

Mega-Fire Effect on Pyrophilous Microbes

1 **Title:** Mega-fire in Redwood Tanoak Forest Reduces Bacterial and Fungal Richness and Selects
2 for Pyrophilous Taxa and Traits that are Phylogenetically Conserved

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4 **Running Title:** Mega-Fire Effect on Pyrophilous Microbes

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19

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24 **Abstract:**

25 Mega-fires of unprecedented size, intensity, and socio-economic impacts have surged
26 globally due to climate change, fire suppression, and development. Soil microbiomes are critical
27 for post-fire plant regeneration and nutrient cycling, yet how mega-fires impact the soil
28 microbiome remains unclear. We had a serendipitous opportunity to obtain pre- and post-fire
29 soils from the same sampling locations because the 2016 Soberanes Fire, a mega-fire burning
30 >500 Km², burned with high severity throughout several of our established redwood-tanoak
31 plots. This makes our study the first to examine microbial fire response in redwood-tanoak
32 forests. We re-sampled soils immediately post-fire from two burned plots and one unburned plot
33 to elucidate the effect of mega-fire on soil microbiomes. We used Illumina MiSeq sequencing of
34 16S and ITS1 to determine that both bacterial and fungal richness were reduced by 38-70% in
35 burned plots, with richness unchanged in the unburned plot. Fire altered composition by 27% for
36 bacteria and 24% for fungi, whereas the unburned plots experienced no change in fungal and
37 negligible change in bacterial composition. We observed several pyrophilous taxa previously
38 observed in Pinaceae forests, indicating that these microbes are likely general fire-responders
39 across forest types. Further, the pyrophilous taxa that positively responded to fire were
40 phylogenetically conserved, suggesting shared evolutionary traits. For bacteria, fire selected for
41 increased Firmicutes and Actinobacteria. For fungi, fire selected for the Ascomycota classes
42 Pezizomycetes and Eurotiomycetes and for a Basidiomycota class of heat-resistant
43 Geminibasidiomycete yeasts. We hypothesize that microbes share analogous fire response to
44 plants and propose a trait-based conceptual model of microbial response to fire that builds from
45 Grime's Competitor-Stress tolerator-Ruderal framework (C-S-R) and its recent applications to

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46 microbes. Using this framework and established literature on several microbial species, we
47 hypothesize some generalizable principals to predict which microbial taxa will respond to fire.

48

49 **Introduction**

50 The rise of the mega-fire is an anthropogenic phenomenon with unknown consequences
51 for soil microbes and ecosystem processes. In the past, most wildfires were low severity, high
52 frequency events (Archibald et al., 2013). These low-intensity naturally occurring wildfires
53 helped clear away dead brush, revitalize the soil with nutrient deposition from pyrolyzed
54 material, and assist some plants (such as serotinous pines) with their reproductive cycles (He &
55 Lamont, 2018; Keeley et al., 2011). However, rising global temperatures (Westerling et al.,
56 2006), elongated droughts (Mukherjee et al., 2018), and development at the wildland-urban
57 interface (Spyratos et al., 2007), have led to the rise of catastrophic mega-fires of unprecedented
58 size, intensity, and socio-economic impacts (Stephens et al., 2014). Whereas many
59 Mediterranean ecosystems and plants are adapted to fire and may indeed require fire to
60 reproduce (Keeley et al., 2011), whether plants or their associated soil microbiomes will survive
61 mega-fires remains unknown.

62 The soil microbiome is an important driver of plant diversity and productivity (Van der
63 Heijden et al., 2008), and soil biogeochemical cycling (Crowther et al., 2019). If soil
64 microbiomes do not survive mega-fires, then associated plants, especially those reliant on
65 symbiotic mycorrhizal fungi, may not regenerate (Collier & Bidartondo, 2009). Ectomycorrhizal
66 fungi (EMF) and arbuscular mycorrhizal fungi (AMF) are key partners with plant roots that
67 increase access to soil nutrients in exchange for photosynthetically derived carbon (Brundrett &
68 Tedersoo, 2018). Moreover, soil bacteria and fungi are primarily responsible for litter

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69 decomposition (Glassman et al., 2018), nutrient cycling (Crowther et al., 2019), and soil
70 aggregation (Lehmann et al., 2017), which are essential for ecosystem regeneration. As climate
71 change continues to influence fire regimes with unknown consequences for ecosystem processes
72 (Rogers et al., 2011), it is essential to determine how soil microbes that drive these processes are
73 affected by mega-fires.

74 Previous studies have shown that while fire significantly decreases bacterial and fungal
75 biomass (Dooley & Treseder, 2012) and richness (Pressler et al., 2019), fire is not totally
76 sterilizing, and similar to plants (Keeley et al., 2011), some taxa respond positively and are
77 adapted to fire. Fires are known to shift fungal dominance from Basidiomycota to Ascomycota
78 (Cairney & Bastias, 2007; Pérez-Valera et al., 2018; Semenova-Nelsen et al., 2019), and many
79 Ascomycetes are known to fruit in abundance after fire. Indeed, century-old studies describe
80 “pyrophilous”, or fire loving, fungi from mushroom surveys (Seaver, 1909). Many of these
81 pyrophilous fungi that fruit after fires are in the Ascomycete family Pyronemataceae (El-Abyad
82 & Webster, 1968; McMullan-Fisher et al., 2011; Petersen, 1970) and heat-treated soil has
83 recovered Ascomycetes in the genera *Aspergillus* and *Penicillium* (McGee et al., 2006; Warcup
84 & Baker, 1963). Further, the Ascomycete *Neurospora crassa* is known to have heat activated
85 spores (Emerson, 1948). While less common than Ascomycetes, Basidiomycetes can also
86 respond positively to fire. For example, the Basidiomycete mushroom *Pholiota highlandensis*
87 commonly fruits after wildfires (Raudabaugh et al., 2020), and the EMF species *Rhizopogon*
88 *olivaceotinctus* significantly increased in frequency after a pine forest mega-fire (Glassman et al.,
89 2016). However, less is known about the mycelial response of fungi to fire, and even less is
90 known about bacteria, with less than 3% of studies examining microbial response to fire
91 addressing their composition (Pressler et al., 2019). Yet, recent evidence suggests that

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92 pyrophilous bacteria may also exist (Whitman et al., 2019; Woolet & Whitman, 2020). For
93 example, several taxa of bacteria significantly increased in frequency after a boreal wildfire, in
94 particular the Actinobacteria *Arthrobacter* and the Proteobacteria *Massilia* (Whitman et al.,
95 2019). Currently, most research on pyrophilous microbes is observational, and as such while we
96 know that these taxa respond positively to fire, we do not yet know why.

97 While their small size and immense diversity has limited our understanding of fire effects
98 on microbes, trait-based approaches are providing promising avenues for synthesizing microbes
99 into suites of traits under which selective trade-offs might occur (Lustenhouwer et al., 2020;
100 Malik et al., 2020). Trait strategies and trait syndromes are well established in the plant world
101 including traits for wildfire response (e.g. thick bark, serotinous cones, vegetative re-sprouting)
102 (Keeley et al., 2011; Pausas et al., 2004). Functional traits synthesize the wide diversity of
103 species into trait groups (e.g., seed size and specific leaf area) each of which is associated with
104 specific strategies such as longevity or drought tolerance. Due to energetic costs or evolutionary
105 constraints associated with different functions, it is unlikely that one organism will succeed at all
106 strategies and, therefore, will *trade off* the ability to perform one function for a less costly
107 alternative (Reich, 2014). Identifying traits of pyrophilous microbes and trade-offs among them
108 can improve our ability to model biogeochemical consequences such as carbon cycling under
109 anthropogenically induced changes to fire regimes (Malik et al., 2020). A recent study
110 hypothesized what some broad microbial fire response traits might be (fast growers,
111 thermotolerant structure producers, and resource acquisition of post-fire nutrients) (Whitman et
112 al., 2019). Expanding on this framework and identifying microbes that fit into these trait
113 syndromes in a variety of biomes will provide key insights into microbial fire ecology and
114 improve prediction of fire biogeochemical impacts. The first step in this expansion of the

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115 pyrophilous trait framework is to test the phylogenetic conservation of microbial fire response,
116 meaning testing if more closely related organisms tend to respond to fire in the same way
117 (Martiny et al., 2013). By comparing a clade's fire response to observations made in other fire
118 events and in multiple ecosystems we can better predict how individual taxa will respond even if
119 they are observed post-fire for the first time. This is because traits governing microbial
120 phenotypic responses are often conserved within clades (Martiny et al., 2013). Thus, as the
121 discovery of traits governing pyrophilous microbes' fire response are uncovered, the ecological
122 role of related microbes will be better predicted in future post-fire sampling. For example,
123 bacterial response to both nitrogen addition (Isobe et al., 2019) and simulated global climate
124 change factors was phylogenetically conserved across all perturbations (Isobe et al., 2020),
125 which improves prediction of disturbance response of closely related taxa.

126 Most fire studies use burned areas compared to an unburned control as a substitute for not
127 having pre-fire data from the burned region (Brown et al., 2019; Buscardo et al., 2010; Whitman
128 et al., 2019), laboratory heating experiments (Bruns et al., 2020; Riah-Anglet et al., 2015), or
129 prescribed fire to examine impacts on soil microbes (Brown et al., 2013; Fujimura et al., 2005).
130 While these all provide useful information on microbial response to fire, none of these conditions
131 replicate the size and severity of a mega-fire. Since it is unlikely to have microbial
132 documentation before fires occur, the study of mega-fire impacts must be opportunistic. Two
133 such studies exist, in which pre- and post-fire soil samples from the exact same sampling
134 locations after a stand-replacing fire were available, and both were in Pine forests, and both
135 focused solely on EMF (Baar et al., 1999; Glassman et al., 2016). Existing research on
136 pyrophilous taxa also focuses largely on pine forests (Dove & Hart, 2017; Pressler et al., 2019),
137 so it is unclear whether the same pyrophilous taxa will respond in other forest types or dryland

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138 ecosystems. Expanding our knowledge to non-Pinaceae forests will allow us to determine if
139 pyrophilous taxa and their traits are generalizable or ecosystem specific.

