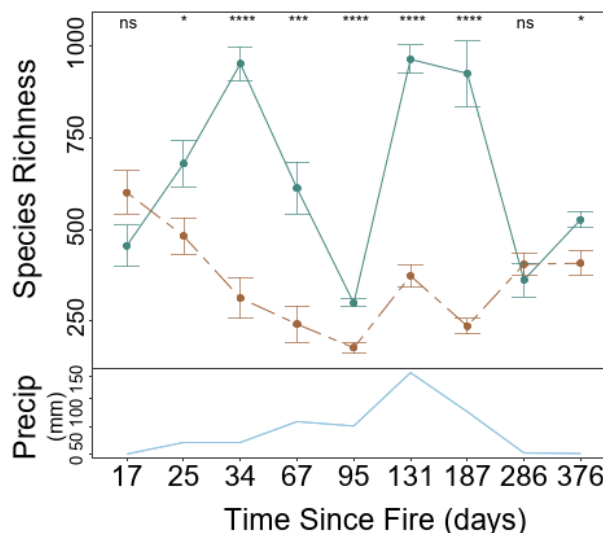
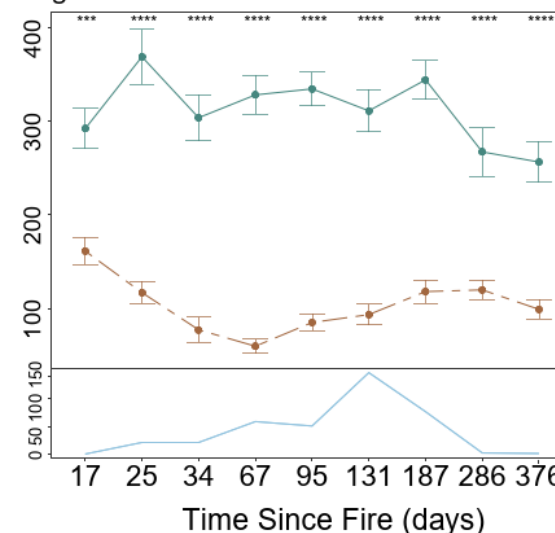**Figure 2.** Change in mean biomass A) archaea/bacteria and B) Fungi and change in mean richness for C) archaea/bacteria and D) fungi in relation to time since fire in days between burned and unburned plots. Precipitation is based on total monthly precipitation (mm) ranging from 0-148mm. The significance of each treatment (burned and unburned) per time point is denoted with an asterisk.
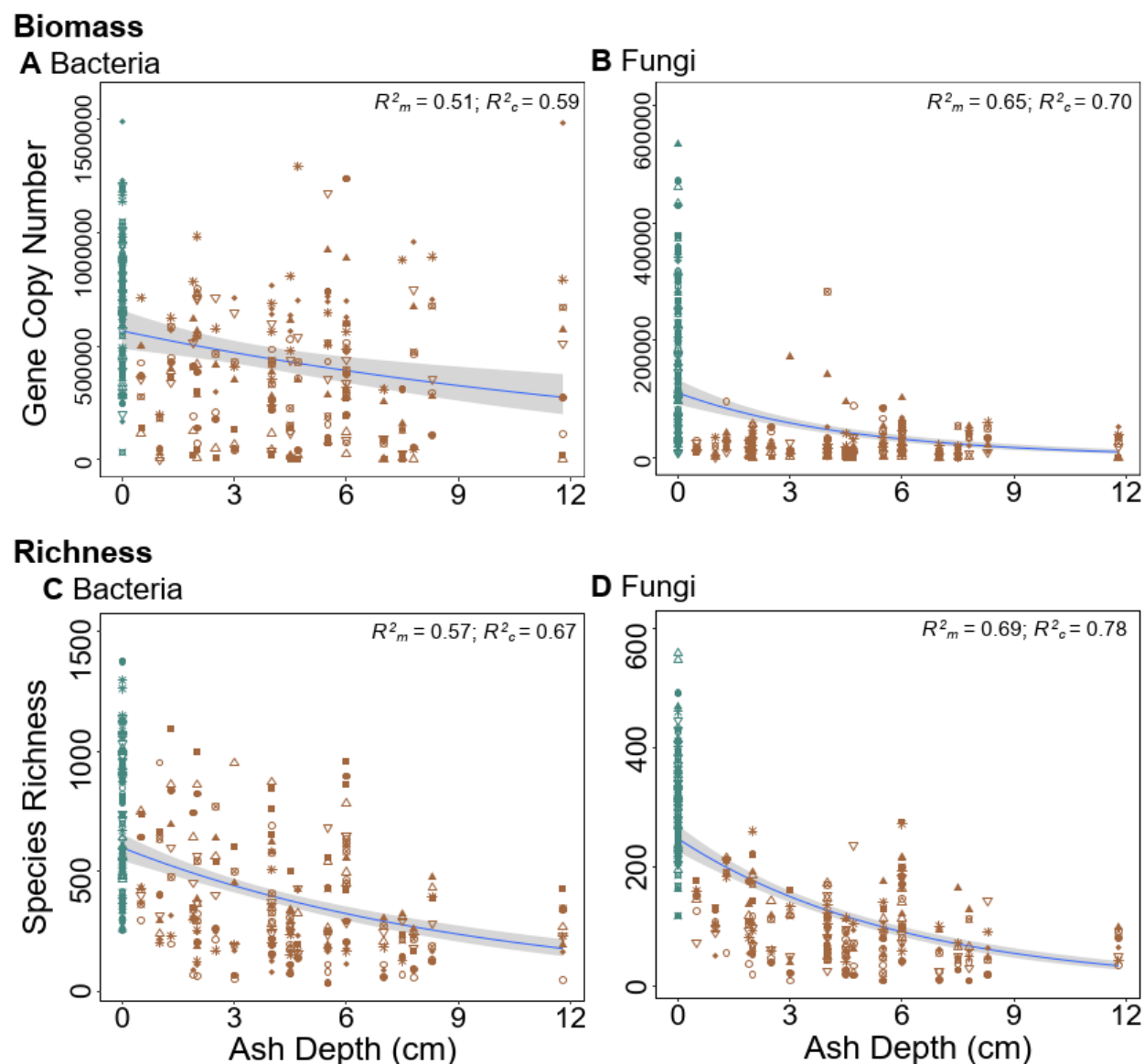
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Figure 3. Change in A) archaeal/bacterial and B) fungal biomass and C) archaeal/bacterial and D) fungal species richness in relation to initial ash depth and its interaction time since fire. The significance of biomass and species richness is based on a negative binomial regression.
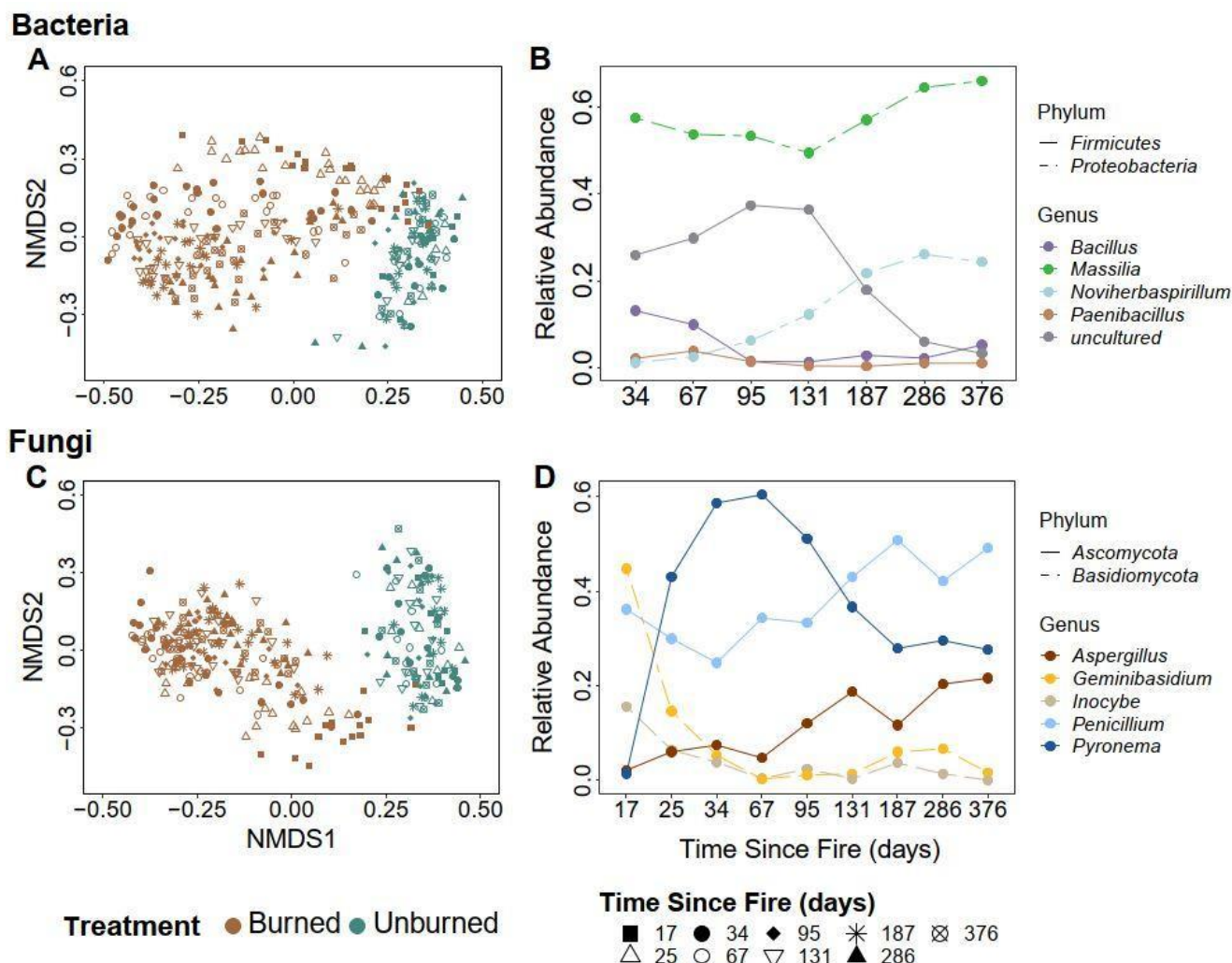
