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Long-term soil fungal community recovery after fire is impacted by climate change
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Abstract:	Though much is known about fungal importance to forest health, there is very little information about factors that impact soil fungal community recovery time after a fire. Soil samples were taken from burn sites within one ecotype of temperate coniferous forest in Utah over a 20-year chronosequence. Sites were selected from available historic burns and were similar in plant community structure, elevation, slope, and aspect. Fungal DNA from these samples was compared to soil from paired unburned sites nearby to measure community similarity and estimate soil fungal recovery rates. Differences between paired burned and unburned sites remained fairly stable over a decadal time scale overall, but fungal community structure was found to recover more quickly in areas with a higher average annual temperatures. A significant positive correlation in community recovery was seen in areas with a difference of as little as two degrees Celsius per year. The only other environmental variable that significantly interacted with time since burn was annual mean precipitation. As global temperatures increase, alpine fires are increasing as well, but these results suggest that fungal community recovery time will be shortened under new climate scenarios.
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2

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4

5 Abstract

6 Though much is known about fungal importance to forest health, there is very little information about
7 factors that impact soil fungal community recovery time after a fire. Soil samples were taken from burn
8 sites within one ecotype of temperate coniferous forest in Utah over a 20-year chronosequence. Sites
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10 slope, and aspect. Fungal DNA from these samples was compared to soil from paired unburned sites
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18 time will be shortened under new climate scenarios.

19

20 Introduction

21 The effect of fires on belowground microbial communities has received increased attention in the past
22 decade due to the importance of microbes to overall ecosystem recovery. Soil microbes interact with
23 plants during disturbance recovery to shape resource availability, community assembly and
24 successional trajectories (Knelman et al., 2015; Sikes et al., 2016; Weidner et al., 2015). Ecosystem
25 recovery from fire disturbance is thus dependent on microbes that facilitate plant succession either
26 directly via obligate symbioses (Dickie et al., 2017) or indirectly via processes such as resource
27 liberation and soil stabilization (Bonner et al., 2019; Claridge et al., 2009; Fuentes-Ramirez et al.,
28 2018). For the purposes of this project, we define "recovery" as resemblance to a nearby unburned
29 plot. It is assumed that no fungal community can be fully "recovered" given that communities are
30 always changing. Unburned fungal communities are also under constant flux, but as burned
31 communities begin to more closely resemble adjoining unburned sites, we treat that as "recovery" in
32 the sense that fire effects are beginning to give way to other site-level forces such as edaphic
33 properties and plant community influences.

34

35 Currently, the reported effects of fire on belowground microbial communities have few consistencies
36 other than a general agreement that full recovery to pre-fire conditions takes place on a decadal time
37 scale (Holden et al., 2013; Köster et al., 2014; Treseder et al., 2004). Reported differences between

studies include varied recovery times for bacteria and fungi (Bárcenas-Moreno et al., 2011; Bárcenas-Moreno & Bååth, 2009) and divergent effects of fire on microbial diversity and abundance in differing biomes (Allison et al., 2010; Dove & Hart, 2017; Hansen et al., 2019). The majority of studies have focused on time since fire as the main effect in their particular ecosystems, and the contrasting details about microbial recovery could be specific to the climatic and edaphic properties of the biomes in which they were observed.

Warmer and drier conditions in many ecosystems due to climate change are increasing the frequency and impact, and decreasing the predictability of, wild fires (Abatzoglou & Williams, 2016; Flannigan et al., 2009). Thus, it is important to continue building knowledge of how soil microbes respond to fires. Furthermore, it is important to understand not only how future climate scenarios alter fire regimes, but whether they will alter the recovery responses of microbial communities in those systems. Here, we conducted an observational experiment along a 20-year fire chronosequence, comparing paired burned and unburned sites along an annual mean temperature gradient in a montane ecosystem dominated by pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma)* forests in Utah, USA. This ecosystem is expected to continue warming at a faster rate than most other biomes with a 20-year projected climate that includes an annual mean temperature of 2 deg C above baseline according to the IPCC AR5 regional synthesis report (Barros et al., 2014). The study design allowed us to test the hypothesis that a warmer climate could alter belowground microbial recovery rates after fires within a single biome.

Methods:

Overview

A range of historic fire events was used to select 11 forested regions of Utah that had burned between 1 and 20 years prior to our study. Each burned site was paired with an adjacent unburned site to serve as controls, giving us a total of 22 sites. Sites were selected to maximize similarity across a range of environmental variables. At each site, we collected burned and unburned soil from the organic horizon of 3 locations, measured canopy and ground cover vegetation, and collected vegetation samples for identification and herbarium curation. We used meta-amplicon sequencing to characterize fungal community structure from each soil sample.

