

Contrasting fungal responses to wildfire across different ecosystem types

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Abstract

Wildfire affects our planet's biogeochemistry both by burning biomass and by driving changes in ecological communities and landcover. Some plants and ecosystem types are threatened by increasing fire pressure while others respond positively to fire, growing in local and regional abundance when it occurs regularly. However, quantifying total ecosystem response to fire demands consideration of impacts not only on aboveground vegetation, but also on soil microbes like fungi, which influence decomposition and nutrient mineralization. If fire-resistant soil fungal communities co-occur with similarly adapted plants, these above- and belowground ecosystem components should shift and recover in relative synchrony after burning. If not, fire might decouple ecosystem processes governed by these different communities, affecting total functioning. Here, we use a natural experiment to test whether fire-dependent ecosystems host unique, fire-resistant fungal communities. We surveyed burned and unburned areas across two California ecosystem types with differing fire ecologies in the immediate aftermath of a wildfire, finding that the soil fungal communities of fire-dependent oak woodlands differ from those of neighbouring mixed evergreen forests. We discovered furthermore that the latter are more strongly altered compositionally by fire than the former, suggesting that differences in fungal community structure support divergent community responses to fire across ecosystems. Our results thus indicate that fire-dependent ecosystems may host fire-resistant fungal communities.

KEYWORDS

climate change, community ecology, environmental DNA, fire, fungi, soil

1 | INTRODUCTION

Biotic and abiotic processes together drive the Earth's biogeochemical cycles. The planet's largest carbon fluxes, photosynthesis and decomposition (Raich & Schlesinger, 1992) are governed by plants, microorganisms and their mutual biotic interactions (Falkowski et al., 2008; Swift et al., 1979; Van Der Heijden et al., 2008). Abiotic disturbances like wildfire can release large amounts of carbon purely through combustion (Van Der Werf et al., 2017), but they also affect the Earth's carbon cycle by setting in motion longer-term biotic

changes in impacted ecosystems and regions (Bond et al., 2005; Hébert-Dufresne et al., 2018). As accelerating climate change alters global fire regimes (Westerling et al., 2006), measuring how fire affects ecosystems biotically alongside its more apparent immediate abiotic consequences, which can include not only combustion emissions but also biogeochemical soil changes (Cook, 1994; Hartshorn et al., 2009), is becoming increasingly important.

Perhaps in part because our modern ecosystem concept has itself grown out of the study of plant communities (Tansley, 1935), researchers seeking to quantify ecosystem change and recovery

after wildfire tend to focus on the aboveground responses of vegetation (e.g. Bartels et al., 2016; Forrestel et al., 2011). From this body of work, we have learned that just as variability exists in wildfire spread and intensity (Van Wagtenonk et al., 2018), so also is it found in the response of plant species and ecosystems to fire (Gärtner et al., 2014), which is a legacy of fire's pervasive influence on plant evolution (Keeley et al., 2011). In fact, while ecosystem development and distribution were historically conceptualized as a deterministic ontogenetic consequence purely of climate (Clements, 1936; Holdridge, 1947), we now know that a number of ecosystems may instead be better described as fire-dependent, or 'pyrogenic'. This means that their regional occurrence is driven also in large part by their requirement for regular fire (Bond et al., 2005), and furthermore, that they may contain plant species whose traits themselves allow fires to more easily ignite and spread (Ellair & Platt, 2013).

However, no ecosystem is composed of plants alone, which means that measuring one only by its constituent plant populations is incomplete at best. Aboveground vegetation is supported by and interacts with many other organisms (Van Der Heijden et al., 2008), including a vast community of root-associated soil microbes like mycorrhizal fungi, which enhance plant nutrient uptake and growth (Smith & Read, 2008). Moreover, it is not obvious that the impacts of disturbances like fire should be felt symmetrically by plant and soil microbial communities since the immediate effects imposed on them differ, with soil communities comparatively buffered from temperature changes and, relative to plants, shielded from direct tissue loss (Raison et al., 1986). Because the fates of these co-occurring, interacting organisms are inevitably intertwined, asynchrony in the fire responses of plants and soil microbes could affect long-term ecosystem recovery. The effects of fire on soil microbial communities thus merit investigation on both philosophical and pragmatic grounds.

Soil fungi are intimately linked to both photosynthesis and decomposition (Smith & Read, 2008; Van Der Wal et al., 2015) and may be especially vulnerable to fire (Dooley & Treseder, 2012; Pressler et al., 2019). Naturalists have long noted that several characteristic Ascomycota genera appear to thrive after wildfire (Warcup, 1990; Wicklow, 1975) and that wildfires initiate successional sequences belowground (Baar et al., 1999; Visser, 1995). Yet just as a wide range of plant and ecosystem responses to fire have been observed, so also does the fire response of the soil fungal community vary (Chen & Cairney, 2002; De Román & De Miguel, 2005; Hansen et al., 2019). Fungi have developed a variety of evolutionary adaptations to fire, like dormant or heat-resistant spores and sclerotia (Nguyen et al., 2012; Peay et al., 2009), and it follows that communities where species with such adaptations are common might be less compositionally altered by wildfire than others. Indeed, some evidence indicates that pyrogenic ecosystems might host, alongside their fire-adapted plant communities, distinct soil fungal communities that resist fire-related change (Hansen et al., 2019; Oliver et al., 2015). However, others have also observed significant short-term rearrangement of fungal community structure after fire even within these ecosystem types (Semenova-Nelsen et al., 2019).