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Figure 4. NMDS plot of A) bacterial and C) fungal community composition with colors denoting treatment and shape indicating time since fire (days). The NMDS is based on 3-dimensions and has a stress value of 0.11 for bacteria and 0.12 for fungi. The shift in the dominant B) bacterial and D) fungal genera over time, the color denoting the genera and line shape denoting the phyla.
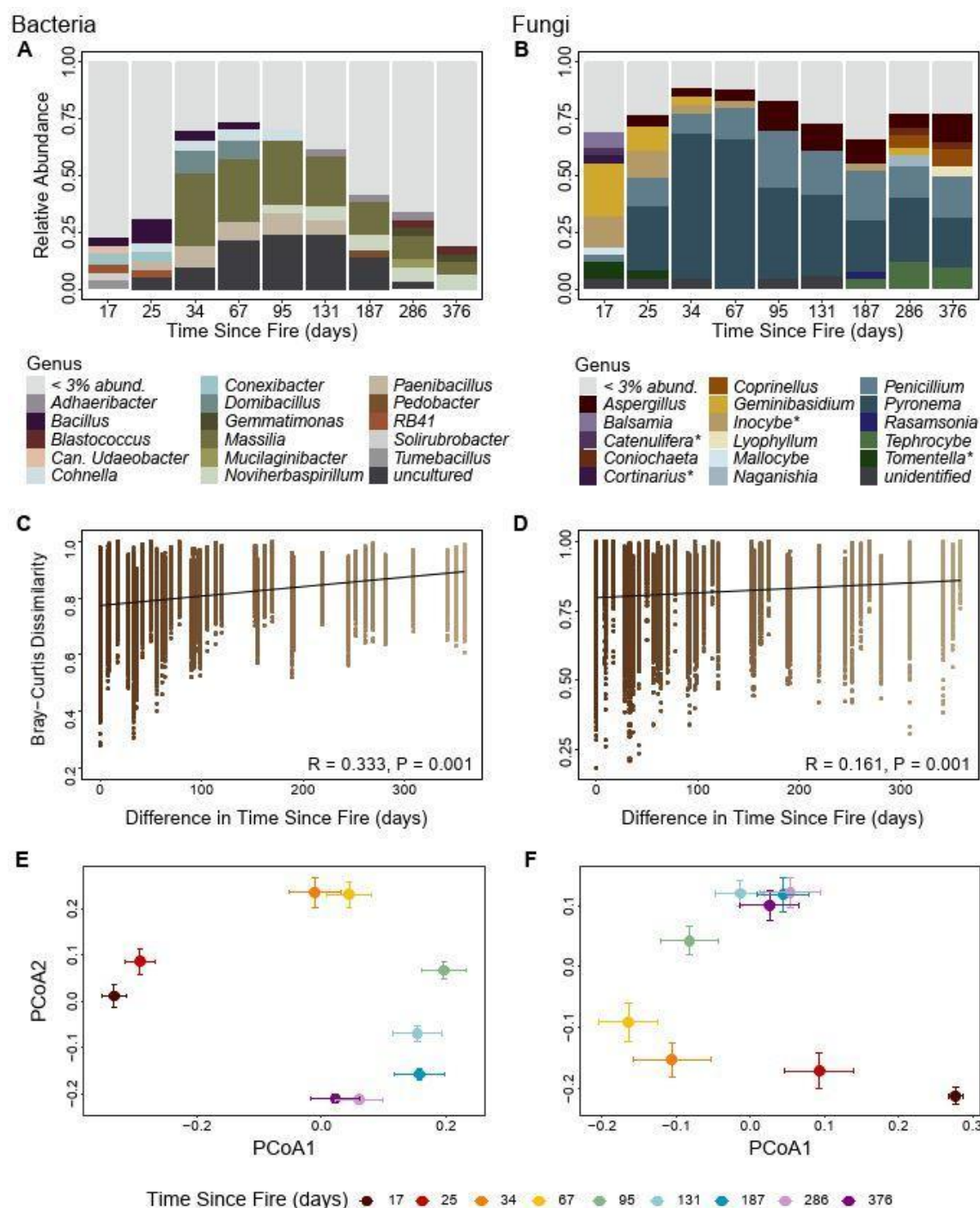
Figure 5. Burned communities relative abundance at the genus level for A) archaea/bacteria and B) fungi based on taxa more than 3% sequence abundant at each time point. An asterisk next to the genera denotes the ectomycorrhizal fungal guild. The succession of the burned communities of C) archaea/bacteria and D) fungi is based on Mantel testing of the correlation between Bray-Curtis community dissimilarity and Euclidean temporal distances. Turnover of E) archaea/bacterial and F) fungal burned community composition per Bray-Curtis community dissimilarity between sampling time points (days) represented as the mean and standard error. Note time points farther apart indicate a community