140 The California redwood (*Sequoia sempervirens*) and tanoak (*Notholithocarpus*
141 *densiflorus*) forest is a charismatic forest of coastal California and southern Oregon that is
142 adapted to high fire frequency with traits including thick bark and vegetative re-sprouting (Paul
143 Zinke, 1988; Stephens et al., 2007). Redwood-tanoak forests are also culturally significant with
144 tanoak acorns as a staple of the Native American diet (Meyers et al., 2006). These forests are
145 now highly threatened by both the invasive pathogen *Phytophthora ramorum*, causative agent of
146 Sudden Oak Death (SOD), and changing fire regimes (Metz et al., 2013; Simler et al., 2018). It is
147 possible that their associated soil microbiomes, including the AMF associated with redwoods
148 (Afek et al., 1994) and EMF associated with tanoaks (Bergemann & Garbelotto, 2006) may help
149 them survive these unprecedented disturbances. Yet, their wildfire response remains completely
150 uncharacterized.

151 Here, we take advantage of the 2016 Soberanes Fire, a mega-fire burning >500 Km²,
152 which burned through our study plots established to examine the impacts of SOD on redwood-
153 tanoak forest microbiomes (Meentemeyer et al., 2008) (Figure 1). We were able to sample soils
154 from two burned and one unburned plot immediately post-fire so we could assess what microbes
155 survived the mega-fire before rain could disperse in new microbes. Because we had an unburned
156 plot, we were able to capitalize on a before-after control impact (BACI) (Conquest, 2000)
157 experimental design for increased inference. We thus tested the following hypotheses: H1) the
158 mega-fire would significantly decrease bacterial, total fungal, and mycorrhizal richness in
159 comparison to the control plot, H2) fungal composition would shift from Basidiomycete to
160 Ascomycete dominated, and H3) pyrophilous bacterial and fungal taxa would emerge and might

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161 have similarities to previously described pyrophilous taxa from pine-forests and would fit into a
162 trait-based conceptual model based on post-fire resource acquisition, thermotolerance, or fast
163 growth or colonization (Whitman et al 2019). Finally, we hypothesized that H4) adaptation to
164 fire might be a phylogenetically conserved trait, as has been indicated for microbial response to
165 nitrogen disturbance (Isobe et al., 2019).

166

167 **Materials and Methods**

168 *Plot Description and soil sampling scheme:* In 2006 and 2007, one hundred fourteen 500 m²
169 circular plots were established in redwood forests across the California Big Sur region to study
170 the effects of the emerging SOD outbreak (Meentemeyer et al., 2008). Big Sur has an average
171 rainfall of 911mm/year, with most rain falling from October through April, and an average
172 temperature range of 10.1°C to 16.1°C (Potter, 2016). On January 14th and February 4th 2013,
173 soil was collected to determine soil microbial composition from a subset of those plots selected
174 for dominance of tanoak as the only EMF host, accessibility from the road so as to keep soils on
175 ice immediately after sampling, and similarity in slope, aspect, and elevation. We collected 12
176 soil cores at 2,6, and 10m from the plot center in 4 cardinal directions in an attempt to adequately
177 sample the soil microbial communities across the entire plot (Figure 1B). The top 10cm of soil
178 was collected using field sterilized (with 70% EtOH) Bond 8050 Releasable Bulb Planters (~250
179 mL of soil). From July 22-October 12, 2016, the Soberanes Fire burned 534 km² in Big Sur,
180 burning with high severity throughout a significant portion of the fire including two of our plots
181 (Potter, 2016)(Figure 1A). On the day that the fire was officially declared over (October 12,
182 2016), we were able access and collect soil samples from the exact same sampling locations
183 (using GIS, meter tape, and notes) in one unburned (plot 058) and two burned plots (plots 601

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184 and 603). For each plot, all tree species identification, size, and dead versus alive status were
185 geographically mapped in 2006, 2010 and 2013 (Figures S1-S3). All plots were in UTM zone 10
186 and slopes ranged from 19-34°, elevations from 491-744m, and distances to the coast from 4.1-
187 6.4km (Table S1).

188

189 *DNA Extraction and Storage:* Soils were stored on ice in the field and homogenized the next day
190 using a 2mm sieve and sterilizing with 70% EtOH between samples. For DNA extraction, 0.25g
191 of soil was weighed and placed into tubes from the MoBio Power Soil DNA Extraction Kit and
192 stored at 4°C. DNA was extracted within the week, following manufacturer's protocols and
193 stored at -20°C until analyzed.

194

195 *PCR Amplification of rRNA:* Bacteria and fungi were characterized using the 515F-806R primer
196 pair to characterize the V4 region of the bacterial 16S rRNA gene (Caporaso et al., 2011) and the
197 ITS1F-2 primer pair (White et al., 1990) adapted for Illumina MiSeq (Smith & Peay, 2014) to
198 characterize the ITS1 region of the fungal internal transcribed spacer region (Schoch et al.,
199 2012). PCR recipe included 1µL of template DNA (in some cases diluted 1:10 to overcome
200 inhibitors), 2µL of each primer at 10µM concentration, 12.5µL of Accustart Toughmix
201 (Quantabio, Beverly, MA, USA), and 7.5µL of PCR grade water for a total reaction volume of
202 25µL. Thermocycler conditions began with denaturation at 94°C for 3 min; followed by 29
203 amplification cycles for 16S of 45 s at 94°C, 1 min at 50°C, 90 sec at 72°C, followed by a 10-
204 min final extension at 72°C; and for ITS: 30 s at 94°C, 30 sec at 52°C, 30 sec at 68°C, with a 10-
205 min final extension at 68°C. A mock community (ZymoBiomics, Zymo, Irvine, CA) and
206 negative DNA extractions and PCRs were also amplified and sequenced.

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207

208 *Illumina library preparation and sequencing:* PCR products were pooled and cleaned as
209 previously established (Glassman et al., 2018), with PCR products for 16S or ITS libraries
210 pooled based on band strength from gel electrophoresis, using either 1 μ L, 2 μ L, or 3 μ L of the
211 PCR product, using 3 μ L for the weakest bands and 1 μ L for the strongest. Pooled PCR products
212 of either 16S or ITS were cleaned with AMPure magnetic beads (Beckman Coulter Inc., Brea,
213 California, USA), quality checked for concentration and amplicon size using the Agilent 2100
214 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA) at the Institute for Integrative
215 Genome Biology (IIGB) at University of California, Riverside (UCR) then pooled at a 60:40 ITS
216 to 16S ratio. The combined library was sequenced with an Illumina MiSeq 250bp paired-end run
217 at the UCR IIGB.

218

219 *Bioinformatics and OTU Table Construction:* Demultiplexed sequences were received from the
220 Institute for Integrative Genome Biology (IIGB) UCR core and raw reads were analyzed for
221 quality with FastQC, and primers and barcodes were trimmed with Cutadapt v. 1.16 (Martin,
222 2011). We then used UPARSE v11 (Edgar, 2013) to merge forward and reverse reads with
223 fastq_mergepairs, quality filtered with fastq_filter with fastq_maxee of 0.5, dereplicated
224 sequences, removed singletons, and clustered 97% OTUs following established protocols
225 (Glassman et al., 2018). For 16S, 5.2 million (M) reads were analyzed, 4.6M (88.6%) merged
226 under the constraints for quality control, and 4.3M reads (94.4%) passed the filtering step at an
227 expected error rate of 0.5. OTUs were then assigned taxonomic information using a RDP
228 classifier and the GreenGenes database (DeSantis et al., 2006) (accessed 4/25/2019) in QIIME
229 1.9.1 (Caporaso et al., 2010). Samples identified as mitochondria, chloroplasts, or unidentified

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230 were removed, leaving a remaining 14,282 OTUs. For ITS1, 9.2M reads were analyzed, 7.5M
231 (81%) merged, and 5.6M (75.6%) passed the filtering step. Fungal taxonomy was assigned to
232 97% OTUs using the QIIME 1.9.1 BLAST protocol and the UNITE database (Kõljalg et al.,
233 2005) (accessed 5/13/2019). Samples not identified as Kingdom Fungi were removed, resulting
234 in 3,328 OTUs. Sequences were submitted to the National Center for Biotechnology Information
235 Sequence Read Archive under BioProject accession number PRJNA659056.

236

237 *Data Analysis*

238 All statistical analyses and figures were produced in R 4.0.2 (R Core Team, 2020) and all
239 scripts are available at: <https://github.com/sydneyg/SoberanesFire>. In order to accurately
240 compare richness across samples with uneven sequencing depth, samples were rarefied to an
241 even sequencing depth per sample (10,367 for bacteria and 12,089 for fungi) using the “rarefy”
242 function in the Vegan R package (Oksanen, 2007). In this process negative DNA extractions and
243 negative PCRs were removed due to low sequencing depth. Mock communities were examined
244 and removed prior to analysis. Alpha diversity metrics were calculated with the “estimate”
245 function (observed species, ACE and Chao1) in the BioDiversityR package (Kindt, 2019) and
246 with the “diversity” and “exp” functions (Shannon, Simpson) in Vegan (Oksanen, 2007). ACE,
247 Chao1 and observed Species were highly correlated for both bacteria (Figure S4 A& B) and
248 fungi (Figure S4 B&C) so all analyses and figures are based on observed species number after
249 rarefaction. Shannon metrics were used to detect changes in evenness and Simpson was used to
250 detect changes in dominance. Normality was tested with a Shapiro test, then ANOVA was used
251 to test the effect of fire versus time on bacterial and fungal richness, followed by a post-hoc
252 Tukey HSD test. Percent reduction in species richness was computed using the average species

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253 richness in each plot before and after the fire. Species accumulation curves were also constructed
254 using “speccacum” function in Vegan (Oksanen, 2007). Richness figures were created in ggplot2
255 (Wickham, Chang, et al., 2019).

