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Research Article

RESEARCH ARTICLE

Soil fungal community composition and functional similarity shift across distinct climatic conditions

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One sentence summary: Over changing climatic conditions, fungal community composition may differ, but for some mutualist groups, their function could be retained.

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ABSTRACT

A large part of ecosystem function in woodland systems depends on soil fungal communities. However, global climate change has the potential to fundamentally alter these communities as fungal species are filtered with changing environmental conditions. In this study, we examined the potential effects of climate on host-associated (i.e. tree-associated) soil fungal communities at climatically distinct sites in the Tehachapi Mountains in California, where more arid conditions represent likely regional climate futures. We found that soil fungal community composition changes strongly across sites, with species richness and diversity being highest at the most arid site. However, host association may buffer the effects of climate on community composition, as host-associated fungal communities are more similar to each other across climatically distinct sites than the whole fungal community. Lastly, an examination of functional traits for ectomycorrhizal fungi, a well-studied guild of fungal mutualist species, showed that stress-tolerant traits were more abundant at arid sites than mesic sites, providing a mechanistic understanding of these community patterns. Taken together, our results indicate that fungal community composition will likely shift with future climate change but that host association may buffer these effects, with shifts in functional traits having implications for future ecosystem function.

Keywords: functional traits; global change ecology; host association; mutualisms; oak woodland; soil fungi

INTRODUCTION

Soil fungi contribute to a variety of ecosystem functions such as decomposition of organic matter, nitrogen and phosphorus cycling, and carbon storage (Treseder and Lennon 2015). Climate change has the potential to affect these functions by changing fungal community composition through warming (Geml *et al.* 2016; Treseder *et al.* 2016; Oliverio, Bradford and Fierer 2017) and more variable precipitation regimes (Hawkes and Keitt 2015; Averill, Waring and Hawkes 2016; Keitt *et al.* 2016). This, in turn, could alter rates of plant litter decomposition, carbon sequestration and nitrogen mineralization, amongst other integral processes (Treseder 2016; Aamir *et al.* 2019; Cavicchioli *et al.* 2019). Therefore, understanding specifically how climate variation alters fungal community composition is critical to understanding the whole ecosystem function in the face of climate change.

While changes in climate can impact fungal community composition (Classen *et al.* 2015; Andrew *et al.* 2016; Peay *et al.* 2017), the direction and strength of these effects are variable across systems (Rillig, Treseder and Allen 2002; Compant, Van Der Heijden and Sessitsch 2010), especially when considering

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the different effects on functional groups (i.e. saprotrophs, symbiotrophs and pathotrophs) and species guilds (e.g. ectomycorrhizal fungi, arbuscular mycorrhizal fungi) (Mohan *et al.* 2014; Geml *et al.* 2015; Asemaninejad *et al.* 2018). However, trait-based approaches may reveal unifying patterns across these apparently discordant responses because they allow us to group taxa by function and therefore link fungal identity to mechanistic responses (Aguilar-Trigueros et al. 2014, 2015; Crowther *et al.* 2014; Koide, Fernandez and Malcolm 2014; Morgado *et al.* 2015; Rillig *et al.* 2015). By incorporating a trait-based approach to fungal community ecology, we can address a fundamental question: Will fungal communities continue to provide the same functions under the stress of climate change (Pickles *et al.* 2012)? By linking climate-driven shifts in fungal community composition with functional traits, we can begin to connect changes in species diversity with ecosystem function.

Of fungal functional traits, modes of nutrient acquisition—in particular for species engaging in mutualisms with plant hosts—are especially crucial for understanding the effects of environmental filtering on ecosystem function. Symbiotrophs are mutualist fungi that associate with plant hosts, and mycorrhizae are a subset of this group that specialize in associations with plant roots in which the plant exchanges carbon resources for the mycorrhiza's soil-derived nitrogen and phosphorus (Smith and Read 2008). Mycorrhizae play a major role in ecosystem function, as they provide almost half of a tree's organic nitrogen budget (Zhang *et al.* 2019) and contribute the bulk of new carbon into soil (Zhang *et al.* 2018). Additionally, mycorrhizal groups (i.e. arbuscular mycorrhizal and ectomycorrhizal fungi) differ in the amount of carbon they input to soil (Averill, Turner and Finzi 2014) and their respective nitrogen and phosphorus benefits to their hosts (Teste, Jones and Dickie 2019). Therefore, understanding changes in mycorrhizal communities in particular can provide insight into changing ecosystem functions in the future (van der Heijden *et al.* 2015).

Given that mycorrhizae are host-associated and therefore rely on a mutualism to fulfill their metabolic demands, there is potential for mutualisms to withstand climate-driven changes in fungal community composition. Most generally, we would expect that, when comparing the microbial community of a single host species to the community at large, host-associated communities are more similar to each other than to the regional pool of species, which includes mutualist species (Peiffer *et al.* 2013; Lebeis 2015; Adair and Douglas 2017); taking this in the context of climate change, plant–host association has the potential to dampen the effects of climate on community turnover, as fungal associates are more similar across differing climatic conditions within a single host species than the entire species pool (Nuccio *et al.* 2016). For mutualist species (i.e. mycorrhizal partners) specifically, species in these functional groups may be even more similar across sites than the whole host-associated community.