turnover, and closer together represent a lack of change for the given time periods. In general, bacteria experience turnover starting at 25 days post-fire and cease at 286 days post-fire, and fungi from 25 days post-fire up to 131 days post-fire where turnover ceased.
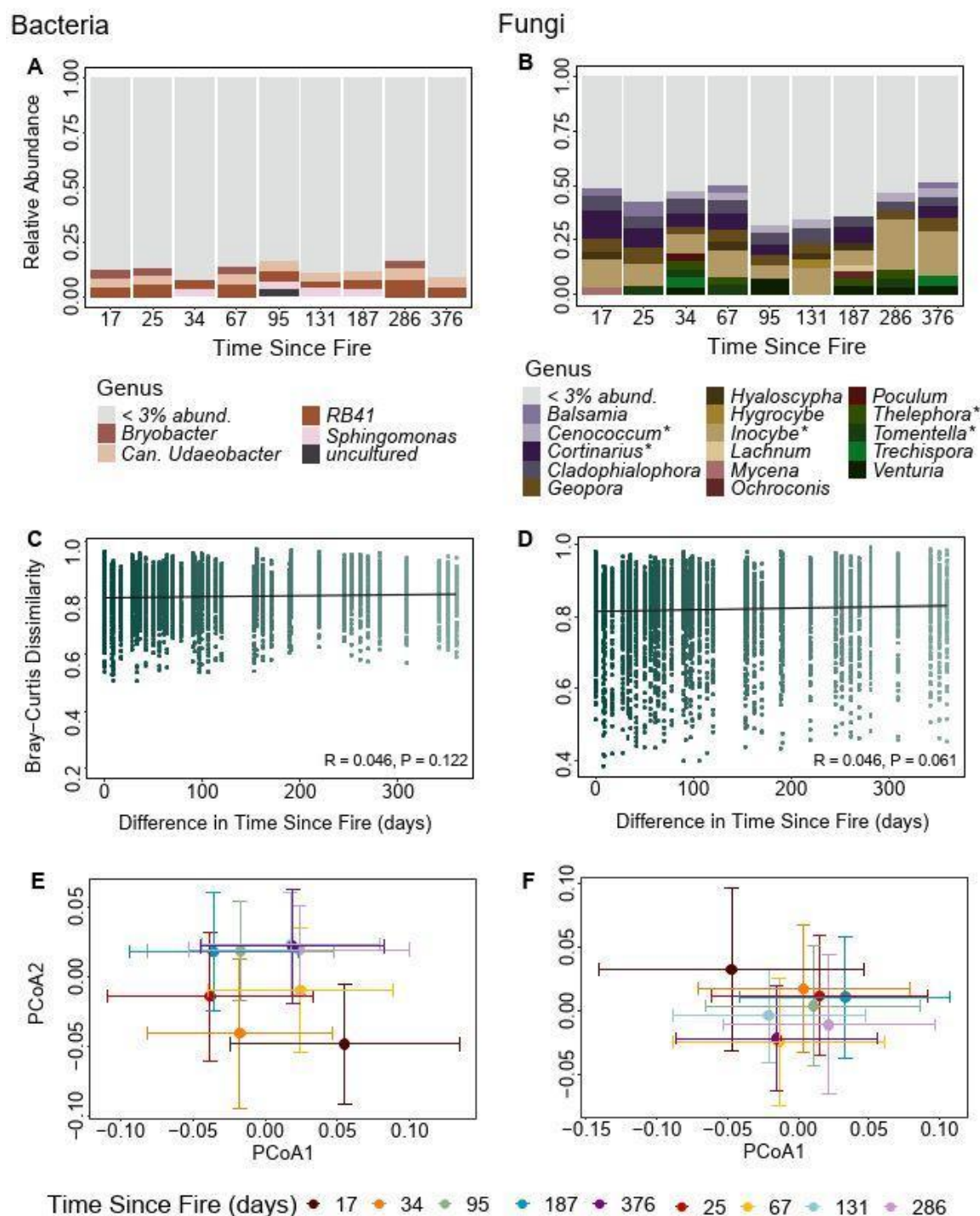
Figure 6. Unburned communities relative abundance at the genus level for A) archaea/bacteria and B) fungi based on taxa more than 3% sequence abundant at each time point. An asterisk next to general denotes ectomycorrhizal fungal guild. The succession of the unburned communities of C) archaea/bacteria and D) fungi is based on Mantel testing of the correlation between Bray-Curtis community dissimilarity and Euclidean temporal distances. Turnover of E) archaea/bacterial and F) fungal unburned community composition per Bray-Curtis community dissimilarity between sampling time points (days) represented as the mean and standard error. Note the lack of community turnover as represented by the overlapping time points.

