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Drought mediates the response of soil fungal communities post-wildfire in a Californian grassland and coastal sage scrubland

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A B S T R A C T

There is a knowledge gap surrounding how drought and wildfire, two increasingly frequent disturbances, will alter soil fungal communities. Moreover, studies that directly compare ambient and drought-treated soil fungal communities in the context of wildfire are exceptionally scarce. We assessed the response and recovery of soil fungal communities and functional guilds in two sites – a grassland and a coastal sage shrubland – after a severe wildfire burned a long-term drought experiment. We collected soil samples at four collection dates over an eight-month period after wildfire and amplified fungal DNA. We predicted that fungal communities within the drought and ambient treatments would differ significantly across collection dates owing to differing responses to post-wildfire conditions. Richness was stable across collection dates, regardless of precipitation treatment, in both sites. Differences between treatments were significant at every collection date with respect to taxonomical community composition. Differences in community composition between collection dates within each treatment were also significant. Additionally, the monotonic trends of drought and ambient communities over time differed in strength and direction. Differences in shrubland functional guild composition across collection dates and contrasting trends suggest a drought-dependent shift after the fire. Overall, we conclude that drought mediates how soil fungal communities respond after a wildfire in the long term, however drought effects may differ across ecosystems.

1. Introduction

To predict alterations in soil carbon under increasing global changes, we must understand how mediators of soil carbon fluxes, particularly fungal communities, are affected by prolonged periods of drought and increasing occurrences of wildfires (Chapin et al., 2011; Treseder and Lennon, 2015; Allison and Goulden, 2017; Schimel, 2018; Glassman et al., 2023). However, we are still uncertain about how drought and wildfire influence fungal community composition and richness, and importantly, under what timescales these communities recover from such disturbances. Recently, studies have evaluated how fungal communities respond to either drought or wildfire, but none have examined the effects of prolonged drought on post-fire recovery (Richter et al., 2000; Harmon et al., 2011; Dooley and Treseder, 2012; Kutorga et al., 2012; Barnard et al., 2013; Holden et al., 2013, 2015; Matulich and Martiny, 2015; Martiny et al., 2017; Treseder et al., 2018; Romero-Olivares et al., 2019; Whitman et al., 2019). Microbial community composition typically changes under drought or after the occurrence of wildfires, leading to shifts in ecosystem functions (Wieder et al., 2013; Berlemont et al., 2014; Todd-Brown et al., 2014; Leff et al., 2015; Martiny et al., 2017; Glassman et al., 2018). Importantly, prolonged periods of drought and wildfires are expected to increase in frequency and severity in North America in the coming century (Gillett, 2004; Balshi et al., 2009; Cayan et al., 2010; Cook et al., 2015; Gibson et al., 2020). Thus, how soil fungal communities respond under prolonged periods of drought and after the occurrence of wildfires is important for understanding how the combination of such disturbances alter ecosystem processes such as soil carbon storage.

Fire can affect the richness of fungal communities either directly through heat-induced mortality, or indirectly by changing the physical and biochemical conditions in an ecosystem (Holden et al., 2013, 2015). Fungi are most abundant at the surface soil (0–5 cm), where temperatures are the highest during wildfire (Fierer et al., 2003; Ice et al., 2004). In fact, fungal richness can be reduced for months to years following fires (Pressler et al., 2019; Glassman et al., 2023). Yet, some fungal taxa are resilient to wildfire (Pattinson et al., 1999; Xiang et al., 2015; Köster et al., 2021). Indeed, it is possible that wildfire might act as an environmental filter selecting for the same resilient taxa in drought versus ambient communities, resulting in those communities becoming more similar in composition. Alternatively, post-wildfire conditions might differentially influence drought versus ambient communities by eliciting unique changes on different pre-existing communities. Notably, there is limited research on the short-term effects that occur after a wildfire, as it is difficult to collect samples so soon after a wildfire occurs (Packard

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et al., 2023).

Drought is an important environmental condition affecting fungal communities (Sanaullah et al., 2012; Ochoa-Hueso et al., 2018). Previous experiments at the Loma Ridge Global Change Experiment, located in a grassland and coastal sage scrubland in Southern California, indicate that fungal communities indeed shift in response to reduced precipitation (Allison et al., 2013; Berlemont et al., 2014; Martiny et al., 2017; Finks et al., 2021). However, the effect of post-wildfire conditions on the differences between ambient and drought-treated fungal communities is yet to be evaluated. Given the increasing frequency and intensity of both drought and wildfire events, understanding the effect of their interaction on fungi, who play critical roles in decomposition and nutrient cycling, is crucial. Based on drought's significant effects on shaping fungal communities, we hypothesize that drought and ambient communities will have different responses to the aftermath of wildfire.