256 We used FunGuild (Nguyen et al., 2016) to analyze the effects of fire on EMF, AMF and
257 saprobic fungi. We applied FunGuild to the unrarefied fungal OTU table, then only included
258 “Highly Probable” guild assignments. These OTUs were then selected from the rarefied full
259 fungal dataset using a “semi_join” function from the tidyverse R package (Wickham, Averick, et
260 al., 2019), resulting in a total of 463 OTUs, including 222 EMF, 25 AMF, and 76 saprobic fungi.
261 Changes in per guild species richness were then calculated.

262 For bacterial and fungal community composition, we calculated dissimilarity matrices as
263 in (Glassman et al., 2018), using the “avgdist” function in Vegan (Oksanen, 2007). OTU tables
264 were normalized by subsampling to the lowest common sampling depth 100×, then the median
265 of the Bray–Curtis dissimilarity matrices calculated from each of subsampled OTU tables was
266 square root transformed. We then tested the effect of time and fire on bacterial and fungal
267 community composition with a two-way Permutational multivariate analysis of variance
268 (PERMANOVA) (Anderson et al., 2008) as implemented with the Vegan “adonis” function. We
269 visualized community compositional differences with nonmetric multidimensional scaling
270 (NMDS) with the Vegan “metaMDS” function and used the Vegan “envfit” function to
271 determine which taxa correlated well with ordination space, correcting for multiple tests with a
272 Benjamini-Hochberg correction.

273 We identified pyrophilous taxa with four approaches. First, we identified taxa that
274 correlated well with ordination space with “envfit” as described above. Second, we calculated
275 percent changes in sequence abundance of dominant taxa (over 1% sequence abundant) before

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276 and after fire in the burned plots and visualized the most abundant taxa summarized by genera
277 with rank abundance curves. Third, we used indicator species analysis (ISA) to identify
278 microbial indicators in the burned plots before and after the fire using the “multipatt” function in
279 the Indicspecies package (Cáceres & Jansen, 2019). Finally, we ran the raw OTU tables through
280 DESeq2 (Love et al., 2019) to identify log-fold changes in abundance of each OTU in the burned
281 plots before and after fire. We then used the DESeq2 output to determine if the taxa that
282 positively or negatively responded to fire were phylogenetically conserved using established
283 protocols (Isobe et al., 2019). In brief, we created circular phylogenies using maximum
284 likelihood trees using the RAxML pipeline (Stamatakis, 2014) for 16S and ITS1 and then
285 assigned each OTU a positive or negative response to fire based on the DESeq2 analysis. Then
286 the tree was examined for the deepest node at which >90% of the OTUs shared the same
287 response (positive or negative). These groups were then binned into consensus clades and the
288 mean depth of the consensus clades was calculated with consenTRAIT (Martiny et al., 2013) as
289 implemented with the Castor “get_trait_depth” function using 1,000 permutations. The
290 consensus clades were then mapped onto the phylogeny and colored to visualize evolutionary
291 relationships of taxa exhibiting positive or negative responses to fire using the Interactive Tree of
292 Life (ITOL) (Letunic & Bork, 2007). The taxonomy of clades whose response was significantly
293 more positive or negative than expected by chance was identified with a two-tailed exact test
294 (Mc. Donald, 2015) against the equal distribution of positive and negative responses within each
295 taxonomic group. Because of some of the known issues with using ITS for phylogenetic analyses
296 an attempt to strengthen our phylogeny using GhostTree (Fouquier et al., 2016) was made.
297 However, due to the inherent bias towards EMF in the GhostTree backbone phylogenies,
298 aligning our OTUs to GhostTree resulted in the loss of 61.4% of OTUs despite multiple attempts

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299 to correct for this, thus rendering the GhostTree derived phylogenies not suitable for our
300 analyses. Therefore, we decided to move forward with ITS based analysis under the guiding
301 principle that the trends and clustering observed in our analysis, supported by literature and our
302 other analyses, are still meaningful despite the potential weakening of statistical conclusions due
303 to the limitations of ITS.

304

305 **Results**

306 *Change in Microbial Richness After Fire:* After rarefaction, we found a total of 12,322 bacterial
307 and 2,878 fungal OTUs. In the burned plots (Plots 601 and 603), we found 9,116 bacterial and
308 1,869 fungal OTUs pre-fire, and 6,172 bacterial and 987 fungal OTUs post-fire. Fire
309 significantly reduced both bacterial and fungal observed species richness in the burned plots,
310 whereas richness remained unchanged in the unburned plot (Figure 2). Results did not differ if
311 we treated samples independently ($F_{1,44} = 23.75$, $p < 0.001$,) versus if we counted them as nested
312 within plots ($F_{1,1} = 65.73$, $p < 0.001$,). For both bacteria and fungi, number of observed taxa
313 decreased in plot 601 by approximately 40% (37.6% for fungi and 40.1% for bacteria). In plot
314 603, bacterial richness declined by 52.2% and fungal richness declined by a whopping 70%. This
315 is in contrast to the unburned plot (058) which had equivalent richness to the burned plots 601
316 and 603 pre-fire but experienced no change in either bacterial or fungal richness during the three
317 years (Figure 2; Table S2). Fire also resulted in large and significant evenness reductions
318 (Shannon diversity index decreased by 82-83% for fungi and 65-78% for bacteria) and large
319 increases in dominance in the burned plots (measured as the inverse of Simpson's index
320 (Whittaker, 1965), which increased by 71-78% for fungi and by 76-82% for bacteria) with no
321 significant change in either index for the unburned plot (Table S2). EMF richness decreased by

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322 68% in one burned plot (plot 603), was unchanged in the other burned plot, but increased by
323 26% over the 3-year time span in the unburned plot (Figure S5). AMF and saprobic richness both
324 decreased in burned plots (saprobes: 69% in plot 601 and 76% in plot 603; AMF: 60% in plot
325 601 and 80% in plot 603) and both increased in the unburned plot over time (saprobes: 24%;
326 AMF: 83%; Figure S5).

327

328 *Change in Microbial Composition After Fire:* Fire resulted in a large and significant change in
329 bacterial (Adonis $R^2 = 0.27$, $p < 0.001$) and fungal (Adonis $R^2 = 0.24$, $p < 0.001$) community
330 composition, while the unburned plot experienced no change in fungal composition and a small
331 change in bacterial composition ($R^2 = 0.09$, $p < 0.01$; Figure 3, Figure S6). Compositional
332 changes in bacteria were largely driven by increases in the Actinobacteria and Firmicutes phyla
333 post-fire and decreases in the Proteobacteria, Gemmatimonadetes, Verrumicrobia, Chloroflexi,
334 Elusimicrobia, Planctomycetes, Acidobacteria, Bacteroidetes, and Saccharibacteria phyla (Figure
335 3B). Compositional changes in fungi were driven by large increases in the Basidiomycete genus
336 *Basidioascus* and the Ascomycete genus *Penicillium* and decreases in the Mucoromycota genus
337 *Mortierella*, and the Ascomycete genera *Ilyonectria*, *Metarhizium*, *Cladophialphora*, *Pectenia*,
338 *Humicola*, and *Exophiala* (Figure 3D).

339

340 *Change in Relative Sequence Abundance of Bacterial Taxa After Fire:* Pre-fire, bacterial OTUs
341 dominating ($\geq 1\%$ of sequence abundance) the burned plots were primarily Proteobacteria
342 (84.4%) and Acidobacteria (15.6%) with the most dominant taxa, Proteobacteria species in
343 *Bradyrhizobium* and *Rhodoplanes*, occupying around 2.3% sequences each (Figure 4A; Table
344 S3). Post-fire, there was a shift in the dominant phyla ($\geq 1\%$ total sequences), with a loss of

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345 Proteobacteria and a dominance of Firmicutes (82%) and Actinobacteria (18%). The most
346 abundant taxon also had an increase in dominance, a Firmicute in the genus *Sporosarcina*,
347 dominating 6.9% of the sequences, followed by Firmicutes genera *Fictibacillus*,
348 *Thermoflavimicrobium*, *Bacillus*, *Solibacillus*, *Cohnella*, and Actinobacteria genera
349 *Micromonospora*, *Pseudonocardia*, and the family Micromonosporaceae (Figure 4A).
350
351 *Change in Relative Sequence Abundance of Fungal Taxa After Fire: Pre-fire, fungal taxa $\geq 1\%$*
352 *sequence abundance were dominated 62% by the phylum Basidiomycota, followed by 25%*
353 *Mucoromycota, 10% to Ascomycota, and 3% unidentifiable to phylum (Figure 4B; Table S4).*
354 *Pre-fire, the most dominant fungi were the Basidiomycete *Hygrocybe acutoconica* (5.94%) and*
355 *the Mucoromycete *Mortierella baineri* (4.62%). Post-fire, among the most abundant taxa,*
356 *Ascomycota dominated (65%), with Basidiomycota falling to 35%, and a complete loss of the*
357 *Mucoromycota. There was also a large increase in dominance with the most abundant taxon*
358 *post-fire, a Basidiomycete Geminibasidiomycete yeast *Basidioascus undulatus*, accounting for*
359 *28% of the sequences (Figure 4B). The other top taxa were dominated by genera in the*
360 *Ascomycota *Penicillium* 13.1% and *Fusarium* 1.2% and the family Pyronemataceae (*Tricharina**
361 *13.6%, *Peziza* 10.2%, *Anthracobia* 7.6%, *Scutellina* 7.2%, *Pyronema* 4.2%).*
362
363 *Bacterial indicator species: Bacterial indicator species analysis (ISA) revealed 86 indicator*
364 *OTUs shared between the burned plots pre-fire, and 21 OTUs indicative of the post-fire*
365 *community (Table S5). The top ten taxa identified for the post-fire grouping were two OTUs*
366 *from the Firmicutes family Thermoactinomycetaceae, one OTU from the Actinobacteria family*

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367 Thermomonosporaceae, OTUs from the Firmicutes genera *Thermoflavimicrobium*, *Fictibiacillus*,
368 *Cohnella*, *Paenibacillus*, *Bacillus*, *Tepidibacterium*, and the Actinobacteria genus *Streptomyces*.