679 **Reference**

680 Agerer, R. (2001). Exploration types of ectomycorrhizae. *Mycorrhiza*, *11*(2), 107–114.
681   https://doi.org/10.1007/s005720100108
682 Allen, M. F., & Kitajima, K. (2013). In situ high-frequency observations of mycorrhizas. *New*
683   *Phytologist*, *200*(1), 222–228. https://doi.org/10.1111/nph.12363
684 Averill, C., & Hawkes, C. V. (2016). Ectomycorrhizal fungi slow soil carbon cycling. *Ecology*
685   *Letters*, *19*(8), 937–947. https://doi.org/10.1111/ele.12631
686 Bailey, A. C., Kellom, M., Poret-Peterson, A. T., Noonan, K., Hartnett, H. E., & Raymond, J.
687   (2014). Draft Genome Sequence of Massilia sp. Strain BSC265, Isolated from Biological
688   Soil Crust of Moab, Utah. *Genome Announcements*, *2*(6), e01199-14, 2/6/e01199-14.
689   https://doi.org/10.1128/genomeA.01199-14
690 Baldani, J. I., Rouws, L., Cruz, L. M., Olivares, F. L., Schmid, M., & Hartmann, A. (2014). The
691   Family Oxalobacteraceae. In E. Rosenberg, E. F. DeLong, S. Lory, E. Stackebrandt, & F.
692   Thompson (Eds.), *The Prokaryotes* (pp. 919–974). Springer Berlin Heidelberg.
693   https://doi.org/10.1007/978-3-642-30197-1_291
694 Baldrian, P. (2016). Forest microbiome: Diversity, complexity and dynamics. *FEMS*
695   *Microbiology Reviews*, fuw040. https://doi.org/10.1093/femsre/fuw040
696 Barnard, R. L., Osborne, C. A., & Firestone, M. K. (2013). Responses of soil bacterial and fungal
697   communities to extreme desiccation and rewetting. *The ISME Journal*, *7*(11), 2229–2241.
698   https://doi.org/10.1038/ismej.2013.104
699 Barro, S. C., & Conard, S. G. (1991). Fire effects on California chaparral systems: An overview.
700   *Environment International*, *17*(2–3), 135–149. https://doi.org/10.1016/0160-
701   4120(91)90096-9
702 Barton, K. (2020). *MuMIn: Multi-Model Inference* (R package version 1.43.17.) [Computer
703   software]. https://CRAN.R-project.org/package=MuMIn
704 Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity.
705   *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-
706   8238.2009.00490.x
707 Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology*
708   *and Evolution*, *9*, 191–193.
709 Bliss, C. I. (1953). *Fitting the negative binomial distribution to biological data (with "Note on*
710   *the efficient fitting of the negative binomial" by R. A. Fisher), Biometrics, 9,* (9th ed.).
711   Biometrics.
712 Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A.,
713   Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger,
714   K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A.
715   M., Chase, J., … Caporaso, J. G. (2019). Reproducible, interactive, scalable and
716   extensible microbiome data science using QIIME 2. *Nature Biotechnology*, *37*(8), 852–
717   857. https://doi.org/10.1038/s41587-019-0209-9
718 Bruns, T. D., Chung, J. A., Carver, A. A., & Glassman, S. I. (2020). A simple pyrocosm for
719   studying soil microbial response to fire reveals a rapid, massive response by Pyronema
720   species. *PLOS ONE*, *15*(3), e0222691. https://doi.org/10.1371/journal.pone.0222691
721 Cairney, J. W. G., & Bastias, B. A. (2007). Influences of fire on forest soil fungal
722   communitiesThis article is one of a selection of papers published in the Special Forum on
723   Towards Sustainable Forestry — The Living Soil: Soil Biodiversity and Ecosystem

Function. *Canadian Journal of Forest Research*, *37*(2), 207–215. https://doi.org/10.1139/x06-190

Callahan, B. J., McMurdie, P. J., & Holmes, S. P. (2017). Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *The ISME Journal*, *11*(12), 2639–2643. https://doi.org/10.1038/ismej.2017.119

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6891), 844–848. https://doi.org/10.1038/nature00812

Capitanio, R., & Carcaillet, C. (2008). Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. *Forest Ecology and Management*, *255*(3), 431–439. https://doi.org/10.1016/j.foreco.2007.09.010

Caporaso, J. G., Lauber, C. L., Walters, W. A., Berg-Lyons, D., Lozupone, C. A., Turnbaugh, P. J., Fierer, N., & Knight, R. (2011). Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *Proceedings of the National Academy of Sciences*, *108*(Supplement_1), 4516–4522. https://doi.org/10.1073/pnas.1000080107

Carey, C. J., Glassman, S. I., Bruns, T. D., Aronson, E. L., & Hart, S. C. (2020). Soil microbial communities associated with giant sequoia: How does the world's largest tree affect some of the world's smallest organisms? *Ecology and Evolution*, *10*(13), 6593–6609. https://doi.org/10.1002/ece3.6392

Certini, G., Moya, D., Lucas-Borja, M. E., & Mastrolonardo, G. (2021). The impact of fire on soil-dwelling biota: A review. *Forest Ecology and Management*, *488*, 118989. https://doi.org/10.1016/j.foreco.2021.118989

Collins, S. L. (1990). Patterns of Community Structure During Succession in Tallgrass Prairie. *Bulletin of the Torrey Botanical Club*, *117*(4), 397–408. https://doi.org/10.2307/2996837

Collins, S. L., Micheli, F., & Hartt, L. (2000). A method to determine rates and patterns of variability in ecological communities. *Oikos*, *91*(2), 285–293. https://doi.org/10.1034/j.1600-0706.2000.910209.x

Cordero, R. J., & Casadevall, A. (2017). Functions of fungal melanin beyond virulence. *Fungal Biology Reviews*, *31*(2), 99–112. https://doi.org/10.1016/j.fbr.2016.12.003

Crow, J. F. (1992). An advantage of sexual reproduction in a rapidly changing environment. *The Journal of Heredity*, *83*(3), 169–173. https://doi.org/10.1093/oxfordjournals.jhered.a111187

Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D. K., Lebrija-Trejos, E., Leiva, J. A., Odén, P.-C., Powers, J. S., Rico-Gray, V., Tigabu, M., & Healey, J. R. (2016). Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, *125*(10), 1386–1397. https://doi.org/10.1111/oik.03229

Dix, N. J., & Webster, J. (1995). *Fungal Ecology*. Chapman & Hall.