To determine whether the fungal communities of pyrogenic ecosystems differ in their sensitivity to fire relative to those of other ecosystems, we took advantage of a natural experiment, surveying soil fungal communities across two California ecosystem types with differing fire ecology in the immediate aftermath of a wildfire: mixed evergreen forests dominated by Douglas-fir (*Pseudotsuga menziesii*) trees and neighbouring open Oregon oak (*Quercus garryana*) woodlands. The ecosystems found in this region of the United States have all been shaped in some respect by fire, but these two ecosystem types and their constituent plant species differ in their adaptations to it (Van Wagtenonk et al., 2018). Oak woodland ecosystems, like other savannahs and woodlands with low tree density (Staver et al., 2011a, 2011b), depend upon regular fire (Finney & Martin, 1992; Hastings et al., 1997; Peterson & Reich, 2001). Oregon oaks resist moderate fire, resprout following severe fire (Van Wagtenonk et al., 2018) and produce highly flammable litter (Engber & Varner, 2012). In contrast, mixed evergreen forests are later successional ecosystems (Sawyer, 2007), which can develop as Douglas-firs encroach and overgrow shade-intolerant oaks (Cocking et al., 2014), reducing the likelihood of severe fire with comparatively inflammable litter (Engber et al., 2011). Historically, oak woodlands in this region burned more frequently than mixed evergreen forest, but fire suppression reduced fire frequency in the 20th century (Finney & Martin, 1992; Van Wagtenonk et al., 2018). To help control resulting encroachment of Douglas-fir into oak woodland (Barnhart et al., 1996), prescribed fire has been in use at our study site since the 1980s (Hastings et al., 1997).

Using generalized dissimilarity modelling and multidimensional ordination, we compared fungal communities in each ecosystem type and in locations either affected or unimpacted by recent wildfires in this region. Based on previous studies (Dickie et al., 2009), we predicted that oak woodlands and mixed evergreen forests would **H1** host distinct fungal communities. Because of the different fire regimes characteristic of these plant communities, we also hypothesized that **H2** these two distinct fungal community types would exhibit responses of contrasting magnitude to wildfire, with differences between burned and unburned fungal communities greater within mixed evergreen forests than in fire-dependent oak woodlands.

2 | METHODS

2.1 | Field sites

Our study was carried out at two parks, Trione-Annadel State Park (hereafter Trione-Annadel; 38.4329° N, 122.6324° W) and Hood Mountain Regional Park and Preserve (hereafter Hood Mountain; 38.4601° N, 122.5515° W), in Sonoma County, California, USA, just north of the San Francisco Bay Area. The climate of Sonoma County is typically Mediterranean, with a mean annual temperature of 14°C and annual precipitation of approximately 251 mm ("Climate & Weather Averages in Sonoma, California, USA," n.d.). This region

is characterized by a heterogeneous mixture of mixed evergreen forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and grassy, open woodlands home to trees like Oregon white oak (*Quercus garryana*). Mixed evergreen forests here commonly also contain madrone (*Arbutus menziesii*) and California laurel (*Umbellularia californica*) (Finney & Martin, 1992). Historically, California mixed evergreen forests in this region had fire intervals of ten to fifteen years, while intervals in the oak woodlands at Trione-Annadel were often shorter than ten years (Finney & Martin, 1992).

Portions of Trione-Annadel and Hood Mountain burned during the October 2017 North Bay wildfires, which consumed over 90,000 hectares and claimed 44 lives (Nauslar et al., 2018). In December 2017, we collected soil from burned and unburned areas in both parks (Figure 1). At Trione-Annadel, we established twelve sites (Figure 1): three each in burned and unburned oak woodlands and mixed evergreen forest. At each site, we selected five trees of the focal species (*Q. garryana* or *P. menziesii*, respectively) located at least 5 m apart from one another and used an ethanol-sterilized trowel to collect soil from the top ten centimetres approximately one metre from the trunk, after gently clearing loose duff and litter. We did not quantify organic horizon depth prior to sampling. At Hood Mountain, we established three sites each in burned and unburned mixed evergreen forests (a total of six sites; Figure 1) and collected soil according to the same protocol. Ninety unpooled soil samples were collected in total. Each sample was kept separate and transported back to Stanford University at 4°C for processing. From each sample, a 0.25 g subsample was frozen at -80°C for later DNA extraction, amplification and sequencing. A second portion of soil was air-dried for measurement of pH in CaCl₂ and determination

of carbon and nitrogen content using an elemental analyser. Nine samples were lost during a laboratory move, leaving 81 in total for chemical analyses.