Certain fungal guilds may respond differently to wildfire and drought than others (Treseder et al., 2004; Day et al., 2019). A guild is a group of species that use similar resources and perform similar functions (Root, 1967). The benefit of examining fungal guilds is to gain insight into functions these groups perform and how they might influence ecosystem processes. For instance, fungi occupying the saprotroph guild are associated with high decomposition potential (Allison and Treseder, 2011), which is important for regulating soil carbon storage and release (Dighton, 2018). In contrast, the symbiotroph guild consists of fungi who form mutualistic relationships with other organisms (Hoeksema et al., 2010). These include mycorrhizal fungi, who colonize the roots of plants and trees, providing nutrients and protection and receiving carbohydrates (Miller and Jastrow, 2000). Pathotrophs, on the other hand, consist of parasitic fungi that secure nutrients by attacking host cells (Dighton, 2018). By examining individual responses of fungal guilds to drought and post-wildfire conditions, better predictions can be made for future shifts in soil carbon dynamics under changing climate conditions (Treseder et al., 2004; Allison and Treseder, 2011).

In 2020, the Silverado Fire burned through Loma Ridge, providing a unique opportunity to evaluate the effect of post-wildfire conditions on fungal communities within a drought manipulation. We evaluated soil fungal community composition in the Loma Ridge experiment at four collection dates spanning from 11 days (the earliest date we were cleared to sample) to eight months after the fire. Again, we hypothesized that drought-treated soil fungal communities will respond differently from ambient communities in the aftermath of a wildfire. Accordingly, we predict that soil fungal communities from the drought plots will follow significantly different patterns from those in ambient plots across collection dates.

2. Methods

2.1. Field site

The Loma Ridge experiment is in the Santa Ana mountains in northern Irvine, California (33°44′N, 117°42′W). The experiment manipulates precipitation in a California grassland and coastal sage scrubland. The grassland consists mainly of the Eurasian species *Bromus diandrus (described by (d.b.) Albrecht Willhelm Roth)* and *Avena fatua (d.b. Carl von Linnaeus)* and the native *Dendra fasciculata (d.b. Edward Lee Greene)*. The shrubland is occupied by the crown-sprouting shrub species of *Artemesia californica (d.b. Christian Friedrich Lessing)*, *Malosma laurina (d.b. Thomas Nuttall),* and *Salvia mellifera (d.b. Edward Lee Greene)*. The soil for the grassland and shrubland is a Myford sandy loam (California Soil Resource Lab, UC Davis, https://casoilresource.lawr.ucdavis.edu/soilweb-apps/). The climate is Mediterranean, with an average annual precipitation of 325 mm. Precipitation data has been collected from the site since 2007 and can be viewed at http://hydstra.ocpublicworks.com/web.htm (Hicks Canyon site). The site experienced a total of 136 mm of precipitation throughout the collection period, with most of the precipitation occurring after the second collection date (Fig. S1).

2.2. Experimental design

Drought treatments commenced in February 2007. The grassland and shrubland each contained four ambient plots paired with four drought plots (Plot dimensions are 12.2 m × 6.1 m in the grassland and 18.3 m × 12.2 m in the shrubland). Each drought plot was equipped with a retractable canopy that was closed for selected rainstorms, reducing precipitation by approximately 50% compared to ambient plots.

2.3. Wildfire

The Silverado wildfire began on October 26, 2020 and was contained on November 7, 2020. The fire burned 12,466 acres (California Department of Forestry and Fire Protection, https://www.fire.ca.gov/incidents/2020/10/26/silverado-fire/). It burned through Loma Ridge and moved south toward Limestone Canyon, mirroring the Santiago Fire that also burned the plots in October 2007. In the shrubland, the fire was more severe in ambient plots than in drought plots, based on the percentage of plant coverage lost (S. Kimball, unpubl. data). In ambient plots, where plant coverage was 60% on average, the fire reduced cover to 10%. In drought plots, where plant cover was already lower at 20%, fire reduced the average coverage to 10%. Plant coverage loss was not quantitatively measured in the grassland, however upon inspection at the first sampling date, both drought and ambient plots were similarly devoid of almost all cover (Fig. S2). The drought shelters in both sites, which were destroyed by the wildfire, were fully repaired by January 2021, at which point the drought treatment resumed.

2.4. Sample collection

Soil samples were taken from the Loma Ridge grassland and coastal shrubland plots 11 days, two months, four months, and eight months post-fire (November 18th, 2020, December 22nd, 2020, February 26th, 2021, and June 23rd, 2021, respectively). An auger sterilized between uses was used to take two 2 cm diameter x 10 cm deep cores per plot. Each core was divided into 5 depths (0–2 cm, 3–4 cm, 5–6 cm, 7–8 cm, and 9–10 cm). We separated samples by depth in case fungal responses to the fire varied significantly by depth. Soil was composited and homogenized within each plot at each depth. Samples were kept on ice for transport to University of California Irvine, where they were stored at −70 °C. DNA was extracted using the ZYMObiomics DNA Miniprep Kit (D4300).