Donato, D. C., Campbell, J. L., & Franklin, J. F. (2012). Multiple successional pathways and precocity in forest development: Can some forests be born complex? *Journal of Vegetation Science*, *23*(3), 576–584. https://doi.org/10.1111/j.1654-1103.2011.01362.x

Dooley, S. R., & Treseder, K. K. (2012). The effect of fire on microbial biomass: A meta-analysis of field studies. *Biogeochemistry*, *109*(1/3), 49–61.

Dove, N. C., & Hart, S. C. (2017). Fire Reduces Fungal Species Richness and In Situ Mycorrhizal Colonization: A Meta-Analysis. *Fire Ecology*, *13*(2), 37–65. https://doi.org/10.4996/fireecology.130237746

771   Dunn, P. H., Wells, W. G. I., Dickey, J., & Wohlgemuth, M. (1982). *Role of Fungi in Postfire*
772   *Stabilization of Chaparral Ash Beds* (PSW-58, pp. 378–381) [Gen. Tech. Rep]. Pacific
773   Southwest Forest and Range Experiment Station, Forest Service, U.S.U.S. Department of
774   Agriculture.
775   Egler, F. E. (1954). Vegetation science concepts I. Initial floristic composition, a factor in old-
776   field vegetation development with 2 figs. *Vegetatio*, *4*(6), 412–417.
777   https://doi.org/10.1007/BF00275587
778   Eisenhauer, N., Schulz, W., Scheu, S., & Jousset, A. (2013). Niche dimensionality links
779   biodiversity and invasibility of microbial communities. *Functional Ecology*, *27*(1), 282–
780   288. https://doi.org/10.1111/j.1365-2435.2012.02060.x
781   Enright, D. J., Frangioso, K. M., Isobe, K., Rizzo, D. M., & Glassman, S. I. (2021). Mega-fire in
782   Redwood Tanoak Forest Reduces Bacterial and Fungal Richness and Selects for
783   Pyrophilous Taxa and Traits that are Phylogenetically Conserved. *BioRxiv*,
784   2021.06.30.450634. https://doi.org/10.1101/2021.06.30.450634
785   Evans, S. E., & Wallenstein, M. D. (2012). Soil microbial community response to drying and
786   rewetting stress: Does historical precipitation regime matter? *Biogeochemistry*, *109*(1/3),
787   101–116.
788   Fierer, N., Jackson, J. A., Vilgalys, R., & Jackson, R. B. (2005). Assessment of Soil Microbial
789   Community Structure by Use of Taxon-Specific Quantitative PCR Assays. *Applied and*
790   *Environmental Microbiology*, *71*(7), 4117–4120.
791   https://doi.org/10.1128/AEM.71.7.4117-4120.2005
792   Fischer, M. S., Stark, F. G., Berry, T. D., Zeba, N., Whitman, T., & Traxler, M. F. (2021).
793   *Pyrolyzed substrates induce aromatic compound metabolism in the post-fire*
794   *fungus,Pyronema domesticum* [Preprint]. Microbiology.
795   https://doi.org/10.1101/2021.03.15.435558
796   Fujimura, K. E., Smith, J. E., Horton, T. R., Weber, N. S., & Spatafora, J. W. (2005). Pezizalean
797   mycorrhizas and sporocarps in ponderosa pine (Pinus ponderosa) after prescribed fires in
798   eastern Oregon, USA. *Mycorrhiza*, *15*(2), 79–86. https://doi.org/10.1007/s00572-004-
799   0303-8
800   Gao, C., Montoya, L., Xu, L., Madera, M., Hollingsworth, J., Purdom, E., Singan, V., Vogel, J.,
801   Hutmacher, R. B., Dahlberg, J. A., Coleman-Derr, D., Lemaux, P. G., & Taylor, J. W.
802   (2020). Fungal community assembly in drought-stressed sorghum shows stochasticity,
803   selection, and universal ecological dynamics. *Nature Communications*, *11*(1), 34.
804   https://doi.org/10.1038/s41467-019-13913-9
805   Gassibe, P. V., Fabero, R. F., Hernández-Rodríguez, M., Oria-de-Rueda, J. A., & Martín-Pinto,
806   P. (2011). Fungal community succession following wildfire in a Mediterranean
807   vegetation type dominated by Pinus pinaster in Northwest Spain. *Forest Ecology and*
808   *Management*, *262*(4), 655–662. https://doi.org/10.1016/j.foreco.2011.04.036
809   Glassman, S. I., Levine, C. R., DiRocco, A. M., Battles, J. J., & Bruns, T. D. (2016).
810   Ectomycorrhizal fungal spore bank recovery after a severe forest fire: Some like it hot.
811   *The ISME Journal*, *10*(5), 1228–1239. https://doi.org/10.1038/ismej.2015.182
812   Glassman, S. I., Randolph, J. W., Saroa, S. S., Capocchi, J. K., Walters, K. E., Pulido-Chavez,
813   M. F., & Larios, L. (2021). *Prescribed versus wildfire impacts on exotic plants and soil*
814   *microbes in California grasslands* [Preprint]. Ecology.
815   https://doi.org/10.1101/2021.09.22.461426
816   Gottlieb, D. (1950). The physiology of spore germination in fungi. *The Botanical Review*, *16*(5),
817   229–257. https://doi.org/10.1007/BF02873609

818   Grady, E. N., MacDonald, J., Liu, L., Richman, A., & Yuan, Z.-C. (2016). Current knowledge
819   and perspectives of Paenibacillus: A review. *Microbial Cell Factories*, *15*(1), 203.
820   https://doi.org/10.1186/s12934-016-0603-7