2.2 | Molecular work and bioinformatics

DNA was extracted from 0.25 g of each soil sample with a Qiagen DNeasy PowerSoil kit according to the manufacturer's instructions (Qiagen; Hilden, Germany); one of our 90 samples did not extract successfully. The fungal internal transcribed spacer (ITS) region was amplified using polymerase chain reaction (PCR) in a 96-well plate using modified version of the ITS1F-KYO1 and ITS2-KYO2 primers (Toju et al., 2016). Primer modification allowed molecular tags for multiplexing to be attached with a second PCR following Toju et al. (2016). Product was verified with gel electrophoresis and then cleaned using a magnetic bead purification method (Talbot et al., 2014). After fluorometric DNA quantification using Qubit (Thermo Fisher Scientific; Waltham, MA, USA), we pooled samples at equimolar concentration and submitted our library for 2 × 300 Illumina MiSeq sequencing at the Stanford Functional Genomics Facility. Raw sequences are deposited in the United States National Center for Biotechnology Information Sequence Read Archive (Accession no. PRJNA679734).

We received a total of 13,872,586 demultiplexed reads across our 89 samples, with an average of 155,872 reads per sample. Using a DADA2 ITS pipeline (Callahan et al., 2016), we quality filtered, denoised, merged forward and reverse reads, and removed chimeric sequences. Parameters used followed those recommended

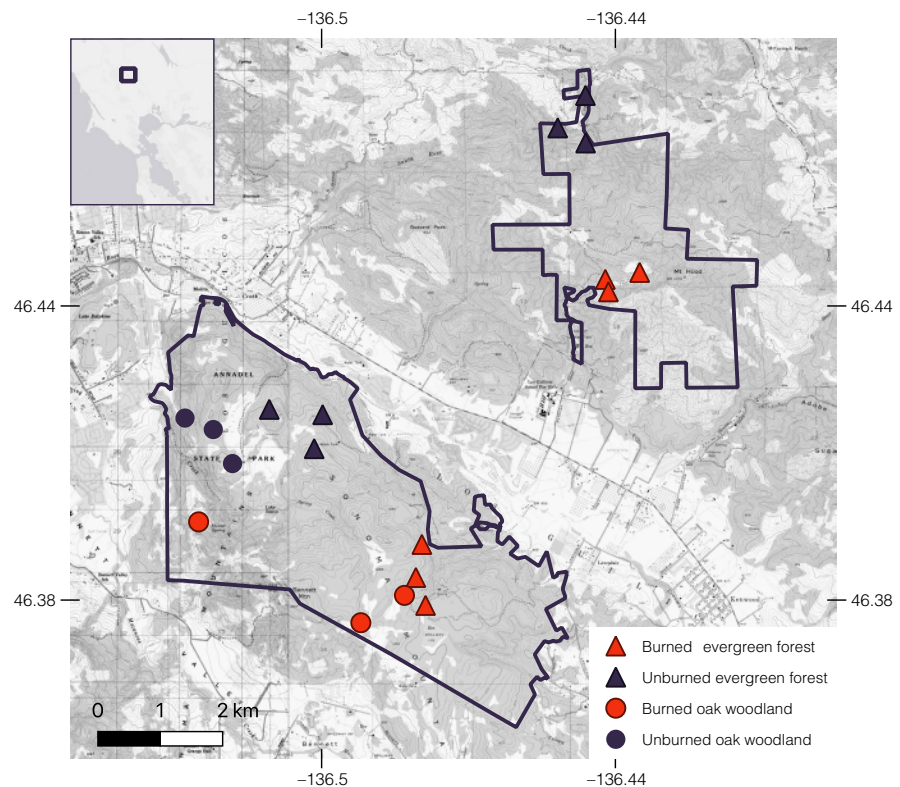


FIGURE 1 Sampling site locations in Hood Mountain Regional Park and Preserve and Trione-Annadel State Park (both outlined) in Sonoma county, California, United States. Park boundaries are drawn according to the specifications of the California State Park Department and Sonoma County Regional Parks Office. The inset depicts the location of the study sites relative to the greater San Francisco Bay Area, California, United States.

(Callahan, n.d.), but with the quality score minimum for read truncation changed from two to nine in order to improve output quality. We retained 12,719,576 reads, with an average of 144,541 per sample; two low-quality samples did not pass quality filtering. Since ecological inference is not hindered by the use of amplicon sequence variants rather than operational taxonomic units (Glassman & Martiny, 2018; Pauvert et al., 2019) and the former conserves information relative to the latter, we did not perform any post hoc operational taxonomic unit clustering. We used the DADA2 default naïve Bayesian classifier (Wang et al., 2007) to assign taxonomy to amplicon sequence variants based on the UNITE database (Kõljalg et al., 2013), then classified taxa to functional guild with FUNGuild (Nguyen et al., 2016). FUNGuild classifications are not mutually exclusive (that is, a single amplicon sequence variant may be classified as belonging to more than one functional guild), but for subsequent analyses we assigned a single functional category to each using the following order of priority: mycorrhizal > pathogenic > saprotrophic. Prior to analyses, we rarefied samples to an even read depth while trying to maintain maximum sample coverage, retaining 13,365 reads per sample. We removed one sample with fewer than this quantity of reads, leaving us with 86 samples for downstream community analysis. Our final data set contained 9813 amplicon sequence variants, of which we assigned 2627 as saprotrophic, 1142 as mycorrhizal and 843 as pathogens. Of the 1142 mycorrhizal amplicon sequence variants, 884 (77.4%) were ectomycorrhizal and 175 (15.3%) were arbuscular mycorrhizal, which we attribute both to the dominance of ectomycorrhizal plant species at our study sites and our use of ITS primers, which are not preferred for arbuscular mycorrhizal fungi (Hart et al., 2015). In our primary downstream analyses, we do not distinguish between different types of mycorrhizal fungi.