2.5. DNA sequencing

Samples and their controls were processed randomly and nanodropped before PCR. A 2-step PCR was conducted to amplify the fungal ITS2 region. We used the non-specific $ITS7_o$ forward primer and ITS4 reverse primer to capture the fungal community (Ihrmark et al., 2012; Kohout et al., 2014). The first PCR was a 12.5 μl total volume reaction, consisting of 6.25 μl of goTaq green PCR mix, 4.25 μl of PCR-grade water, 0.5 μl each of the forward and reverse primer, and 1 μl of template. The cycle parameters were as follows: 95 °C for 3 min, then 29 cycles of 90 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min, followed by a final elongation phase of 72 °C for 10 min. After the first step PCR, individual wells were bead cleaned with AmpureX beads at 1X concentration. For the 2nd step PCR, the total reaction volume was 25 μl. This mix consisted of 12.5 μl of goTaq green PCR mix, 0.5 μl PCR-grade water, 5 μl of template, and 3.5 μl each of the i5 and i7 index primers. The cycle parameters were as follows: 95 °C for 3 min, then 10 cycles of 90 °C for 30 s, 55 °C for 30 s, and 68 °C for 1 min, followed by a final elongation phase of 68 °C for 5 min. After the 2nd step PCR, 8 μl of product was loaded on a 1.5% agarose gel. Products were pooled based on band intensity with four categories: strong, medium, weak, and very weak. A final bead clean was performed on the pooled sample. Samples were then submitted to the UCI Genomics High-Throughput Facility, where quality was checked using bioanalyzer (Agilent 2100), KAPA QPCR, and Qubit. Samples were then sequenced there with Illumina MiSeq PE300.

2.6. Bioinformatics

We used the AMPtk pipeline to process sequencing data (v. 1.5.4) (Nguyen et al., 2016; Palmer et al., 2018). A total of 7,449,421 reads were trimmed, quality filtered, and clustered in operational taxonomic units (OTUs) using a 97% sequence similarity cutoff. AMPtk assigned taxonomy through global alignment of OTUs using VSEARCH and SINTAX (Edgar, 2016). AMPtk classified taxonomy for 6741 total OTUs. Of these classifications, FUNGuild classified 1051 OTUs as saprotrophs, 418 as symbiotrophs, and 308 as pathotrophs (Nguyen et al., 2016). To account for uneven sequencing depth, OTUs were rarefied to 1175 sequences per sample using the vegan package in R (v. 2.6–2)(Dixon, 2003). All figures were generated with ggplot2 in R and formatting polished in Adobe Illustrator 2023 (v. 27.2)(Wickham, 2011).

2.7. Statistics

Taxonomic community composition. Rarefied OTU tables were used to calculate relative abundance (i.e., percentages) of each OTU by dividing the count of that OTU by the count of all OTUs and multiplying the result by a hundred. Bray Curtis dissimilarities were calculated from square root transformed rarefied OTU tables. These tables were used in statistical tests including permutational multivariate analysis of variance (PERMANOVA) in Primer v6 (Anderson et al., 2008; Clarke & Gorley, 2006). We performed separate PERMANOVAs for each site. Our two fixed factors were treatment (2 levels) and collection date (4 levels). We nested block (4 levels) within site as a random factor to account for the blocked design of the experiment. We also nested soil depth (5 levels) as a random factor within block, since samples collected at multiple soil depths were not independent. To illustrate taxonomical similarities between samples, we performed nonmetric multidimensional scaling on samples using the 'metaMDS' function in vegan (Dixon, 2003). We calculated percent variance explained by each significant factor by dividing the estimated component of variation of a given factor by the sum of the estimated components of variation for all significant factors plus the residuals.

Guild community composition. We calculated the relative abundance of each of the three guilds (saprotroph, pathotroph, & symbiotroph) for each sample. We generated a dissimilarity matrix and performed PERMANOVAs and pairwise tests using the same approach as for taxonomic community composition.

Richness. We calculated richness by summing the number of unique taxa within each sample using the 'specnumber()' function provided by the vegan package. We then performed a linear mixed effects model using the 'lme4′ package in R (Bates et al., 2015). Our linear model followed the general form (richness ~ treatment + collection date + soil depth + block + (1|block:soil depth) + interactions). We performed a type III analysis of variance (ANOVA) on our model with Satterwaithe's method using the 'anova' function from 'stats' (Chambers and Hastie, 2017). We followed up with post-hoc pairwise tests using the 'pairs' function of the 'emmeans' package using Tukey's method to adjust for multiple comparisons (Searle et al., 1980).

Species indicator analysis. We calculated species indicators using the 'indicspecies' package in R (De Cáceres et al., 2011). We used the 'multipatt' function to calculate species indicators for drought versus ambient treatments by comparing OTUs between ambient and drought plots. We also calculated species indicators for immediate post-fire communities for comparing OTUs between samples collected at the first collection date and last collection date. We then outputted species indicators at an alpha value of 0.01.