369

370 *Fungal indicators species*: Fungal ISA identified 13 indicator taxa for the burned plots pre-fire
371 and 5 indicator taxa post-fire (Table S6). The 13 pre-fire taxa identified were 4 species from the
372 Mucoromycota genus *Mortierella* and the rest Ascomycetes belonging to the genera *Polyphilus*,
373 *Pycnopeziza*, *Thelonectria*, *Pectenia*, *Cladophialophora*, and *Phomopsis*. The five fungal
374 indicators of the post-fire group were all Ascomycetes, one in the Aspergillaceae, *Penicillium*
375 *decumbens*, and the rest in the Pyronemataceae: *Anthracobia* sp., *Geopyxis alpina*, *Peziza*
376 *vacinii*, and *Tricharina praecox*.

377

378 *Phylogenetic conservation of pyrophilous taxa*: Lineages of both bacteria and fungi that
379 negatively or positively respond to fire appear to be phylogenetically conserved at the class level
380 for fungi and the phylum level for bacteria (Figures 5 & 6). There is strong clustering of bacteria
381 positively responding to fire in the Firmicutes and Actinobacteria and a few positive responders
382 in the Acidobacteria (Figure 5; Table S7). All other phyla belonged to consensus clades that
383 either did not show the patterned response to fire or responded negatively. For fungi, the lineages
384 that positively respond to fire include the Ascomycete class Pezizomycetes (containing
385 Pyronemataceae) and the Basidiomycete class Geminibasidiomycetes (containing *Basidioascus*)
386 (Figure 6; Table S8). There are also positive interactions sprinkled within some of the other
387 classes, which appear to be conserved at the order level rather than class level, namely the
388 Eurotiomycetes order Eurotiales (contains Aspergillaceae) and the Agaricomycete order

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389 Russulales. All other groups belonged to consensus clades that responded negatively or did not
390 show the phylogenetic patterned response.

391

392 **Discussion**

393 Here, we take advantage of the 2016 Soberanes Fire burning through our plots and show
394 for the first time the effects of a mega-fire on bacterial and fungal communities with a rare pre-
395 and post-fire dataset in a redwood tanoak forest. In accordance with our hypotheses, the mega-
396 fire significantly decreased bacterial and fungal richness (H1) (Figure 2); fungal composition
397 shifted from Basidiomycete to Ascomycete dominated (H2) (Figure 4); many pyrophilous taxa
398 previously identified from other biomes appeared in a redwood tanoak forest and are likely
399 generalizable and may fall into trait categories analogous to plants (H3); and adaptation to fire is
400 likely a phylogenetically conserved trait across bacteria (Figure 5) and fungi (Figure 6) (H4).

401 We found that the mega-fire led to large and significant reductions in bacterial and fungal
402 richness. Reduction in microbial richness is a typical result after fire (Brown et al., 2019; Day et
403 al., 2019; Pérez-Valera et al., 2018; Whitman et al., 2019), however the degree to which fire
404 affects richness varies. In our study, fire reduced the average species richness per sample by up
405 to 52% for bacteria and up to 70% for fungi (Figure 2). In contrast, a meta-analysis of fungal
406 response to fire found an average richness reduction of 28% (Dove & Hart, 2017). However, the
407 range for both fungal (12-80%) (Brown et al., 2019; Pulido-Chavez et al., 2021) and bacterial
408 (20-58%) (Brown et al., 2013; Pérez-Valera et al., 2018) richness reduction can be quite large.
409 This is likely due to differences in fire severity, which is often not measured or consistently
410 reported in post-fire microbial surveys, despite that more severe fires have been shown to have
411 greater impacts on the soil community (Whitman et al., 2019). Moreover, when reported, it is

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412 based on plant mortality measured at coarse levels (30km² in the case of the Soberanes Fire)
413 (Potter, 2016) that do not correspond well to the scale of the soil core and can lead to wide
414 disparities in the presence or absence of live plants, duff, or ash in soil cores all taken in high
415 severity defined fire zones. We also found that EMF richness declined following fire, which
416 makes sense given large host mortality, and is in accordance with other high severity fires in pine
417 forests (Glassman et al., 2016; Pulido-Chavez et al., 2021; Reazin et al., 2016). This large-scale
418 reduction in the microbial richness can have far reaching impacts on the surrounding ecosystem
419 from radically altered nutrient cycling (Crowther et al., 2019) to the inability to reestablish
420 critical plant species (Van der Heijden et al., 2008).

421 The mega-fire led to large compositional shifts in both bacterial (27%) and fungal (24%)
422 communities (Figure 3). Studies often report significant changes in fungal compositional
423 turnover post-fire but variable change in bacterial composition (Pérez-Valera et al., 2018;
424 Pressler et al., 2019). However, sampling immediately post-fire does reveal significant
425 reductions in bacterial richness and evenness (Brown et al., 2019; Ferrenberg et al., 2013) and
426 one study showed with increasing fire severity the reduction in richness and evenness becomes
427 more drastic (Brown et al., 2019). Depending on the biome, changes in microbial composition
428 can be as short lived as 21 days after simulated soil heating (Bárcenas-Moreno & Bååth, 2009) or
429 as long as 19 years post-fire in a Spanish Mediterranean ecosystem (Pérez-Valera et al., 2018). A
430 study in a Chinese pine forest speculated that bacterial composition would recover within one
431 growing season based on data from 6 months post-fire (Li et al., 2019). This disparity in
432 resilience is likely due to differences in fire severity and timing of post-fire sampling. Fires that
433 are not as severe often produce smaller shifts in bacterial and fungal composition (Buscardo et
434 al., 2010). The effect of fire on microbial richness and composition is also likely more transient

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435 in some biomes and longer lasting in others. As such, studies that sample 1-2 years post-fire may
436 miss changes in bacterial and fungal communities depending on the biome. In the case of our
437 data, these observed changes stemmed from a severe mega-fire where the changes to the
438 landscape can be quite drastic and took place in a well-established forest and therefore recovery
439 could take much longer.

440 Changes in dominance can be important indicators of how post-fire microbial
441 communities assemble, as has been documented in plant communities (Moser & Wohlgemuth,
442 2006). Fires often lead to shifts in plant community evenness to increased dominance by specific
443 fire-adapted species such as long leaf pine (Glitzenstein et al., 1995), *Ceanothus* shrubs (Lawson
444 et al., 2010), or Manzanita in chaparral systems (Vogl & Schorr, 1972). These effects can be
445 more pronounced when fire severity increases (Kuenzi et al., 2008). Fire similarly alters
446 microbial community assembly processes (Ferrenberg et al., 2013). Here, we find patterns of fire
447 induced-dominance in microbial communities, with a single fungal taxon (*Basidioascus*
448 *undulates*) dominating 28% and a single bacterial taxon (*Sporosarcina spp.*) dominating 7% of
449 the sequences post-fire. While changes in dominance have been documented in microbial
450 communities post-fire (Pérez-Valera et al., 2018; Whitman et al., 2019), they are at lower levels
451 (2-4% for most abundant taxon) likely because they sampled later after the fire and after the first
452 rains post-fire thus obscuring initial compositional shifts. An experimental fire in laboratory
453 “pyrocasm” (a small-scale highly controlled experimental fire to test the effects of fire on soil
454 samples) similarly found huge increases in dominance with the most abundant taxon *Pyronema*
455 *domesticum* occupying 57% of the sequences within 2 weeks of the fire (Bruns et al., 2020). We
456 interpret this level of dominance to indicate the opening of niche space due to massive microbial

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457 death of the pre-fire dominants that allows the few microbial taxa that are thermotolerant or
458 capable of capitalizing on post-fire resources or eating microbial necromass to take over.