2.3 | Statistics

All statistical analyses were carried out with R (R Core Team, 2018) and package Phyloseq (McMurdie and Holmes, 2013), while plots were generated with GGPLOT2 (Wickham, 2016) and COWPLOT (Wilke, 2019). For each of our samples, we acquired remotely sensed measures of tree canopy cover and fire-caused canopy damage from county-specific gridded data products (Tukman Geospatial LLC, 2019), which we used in downstream modelling. Though vegetation and fire damage were verified at all sites in the field, two of our burned sampling locations were not covered by the fire canopy damage data product. We assigned them values identical to their nearest neighbours.

We used generalized dissimilarity modelling as implemented in R package gdm (Fitzpatrick et al., 2020) to compare the relative influences of geography, fire (categorical, as assigned in the field, as well as continuous, as remotely sensed canopy damage), soil chemistry and categorical (mixed evergreen forest vs. oak woodland) and continuous (remotely sensed per cent canopy cover) ecosystem properties on soil fungal community similarity. With partial canonical correspondence analysis as implemented in R package vegan

(Oksanen et al., 2019), we then assessed correlations with the environmental factors identified *via* generalized dissimilarity modelling as significant at $\alpha = 0.05$ among the 25 most abundant fungal genera, controlling for spatial autocorrelation of samples following Fletcher and Fortin (2018). We chose to focus on environmental factors that our upstream analysis identified as important because generalized dissimilarity modelling is robust to multicollinearity among predictors (Glassman et al., 2017), which we anticipated *a priori* due to the established influence of fire on soil chemistry (Neary et al., 1999) and the inherent link between fire category and remotely sensed canopy damage. We note also that selective rather than complete inclusion of environmental covariates is generally encouraged in canonical correspondence analysis (Oksanen, 2019). To verify that canonical correspondence analysis was appropriate for our data set, we also first confirmed that the community matrix maximum axis length calculated *via* detrended correspondence analysis was greater than 4, following Lepš and Šmilauer, (1999). For both generalized dissimilarity modelling and partial canonical correspondence analysis, the subset of samples with both fungal community and complete soil chemistry data ($n = 75$) were used. To assess mean site-level differences in fungal communities, we used permutational analysis of variance as implemented in *adonis* from R package *vegan* (Oksanen et al., 2019) with Bray–Curtis dissimilarities, comparing the effects of fire (burned vs. unburned), ecosystem type (mixed evergreen forest vs. oak woodland) and the interaction between the two.

To compare richness of functional guilds between different ecosystem and fire categories (burned vs. unburned), we used generalized linear mixed effects models as implemented in R package *lme4* (Bates et al., 2015), treating each sample as an individual replicate. We included categorical fixed effects for fire, ecosystem and an interaction between the two, as well as a random effect for site to account for spatial autocorrelation as recommended by Zuur et al. (2009). We tested the significance of terms in our generalized linear mixed effects models with ANOVA from R package *car* (Fox & Weisberg, 2011), utilizing type II sum of squares for p-value calculation by default and type III only if the interaction term was identified as significant at $\alpha = 0.05$ (Langsrud, 2003). For count variables like richness, models used a Poisson distribution, while proportional abundance models used a Gaussian distribution. For post hoc identification of significant differences between groups in linear mixed effects models, we used *lsmeans* from R package *lsmeans* with Tukey-adjusted p-values (Lenth, 2016). We used the same analytical approach to examine variation in soil chemistry, employing an identically structured Bayesian linear mixed effects model with default priors as implemented in R package *blmer* (Chung et al., 2013) for soil pH, as a frequentist model failed to converge.

3 | RESULTS

In support of **H1**, fungal community structure, in terms of richness and composition, significantly varied across our study sites. There was a strong effect of fire on total richness ($\chi^2 = 15.3541, p < .001$)

but no effect of ecosystem type—that is, evergreen forest vs. oak woodland ($\chi^2 = 2.78$, $p = .095$; Figures 2a, 3a; Table S1). Both ecosystem type ($\chi^2 = 19.53$, $p < .001$) and fire ($\chi^2 = 9.20$, $p < .001$; Table S1) significantly affected mycorrhizal richness; post hoc Tukey testing suggested that this was driven by variation between ecosystems in responses to fire (Figure 2b; Table S2). Indeed, in support of H2, there was a significant interaction between the two factors, indicating that the effect of fire on mycorrhizal fungal richness varied with ecosystem type ($\chi^2 = 9.07$, $p = .003$; Table S1). Investigation specifically of ectomycorrhizal or arbuscular mycorrhizal richness returned qualitatively equivalent results (Figure S1), with the exception that arbuscular mycorrhizal communities were generally more species-rich in oak woodlands than in mixed evergreen forests (Figure S1b), which was not the case with ectomycorrhizal communities (Figure S1a). Richness of saprotrophic communities varied significantly with both fire ($\chi^2 = 15.13$, $p < .001$) and ecosystem type ($\chi^2 = 5.23$; $p = .022$; Figure 2c), and pathogen communities were not significantly affected by any tested factor (Figure 2d).