821   Gray, L., & Kernaghan, G. (2020). Fungal Succession During the Decomposition of
822   Ectomycorrhizal Fine Roots. *Microbial Ecology*, *79*(2), 271–284.
823   https://doi.org/10.1007/s00248-019-01418-3

824   Grishkan, I., Korol, A. B., Nevo, E., & Wasser, S. P. (2003). Ecological stress and sex evolution
825   in soil microfungi. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1510),
826   13–18. https://doi.org/10.1098/rspb.2002.2194

827   Gu, H., Lou, J., Wang, H., Yang, Y., Wu, L., Wu, J., & Xu, J. (2016). Biodegradation,
828   Biosorption of Phenanthrene and Its Trans-Membrane Transport by Massilia sp. WF1 and
829   Phanerochaete chrysosporium. *Frontiers in Microbiology*, *7*.
830   https://doi.org/10.3389/fmicb.2016.00038

831   Guhr, A., & Kircher, S. (2020). Drought-Induced Stress Priming in Two Distinct Filamentous
832   Saprotrophic Fungi. *Microbial Ecology*, *80*(1), 27–33. https://doi.org/10.1007/s00248-
833   019-01481-w

834   Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F. B., Ripplinger, J.,
835   Slaughter, P., Gries, C., & Collins, S. L. (2016). codyn: An r package of community
836   dynamics metrics. *Methods in Ecology and Evolution*, *7*(10), 1146–1151.
837   https://doi.org/10.1111/2041-210X.12569

838   Hanes, T. L. (1971). *Succession after Fire in the Chaparral of Southern California*. *41*(1), 27–
839   52. https://doi.org/doi:10.2307/1942434

840   Hart, S. C., DeLuca, T. H., Newman, G. S., MacKenzie, M. D., & Boyle, S. I. (2005). Post-fire
841   vegetative dynamics as drivers of microbial community structure and function in forest
842   soils. *Forest Ecology and Management*, *220*(1–3), 166–184.
843   https://doi.org/10.1016/j.foreco.2005.08.012

844   Hernández-Rodríguez, M., Oria-de-Rueda, J. A., & Martín-Pinto, P. (2013). Post-fire fungal
845   succession in a Mediterranean ecosystem dominated by Cistus ladanifer L. *Forest
846   Ecology and Management*, *289*, 48–57. https://doi.org/10.1016/j.foreco.2012.10.009

847   Homyak, P. M., Sickman, J. O., Miller, A. E., Melack, J. M., Meixner, T., & Schimel, J. P.
848   (2014). Assessing Nitrogen-Saturation in a Seasonally Dry Chaparral Watershed:
849   Limitations of Traditional Indicators of N-Saturation. *Ecosystems*, *17*(7), 1286–1305.
850   https://doi.org/10.1007/s10021-014-9792-2

851   Iffis, B., St-Arnaud, M., & Hijri, M. (2014). Bacteria associated with arbuscular mycorrhizal
852   fungi within roots of plants growing in a soil highly contaminated with aliphatic and
853   aromatic petroleum hydrocarbons. *FEMS Microbiology Letters*, *358*(1), 44–54.
854   https://doi.org/10.1111/1574-6968.12533

855   J., E. de los M., A., M., & F., V. (2001). Metabolic profiles and aprE expression in anaerobic
856   cultures of Bacillus subtilis using nitrate as terminal electron acceptor. *Applied
857   Microbiology and Biotechnology*, *57*(3), 379–384.
858   https://doi.org/10.1007/s002530100749

859   Kalayu, G. (2019). Phosphate Solubilizing Microorganisms: Promising Approach as
860   Biofertilizers. *International Journal of Agronomy*, *2019*, 1–7.
861   https://doi.org/10.1155/2019/4917256

862   Kaur, N., Seuylemezian, A., Patil, P. P., Patil, P., Krishnamurti, S., Varelas, J., Smith, D. J.,
863   Mayilraj, S., & Vaishampayan, P. (2018). Paenibacillus xerothermodurans sp. Nov., an
864   extremely dry heat resistant spore forming bacterium isolated from the soil of Cape

865   Canaveral, Florida. *International Journal of Systematic and Evolutionary Microbiology*,
866   *68*(10), 3190–3196. https://doi.org/10.1099/ijsem.0.002967
867 Kindt, R., & Coe, R. (2005). *Tree diversity analysis. A manual and software for common*
868   *statistical methods for ecological and biodiversity studies*. World Agroforestry Centre
869   (ICRAF).
870 Kinzig, A. P., & Pacala, S. (2013). 9. Successional Biodiversity and Ecosystem Functioning. In
871   *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical*
872   *Extensions (MPB-33)* (pp. 175–212). Princeton University Press.
873   https://doi.org/10.1515/9781400847303.175
874 Koide, R. T., Fernandez, C., & Malcolm, G. (2014). Determining place and process: Functional
875   traits of ectomycorrhizal fungi that affect both community structure and ecosystem
876   function. *New Phytologist*, *201*(2), 433–439. https://doi.org/10.1111/nph.12538
877 Kõljalg, U., Larsson, K.-H., Abarenkov, K., Nilsson, R. H., Alexander, I. J., Eberhardt, U.,
878   Erland, S., Høiland, K., Kjøller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A. F. S.,
879   Tedersoo, L., & Vrålstad, T. (2005). UNITE: A database providing web-based methods
880   for the molecular identification of ectomycorrhizal fungi. *New Phytologist*, *166*(3), 1063–
881   1068. https://doi.org/10.1111/j.1469-8137.2005.01376.x
882 Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K., & Schloss, P. D. (2013).
883   Development of a Dual-Index Sequencing Strategy and Curation Pipeline for Analyzing
884   Amplicon Sequence Data on the MiSeq Illumina Sequencing Platform. *Applied and*
885   *Environmental Microbiology*, *79*(17), 5112–5120. https://doi.org/10.1128/AEM.01043-
886   13
887 Krappmann, S., & Braus, G. H. (2005). Nitrogen metabolism of *Aspergillus* and its role in
888   pathogenicity. *Medical Mycology*, *43*(s1), 31–40.
889   https://doi.org/10.1080/13693780400024271
890 Kües, U., & Liu, Y. (2000). Fruiting body production in basidiomycetes. *Applied Microbiology*
891   *and Biotechnology*, *54*(2), 141–152. https://doi.org/10.1007/s002530000396
892 Kummerow, J., Alexander, J. V., Neel, J. W., & Fishbeck, K. (1978). Symbiotic Nitrogen
893   Fixation in Ceanothus Roots. *American Journal of Botany*, *65*(1), 63–69.
894   https://doi.org/10.2307/2442555
895 Lagashetti, A. C., Dufossé, L., Singh, S. K., & Singh, P. N. (2019). Fungal Pigments and Their
896   Prospects in Different Industries. *Microorganisms*, *7*(12), 604.
897   https://doi.org/10.3390/microorganisms7120604
898 Li, X., Rui, J., Mao, Y., Yannarell, A., & Mackie, R. (2014). Dynamics of the bacterial
899   community structure in the rhizosphere of a maize cultivar. *Soil Biology and*
900   *Biochemistry*, *68*, 392–401. https://doi.org/10.1016/j.soilbio.2013.10.017
901 Liu, C. M., Kachur, S., Dwan, M. G., Abraham, A. G., Aziz, M., Hsueh, P.-R., Huang, Y.-T.,
902   Busch, J. D., Lamit, L. J., Gehring, C. A., Keim, P., & Price, L. B. (2012). FungiQuant: A
903   broad-coverage fungal quantitative real-time PCR assay. *BMC Microbiology*, *12*(1), 255.
904   https://doi.org/10.1186/1471-2180-12-255
905 Livne-Luzon, S., Shemesh, H., Osem, Y., Carmel, Y., Migael, H., Avidan, Y., Tsafrir, A.,
906   Glassman, S. I., Bruns, T. D., & Ovadia, O. (2021). High resilience of the mycorrhizal
907   community to prescribed seasonal burnings in eastern Mediterranean woodlands.
908   *Mycorrhiza*, *31*(2), 203–216. https://doi.org/10.1007/s00572-020-01010-5
909 Martin, M. (2011). *Cutadapt removes adapter sequences from high-throughput sequencing*
910   *reads*. https://journal.embnet.org/index.php/embnetjournal/article/view/200/458