Mann-Kendall trend analysis. To compare communities between ambient and drought treatments, we used the Mann-Kendall test for monotonic trends over time for taxonomic community composition, guild community composition, and the top 20 most significant species indicators per each treatment (Mann, 1945; De Cáceres et al., 2019). We separated samples based on treatment and site. We used the 'mk.test' function provided by the 'trend' package in R to generate a z quantile, tau statistic, and P value for each treatment per each site (Pohlert, 2023). The tau statistic ranges from −1 to 1, where a value of −1 indicates a strong decreasing trend, 0 indicates no trend, and 1 indicates a strong increasing trend (Mann, 1945).

Hypothesis testing. We checked for significant interactions between treatment and collection date on taxonomic community composition, guild community composition, or richness. Our hypothesis would be supported if we observed a significant interaction between treatment and collection date as indicated by ANOVA or PERMANOVA and if drought-treated and ambient communities had significantly different trends over time as indicated by the Mann-Kendall test.

2.8. Accession numbers

Sequences have been deposited in the NCBI Sequence Read Archive under the accession number PRJNA1027485.

3. Results

3.1. Taxonomy and guilds

We investigated the response of ambient and drought-treated soil fungal communities to post-wildfire conditions after a recent wildfire burned through a decade-long global change experiment. In both the grassland and shrubland, *Ascomycota* was the dominant phylum in both treatments (Fig. S3). Specifically, the average relative abundance of *Ascomycota* in the grassland was 75.0% in ambient communities and 73.8% in drought communities. In the shrubland, *Ascomycota* was slightly lower in the drought community, at about 66.5% compared to 75.3% in ambient communities. However, the difference was not significant ($P = 0.118$). *Basidiomycota* was the next dominant phylum in both sites. While the average relative abundance of *Basidiomycota* was similar between treatments in the grassland, the drought community in the shrubland had a significantly higher abundance compared to ambient (drought: 28.8%, ambient: 20.6%, $P = 0.026$). These phyla were followed by *Mortierellomycota, Chytridiomycota,* and *Glomeromycota*, found in similar abundances in both treatments and across both sites.

Saprotrophs were the most abundant guild in both sites and across treatments. Saprotrophs were similarly abundant across site and treatment, ranging from 61.9% to 73.2% (ambient vs. drought $P = 0.177$ in the grassland and $P = 0.743$ in the shrubland). In the grassland, pathotrophs were more abundant in drought plots, where their average relative abundance was 25.2% compared to 18.1% in ambient plots ($P = 0.001$). In the grassland, symbiotrophs were also more abundant in drought plots, where their average relative abundance was 12.9% compared to 9.8% in ambient plots ($P = 0.001$). In the shrubland, pathotroph and symbiotroph abundance were similar across treatments ($P = 0.976$ for pathotrophs and $P = 0.259$ for symbiotrophs).

3.2. Taxonomic community composition

PERMANOVAs of the grassland and shrubland sites showed significant interactions of treatment and collection date in both sites (Fig. 1, Table 1, $P = 0.001$ for both). In the grassland, treatment explained the most variation (5.74%), while in the shrubland, collection date explained the most (4.69%). Soil depth significantly affected community composition in the grassland but not the shrubland and did not interact

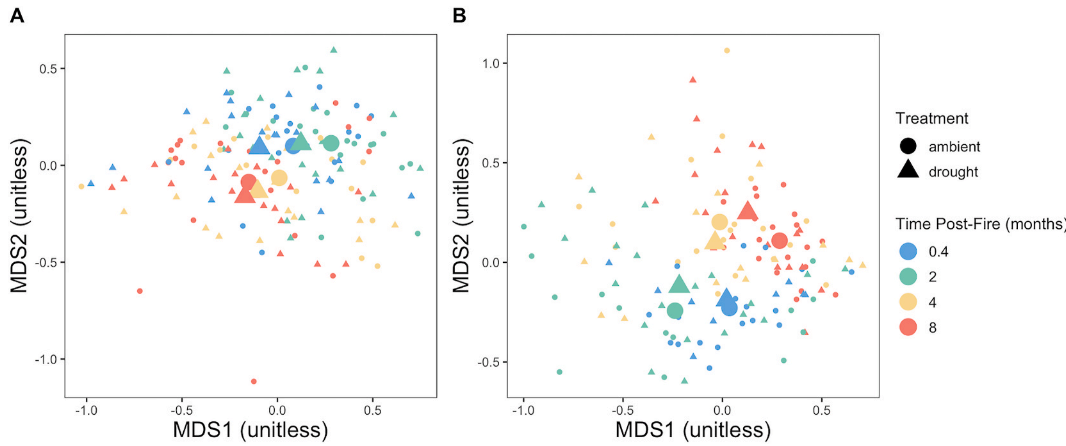

Fig. 1. Nonmetric-multidimensional scaling of fungal OTUs in the grassland (A), and in the coastal sage scrubland (B). Each smaller symbol designates a subsample of fungal OTUs at a given depth (n = 151 for grassland, n = 145 for shrubland). Treatment is represented by the shape of the symbol. Time after the fire is represented by the color of the symbol. Larger symbols are means within treatment and collection date. Community composition varied significantly between treatment (P = 0.001), timepoint (P = 0.001), and their interaction (P = 0.001) for both sites.