The proportional abundance of mycorrhizal sequences in our samples was significantly affected by ecosystem type ($\chi^2 = 11.27$, $p < .001$) and an interaction between ecosystem type and fire ($\chi^2 = 8.49$, $p = .004$; Figure 3b; Table S3). Just as with overall richness, mycorrhizal proportional abundance was thus differently affected by fire in oak woodlands and evergreen forests, in support of H2. The proportional abundances of saprotrophic and pathogenic fungi were not significantly affected by any tested factor.

Our full generalized dissimilarity model was highly significant ($p < .001$) and explained 54.72% of the deviance in fungal community structure (Figure 4). Backward variable elimination with *gdm*.*varImp* identified geographical distance, ecosystem type, fire, per cent canopy cover, soil pH and soil carbon content as significant

predictors ($p < .05$) while excluding canopy damage and soil nitrogen content. We used this subset of significant environmental factors as predictors in our downstream partial canonical correspondence analysis.

Partial canonical correspondence analysis on the 25 most abundant fungal genera confirmed significant effects of fire ($F = 5.99$, $p = .001$), ecosystem type ($F = 3.06$, $p = .003$; Figure 5a), soil pH ($F = 2.29$, $p = .01$) and soil C (%) ($F = 2.05$, $p = .03$). Permutational analysis of variance with the full set of amplicon sequence variants averaged by site revealed significant effects of fire ($F = 4.31$, $p = .001$), ecosystem type ($F = 4.79$, $p = .001$) and, in support of H2, an interaction between the two ($F = 2.63$, $p = .006$; Table S4). Nonmetric multidimensional scaling ordination using Bray–Curtis dissimilarities illustrated this starkly, with extreme separation between burned and unburned mixed evergreen forest sites and weaker separation between burned and unburned oak woodland sites (Figure 5b).

Linear mixed effects modelling detected a marginally significant effect of fire on soil nitrogen content ($\chi^2 = 4.04$, $p = .044$; Figure S2b), but post hoc Tukey testing did not identify any differences among groups. Soil carbon content was not significantly affected by any tested factor (Figure S2a). Soil pH was affected significantly by fire ($\chi^2 = 27.41$, $p < .001$), ecosystem type ($\chi^2 = 9.65$, $p = .002$) and an interaction between the two ($\chi^2 = 8.56$, $p = .003$; Figure S2c).

4 | DISCUSSION

We discovered (1) that fungal communities differ between California oak woodland ecosystems and neighbouring mixed evergreen forests, in support of H1, and (2) that oak woodland fungal communities exhibit less change after wildfire than mixed evergreen forest fungal

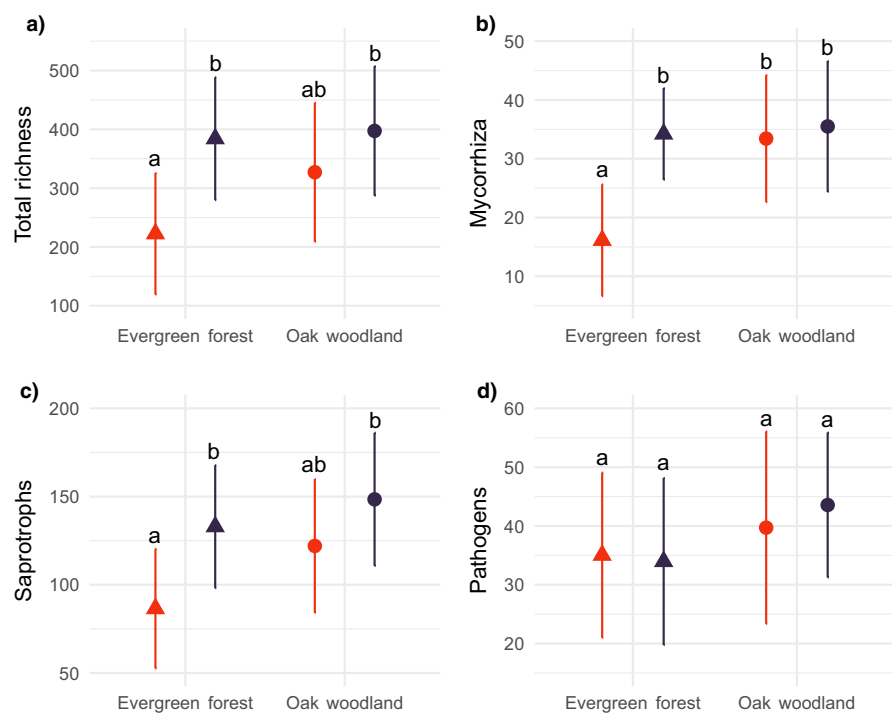


FIGURE 2 Total fungal richness (a) and richness of three functional guilds (b–d) as classified by FUNGuild (Nguyen et al., 2016). Circles and triangles represent means, while error bars represent one standard deviation above and below. Red represents fire-affected ecosystems, while dark blue represents unburned ecosystems. Shared letters indicate no significant difference between groups at $\alpha = .05$.