459 After fire, we found a complete turnover in the abundant bacterial taxa (>1% sequence
460 abundant) from Proteobacteria and Acidobacteria domination to Firmicutes and a few
461 Actinobacteria (Figure 4). These changes are likely driven by thermotolerance of endospore
462 forming Firmicutes, which have also been found to increase in abundance following laboratory
463 heat treatments of soil samples (Filippidou et al., 2016; Jurburg et al., 2017) and soon after
464 Mediterranean fires (Pérez-Valera et al., 2020). Post-fire environments are often characterized by
465 increases in pH (Neary et al., 1999), which may favor both thermotolerant and alkaline tolerant
466 Actinobacteria (Shivlata & Tulasi, 2015). Of the specific genera dominating our communities
467 post-fire, only *Thermoflavimicrobium* (Yoon et al., 2005) and *Sporosarcina* (Jurburg et al., 2017)
468 have previously been shown to increase after laboratory heating. Other studies have shown an
469 increase in Actinobacteria and Firmicutes post-fire, though only the *Bacillus spp.* in our study is
470 a potentially shared taxon with those other studies (Ferrenberg et al., 2013; Li et al., 2019;
471 Whitman et al., 2019). In contrast, most other groups of bacteria negatively responded to fire, or
472 only responded positively sporadically within a clade (Figure 5). Lineages can have differing
473 responses within a clade when lineages challenged with the same evolutionary pressures do not
474 respond the same way (Isobe et al., 2019). Furthermore, the degree to which a trait is conserved
475 within lineages may reflect the genetic complexity of the response or trait, with more complex
476 responses being less conserved due to needing many pathways to be conserved across all taxa of
477 a lineage (Isobe et al., 2019). It may be then that the genetic drivers of Firmicutes' response to
478 fire are either less genetically complex or more genetically integral to that phylum while
479 Actinobacteria's response may be genetically varied or require the conservation of a greater

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480 number of genetic pathways in order to successfully adapt to fire. Finally, as this study is among
481 the first to comprehensively characterize the soil microbiome of the charismatic redwood-tanoak
482 forests, we note a few similarities in our pre-fire soils with a recent bacterial study of coastal
483 redwood roots which also showed the most abundant taxa as *Bradyrhizobium* and *Rhodoplanes*
484 (Willing et al., 2020). Additionally, a study of the microbial composition of the coastal
485 redwood's sister genus, the giant sequoia (*Sequoiadendron giganteum*), also showed domination
486 by *Bradyrhizobium* and Sinobacteraceae sp. of the Proteobacteria (Carey et al., 2019). The
487 similarities with the giant sequoia soil communities also extend to fungi, with *Hygrocybe*
488 dominating both our redwood forests pre-fire and in the giant sequoia forest.

489 After the fire, the fungal communities were dominated (28%) by the yeast *Basidioascus*
490 *undulates*, which was rare (0.05%) pre-fire. *Basidioascus* and *Geminibasidium* are newly
491 described heat-resistant and xerotolerant Basidiomycete yeasts isolated from laboratory heat-
492 treatments to soil (Nguyen et al., 2013). *Basidioascus* was originally described as an Ascomycete
493 because their spores were spuriously described as single-spored asci. Perhaps the visual
494 similarity to Ascomycetes is representative of convergent evolution with other ascomycetes,
495 which are more often associated with fire (Cairney & Bastias, 2007). Only one other wildfire
496 study has found *Basidioascus* to increase post-fire (Pulido-Chavez et al., 2021) though not with
497 the level of dominance in our study. A couple recent studies have found an increase in
498 dominance of the sister genus *Geminibasidium*, including a study of a *Pinus ponderosa* forest in
499 the American Pacific Northwest (Pulido-Chavez et al., 2021) and a study of *Larix* and *Betula*
500 dominated forests in northeastern China (Yang et al., 2020). *Geminibasidium* was also present at
501 0.05% sequence abundance, the same amount as our pre-fire soil, in an unburned giant sequoia
502 forest (Carey et al., 2019). While Geminibasidiomycetes are positively selected for by fire

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503 (Figure 6) likely due to their thermotolerance and xerotolerance (Nguyen et al., 2013), they have
504 been missed by existing descriptions of pyrophilous fungi that are mainly based on fruiting body
505 surveys (McMullan-Fisher et al., 2011).

506 Despite the most dominant post-fire fungus being a Basidiomycete, overall the
507 community shifted from Basidiomycete to Ascomycete dominated post-fire, with particular
508 increases in the Pezizomycete and Eurotiomycete lineages (Figure 6). The shift from
509 Basidiomycete to Ascomycete dominance is well established in the post-fire fungal literature
510 (Cairney & Bastias, 2007) with similar findings across diverse biomes ranging from
511 Mediterranean shrublands of Spain (Pérez-Valera et al., 2018) to pine savannas of the American
512 southeast (Semenova-Nelsen et al., 2019). Four of the five fire indicator taxa (Table S6) belong
513 to the Pyronemataceae, which have long been known to fruit extensively after fires (Seaver,
514 1909). In addition to evidence from fruiting body surveys, the Pyronemataceae genus *Pyronema*
515 can also dominate belowground mycelium by as much as 60% after experimental laboratory fires
516 (Bruns et al., 2020) and increased 100 fold in frequency after prescribed fires in a *P. ponderosa*
517 forest (Reazin et al., 2016). *Geopyxis alpina* was also an indicator of fire, and at least two species
518 of *Geopyxis* species are known to fruit exclusively on burned soil (Wang et al., 2016). The
519 Pyronemataceae produce sporocarps that are small orange cup fungi that appear on pyrolyzed
520 material after burning (El-Abyad & Webster, 1968). It is possible that their color or morphology
521 makes them better adapted to post-fire scenarios, for example many of them are orange and
522 contain carotenoids (Carlile & Friend, 1956) which may add UV protection (Luque et al., 2012).
523 However, it is also likely that they survive fires due to their ability to form resistant propagules
524 called sclerotia (Smith et al., 2015) which may be thermotolerant (Richter & Barnard, 2002).
525 While Eurotiomycetes are widespread fungi, it is possible that their ability to grow fast and

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526 produce ubiquitous spores help them colonize open niche space after fires, as they were similarly
527 common after wildfires in a Canadian boreal forest (Whitman et al., 2019) and in northeastern
528 China (Yang et al., 2020). This would be analogous to the fast-colonization trait of fire adapted
529 plants sprouting in the newly opened niche of burn zones (Keeley et al., 2011). Moreover,
530 several species of *Aspergillus* and *Penicillium* have evidence of heat activated spores (Warcup &
531 Baker, 1963). Much like our reasoning for why some bacterial clades responded better to fire, the
532 Pezizomycetes may all share a similar, conserved response to fire that is less genetically
533 complex, more basal, or more deeply conserved than the response exhibited by the Eurotiales,
534 which may explain why all lineages within the Pezizomycetes responded positively to fire while
535 not all lineages of the Eurotiomycetes did (Figure 6). When discussing the phylogenetic signal
536 obtained in our analyses, we are aware of the limitations of ITS based phylogenies compared
537 with phylogenies constructed involving 18S or 28S data and therefore the statistical significance
538 portrayed in our consentRAIT analysis (Figure 6) may not be as reliable as the analysis done
539 with the 16S phylogeny (Figure 5). However, we feel confident in continuing to draw
540 meaningful conclusions from our phylogenetic analysis as the observed signal (either positively
541 or negatively responding) is tightly clustered within clades, and the positively responding taxa
542 from which we form additional hypotheses (eg. Pyronemataceae, Eurotiales,
543 Geminibasidiomycetes) have strong support in the literature behaving as observed. Future
544 phylogenetic studies on pyrophilous fungi would benefit from sequencing which includes 18S or
545 28S information.

546 Critically analyzing similarities between certain groups of pyrophilous microbes has
547 brought us to the hypothesis that there may be certain traits that characterize a microbe's ability
548 to thrive post-fire, which should be able to be placed into a conceptual framework (H3). These

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549 traits may be analogous to the traits exhibited by fire-tolerant plants (e.g. thick bark, production
550 of serotinous cones, etc.), which themselves fall into fairly well defined suites (vegetative re-
551 sprouters, structural resistance to fire, and rapid colonizers post-fire) (Keeley et al., 2011). We
552 thus propose that microbes survive fire by analogous traits to plants and build from Grime's
553 Competitive-Stress-Ruderal (C-S-R) model (Grime, 1977), its adaptation to mycorrhizal fungi
554 (Chagnon et al., 2013) and to microbial decomposers (Malik et al., 2020), and a recent study
555 from a Canadian boreal forest fire (Whitman et al., 2019). Pyrophilous microbes appear to
556 survive fire via trade-offs among microbial ability acquire post-fire resources (analogous to
557 Grime's C), tolerate heat or desiccation (analogous to Grime's S), or early colonize or grow fast
558 (analogous to Grime's R) (Figure 7). Furthermore, as trade-offs among traits can be used to
559 predict decomposition rates among wood decomposer fungi (Lustenhouwer et al., 2020), we
560 predict that trade-offs among fire response traits might enable prediction of post-fire
561 biogeochemical cycling. For example, the DEMENT model uses traits to improve forecasting of
562 soil carbon by considering trade-offs between a microorganism's ability to decompose litter
563 versus tolerate drought (Allison & Goulden, 2017). Similarly, trade-offs between a microbe's
564 ability to survive fire by thermotolerance versus decomposing pyrogenic organic matter might
565 predict changes in carbon cycling post-fire. This could be further highlighted by a trade-off of
566 post-fire nutrient acquisition strategy microbes growing slowly as they work to breakdown
567 recalcitrant carbon forms present in PyOM, slowly releasing this carbon for cycling, as opposed
568 to fast-growing microbes taking advantage of easily accessible labile carbon. We hypothesize
569 that several known pyrophilous taxa observed in this study and in others would fall into these
570 suites of traits. For post-fire resource acquisition, basidiomycetes such as *Pholiota highlandensis*
571 or *Lyophyllum atratum* might be more likely to degrade pyrolyzed organic matter due to their

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572 enzymatic capabilities, as supported by recent sequencing of their genomes (Steindorff et al.,
573 2020), and *Fusarium* may be capable of denitrifying highly abundant nitrogen (Maeda et al.,
574 2015). For thermotolerance, *Neurospora crassa* has heat-activated spores and *Rhizopogon*
575 *olivaceotinctus* has spores that increase after heat treatment (Bruns et al., 2019; Emerson, 1948)
576 and *Pyronema* may produce thermotolerant sclerotia (Moore, 1962). *Aspergillus* and *Penicillium*
577 are likely fast-colonizers due to highly abundant spore production. However, it is also possible
578 that certain species fall along a continuum of traits and that trade-offs may not be so strict. For
579 example, but *Aspergillus* and *Penicillium* species are also likely thermotolerant (Warcup &
580 Baker, 1963), and some *Penicillium* species have been found to degrade polycyclic aromatic
581 hydrocarbons (PAHs), such as those that might be produced through combustion (Leitão, 2009).
582 Similarly, the yeast *Basidioascus* tolerates stress with its xero- and thermo-tolerance but as a
583 yeast may also be a fast-colonizer since it is unicellular. As our hypothesis regarding post-fire
584 microbial trait suites expands, it may evolve into a more multi-faceted niche space as is currently
585 used in plant trait models (Díaz et al., 2016).