Table 1
Results of PERMANOVA analysis of fungal taxonomic community composition across sites.

Factor	df	Pseudo-F	P[a]	% Variance Explained
Grassland				
Treatment	1	7.37	**0.001**	**5.74**
Soil depth	16	1.23	**0.001**	**2.54**
Collection date	3	4.41	**0.001**	**5.52**
Block	3	3.20	**0.001**	**5.91**
Treatment x Soil depth	16	0.81	1.000	
Treatment x Collection date	3	1.55	**0.001**	**2.36**
Soil depth x Collection date	48	0.75	1.000	
Residuals	52			77.94
Shrubland				
Treatment	1	3.48	**0.001**	**1.71**
Soil depth	16	0.62	1.000	
Collection date	3	5.46	**0.001**	**4.69**
Block	3	3.19	**0.001**	**3.72**
Treatment x Soil depth	16	0.48	1.000	
Treatment x Collection date	3	2.97	**0.001**	**4.52**
Soil depth x Collection date	48	0.40	1.000	
Residuals	22			85.36

[a] Significant P-values in bold.

with any other factors in either site.

Ambient and drought-treated communities differed significantly in trends across time in both sites, as determined via the Mann-Kendall test. In the grassland, ambient communities displayed no overall trend across time (Table 2, tau = 0.008, P = 0.538) while drought-treated communities had a significant downward trend over time (tau = −0.195, P < 0.001). We observed the opposite response in the shrubland, where ambient communities trended significantly downward (tau = −0.149, P < 0.001) and drought treated communities had no evidence of a trend (tau = 0.019, P = 0.208).

Table 2
Mann-Kendall trend tests on fungal taxonomic community composition for ambient and drought-treated communities in the grassland and coastal sage scrubland.

Treatment	Tau	Z	P[a]
Grassland			
Ambient	0.01	0.61	0.538
Drought	−0.20	−15.85	**0.001**
Shrubland			
Ambient	−0.15	−11.29	**0.001**
Drought	0.02	1.26	0.208

[a] Significant P-values in bold.

Our hypothesis predicts that post-fire recovery would differ between treatments. In addition to the significant treatment and collection date interactions in both sites, pairwise comparisons between treatments were significant at each collection date (Table S1, P < 0.003 for each collection date in both sites). Pairwise comparisons of collection dates within each treatment were also all significantly different (Table S2, P < 0.024 for every comparison). Not only were ambient and drought-treated communities changing across collection dates, they followed significantly different trends. Taken together, we find support for our hypothesis regarding taxonomic community composition.

3.3. *Guild community composition*

Fungal guild community composition, a proxy for community functional potential, was significantly affected by treatment and collection date individually in both sites (Table 3). However, the interaction between treatment and collection date was significant only in the shrubland (P = 0.013), where it explained the most variation. Pairwise comparisons between treatments at each collection date in the shrubland show ambient and drought communities were significantly different at the first collection date (Table S3, P = 0.001), but not

Table 3
Results of PERMANOVA analysis of fungal guild community composition across sites.

Factor	df	Pseudo-F	P[a]	% Variance Explained
Grassland				
Treatment	1	26.50	**0.001**	**12.34**
Soil depth	16	0.98	0.486	
Collection date	3	3.49	**0.005**	**2.54**
Block	3	6.30	**0.001**	**10.79**
Treatment x Soil depth	16	0.46	0.989	
Treatment x Collection date	3	0.78	0.561	
Soil depth x Collection date	48	0.50	1.000	
Residuals	60			74.33
Shrubland				
Treatment	1	0.45	0.661	
Soil depth	16	0.24	1.000	
Collection date	3	6.90	**0.001**	**4.50**
Block	3	2.63	**0.032**	**1.31**
Treatment x Soil depth	16	0.21	1.000	
Treatment x Collection date	3	3.50	**0.013**	**4.64**
Soil depth x Collection date	48	0.25	1.000	
Residuals	20			89.56

[a] Significant P-values in bold.

significant at subsequent collection dates. In the grassland, guild composition was also significantly different between drought and ambient at the first collection date ($P = 0.014$), as well as the second and last collection date ($P < 0.003$ for both dates). Pairwise comparisons of collection dates within each treatment show that guild composition was similarly unchanging for both ambient and drought communities across time (Table S4). However, Mann-Kendall test results again revealed differences between drought and ambient community trends across time. In the grassland, ambient communities had a significantly increasing trend (Table 4, tau = 0.065, $P < 0.001$) and drought-treatment communities showed a significantly decreasing trend (tau = −0.101, $P < 0.001$). In the shrubland, ambient communities followed a significantly downward trend (tau = −0.104, $P < 0.001$) while drought communities displayed no overall trend (tau = 0.001, $P = 0.381$). Overall, we find some support for our hypothesis with respect to the community guild patterns across time mainly in the shrubland.