If mutualists are indeed buffered from climate impacts on composition by their hosts, this could imply the conservation of host function given future climate change because their mutualists will retain their own function. While mycorrhizal partners may remain similar in composition, changes in relative abundance of species functional traits could conserve host function (Eduardo *et al.* 2018; Yan *et al.* 2018). Thus, by filtering the membership of the fungal community (Kiers *et al.* 2003), host trees may maintain mycorrhizal mutualism function across drastically different climates, thereby preserving ecosystem functions provided by their mycorrhizae. Therefore, understanding how to preserve host and mutualist function remains crucial for management and conservation strategies concerning woodland systems to adapt to climate change.

In this work, we use three climatically distinct sites to (i) quantify changes in fungal community composition, (ii) test the effects of host association on these shifts and (iii) measure the turnover in relative abundance of ectomycorrhizal species functional traits. An observational approach like the one taken here provides a spatial advantage to small-scale experiments by letting community assembly occur over a landscape (Bennett, Kasel and Tibbits 2009). Additionally, oak woodland systems in California are likely to experience range contractions and northward shifts as a result of changing temperatures and precipitation (Kueppers *et al.* 2005); therefore, they are representative of woodlands in Mediterranean climates globally, which are likely to experience range contractions as a result of increasing temperature, drought and more variable precipitation (IPCC 2014). However, little is known about whether fungal associates can withstand or ameliorate climate change effects. Our site—the Tejon Ranch in the Tehachapi Mountains of California—is particularly ideal to test questions about climate effects on host-associated soil fungal communities because some hosts are constant across climatic conditions and there are distinct shifts in climate within a geographically constrained area (8 km) (McCullough *et al.* 2016). We first ask how fungal community composition responds to climate when holding host identity constant, and hypothesize that both richness and diversity will be highest at cooler, wetter sites than hot, dry sites (Peay *et al.* 2017). Across climatic conditions, soils in dry sites tend to be nutrient-poor compared to wet sites (Talmon, Sternberg and Grünzweig 2011; Delgado-Baquerizo *et al.* 2013; Jiao *et al.* 2016); therefore, arid environments will likely support fewer fungal species than their mesic counterparts (Maestre *et al.* 2015). Next, we ask how mycorrhizal association may drive convergence of fungal communities, and hypothesize that communities of mycorrhizal species are more similar across sites than whole host-associated communities. Potential fungal partners are likely filtered by their hosts based on the efficacy of nutrient acquisition given carbon costs (Dickie 2007; Vályi *et al.* 2016; Powell and Rillig 2018), and we expect host selectivity to override the filtering effects of climate across sites. Lastly, we ask how the functional trait composition of fungal mutualists reflects climate conditions in our sites, and hypothesize that functional traits will reflect the environment in which the species are found. Because ectomycorrhizal fungi provide nutrients and water to hosts (Tedersoo, May and Smith 2010), we anticipated that differences in composition in this community might reflect divergent tree nutritional needs (Moeller, Peay and Fukami 2014). In this case, we explore the functional traits of ectomycorrhizal fungi and predict that functional traits considered adaptive for stressful environments, in particular rhizomorph formation and foraging type, will be found in higher abundance in arid compared to mesic sites (Moeller, Peay and Fukami 2014).

MATERIALS AND METHODS

Field site and sample collection

We collected all samples in April 2018 at Tejon Ranch in the Tehachapi Mountains of California (34° 5' 80' N, 118° 3' 50' W, Fig. 1A and B). April represents the full-leaf-out period for the main host plant species, as well as peak growth for most understory plants. The mountain range is characterized by diverse oak woodland habitats (Davis and Sweet 2012), with valley oaks (*Quercus lobata*) distributed widely across elevations between 300 and 1830 m. The Tehachapi mountain range experiences a Mediterranean climate and is representative of California oak woodland ecosystems; therefore, Tejon is an especially fitting