586 We propose that this trait based conceptual model works for pyrophilous bacteria as well
587 as fungi (Figure 7). For example, for post-fire resource acquisition, there are a few studies
588 claiming *Arthrobacter* may be capable of degrading pyrogenic organic matter (Fernández-
589 González et al., 2017; Woolet & Whitman, 2020) and so may *Nocardiodes* (Woolet & Whitman,
590 2020). It is also possible that ammonifying bacteria may be able to capitalize on post-fire high
591 nitrogen content (Johnson & Curtis, 2001), and indeed one study did find that ammonifying
592 bacteria increased post-fire while ammonia-oxidizing bacteria did not (Aceá & Carballas, 1996).
593 For thermotolerance, members of the Firmicutes are good candidates since they are almost all
594 spore-forming bacteria (Barberán et al., 2017; Filippidou et al., 2016). For fast growth or

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595 colonization, the Proteobacteria genus *Massilia* has been hypothesized as a fast responder due to
596 a predicted high 16S copy number (Nemergut et al., 2016; Whitman et al., 2019). We believe
597 that categorizing pyrophilous microbes into traits will improve prediction of biogeochemical
598 cycling post-fire. Just as redwoods survive fire with thick bark and tanoaks are vegetative re-
599 sprouters, it is likely that microbes have similar strategies and this diversity of fire-responsive
600 traits both above and belowground will enhance forest resilience to the unprecedented rise of
601 mega-fires. However, whether they will recover from synergistic effects of introduced pathogens
602 and global change (Simler et al., 2018) remains unclear.

603

604 **Conclusions**

605 In conclusion, we present the first study examining the immediate effects of a megafire
606 on both bacterial and fungal communities with a rare data set of pre- and post-fire samples and
607 also the first study to comprehensively characterize the soil microbial communities of a redwood
608 tanoak forest. We know of only two other instances where pre- and post-fire samples from the
609 same locations exist (Baar et al., 1999; Glassman et al., 2016), but both were in pine forests,
610 focused only on EMF communities, and both lacked an unburned control. We identified a
611 massive increase in the Basidiomycete yeast *Basidioascus* and the bacterial Firmicutes post-fire,
612 and we showed that pyrophilous bacteria and fungi and their traits are phylogenetically
613 conserved at the class level. By comparing our work to other recent molecular characterizations
614 of post-fire microbes in Pinaceae forests (Bruns et al., 2020; Glassman et al., 2016; Whitman et
615 al., 2019), we can now begin to generalize traits of post-fire microbes to other forest types and
616 compare them to analogous traits in plants (Figure 7). For example, we hypothesize certain
617 bacteria (Firmicutes) and fungi (Pyronemataceae) appear to be able to survive fire with

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618 thermotolerant structures, and other fungi (*Penicillium*) or bacteria (*Massilia*) are fast-
619 responders, and trade-offs might exist among these traits. Future studies of post-fire systems in a
620 broad variety of ecosystems, and experimental determinations of microbial traits, will allow us to
621 further characterize and generalize traits of post-fire microbes so that we can refine our
622 conceptual model and reach the level of knowledge of post-fire traits of plants.

623

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630

631 **Competing Interests**

632 The authors declare no conflicts of interest or competing financial interests in relation to the
633 work described.

634

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Enright et al Figure Captions

Figure Captions

Figure 1: A) Map of the Soberanes Fire of 2016 with fire perimeter in orange. Triangles represent locations of individual plots in the plot network that were sampled in 2013 with burned plots in red and unburned plot in blue. B) Sampling scheme used in all plots with soils collected at 2, 6, and 10 meters from the plot center in each cardinal direction (indicated by inverted blue triangles on sampling scheme).

Figure 2: Fire reduced bacterial (A) total richness and (B) mean per sample richness in burned plots and fungal (C) total richness and (D) mean per sample richness in burned plots. Species accumulation curves represent total pre- and post-fire bacterial and fungal OTUs within the burned plots with transparency around the line representing the standard deviation. Mean per sample richness shown plus and minus the standard error. Colors differentiate sampling in 2013 pre-fire and in 2016 immediately post-fire. Shapes differentiate burned (plots 601 and 603) and unburned plots (plot 58). Statically significant difference in richness was tested using ANOVA (for burned plots, $F_{1,1} = 65.73$, $p < 0.001$, for unburned $F_{1,1} = 0.005$, $p = 0.943$). Letters represent Tukey HSD differences.

Figure 3: NMDS of Bray-Curtis Dissimilarity ordinations comparing bacterial composition A) in unburned plot and B) burned plots and fungal composition in C) unburned plot and D) burned plots with colors indicating the 2013 pre-fire and 2016 post-fire samplings shapes differentiating burned and unburned plots. Ellipses represent 95% confidence interval from the centroid for each group. Notice the difference in scales for all NMDS with much smaller scales for NMDS axes in

unburned plots representing a much smaller degree of compositional turnover than for burned plots with much larger axes. Adonis R^2 and p-values represent the difference in composition for pre- versus post-fire. Envfit model depicts which taxa are driving the changes in community composition for B) bacterial or D) fungal communities. The top phyla contributing to change are shown. Identification of the top contributors was done by R^2 value after constraining p value at less than 0.001 and adjusted p -value to less than 0.01.

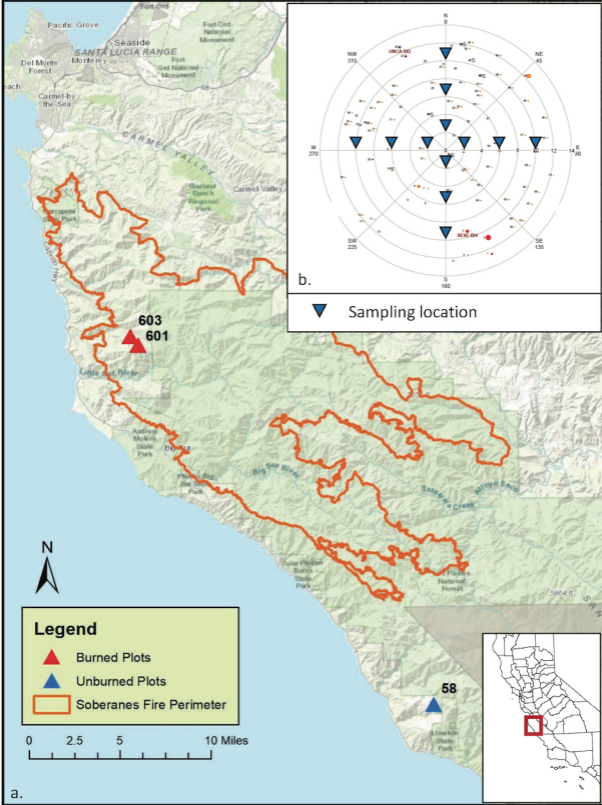
Figure 4: Rank abundance curves of taxa $\geq 1\%$ sequence abundant for bacteria and fungi pre-fire (top) vs. post-fire (bottom) grouped by genus and colored by phyla. Where genus level identification could not be determined, a higher order of classification is given.