3.4. Richness

ANOVA results indicated that collection date was not a significant factor affecting richness in either site, while treatment significantly affected richness only in the grassland (Table 5, treatment $P = 0.011$). We did not observe significant interactions between treatments and collection date in either site. Richness values between ambient and drought communities were similar at every collection point for both sites (Fig. 2, Table S5). In addition, richness was similar between collection dates within each treatment for each pairwise comparison of collection dates (Table S6). Thus, we did not find support that post-fire conditions affected richness differently across treatments.

3.5. Species indicator analysis

In the grassland, there were 94 indicator species for the drought treatment. The top 3 most significant indicator species in the drought category were a species of the order Hypocreales, a species of the genus *Mortierella*, and a species of the genus *Lectera* ($P = 0.001$ for all). There were 100 indicator species in the 11 days post-fire category. The top 3 most significant fungal indicator species were the species *Mortierella alpina*, a species of the order Pleosporales, and a species of the genus *Fusarium* ($P = 0.001$ for all).

In the coastal sage shrubland, we observed 41 indicator species for the drought treatment. The top 3 most significant species were a species of the family *Didymellacae*, a species of the genus *Alternaria*, and a species of the genus *Preussia* ($P < 0.001$ for all). We observed 132 indicator species for the 11 days post-fire category. The top 3 species were a species of unknown phylum, a species of the genus *Dominikia*, and a species of the genus *Penicillium* ($P < 0.001$ for all). A spreadsheet of all indicator species with taxonomy is available in the supplement.

With respect to our hypothesis, the trend analyses for the top 20 species indicators per treatment per site revealed some differences in ambient and drought community patterns across time. Ambient and drought-treated communities in the grassland followed similar trends across time, and both trends were significantly downward (Table 6, ambient tau = −0.099, $P < 0.001$, drought tau = −0.124, $P < 0.001$). In the shrubland, however, ambient communities had a significantly downward trend, while the drought-treated community showed no significant trend. In this context, we find support for our hypothesis with respect to species indicator community patterns, but only in the shrubland.

Table 4
Mann-Kendall trend tests on fungal guild composition for ambient and drought-treated communities in the grassland and coastal sage scrubland.

Treatment	Tau	Z	P[a]
Grassland			
Ambient	0.07	4.96	**0.001**
Drought	−0.10	−8.20	**0.001**
Shrubland			
Ambient	−0.10	−7.88	**0.001**
Drought	0.01	−0.87	0.381

[a] Significant P-values in bold.

Table 5
Type III ANOVA results of fungal richness.

Factor	df	Pseudo-F	P[a]
Grassland			
Treatment	1	6.77	**0.011**
Soil depth	4	7.01	**4.57e-5**
Collection date	3	1.32	0.270
Block	1	8.35	**0.004**
Treatment x Soil depth	4	0.29	0.886
Treatment x Collection date	3	0.42	0.741
Soil depth x Collection date	12	0.30	0.988
Treatment x Soil depth x Collection date	12	0.59	0.838
Shrubland			
Treatment	1	0.77	0.382
Soil depth	4	2.01	0.098
Collection date	3	0.56	0.643
Block	1	2.56	0.112
Treatment x Soil depth	4	0.59	0.674
Treatment x Collection date	3	0.31	0.821
Soil depth x Collection date	12	0.71	0.732
Treatment x Soil depth x Collection date	12	0.60	0.838

[a] Significant P-values in bold.

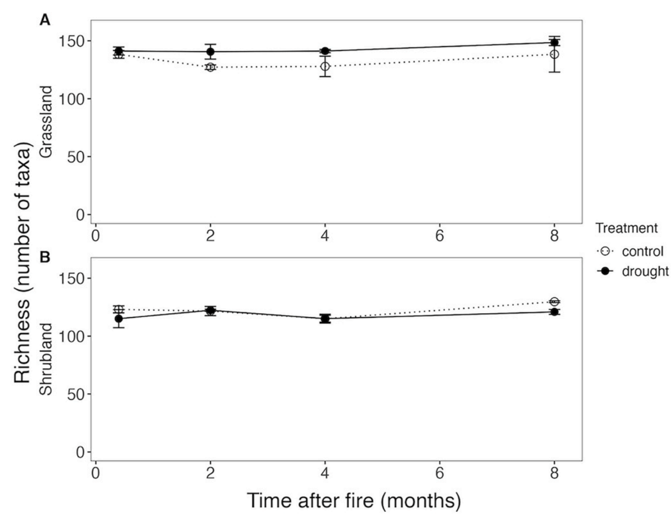

Fig. 2. Fungal richness, measured in number of taxa, across collection date in the grassland (A) and the coastal sage scrubland (B). Symbols are means ±1SE of ~4 subsamples. There were no significant differences across treatment or collection dates.