communities, supporting H2 and qualitatively mirroring the overall differences in fire ecology represented by the two ecosystem types themselves. In oak woodland systems, which require regular fire (Hastings et al., 1997), fungal communities appear to be only mildly altered by burning (Figure 3; 5b). In contrast, fire starkly rearranged fungal communities in mixed evergreen forests.

Biotic and abiotic environmental filtering structure fungal communities at the largest spatial scales (Tedersoo et al., 2014; Větrovský et al., 2019), but dispersal limitation and interspecific competition also create significant patchiness, especially at finer scales (Smith et al., 2018; Tedersoo et al., 2003). Despite this heterogeneity, our generalized dissimilarity model demonstrated that geographical distance influenced fungal community structure less than ecosystem type at this landscape scale (Figure 4), which suggests that variation in environmental filtering between mixed evergreen forests and oak woodlands is a key determinant of fungal community

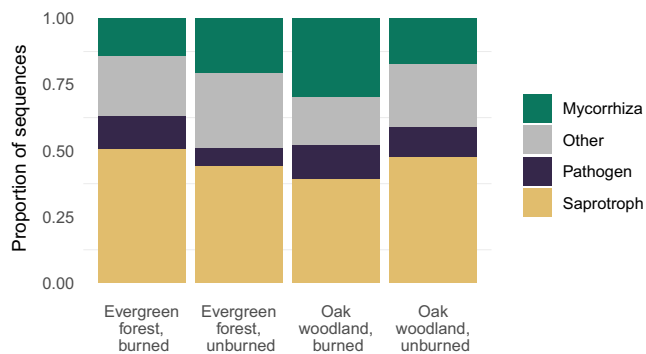


FIGURE 3 Mean proportional sequence abundances for the four different combinations of fire and ecosystem type, colour-coded according to functional guild.

assembly in this region. Differences in the symbiont preferences of locally abundant ectomycorrhizal host species (i.e. Douglas-firs and oaks) between the two systems likely affect community assembly of these fungal guilds (Rasmussen et al., 2017) and such differences in plant community could also indirectly affect soil microbial community assembly more broadly by altering soil chemistry (Waring et al., 2015). Additionally, differences in fire frequency between these two ecosystem types (Van Wagtenonk et al., 2018) could contribute to the development of different belowground communities as well as aboveground.

Just as fungal community structure differed between evergreen forests and oak woodlands, so also did fungal fire response. We observed stronger compositional separation between burned and unburned sites in mixed evergreen forests than between those in oak woodlands (Figure 4b). In particular, mycorrhizal richness and proportional abundance were reduced by fire in mixed evergreen forests (Figures 1b, 2) while neither of these measures were impacted in oak woodlands (Figures 1b, 2a,b). These findings support prior research showing that coniferous forests shift markedly towards a species-poor, fire-adapted mycorrhizal community when burned (Glassman et al., 2016; Taylor & Bruns, 1999), but they also demonstrate that such a response may not be common in other ecosystem types. Indeed, some mycorrhizal genera like *Rhizopogon* or *Cenococcum*, of which the latter was associated with oak woodlands in our study (Figure 5a), are resilient to heat (Kipfer et al., 2010; Peay et al., 2009), and communities where such adaptations are already common among dominant taxa are likely to change less than others. It is probable, moreover, that such fungal communities will be found where ecosystems burn more frequently. By regularly resetting the successional clock and favouring fire-adapted fungi, such fire regimes may reduce the compositional distance between prefire and