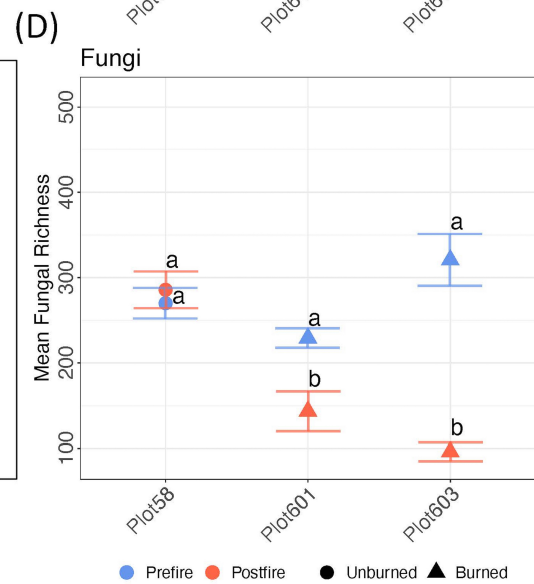
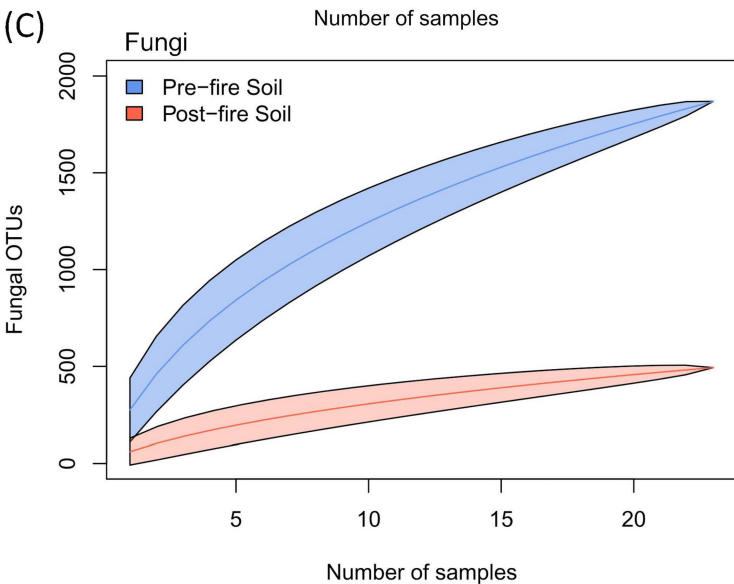
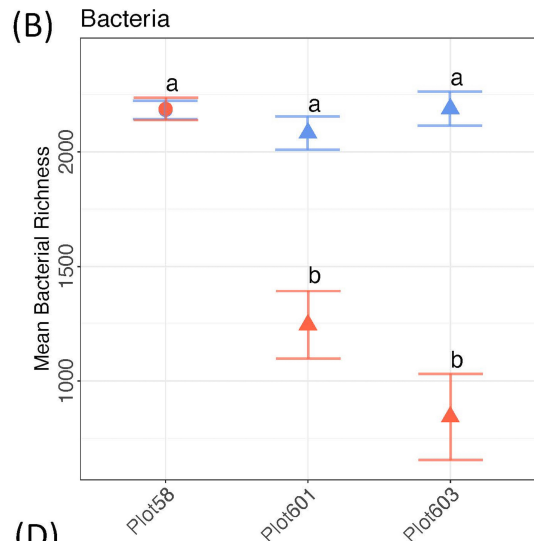
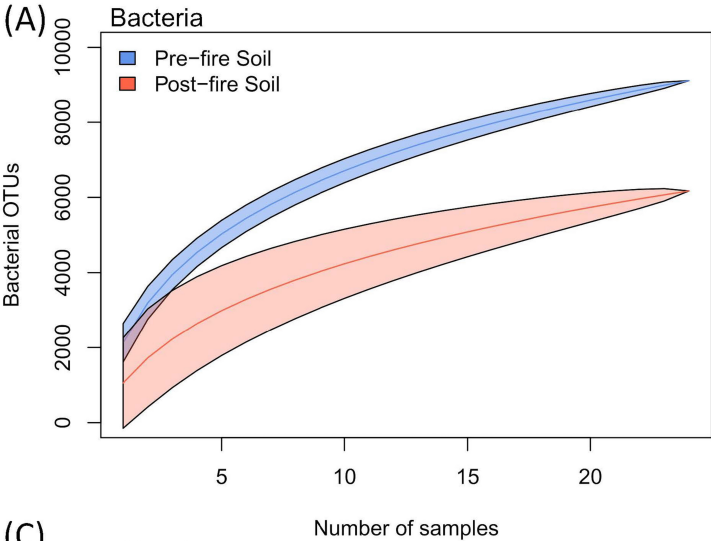
Figure 5: Circular phylogeny of all bacterial OTUs observed based on 16S rRNA. Consensus Lineage refers to the response to fire as measured using DeSEQ2 analysis. Lineages are colored based on positive (blue) or negative (orange) response to fire. The colored bars circling the outside of the phylogeny correspond to each OTUs respective phyla.

Figure 6: Circular phylogeny of all fungal OTUs observed based on ITS1. Consensus Lineage refers to the response to fire as measured using DeSEQ2 analysis. Lineages are colored based on positive (blue) or negative (orange) response to fire. The colored bars circling the outside of the phylogeny correspond to each OTUs respective class.

Figure 7: Conceptual model of hypothesized trait suites for post fire microbes, in comparison to analogous trait suits of fire adaptation in plants. Grimes CSR ecological trade-off directions are

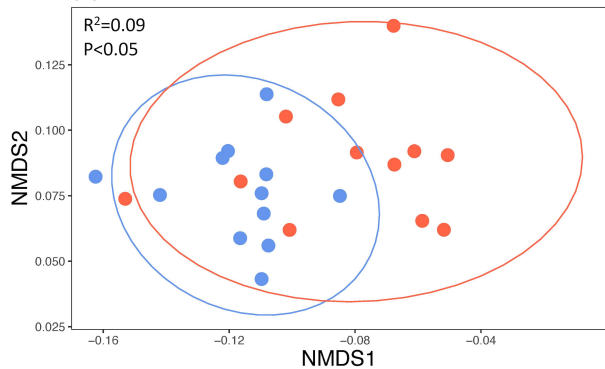
placed inside the triangle following where the corresponding pyrophilous microbial trait suite is hypothesized to relate. A color gradient between trait suites represents that these suites may not be exclusive but rather taxa may fall along a gradient between trait suites. A representation of the microbial trait is placed at each corner (Fast colonization = replicating bacteria, Thermotolerance = fungal sclerotium, Post-fire nutrient acquisition = colonized charcoal) along with an analogous plant trait representation (fast herbaceous growth, serotinous cone, root nodule forming post-fire colonizer, respectively). A brief description of the pyrophilous trait suites and hypothesized taxa placement is located on the right side of the figure.



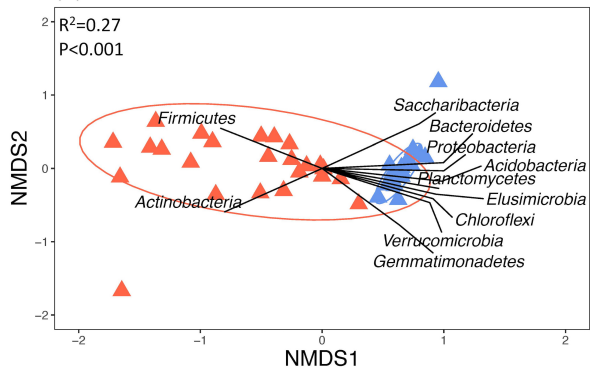


● Prefire ● Postfire ● Unburned ▲ Burned

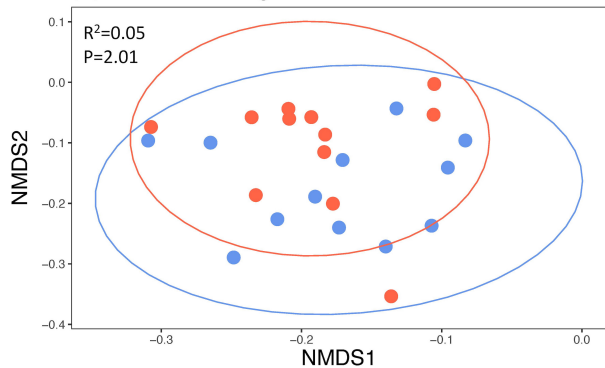
(A) Unburned Bacteria



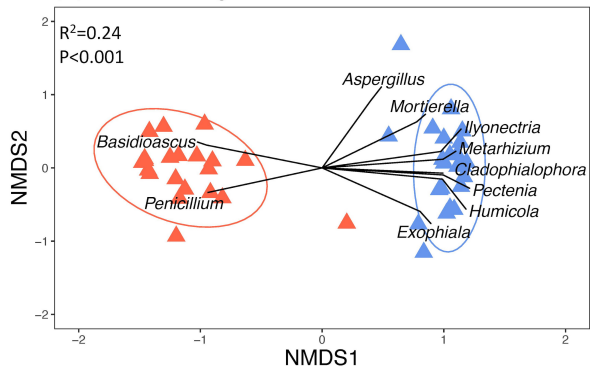
(B) Burned Bacteria



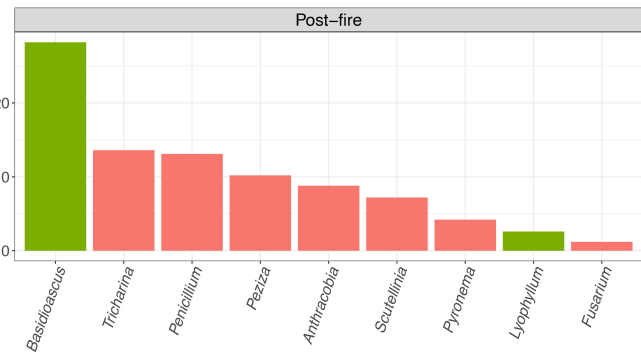
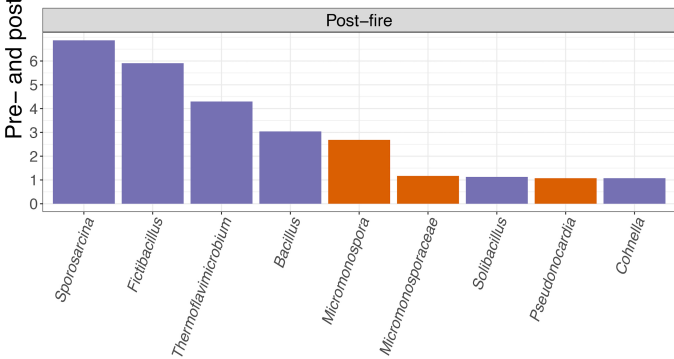
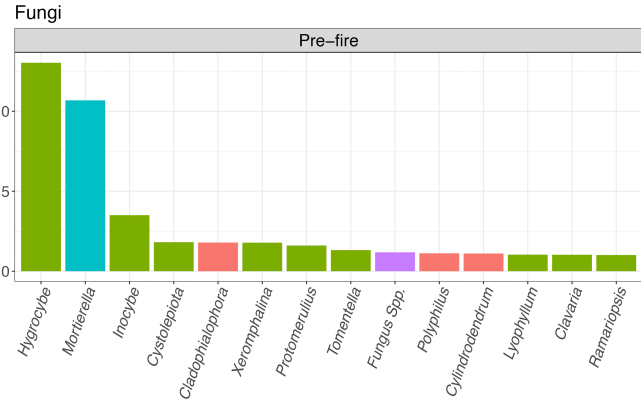
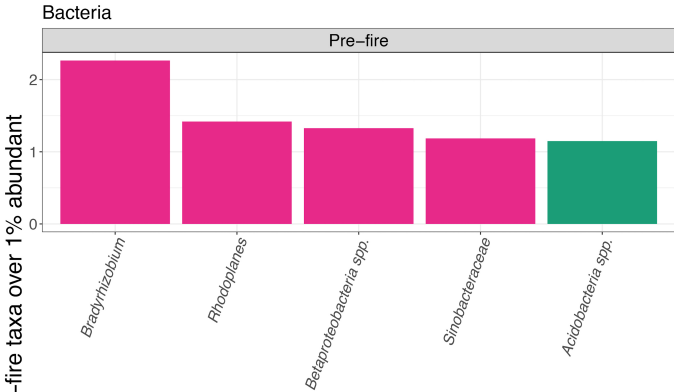
(C) Unburned Fungi