Table 6
Mann-Kendall trend tests on the top 20 most significant species indicators for ambient and drought-treated communities in the grassland and coastal sage scrubland.

Treatment	Tau	Z	P[a]
Grassland			
Ambient	−0.10	−7.68	**0.001**
Drought	−0.12	−10.07	**0.001**
Shrubland			
Ambient	−0.04	−2.94	**0.001**
Drought	0.03	−1.70	0.089

[a] Significant P-values in bold.

4. Discussion

Our study addresses an important knowledge gap regarding the short-term response of drought-treated soil fungal communities to post-wildfire effects. We found some support for our hypothesis that drought communities respond differently to post-fire conditions. In addition to significant treatment x collection date interactions, a trend analysis of taxonomic community composition demonstrated that drought and ambient communities followed differing trends in both sites (Table 2). Furthermore, we observed opposing trends between drought-treated and ambient communities with respect to guild composition. Unexpectedly, we did not find that post-wildfire effects influenced richness in either site (Table 5, Fig. 2). Additionally, we found several indicator species for the 11 days post-fire collection date (Supplementary spreadsheet). While the top 20 species indicators of the drought and control treatments followed similar trends in the grassland, they had significantly different patterns in the shrubland (Table 6). These results were achieved through a rare opportunity to directly compare ambient and drought-treated fungal communities in the immediate aftermath of a wildfire.

4.1. Fungal response to post-wildfire conditions

We found support for our hypothesis that drought communities would respond differently to post-fire conditions with respect to taxonomic community composition (Table 1, Fig. 1). Treatment and collection date interacted significantly to influence community composition in both sites. Additionally, pairwise comparisons showed ambient and drought communities were significantly different from each other at each collection date (Table S1), and communities at every collection date were significantly different from each other within each treatment (Table S2). These results suggest strong and persistent differences between ambient and drought treated communities across time, and ambient and drought-treated communities differed in the direction and strength of their monotonic trends (Table 2). A possible reason for the persistent differences between the communities is a unique response of drought-exposed soil fungal communities to post-fire conditions (Buscardo et al., 2015; Hansen et al., 2019; Hinojosa et al., 2019; Köster et al., 2021). At the Loma Ridge, the drought manipulation has lasted for more than 15 years. This prolonged drought has led to significant changes in microbial communities and soil composition (Alster et al., 2013, 2021; Treseder et al., 2018; Malik et al., 2020). Studies that directly compare wildfire effects on drought versus ambient fungal communities are rare, but one examining fungal community structure via ester-linked fatty acids found that fungal communities in burned soils were different when exposed to drought (Hinojosa et al., 2019).

We also found significant treatment and collection date interactions influencing functional guild composition in the shrubland but not the grassland (Table 3). Pairwise comparisons between treatments revealed that guild composition of ambient and drought communities in the shrubland were only significantly different at the first collection date (Table S3). Indeed, pairwise comparisons between collection dates showed that guild composition was relatively unchanging for both treatments in both sites (Table S4). Yet, Mann-Kendall analysis revealed that drought and ambient treatments followed different trends for both sites (Table 4). Our finding highlights that fungal responses to drought and post-wildfire conditions may vary depending on site. Indeed, previous studies suggest that fungal communities of some ecosystem types can be less affected by drought and wildfire than others (Smith et al., 2021). Thus, the function of the fungal community—to the extent that it is influenced by guild structure—may not be influenced by post-wildfire conditions in some ecosystems, even if taxonomy shifts. We are currently unaware of any other studies measuring guild compositional changes in soil fungi under drought and post-fire conditions.

Interestingly, richness was not affected by significant interactions between treatment and collection date in either site (Table 5). Indeed, richness was similar between drought and ambient communities at each collection date in both sites (Table S5, Fig. 2). Furthermore, richness was similar between all collection dates for each treatment for both sites (Table S6). This was an unexpected finding, as some previous studies demonstrate that wildfire reduces richness of soil fungal communities (Day et al., 2019; Pulido-Chavez et al., 2021). Nevertheless, our result is consistent with other studies where fungal richness was not affected by wildfire (Smith et al., 2021; Stürmer et al., 2022).