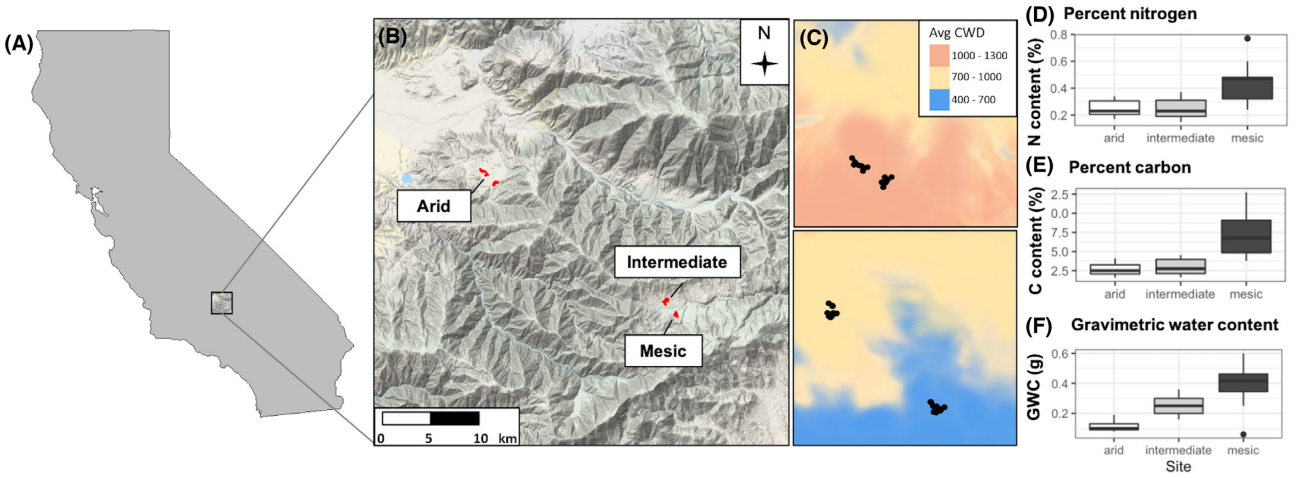

Figure 1. Sampling sites at Tejon Ranch. Tejon Ranch is in south-central California **(A)**. Sampling sites are shown with each dot representing the geographic location of a sampled tree, with topography **(B)** and climate water deficit (CWD) **(C)**. Colors represent average CWD in mm H_2O/year, with arid sites in red, intermediate sites in yellow, and mesic sites in blue. Soil % nitrogen and carbon, and gravimetric water content differ between sites **(D–F)**.

site to examine the effects of climate on community composition and diversity patterns broadly applicable to these particular systems (Myers *et al.* 2000; Sala *et al.* 2000).

Within the Tehachapi Mountain range, a natural range of climate conditions exists, driven by landscape-level patterns in temperature and CWD. CWD is the amount of water by which potential evapotranspiration (PET) exceeds actual evapotranspiration (AET); this term effectively integrates the combined effects of solar radiation, evapotranspiration and air temperature on watershed conditions given available soil moisture derived from precipitation. Across sites, CWD varies as a result of topographically controlled variation in solar radiation, temperature, precipitation and soil water holding capacity (McCullough *et al.* 2016). These sites occur on the same parent material (granite-derived coarse-loamy Haploxerolls, Soil Survey Staff 2019), allowing us to hold substrate constant while quantifying the effect of climate on belowground community composition. We sampled across three sites designated 'mesic', 'intermediate' and 'arid' with a mean increase of ~2°C and a CWD of ~200 mm H_2O per year between consecutive sites (Fig. 1C and D). We chose sites based on preexisting climate grids spanning ~33 000 hectares across the elevational gradient (Davis and Sweet 2012; McCullough *et al.* 2016), and sites are the location of a large-scale ungulate exclosure experiment that tests the effects of herbivore removal under present, near-future and far-future climate scenarios (Orr *et al.* 2020 in submission). Although soils are derived from the same parent material, they differed in % nitrogen and carbon, and gravimetric water content (Fig. 1E–G). These soils and topographically varied landscape support a landscape mosaic ranging from arid scrubland, remnant native forbland and invaded grassland to deciduous and evergreen oak woodlands and montane conifer forest (Supplemental Figure 1).

To characterize the host-associated fungal community, we collected soil samples beneath (i.e. within 20 cm of the trunks of) valley oaks. This design allowed us to collect replicate samples (mesic: n = 15 trees, intermediate: n = 23, arid: n = 15) within a climate site, while controlling for aboveground community composition by holding the dominant tree species constant. We collected two soil cores (5 cm wide and 10 cm deep) on opposite sides of the base of each tree, sampling trees at least 10 m from another tree and at least 15 m away from trees of other species. Soils were kept on ice until transported back to the laboratory, where they were stored at 4°C until processing within one week. Soil samples were homogenized prior to all downstream processing and filtered by sequential filtration through sieves of apertures of 2 and 5.6 mm to remove any remaining pieces of plant litter. From a random subset of soil cores ($n = 23$) representing all three sites, we measured soil % nitrogen and carbon, phosphorus, organic matter (OM), total exchange capacity (TEC), ppm NO_3 and ppm NH_4 (Brookside Laboratories, New Bremen, OH, USA; Table 1). Gravimetric water content was taken for all samples and was measured as the difference between the wet weight and dry weight of soils after drying in an oven at 65°C.

Fungal community deoxyribonucleic acid extraction and sequencing

An amount of 0.25 g soil was extracted from each core ($n = 108$) and kept at 0°C until extraction. Fungal DNA was extracted using the DNEasy Powersoil Kit (Qiagen, Maryland, USA). Extracted deoxyribonucleic acid (DNA) was amplified using polymerase chain reaction (PCR) with forward primers targeting the internal transcribed spacer (ITS) region ITS1F-KYO1 and ITS2-KYO1 (Toju *et al.* 2012). We used the following thermocycler protocol: 3 min at 95°C, 0:30 s at 95°C + 0:30 s at 47°C + 0:30 s at 72°C x35, 5 min at 72°C, ∞ at 4°C. Each sample was given a unique pair of forward and reverse barcodes, ligated on using the following thermocycler protocol: 3 min at 95°C, 0:30 s at 95°C + 0:30 s at 55°C + 0:30 s at 72°C x10, 5 min at 72°C, ∞ at 4°C. Samples were cleaned using AMPure XP beads (Beckman Coulter, Illinois, USA) and diluted to 4 nM. Samples were pooled and sequenced using the Illumina MiSeq platform at the University of California, Santa Barbara Biological Nanostructures Lab.