Site Selection

The Utah Department of Natural Resources sourced Utah fire data for the previous 20 years. 300 GPS points 100 m inside of burn boundaries were used to compile national GIS layers including topography, land use and cover, human impacts, and climate data. Habitats were dominated by Pinyon Pine and Juniper, with common understory plant communities dominated by Asteraceae and

75 Poaceae. Sites were spread across Utah from 38.5 to 41.6 deg latitude and ranged in elevation

76 between 1483m and 2969m, with a median elevation of 1660m (Fig. 1). The annual mean temperature

77 at sites ranged from -7.9C to -3.4C with a median of -5.0C. Soil types were predominantly a mixture

78 Nielsen, Sterling, and Steed series.

79 Using these and other site characteristics (see S.I. Table 1), we built a pairwise distance matrix for

80 every possible combination of variables, and selected a subset of the 300 sites that had minimal land

81 variation, but still maintained substantial ranges in burn chronology and annual mean temperature

82 (see S.I. Fig. 1). Effort was made to reduce site variability, especially in plant community structure, and

83 this took precedence over chronosequence sampling density. All raw site data and full code for

84 selecting study sites can be found in the Supporting Information.

85

Field Collection

87 Photography, site marking, and sample collection protocols were designed before field work began.

88 Three soil samples were collected with sterile utensils from each site at a depth of 5 to 10 cm 0.5m

89 from the site center in the North, East, and West cardinal directions. Soils were frozen at -80° within 6

90 hours of collection. Local plant cover was recorded and photographed and representative plant

91 samples were collected for later identification. International Field Collection Forms were filed for each

92 plant collection and all specimens are housed in the Utah Valley University Herbarium (UVSC).

93

DNA Extraction and Library Preparation

95 Genomic DNA from 0.25g of soil was extracted from each sample using DNeasy PowerSoil Kits

96 (QIAGEN, Venlo, The Netherlands). Fungal DNA was amplified with the ITS1F

97 (CTTGGTCATTTAGAGGAAGTAA; Gardes & Bruns 1993) and ITS2 (GCTGCGTTCTTCATCGATGC;

98 White et al., 1990) primers, modified with the addition of Illumina adaptors (Caporaso et al., 2011)

99 using the following protocol: 98 2 min; 22 cycles of: 98 15 s, 52 30 s, 72 30 s; 72 2 min). After 22

100 cycles, the PCR product was diluted 1:12 and 1 µL of this was used as a template for 8 more rounds

101 of PCR with a 60 deg annealing temperature in which bi-directional barcodes bound to reverse

102 complemented Illumina adaptors acted as primers. Resulting barcoded libraries were cleaned,

103 normalized, and sequenced with the Illumina MiSeq platform (V3 chemistry, 2 × 300 bp).

104

Bioinformatics

106 Reads were demultiplexed and barcode sequences were removed by the sequencing center. Quality

107 filtration and bioinformatics were performed in R. Briefly, we extracted the ITS1 region, filtered forward

108 reads based on quality, utilized a clustering-free Divisive Amplicon Denoising Algorithm (DADA) to

109 infer Amplicon Sequence Variants (ASVs) (Callahan et al., 2016), removed chimeras and potential

110 contaminants and assigned taxonomy against a custom ITS1 database.

111 The ITS1 region of the rDNA was extracted from all raw reads using ITSxpress (Rivers et al., 2018).

112 Quality control on ITSxpress output consisted of removing reads with ambiguous base calls and those

113 with a maxEE of >2, and truncating each read when quality scores dropped below 20. Due to lower

114 quality, and to reduce false-positive detection, reverse reads were not used (Pauvert et al., 2019).

115 Filtered forward reads were subjected to de novo chimera detection and removal in DADA2 and

116 potential contaminants were inferred from extraction negatives and removed from all samples using

117 the prevalence method in the decontam package (Davis et al., 2018). Cleaned and filtered ASVs were

118 assigned taxonomy with the RDP Classifier algorithm against a custom database consisting of the

119 UNITE database (v. 1.12.2017) and a custom set of outgroups including ITS1 sequences from

120 metazoans and viridiplantae taken from NCBI. The outgroups added to UNITE can be found in the

121 Supporting Material. Any sequences matching non-fungal taxa were removed. The remaining ASVs

122 that were unambiguously assigned to fungi were used in all downstream analyses within the phyloseq

123 R package (McMurdie & Holmes, 2013). All sequences have been deposited in the NCBI Sequence

124 Read Archive under the accession PRJNA550446.

125

126 *Statistical Analyses*

127   All analyses were performed in R (Version 3.4.4). A PermANOVA model of community composition

128 as an interactive function of Burn Year, Fire Treatment, and Location was fit using the adonis function

129 of the vegan package (Okansen et al., 2016). A community distance matrix was generated with the

130 vegdist function of the vegan package. The community distance between paired burned and unburned

131 sites at the same location was regressed against time since burn and decadal annual mean

132 temperature in a linear mixed-effect model using the lme4 package (Bates et al., 2015) with paired

133 community distance as a response and annual mean temperature and years since burn as predictors.