Our study is unusual in that there are very few experiments that directly compare drought and ambient microbial communities in the context of wildfire (Brown et al., 2019). Almost none examine soil fungi. An analysis of bacterial community composition after the Silverado fire in our study site found little evidence that the drought treatment altered the bacterial community's response to the wildfire (Barbour et al., 2022). However, it is well supported that fungi and bacteria have distinct responses to wildfire, and that bacteria tend to recover faster than fungi (Brown et al., 2019; Whitman et al., 2019; Caiafa et al., 2023). Indeed, many wildfire studies on fungi focus on the long-term recovery of fire-sensitive symbiotrophs (Jonsson et al., 1999; Xiang et al., 2015; Pulido-Chavez et al., 2021; DeVan et al., 2023). In this context, our study provides some valuable foundational information on the early response of drought-treated communities to post-fire conditions on a short-term scale.

Due to the unforeseen nature of the fire, our study lacked samples collected immediately before the fire. We were cautious with our interpretations, but acknowledge that other environmental factors, including seasonality, could have influenced our samples. Nevertheless, this study provides valuable insight on the early response of soil fungal communities to post-fire conditions. The proximity of our first collection date to the fire, only 11 days after, in addition to our ability to compare drought and ambient communities, presented a unique opportunity. Future research contrasting pre- and post-fire fungal communities under drought would be valuable.

Our study also offers insight into potential changes in ecosystem function owing to drought and wildfire, which are both expected to increase in frequency and severity in the coming century (Westerling et al., 2003; Cayan et al., 2010; Pechony and Shindell, 2010). If the differing response of drought soil fungi communities to wildfire is widespread, then ecosystems undergoing prolonged drought could experience altered function in the aftermath of wildfire.

4.2. Indicator species

We found that the top 20 most significant species indicators for the drought and ambient treatments followed different trends, but only in the shrubland (Table 6). This result complements our findings on guild composition, where we observed a significant treatment x collection date interaction in shrubland communities but not grassland communities. Again, our results suggest community patterns post-fire may vary by site (Smith et al., 2021).

In the grassland, *Mortierella alpina*, a species from the order Pleosporales, and a *Fusarium* species were significant indicators of 11 days post-fire. *Mortierella alpina* belongs to the phylum *Mucoromycota* and is a filamentous fungus commonly found in soil (Anastasi et al., 2005; Buée et al., 2009; Fröhlich-Nowoisky et al., 2015). *Mortierella alpina* is known to be an oleaginous fungus, accumulating a large proportion of lipids within its cells (Ratledge and Wynn, 2002; Wang et al., 2011). It is possible that its ability to store high volumes of lipids allowed it to thrive in post-fire conditions, as it could metabolize those lipids in a nutrient-poor environment (Ray et al., 2019). Pleosporales is an order of fungi comprised of mainly saprotrophs and is found commonly in soil (Kruys et al., 2006). Pleosporales was found to be one of the most abundant orders in another study of a site undergoing yearly prescribed burns (Alem et al., 2020). Lastly, genus *Fusarium* belongs to the order Hypocreales within Ascomycota. *Fusarium* is comprised mainly of saprotrophs and plant pathogens (Edel-Hermann et al., 2015; Torbati et al., 2021).

In the shrubland, an unknown species from the genus *Dominikia* and another unknown species from the genus *Penicillium* were significant indicator species 11 days post-fire. Genus *Dominikia*, belonging to the phylum Glomeromycota, forms symbiotic associations with a wide array of plant species and is widely distributed (Błaszkowski et al., 2015, 2018). While some wildfire studies have found that symbiotrophic fungi are negatively affected by wildfire events, other studies have reported that richness and abundance of Glomeromycota is not severely affected by wildfire (Longo et al., 2014; Xiang et al., 2015; Stürmer et al., 2022). Lastly, genus *Penicillium* is comprised of mainly saprotrophic species and is known to be widely distributed (Yadav et al., 2018). Additionally, many *Penicillium* species have been recorded in extreme environments (Yadav et al., 2018). One previous study found that *Penicillium* was associated with high fire severity (Day et al., 2019).

5. Conclusion

In conclusion, our study suggests that drought mediates the response of soil fungal communities to post-wildfire conditions. The composition and patterns of drought communities over time were different from that of ambient communities regarding taxonomic community composition post-fire. Additionally, drought communities in the shrubland had differing guild composition and monotonic trends post-fire. We also observed differing patterns over time for drought-treated species indicators compared to ambient. If this result is widespread, climate change-induced drought may alter composition and functionality in post-fire conditions in ways that cannot be predicted based on ambient responses.

Data statement

Scripts for this project are accessible on GitHub: https://github.com/melaniehacopian/wildfire_workflow. Sequences have been deposited in the NCBI Sequence Read Archive under the accession number PRJNA1027485.

CRediT authorship contribution statement

Melanie T. Hacopian: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sarai S. Finks:** Writing – review & editing, Resources, Methodology, Data curation. **Kathleen K. Treseder:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Sequences from this manuscript are available online and a GitHub repository is specified in the text. Other data can be made available upon request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2024.109511.

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