Bioinformatics pipeline and data analysis

Forward and reverse reads obtained through Illumina sequencing were processed using USEARCH11 (Edgar 2010). Sequences were merged, and reads with expected error greater than 1 were filtered out. Sequences were then clustered into operational taxonomic units (OTUs, serving as a proxy for species) by 97% similarity using the UPARSE algorithm and assigned taxonomy using the Basic Local Alignment Search Tool (BLAST) from the National

Table 1. Methods of soil characteristic measurements.

Measurement	Method	Citation
% nitrogen	Combustion	(McGeehan and Naylor 1988; Nelson and Sommers 1996)
% carbon	Combustion	(McGeehan and Naylor 1988; Nelson and Sommers 1996)
Phosphorous	Bray II	(Bray and Kurtz 1945)
OM	Weight loss on ignition	(Schulte and Hopkins 1996)
TEC	Calculated using Ca, Mg and K measurements	(Ross 1995)
Nitrate	1 N KCl cadmium reduction	(Dahnke 1990)
Ammonium	1 N KCl cadmium reduction	(Dahnke 1990)

Table 2. Fungal trophic modes and guilds as assigned using FUNGuild.

Trophic mode	Pathotroph
	Saprotroph
	Symbiotroph
Guilds (within symbiotrophs)	Ectomycorrhizal
	Arbuscular mycorrhizal
	Ericoid mycorrhizal
	Orchid mycorrhizal

Table 3. Ectomycorrhizal functional traits chosen for analysis.

Trait	Types
Foraging distance	Short distance
	Medium-distance fringe
	Medium-distance mat
	Medium-distance smooth
	Long distance
Rhizomorph formation	True (forms rhizomorphs)
	False (does not form rhizomorphs)

Center for Biotechnology Information using the University of California, Santa Barbara Knot Computing Cluster. Fungal OTUs were identified and extracted using MEGAN (Huson *et al.* 2016), which uses the Lowest Common Ancestor (LCA) algorithm to assign taxonomy to OTUs. OTUs were then filtered against this list in QIIME (Caporaso *et al.* 2010) to remove any OTUs with an abundance of 0 while keeping singletons. An abundance-scaled OTU table was obtained using cumulative sum scaling (Paulson *et al.* 2013). Paired cores were pooled by replicate (i.e. tree) for downstream analysis.

Functional group characterization

OTUs were assigned trophic modes and guilds using FUNGuild (Nguyen *et al.* 2016; Table 2). Only OTUs that had been assigned to a functional group with the confidence ranking of 'highly probable' or 'probable' were included in downstream analyses (Day *et al.* 2019). To characterize functional traits of ectomycorrhizal OTUs, information regarding rhizomorph formation and foraging type (Table 3) was gathered for each ectomycorrhizal OTU using DEEMY (Agerer and Rambold 2004) and the Ectomycorrhizal Descriptions Database (British Columbia Ectomycorrhizal Research Network 2009). While exact species matches in either database were rare, coarse traits relevant to foraging type are similar at the genus level (Agerer 2001; Moeller, Peay and Fukami 2014)—thus, OTUs were assigned functional traits if there existed genus-level matches in either trait database.

In our analysis of responses of specific fungal functional groups to climate, we focus on ectomycorrhizal and arbuscular mycorrhizal fungi. While arbuscular mycorrhizal fungi (AMF) are often variably sequenced with ITS primers (Lee, Lee and Young 2008), we include AMF in our analyses because of their high abundance relative to other mycorrhizal groups (e.g. ericoid mycorrhizae) in the system.

Statistical methods

All analyses were performed using R version 3.5.1. Data and R code for all analyses are available in a public repository on Github (https://zenodo.org/badge/latestdoi/221615362).

Community composition

We determined if soil characteristics differed by site using one-way analysis of variance (ANOVA). Shannon diversity, species richness and Bray–Curtis dissimilarity were calculated using *vegan* (Oksanen *et al.* 2019). We determined if community composition differed between sites with PerMANOVA using the adonis() function. To visualize differences in community composition, we used non-metric multidimensional scaling (NMDS) using the 'metaMDS()' function in *vegan*.

Soil contributions to fungal community composition and richness

We used redundancy analysis (RDA) and multiple linear regression (MLR) to determine the contribution of soil physicochemical properties and site on community composition and richness, respectively. For the RDA, we used the stepwise model selection function in *vegan* to determine the best model of soil properties and sites as predictor variables and community composition as a response variable. The best model was defined as the combination of predictor variables giving the highest adjusted R^2 value. For the MLR, we used the *MuMin* package (Bartón 2020) for random selection of model parameters to determine the best model describing OTU richness as a response variable. We used the Akaike information criterion (AIC) to evaluate the best-fitting model.

Effects of geographic location on fungal community dissimilarity

We tested for correlation between geographic distance and community dissimilarity and soil environmental characteristics using a Mantel test with 'ecodist' in the *ecodist* package (Goslee and Urban 2007). There were 10 trees for which we could not match bioinformatic data with exact geographic coordinates;

therefore, we assigned an average location to these trees based on coordinates that had been collected but could not be assigned directly to any tree.