134 P-values were obtained using the lmerTest package (Kuznetsova et al., 2017). Differential abundance

135 of taxa between burn treatments was analyzed using a beta-binomial model with the corncob R

136 package (Martin et al., 2020).

137

Results

139

140 No fungal community of any burned site we observed had fully rebounded to the alpha diversity or

141 community structure of its unburned counterpart within the 20 year timeframe that was studied. All

142 samples were dominated by Ascomycota and Basidiomycota, regardless of whether they were burned

143 or not, but the relative dominance of these two main phyla decreased in older sites. In burned sites 14

144 years or older, Ascomycota and Basidiomycota still dominated in terms of relative abundance, but

145 other phyla such as Mucormycota and Olpidiomycota were also more common (Fig. 2). Relative

146 abundance of taxonomic groups did not correlate significantly with annual mean temperature,

147 elevation, latitude, or soil type.

148

149 Alpha diversity was not significantly different overall between aggregated burned and unburned sites

150 (Fig. 3), and there was no consistent pattern between burn status and Shannon diversity in between-

site pairs.Beta diversity was significantly affected by burn status (P = 0.035), time since burn (P=0.001), and annual mean temperature (P=0.001) in an interactive PermANOVA model (S.I. Table 2). Further, there was a significant interaction term between time since burn and annual mean temperature (P=0.002).

Mean community distance between paired burned and unburned sites showed a small but significant decrease over time since burn, congruent with previous research showing the decadal scale of recovery for fungi after fires. However, in this study, we also found that annual mean temperature was an important predictor of the rate of recovery (Fig. 4; LMER; P < 0.0005), and each temperature increase of 1 deg C accounted for an additional 5% community similarity along our full chrono-series (S.I. Table 3).

When location-specific plant community data was added to linear mixed-effect models, no significant correlation between plant cover or plant community and paired fungal community distance was found. Additionally, a Mantel test between plant and fungal community distances showed no significant correlation. These results likely stem from the high similarity in plant communities at each location. Differential abundance analyses yielded 4 fungal families that were significantly enriched in either burned or unburned locations across all sites (S.I. Fig. 2). The basidiomycetes Serendipitaceae and Thelophoraceae had greater abundance and variability in unburned sites, and the ascomycetes Microascaceae and an unclassified family-level taxon in Dothidiales had greater abundance and variability in burned sites.

The broad diversity patterns we observed generally reflect those seen in related research. For example, our forest soils were dominated by Ascomycota and Basidiomycota phyla, but this dominance was reduced over time since burn as other phyla such as Mucormycota, Rozellomycota, and Olpidiomycota became detectably more abundant roughly 14 years after fire. However, where other work in Boreal forests found that Basidiomycota was initially reduced after fire and recovered over time (Sun et al., 2015), our results from this montane biome show Ascomycota following that pattern instead.

Discussion

Though most studies on fungal recovery after fires have taken place in a single biome and focused on chronology as the main predictor, Dove and Hart (2017) showed via meta-analysis that the magnitude of at least the initial fungal community responses to fire can vary based on fire frequency and biome type. These are important observations because they suggest hypotheses to help explain observed discrepancies in fungal recovery trajectories between studies.

Here, we tested whether large-scale climatic factors could also help explain variance within a single biome. Comparing nearby pairs of burned and unburned sites along a forest fire chronosequence showed that climatic conditions can have a role in soil fungal community recovery trajectories. In particular, our observation that annual mean temperature of a site has a small but significant effect on recovery speed is a possible example of how local environmental variation can help explain discrepancies in fungal recovery times after fires.