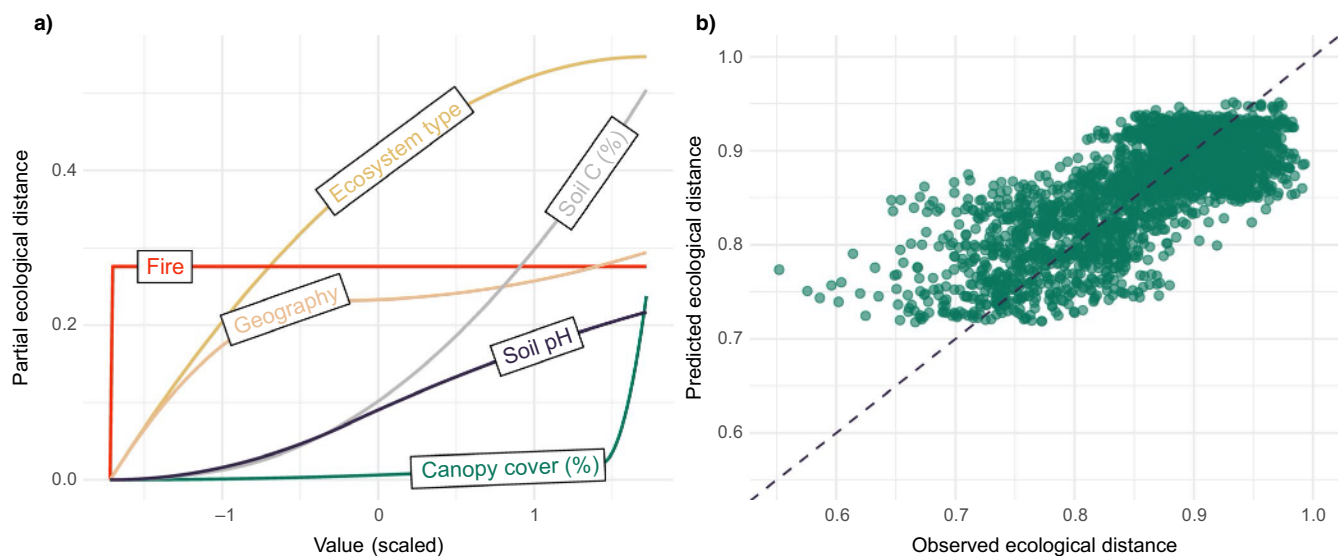


FIGURE 4 Results of generalized dissimilarity modelling of soil fungal communities. (a) Splines represent the community turnover associated with each significant factor over its range of values. Variables are scaled to allow comparison between spline shapes on the same x-axis. (b) Observed ecological distances in our data set compared with values predicted by our generalized dissimilarity model. A dashed one-to-one line represents perfect prediction.

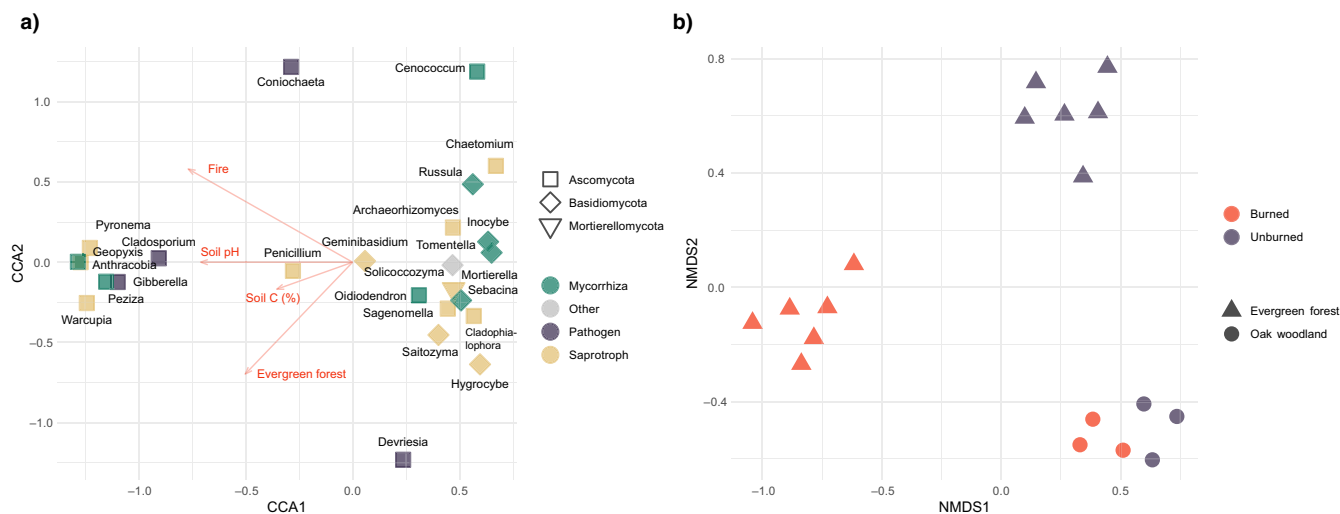


FIGURE 5 Ordination plots representing relative similarity between taxa and sites. (a) Canonical correspondence analysis illustrates the sensitivity of the 25 most abundant fungal genera in our data set to environmental factors, with drivers identified as significant at $\alpha = 0.05$ depicted as red vectors. Each point represents a genus and is shape- and colour-coded according to its Phylum and functional guild, respectively. (b) Nonmetric multidimensional scaling ordination using Bray–Curtis distances shows the relative similarity of mean fungal communities at each site. Here, points represent sites and are shape- and colour-coded according to ecosystem type and fire, respectively.

postfire communities. In contrast, large compositional shifts after fire are likely more possible where longer periods of time without disturbance have allowed fungal communities to change significantly compared to their immediately postfire states (Visser, 1995).