Ectomycorrhizal functional traits

To test the hypothesis that stress-tolerant traits relating to rhizomorph formation and foraging type will be found in higher abundance in arid compared to mesic sites, we assessed differences in the proportion of functional traits across all three sites using chi-square goodness-of-fit. The proportion of reads for each trait was determined by calculating the proportion of reads per trait per site. Therefore, proportions of reads per trait when compared across sites would sum to 1.

Community convergence

Community convergence across functional groups was calculated by dividing the Bray–Curtis distance between two site centroids (e.g. arid–intermediate, intermediate–mesic) and a tree and its site centroid [e.g. arid tree–arid centroid, mesic tree–mesic centroid (Supplemental Figure 2a.i and 2a.ii)], with the expectation that as communities start to converge, this ratio decreases (Supplemental Figure 2b). We calculated these distances using the *usedist* package (Bittinger 2020). We developed this metric in order to compare differences in community mean values and dispersion between datasets of different fungal functional groups—while a PERMANOVA only allows for comparison within datasets, this metric allows us to compare between datasets and their subsets (i.e. between the whole fungal community and ectomycorrhizal fungal OTUs). All OTUs that were not classified to any functional group were excluded from this analysis. We chose to calculate this metric for symbiotrophs, and ectomycorrhizal and arbuscular mycorrhizal species in order to compare species of similar functional identities. For each tree, two values for this ratio were calculated for each site comparison. To summarize all ratios calculated, we calculated the mean ratio for all trees for a single site.

To ensure that results were not due to differences in OTU richness between functional groups, we simulated the reduction in fungal richness that accompanies a focus on a specific functional group. To do this, we downsampled the most OTU rich communities to the lowest number of species in any functional group by randomly excluding OTUs from analysis. For example, when contrasting total fungal communities with ectomycorrhizal communities, we downsampled the total fungal community to $n = 117$ OTUs (the number of ectomycorrhizal species in our dataset). We bootstrapped this calculation for 1000 simulated communities that had been downsampled to control for differences in OTU richness between functional groups. This calculation was repeated for all four functional groups: all fungi (Supplemental Figure 2a.i), symbiotrophs, and arbuscular mycorrhizal and ectomycorrhizal fungi (Supplemental Figure 2a.ii).

Lastly, because our functional groups demonstrated different levels of species evenness (Supplemental Figure 3), we tested the effects of evenness across functional groups on the calculation of this metric. We constructed a 'null model' of randomly generated communities using the 'permatswap()' function in 'vegan' to shuffle read counts between present OTUs and retain the original identity and proportions of absent OTUs. We randomly generated 50 such communities, and performed the same bootstrapping procedure as on the original communities 50 times.

RESULTS

Soil characteristics

Soil % nitrogen and carbon, phosphorus, OM, TEC, ppm NO_3, ppm NH_4 and gravimetric water content were significantly different between sites, with mesic sites generally exhibiting higher resource availability and carbon content [one-way ANOVA, $P < 0.001$, $\alpha = 0.05$, nitrogen: $F(2, 22) = 9.10$, carbon: $F(2, 22) = 14.75$, phosphorus: $F(2, 23) = 39.2$, OM: $F(2, 23) = 24.78$, TEC: $F(2, 23) = 24.75$, NO_3: $F(2, 23) = 10.37$, NH_4: $F(2, 23) = 10.42$, gravimetric water content: $F(2, 23) = 13.95$; Supplemental Figure 4a–h]. Of all soil characteristics measured, only pH was not significantly different between sites [one-way ANOVA, $F(2, 23) = 0.59$, $P = 0.56$; Supplemental Figure 4i].

Fungal community composition

From Illumina MiSeq sequencing, ~2.1 million reads were obtained with 2422 unique OTUs. After filtering the dataset further for OTUs successfully assigned to functional groups, we were left with 1872 OTUs (77%) for downstream analyses (Table 4).

Mean fungal OTU richness per tree (i.e. replicate) was highest in samples from the arid site and lowest in those from the mesic site [Fig. 2A, one-way ANOVA, $F(2, 50) = 80.62$, $P < 0.001$]. Mean fungal Shannon diversity was also highest in the arid site and lowest in the mesic site [Fig. 2B, one-way ANOVA, $F(2, 50) = 82.09$, $P < 0.001$].

In addition to richness, fungal community composition also differed by site for all fungi [PerMANOVA, $F(2, 51) = 12.6$, $P = 0.001$, $\alpha = 0.05$, Fig. 3A] and for fungi grouped by guild [PerMANOVA, $F(2, 51) =$ symbiotrophs: 17.87, ectomycorrhizal fungi = 10.52, arbuscular mycorrhizal fungi = 16.59, saprotrophs: 15.39, pathotrophs: 16.65, $P = 0.001$, Fig. 3B–D, Supplemental Figure 5a and b).

Soil contributions to fungal community composition and richness

The model that described community composition best following stepwise selection was composed solely of site as a predictor variable (adjusted $R^2 = 0.32$, $P = 0.002$). Similarly, OTU richness was best described with a model with only site as a predictor variable (AIC = 183.12, weight = 0.33).

Effects of geographic location on fungal community dissimilarity

Distance was positively correlated with fungal community dissimilarity (one-tailed Mantel $r = 0.83$, $P = 0.001$, Supplemental Figure 6a). However, distance was not correlated with soil characteristics (two-tailed Mantel $r = 0.039$, $P = 0.33$, Supplemental Figure 6b). Black dots indicate significant spatial correlation.