(D) Burned Fungi



● Unburned ▲ Burned ● Pre-fire ● Post-fire



Phylum ■ Acidobacteria ■ Actinobacteria ■ Firmicutes ■ Proteobacteria

Phylum ■ Ascomycota ■ Basidiomycota ■ Mucoromycota ■ Unidentified

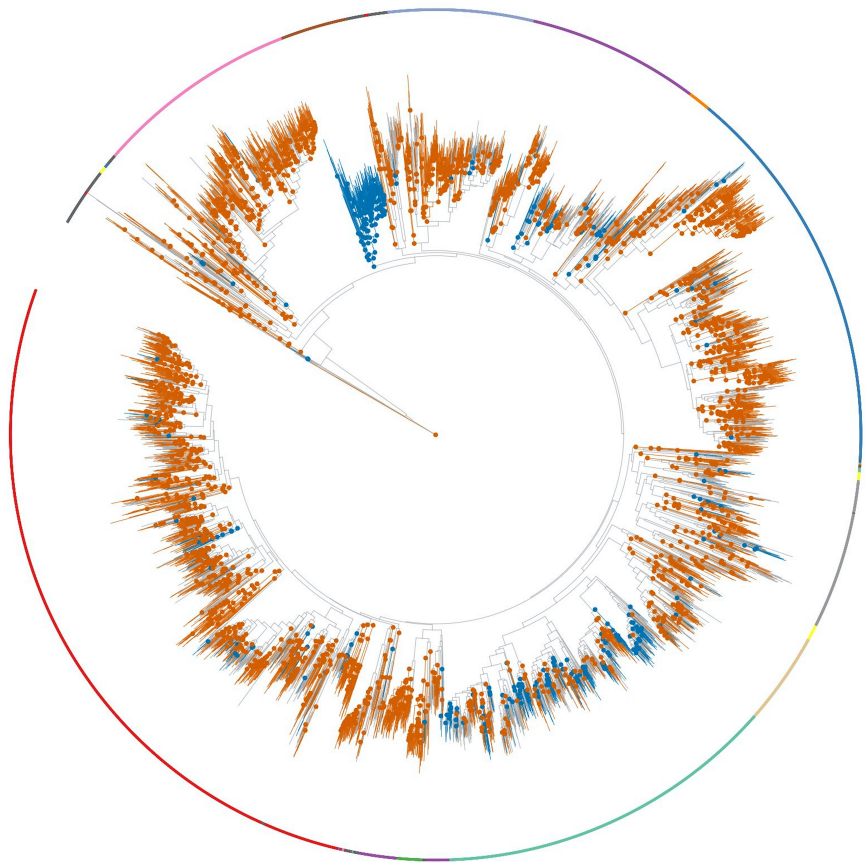
Tree scale: 0.1

Phylum

- Others
- Acidobacteria
- Actinobacteria
- Armatimonadetes
- Bacteroidetes
- Chloroflexi
- Elusimicrobia
- Firmicutes
- Gemmatimonadetes
- Gemmatimonadetes
- Planctomycetes
- Proteobacteria
- Verrucomicrobia
- WS3

Consensus lineage

- Positive
- Negative



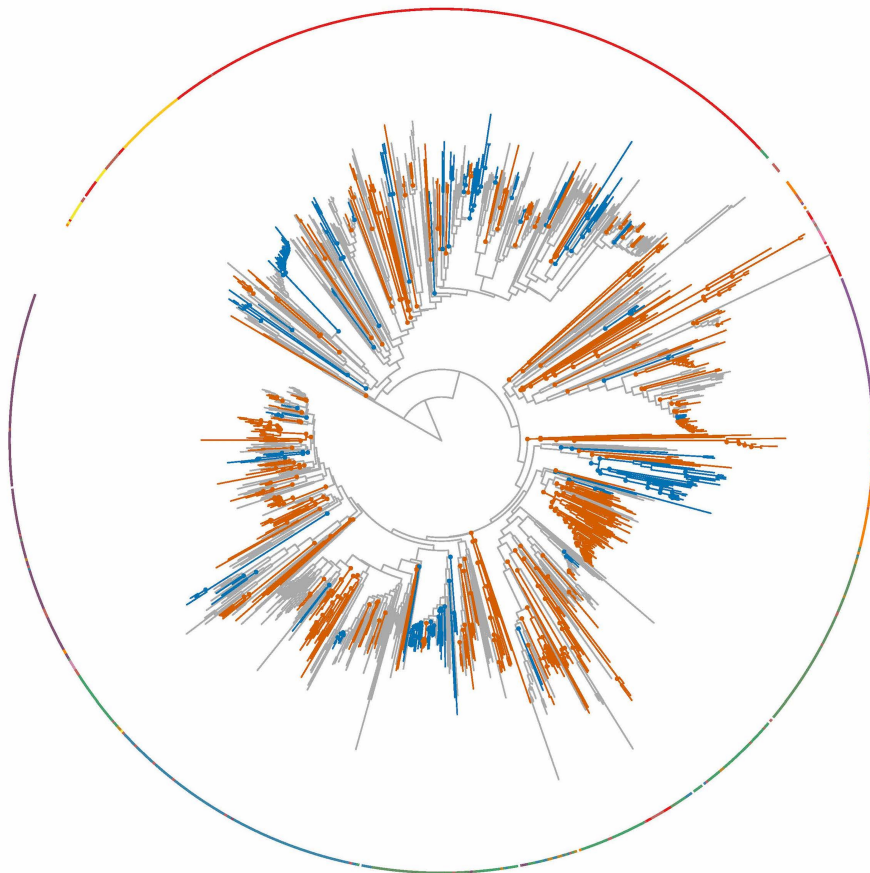
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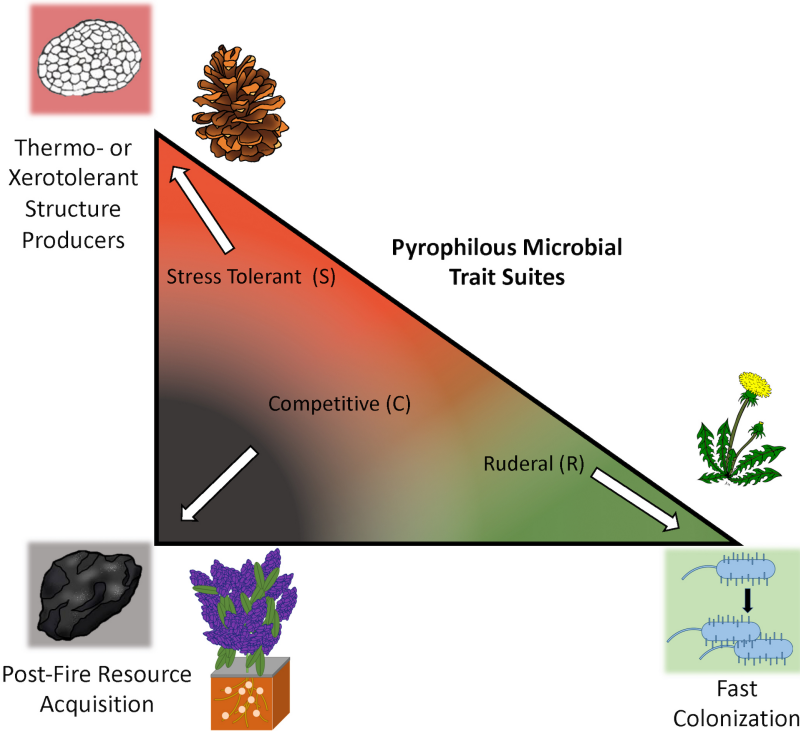
Class

- Agaricomycetes
- Dothideomycetes
- Eurotiomycetes
- Geminibasidiomycetes
- Geoglossomycetes
- Glomeromycetes
- Lecanoromycetes
- Leotiomycetes
- Microbotryomycetes
- Mortierellomycetes
- Pezizomycetes
- Sordariomycetes
- Tremellomycetes
- Umbelopsidomycetes
- unidentified

Consensus lineage

- Positive
- Negative





Post-Fire Resource Acquisition

- Able to breakdown unique resources found after fire (eg. Pyrolyzed organic matter, high nitrogen)
- Able to withstand high pH of deposited ash
- Analogous to post-fire plants that capitalize on high nitrogen in burned soils (e.g. *Ceanothus*)
- Potential taxa:
 - Bacteria: *Arthrobacter*, *Nocardioides*
 - Fungi: *Lyophyllum atratum*, *Pholiota highlandensis*, *Penicillium chrysogenum*

Thermo- or Xerotolerant Structure Producers

- Production of thermotolerant structures (e.g. fungal sclerotia, bacterial endospores)
- Analogous to plant production of thermotolerant structures (e.g. Serotinous cones or thick bark)
- Potential taxa:
 - Bacteria: *Thermoflavimicrobium*, *Bacillus*
 - Fungi: *Pyronema*, *Rhizopogon olivaceotinctus*, *Neurospora crassa*

Fast Colonization

- Fast hyphal extension rates or low doubling time
- Rapid expansion into open niche space
- Analogous to plant vegetative re-sprouting and rapid colonization.
- Potential taxa:
 - Bacteria: *Massilia*
 - Fungi: *Basidioascus*, *Penicillium arenicola*, *Aspergillus*