911 McGee, P. A., Markovina, A.-L., Jeong, G. C. E., & Cooper, E. D. (2006). Trichocomaceae in
912   bark survive high temperatures and fire: Trichocomaceae in bark survive high
913   temperatures and fire. *FEMS Microbiology Ecology*, *56*(3), 365–371.
914   https://doi.org/10.1111/j.1574-6941.2006.00079.x
915 McMullan-Fisher, S. J. M., Tom W. May, Richard M. Robinson, Tina L. Bell, Teresa Lebel,
916   Pam Catcheside, & Alan York. (2011). *Fungi and fire in Australian ecosystems: A review*
917   *of current knowledge, management implications and future directions*. *59*, 70–90.
918 McMurdie, P. J., & Holmes, S. (2013). phyloseq: An R Package for Reproducible Interactive
919   Analysis and Graphics of Microbiome Census Data. *PLOS ONE*, *8*(4), e61217.
920   https://doi.org/10.1371/journal.pone.0061217
921 Monciardini, P., Cavaletti, L., Schumann, P., Rohde, M., & Donadio, S. (2003). Conexibacter
922   woesei gen. Nov., sp. Nov., a novel representative of a deep evolutionary line of descent
923   within the class Actinobacteria. *International Journal of Systematic and Evolutionary*
924   *Microbiology*, *53*(2), 569–576. https://doi.org/10.1099/ijs.0.02400-0
925 Moore, E. J. (1962). The Ontogeny of the Sclerotia of Pyronema Domesticum. *Mycologia*, *54*(3),
926   312–316. https://doi.org/10.1080/00275514.1962.12025004
927 Neary, D. G., Klopatek, C. C., DeBano, L. F., & Ffolliott, P. F. (1999). Fire effects on
928   belowground sustainability: A review and synthesis. *Forest Ecology and Management*,
929   *122*(1–2), 51–71. https://doi.org/10.1016/S0378-1127(99)00032-8
930 Nguyen, H. D. T., Nickerson, N. L., & Seifert, K. A. (2013). Basidioascus and Geminibasidium:
931   A new lineage of heat-resistant and xerotolerant basidiomycetes. *Mycologia*, *105*(5),
932   1231–1250. JSTOR.
933 Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S., &
934   Kennedy, P. G. (2016). FUNGuild: An open annotation tool for parsing fungal
935   community datasets by ecological guild. *Fungal Ecology*, *20*, 241–248.
936   https://doi.org/10.1016/j.funeco.2015.06.006
937 Ofek, M., Hadar, Y., & Minz, D. (2012). Ecology of Root Colonizing Massilia
938   (Oxalobacteraceae). *PLOS ONE*, *7*(7), e40117.
939   https://doi.org/10.1371/journal.pone.0040117
940 Oksanen, J., Blanchet, G. F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R.,
941   O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H.
942   (2018). *Vegan:Community Ecology Package-Version 2.5.2. Ordination Methods,*
943   *Diversity Analysis, and Other Functions for Community and Vegetation Ecologist*.
944 Owen, S. M., Patterson, A. M., Gehring, C. A., Sieg, C. H., Baggett, L. S., & Fulé, P. Z. (2019).
945   Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a
946   ponderosa pine forest. *Soil Biology and Biochemistry*, *139*, 107616.
947   https://doi.org/10.1016/j.soilbio.2019.107616
948 Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., & Ribbens, E. (1996).
949   Forest Models Defined by Field Measurements: Estimation, Error Analysis and
950   Dynamics. *Ecological Monographs*, *66*(1), 1–43. https://doi.org/10.2307/2963479
951 Pandolfi, J. M. (2008). Succession. In S. E. Jørgensen & B. D. Fath (Eds.), *Encyclopedia of*
952   *Ecology* (pp. 3416–3424). Academic Press. https://doi.org/10.1016/B978-008045405-
953   4.00547-4
954 Pena, R., Offermann, C., Simon, J., Naumann, P. S., Geßler, A., Holst, J., Dannenmann, M.,
955   Mayer, H., Kögel-Knabner, I., Rennenberg, H., & Polle, A. (2010). Girdling Affects
956   Ectomycorrhizal Fungal (EMF) Diversity and Reveals Functional Differences in EMF