Differing fire responses by mycorrhizal fungi across evergreen forests and oak woodlands are also in keeping with their close physiological links to the plant communities of the two ecosystem types. Oregon oaks like those at our woodland study sites tend to respond positively to fire, resprouting vigorously even when top-killed by intense burns (Van Wagtenonk et al., 2018). Continued active photosynthesis after fire is likely to better support mycorrhizal populations in these ecosystems relative to mixed evergreen forests (Högberg et al., 2001), where tree mortality may have reduced the belowground carbon flux. Correspondingly, mycorrhizal communities robust to the impact of fire may be better able to furnish nutrients necessary for subsequent plant regrowth. However, differences in fire sensitivity across the two ecosystem types were not restricted to members of the fungal community growing in direct symbiosis with plants. For example, though burned mixed evergreen forests experienced a bloom of fire-adapted saprotrophic genera like *Pyrenoma*, *Geopyxis* and *Warcupia*, these taxa were not strongly associated with oak woodland ecosystems (Figure 5a).

While fungal communities in both ecosystem types were affected by fire, the difference in the magnitude of change suggests both longer temporal scales for recovery and greater perturbation of function in mixed evergreen forests. Indeed, though soil microbial community shifts in pyrogenic ecosystems just after fire can slow decomposition, functional differences dissipate over the course of just a couple of years as communities return to prefire states (Semenova-Nelsen et al., 2019). In contrast, the microbial communities of other ecosystem types, for example boreal forests (Fritze et al., 1993; Holden et al., 2013), may take significantly longer to

return to their prior composition (Oliver et al., 2015). Such persistent community differences suggest that biotically mediated reductions in decomposition rates after disturbance might last longer in these types of ecosystems (Waldrop & Harden, 2008), which could contribute to observed long-term soil carbon retention in needleleaf forests even with repeated burning (Pellegrini et al., 2018).

Differences in fungal community fire sensitivity and fire intensity across ecosystem types may both have contributed to the patterns we have observed. If fire intensity were lower overall in the oak woodlands relative to evergreen forests, this could support differences in fungal responses to fire between the two ecosystem types similar to those we observed (Figure 5b) both due to variation in direct (e.g. less fungal biomass burned) and indirect impacts (e.g. less abiotic change in soil or less plant mortality). Indeed, we found significant differences in soil pH, which is influenced by fire (Certini, 2005), between burned and unburned evergreen forests, but not in oak woodlands (Figure S2). Both in our study (Figure 3a) and others (e.g. Glassman et al., 2017), pH is shown to affect fungal community composition; changes in pH thus represent one of numerous potential mechanisms by which variation in fire intensity could influence the magnitude of fungal community change.

However, generalized dissimilarity modelling also showed that a remotely sensed continuous measure of fire-caused canopy damage was no more informative for community composition than our simple, binary categorization of burned vs. unburned. Thus, variation in fire intensity, at least as can be inferred from remotely sensed vegetation damage, is unlikely to drive the difference in magnitude of fungal community change between ecosystem types by itself. While ground-fire intensity, which may more proximally impact soil fungal communities, is unlikely to correspond perfectly with crown-fire intensity, a recent investigation in a boreal forest found that the latter may in fact be better linked to fungal community change than the

former (Pérez-Izquierdo et al., 2020). We thus expect that environmental filtering due in part to ecosystem fire regime has likely enhanced fungal community differentiation between mixed evergreen forests and oak woodlands in our study system (Bastias et al., 2006; Oliver et al., 2015), which has then entailed variation in community fire sensitivity and itself supported divergent community response patterns. Precisely such variation in fire regime is likely to also contribute to variation in fuel structure, vegetation and fire intensity between the two ecosystem types (Thaxton & Platt, 2006), linking these related yet distinct drivers.

As the Earth's climate changes, so also do its fire regimes (Westerling et al., 2006), which makes understanding ecosystem change and recovery after wildfire increasingly crucial to predicting our planet's biogeochemical and climatic future. Though soil microbial communities drive carbon fluxes of immense magnitude (Falkowski et al., 2008; Raich & Schlesinger, 1992), our knowledge about how species and communities differ in sensitivity to fire is biased towards plants (Keeley et al., 2011; Staver et al., 2011a). Here, we found that soil fungal communities inhabiting pyrogenic oak woodland ecosystems in California are impacted less by wildfire than those in neighbouring mixed evergreen forests, mirroring adaptations present in the plant communities of these ecosystem types. Our results suggest that biotically mediated changes to ecosystem function after fire are likely to vary between different ecosystems both above- and belowground and that fire regime and ecosystem type shape community assembly such that fire resistance in soil fungal communities co-occurs with pyrogenic plant communities. As such, they indicate that recovery of ecosystem structure and function after fire, especially in other ecosystem types, may be a matter not only of plant but also fungal communities.

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AUTHOR CONTRIBUTIONS

GRS and KGP designed the project. GRS performed fieldwork. LCE and GRS performed laboratory work and analysis. GRS wrote the manuscript with input from LCE and KGP.

DATA AVAILABILITY STATEMENT

Raw sequencing data are archived at NCBI SRA (Accession no. PRJNA679734). Processed data and code are available via Dryad (<https://doi.org/10.5061/dryad.x95x69pgv>) Smith et al., 2020.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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