Temperature directly affects microbial activity, but can also influence microbial community composition, competition, and secondary metabolite production (Bárcenas-Moreno & Bååth, 2009; Yogabaanu et al., 2017). Warming temperatures also affect plant succession trajectories (Prach et al., 2007) and plant succession is an important covariate for understanding fungal succession (Davey et al., 2015; Rudgers et al., 2007; Zhang et al., 2018). Taken together, the linkages between plant and fungal succession dynamics and temperature are difficult to uncouple. By limiting our study to a single biome and to sites with very similar plant communities, we were able to isolate, to some degree, the effect of temperature on fungal recovery from fire. Other factors besides plant community have been directly linked to fungal community dynamics, however. For instance, it has been shown that soil pH and nutrient content are strong drivers of fungal community structure (Glassman et al., 2017). Since fire can have a strong impact on soil properties such as pH, C:N ratio, and SOC content (Boerner et al., 2009), it is possible that these edaphic characters varied between burned and unburned paired sites, though these variables were not measured in this study. Additionally, one of the site pairs in this study, burned 13 years prior to observation, had highly similar fungal communities (Fig. 3). Removing this site did not affect the significance of mean annual temperature in our model, but did reduce the effect size. It seems clear that local stochastic processes in community assembly can reduce our ability to detect broader patterns.

In this montane biome, with mean annual temperatures below freezing, liquid water can be a limiting resource for plant and fungal growth (Monson et al., 2002, 2006). An increase in mean annual temperature at these sites likely means more days when fungi can be metabolically active. Our results support this assumption, in that warmer temperatures led to quicker recovery times.

Due to ongoing recent climate change, any chronosequence studies must inevitably deal with the potential covariance of time since burn and mean annual temperature. There was some correlation between these two variables in the present study, with older sites tending toward lower mean annual temperatures, which could be an effect of climate change (S.I. Fig. 2). We were unable, however, to acquire site-specific environmental variables from 20 years prior, to test this due to lower resolution of these observations from that time period.

Additionally, climate warming is inextricably linked to other variables that have been shown to affect fire severity and fire frequency such as reduced soil moisture and increased fuel load (Harvey, 2016). These factors could also be important drivers of fungal recovery trajectories. These legacy factors

228 were not considered in the present study since none of our selected sites had burned in the previous
229 75 years and were from very similar biomes, but they may be important to consider in work of this
230 nature.

231

232 Our results indicate that even within a single biome, slight alterations to climatic variables like mean
233 annual temperature can affect the rate of fungal recovery from fires. This has implications for broader
234 disturbance modeling efforts. For example, the reduction and rebounding of soil fungal communities is
235 important for dynamic vegetation models, but many disturbance models use predictors that are
236 simulated in isolation, neglecting any potential interaction effects (Seidl et al., 2017). As climate warms
237 and fires in these biomes increase in intensity and frequency, the loss of fungal diversity and
238 ecosystem services could be, to some small degree, mitigated by increased recovery rates due to
239 warming in these often frozen montane soils.