957   Community Composition in a Beech Forest. *Applied and Environmental Microbiology*,
958   *76*(6), 1831–1841. https://doi.org/10.1128/AEM.01703-09

959 Pérez-Valera, E., Verdú, M., Navarro-Cano, J. A., & Goberna, M. (2018). Resilience to fire of
960   phylogenetic diversity across biological domains. *Molecular Ecology*, *27*(13), 2896–
961   2908. https://doi.org/10.1111/mec.14729

962 Pérez-Valera, E., Verdú, M., Navarro-Cano, J. A., & Goberna, M. (2020). Soil microbiome
963   drives the recovery of ecosystem functions after fire. *Soil Biology and Biochemistry*, *149*,
964   107948. https://doi.org/10.1016/j.soilbio.2020.107948

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

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

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

976 Pulido-Chavez, M. F., Alvarado, E. C., DeLuca, T. H., Edmonds, R. L., & Glassman, S. I.
977   (2021). High-severity wildfire reduces richness and alters composition of
978   ectomycorrhizal fungi in low-severity adapted ponderosa pine forests. *Forest Ecology*
979   *and Management*, *485*, 118923. https://doi.org/10.1016/j.foreco.2021.118923

980 Rhodes, J. C. (2006). *Aspergillus fumigatus*: Growth and virulence. *Medical Mycology*, *44*(s1),
981   77–81. https://doi.org/10.1080/13693780600779419

982 Riley, K. L., & Loehman, R. A. (2016). Mid-21st-century climate changes increase predicted fire
983   occurrence and fire season length, Northern Rocky Mountains, United States. *Ecosphere*,
984   *7*(11), e01543. https://doi.org/10.1002/ecs2.1543

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

988 Rousk, J., Brookes, P. C., & Bååth, E. (2010). Investigating the mechanisms for the opposing pH
989   relationships of fungal and bacterial growth in soil. *Soil Biology and Biochemistry*, *42*(6),
990   926–934. https://doi.org/10.1016/j.soilbio.2010.02.009

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

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

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

1000 Slepecky, R. A., & Hemphill, H. E. (2006). The Genus Bacillus—Nonmedical. In M. Dworkin,
1001   S. Falkow, E. Rosenberg, K.-H. Schleifer, & E. Stackebrandt (Eds.), *The Prokaryotes:*
1002   *Volume 4: Bacteria: Firmicutes, Cyanobacteria* (pp. 530–562). Springer US.
1003   https://doi.org/10.1007/0-387-30744-3_16

1004 Smith, M. E., Henkel, T. W., & Rollins, J. A. (2015). How many fungi make sclerotia? *Fungal*
1005   *Ecology*, *13*, 211–220. https://doi.org/10.1016/j.funeco.2014.08.010
1006 Taylor, D. L., Walters, W. A., Lennon, N. J., Bochicchio, J., Krohn, A., Caporaso, J. G., &
1007   Pennanen, T. (2016). Accurate Estimation of Fungal Diversity and Abundance through
1008   Improved Lineage-Specific Primers Optimized for Illumina Amplicon Sequencing.
1009   *Applied and Environmental Microbiology*, *82*(24), 7217–7226.
1010   https://doi.org/10.1128/AEM.02576-16
1011 Toljander, J. F., Artursson, V., Paul, L. R., Jansson, J. K., & Finlay, R. D. (2005). Attachment of
1012   di¡erent soil bacteria to arbuscular mycorrhizal fungal extraradical hyphae is determined
1013   by hyphal vitalityand fungal species. *FEMS Microbiol Lett*, 7.
1014 Torti, A., Lever, M. A., & Jørgensen, B. B. (2015). Origin, dynamics, and implications of
1015   extracellular DNA pools in marine sediments. *Marine Genomics*, *24*, 185–196.
1016   https://doi.org/10.1016/j.margen.2015.08.007
1017 Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors Influencing
1018   Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems*, *1*(6),
1019   511–523. https://doi.org/10.1007/s100219900047
1020 Van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R.,
1021   Boller, T., Wiemken, A., & Sanders, I. R. (1998). Mycorrhizal fungal diversity
1022   determines plant biodiversity, ecosystem variability and productivity. *Nature*, *396*(6706),
1023   69–72. https://doi.org/10.1038/23932
1024 Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (Fourth edition).
1025   Springer. https://www.stats.ox.ac.uk/pub/MASS4/.
1026 Wan, W., Qin, Y., Wu, H., Zuo, W., He, H., Tan, J., Wang, Y., & He, D. (2020). Isolation and
1027   Characterization of Phosphorus Solubilizing Bacteria With Multiple Phosphorus Sources
1028   Utilizing Capability and Their Potential for Lead Immobilization in Soil. *Frontiers in*
1029   *Microbiology*, *0*. https://doi.org/10.3389/fmicb.2020.00752
1030 Warcup, J. H., & Baker, K. F. (1963). Occurrence of Dormant Ascospores in Soil. *Nature*,
1031   *197*(4874), 1317–1318. https://doi.org/10.1038/1971317a0
1032 Whitman, T., Whitman, E., Woolet, J., Flannigan, M. D., Thompson, D. K., & Parisien, M.-A.
1033   (2019). Soil bacterial and fungal response to wildfires in the Canadian boreal forest
1034   across a burn severity gradient. *Soil Biology and Biochemistry*, *138*, 107571.
1035   https://doi.org/10.1016/j.soilbio.2019.107571
1036 Woolet, J., & Whitman, T. (2020). Pyrogenic organic matter effects on soil bacterial community
1037   composition. *Soil Biology and Biochemistry*, *141*, 107678.
1038   https://doi.org/10.1016/j.soilbio.2019.107678
1039 Xiang, X., Shi, Y., Yang, J., Kong, J., Lin, X., Zhang, H., Zeng, J., & Chu, H. (2014). Rapid
1040   recovery of soil bacterial communities after wildfire in a Chinese boreal forest. *Scientific*
1041   *Reports*, *4*. https://doi.org/10.1038/srep03829
1042 Yilmaz, P., Parfrey, L. W., Yarza, P., Gerken, J., Pruesse, E., Quast, C., Schweer, T., Peplies, J.,
1043   Ludwig, W., & Glöckner, F. O. (2014). The SILVA and "All-species Living Tree Project
1044   (LTP)" taxonomic frameworks. *Nucleic Acids Research*, *42*(D1), D643–D648.
1045   https://doi.org/10.1093/nar/gkt1209
1046