Community convergence

Increasing levels of host association appeared to drive community convergence: After downsampling to control for OTU number, ectomycorrhizal fungal communities were more similar across sites than the total fungal community (Supplemental Figure 7). The null model of variable community evenness did not reveal any differences in level of convergence between functional groups.

Table 4. Summary of OTUs and read counts. Reads were assigned to functional groups based on taxonomic assignments in FUNGuild. A total of 591 OTUs (38%) were assigned to more than one functional group, and 582 OTUs were not assigned to any functional groups.

Site	Trees sampled	Total reads	Total OTUs	Functional group	Total reads	Total OTUs
Arid	15	617 481	1657	Symbiotrophs	281 490	473
				ECM	10 123	74
				AMF	5871	158
				Ericoid	869	10
				Saprotrophs	503 426	917
				Pathotrophs	311 379	504
				Unassigned	13 060	277
Intermediate	23	1 035 162	1038	Symbiotrophs	312 920	281
				ECM	10 619	53
				AMF	953	65
				Ericoid	1292	8
				Saprotrophs	849 114	596
				Pathotrophs	508 189	318
				Unassigned	29 328	177
Mesic	15	550 480	767	Symbiotrophs	105 435	41
				ECM	14 147	184
				AMF	559	31
				Ericoid	398	4
				Saprotrophs	411 192	459
				Pathotrophs	230 377	247
				Unassigned	16 157	129

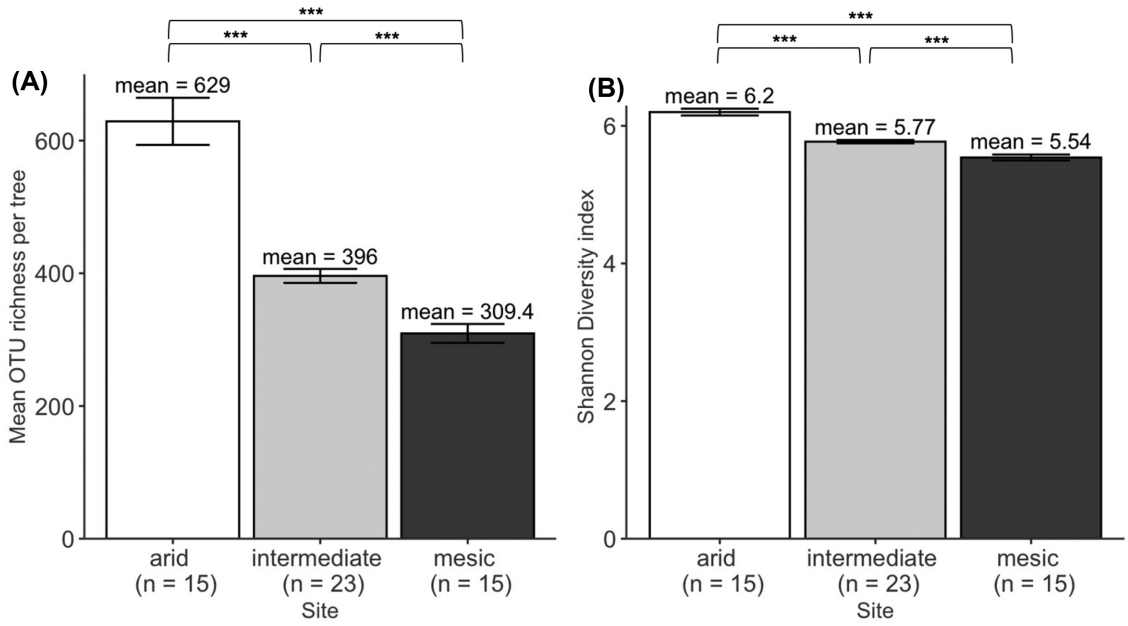

Figure 2. Fungal OTU richness and Shannon diversity. Mean fungal OTU richness and Shannon diversity were compared at three sites: arid, intermediate and mesic. Bars indicate standard error. Mean richness was significantly different between sites, as was Shannon diversity. Asterisks indicate pairwise significance comparisons by Tukey's Honestly Significant Difference tests (***: $P < 0.001$).

Ectomycorrhizal functional trait analysis

Using FUNGuild, we determined that 92 fungal OTUs were ectomycorrhizal. For 64 of these OTUs, we were able to assign trait characteristics for foraging distance and rhizomorph formation at the genus level and assumed that all traits were equally as likely to be described as others (e.g. short-distance foragers not more likely to be described than long-distance ones). We assigned functional traits to each OTU and calculated the mean proportion of functional traits by site.

With regard to foraging distance, the proportion of short-, medium- and long-distance foragers was significantly different between sites (chi-square, $\chi^2(4) = 195.11$, $P < 0.001$, Fig. 4A–C). With regard to rhizomorph formation, the proportion of rhizomorph formers and non-rhizomorph formers was significantly different between sites (chi-square, $\chi^2(2) = 132.47$, $P < 0.001$, Fig. 4D and E).