240

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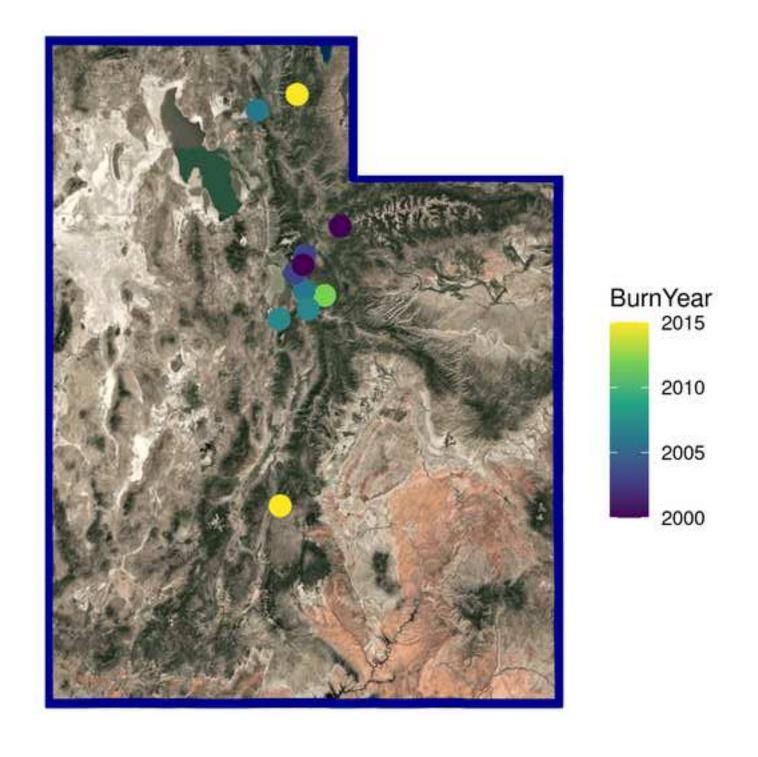
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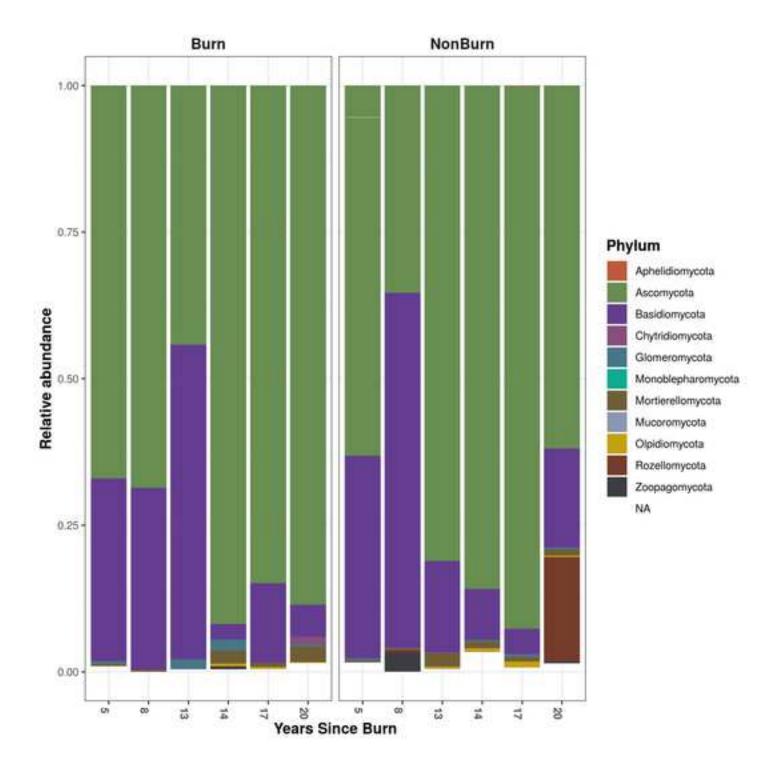
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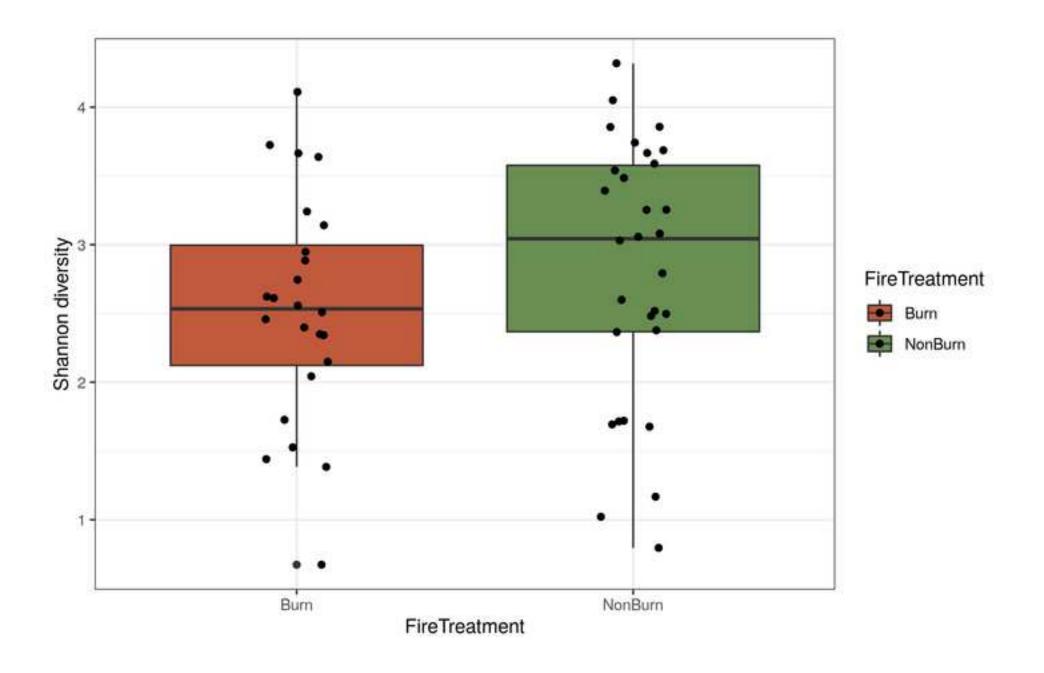
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Figure 1 - Site Map

Figure 2 - Phylum Relabund

Figure 3 - AlphaDiv

Figure 4 - DistVTime

Figure 4 - DistVTime