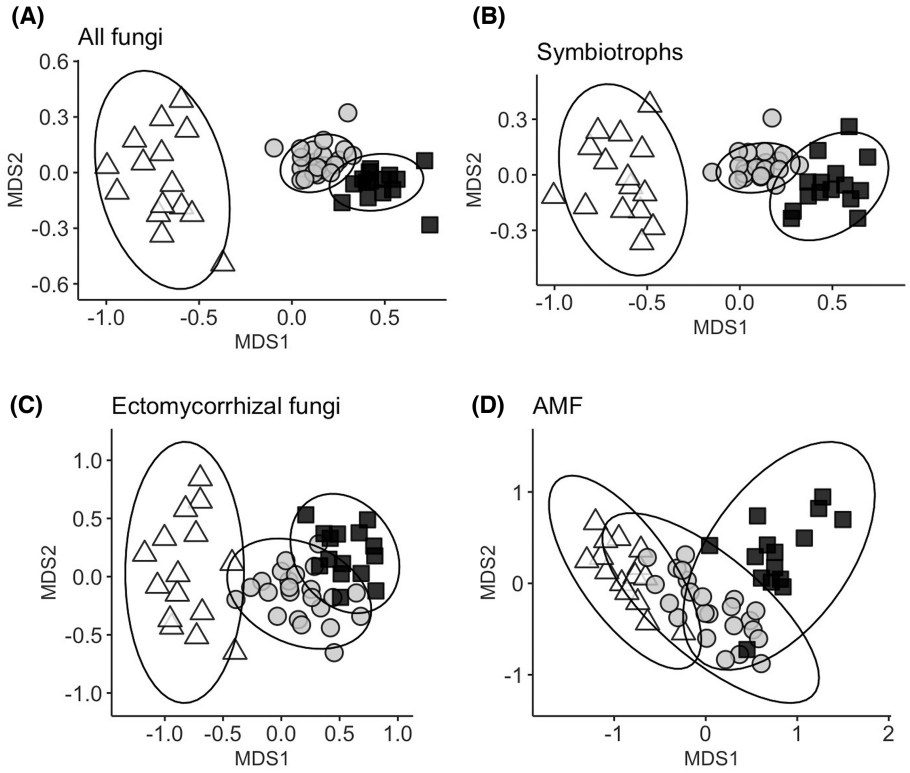

Figure 3. NMDS ordination of fungal communities by guild. Each point in the plot represents one host tree from arid (white triangles), intermediate (grey circles) and mesic (black squares) sites. The distance between points is proportional to the distance between fungal communities, measured by Bray–Curtis dissimilarity. Community clustering was significantly different between sites for all guilds, measured using PerMANOVA with a significance level of $P < 0.001$.

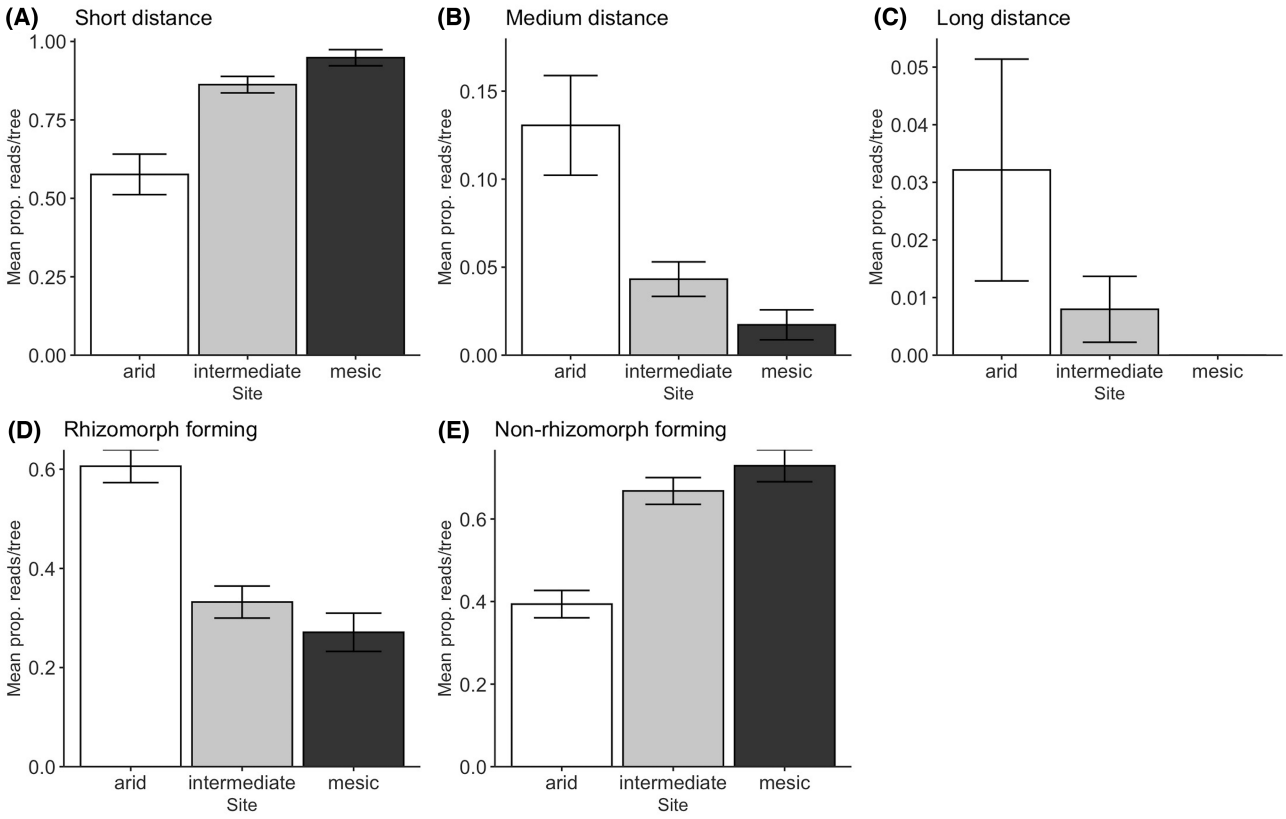

Figure 4. Ectomycorrhizal functional trait distribution across sites. Functional traits were assigned to OTUs, and then mean proportion of reads of each OTU per trait was calculated. Bars indicate standard error.

DISCUSSION

In this study, we found significant differences in fungal community composition across three sites differing largely in local climate representing potential climate in California's oak woodlands in present, near-future and far-future conditions. Fungal species richness in arid sites was twice as high as in mesic sites and Shannon's H (which measures diversity and evenness) in arid sites was 1.5 times that of mesic sites, suggesting a potential increase in Shannon's H of fungal communities in future climate scenarios. Using a Bray–Curtis distance-based metric, we also found that host association buffered fungal communities from change—fungal guilds that displayed strong host association (e.g. ectomycorrhizal and arbuscular mycorrhizal fungi, Fig. 3C and D) were more similar across climatic conditions than the fungal community as a whole (Fig. 3A). Lastly, we examined a subset of species in our dataset for functional trait analysis: Although ectomycorrhizal fungal communities were more similar across distinct climatic conditions than the broader fungal community, subtle shifts in community membership led to higher relative abundance of stress-tolerant traits in arid sites, suggesting some capacity in the system to retain function (e.g. nutrient delivery to host trees) while adjusting to future climate conditions.

The distinct climatic conditions in our study provide insight into how patterns of fungal diversity may change with climate change, though these patterns appear to differ across systems. While some studies find that fungal OTU diversity and richness increase with nutrient availability and moisture (Peay *et al.* 2017), others show the opposite effect (Giauque and Hawkes 2016; Newsham *et al.* 2016) and still others show no or inconsistent effects (Fierer *et al.* 2011; Hendershot *et al.* 2017). Insights into the patterns of community composition we see in our study may be described by a working hypothesis in animal microbiome research, the Anna Karenina Principle (Zaneveld, McMinds and Thurber 2017). Based on the opening line of the eponymous novel by Leo Tolstoy, this hypothesis states that an unhealthy (i.e. stressed due to environmental conditions) host may have a more diverse microbiome than its healthy counterparts (Zaneveld, McMinds and Thurber 2017). Here, we find that tree hosts in arid sites support more dispersed communities than those in mesic sites. Our data demonstrate that if climate change produces greater aridity, future fungal communities may be more speciose than those at present in mesic sites.

We demonstrate that mutualism filters fungal community composition—while hosts at each site have distinct fungal communities from those in other sites, we found that ectomycorrhizal fungal communities were more similar than the whole host-associated community. Here, mutualism appears to reduce the magnitude of community change, as trees can modulate their own rhizospheres and filter potentially disadvantageous mutualists out of their own community (Kiers *et al.* 2011; Ji and Bever 2016). However, we maintain the caveat that community evenness may contribute to the patterns we observed in convergence; for example, communities of ectomycorrhizal species may converge simply because they are more even than the whole fungal community. We look forward to the implementation of this metric with other datasets with highly variable sample evenness to further assess its efficacy as a measure of community convergence.

Though host-associated communities remain similar to each other across distinct climatic conditions, we show that trait space shifts to more costly but higher performing fungi in arid environments. For ectomycorrhizal fungi, foraging distance and rhizomorph formation are determined by the nutrient availability of their environments; for example, we would expect to find more long distance foragers in a nutrient-poor environment because the production of exploratory structures is only worth the high energetic cost when nutrients are depleted and therefore difficult to access (Hobbie 2006). Similarly, we would expect to find more rhizomorph-forming species in dry environments, as rhizomorphs increase the surface area upon which an ectomycorrhizal fungus can detect and extract water from soil (Koide, Fernandez and Malcolm 2014). Given that energetically costly but highly rewarding partners are found in higher abundance in arid sites than mesic, our data suggest that future climates may stress trees, but different sets of fungal partners may buffer this stress. We were able to examine functional traits for ectomycorrhizal fungi because they are relatively well-studied compared to other fungal groups; however, further trait-based approaches to understanding mechanisms behind community turnover for other groups are needed.

Differences in community composition between host-associated and non-host-associated fungi across climatically distinct sites have the potential to scale up to affect ecosystem function. These groups play integral roles in biogeochemical processes, but at different parts of the cycle given their trophic mode—host-associated functional groups such as ectomycorrhizal and arbuscular mycorrhizal fungi release tree photosynthetic products into soil in exchange for the acquisition of nitrogen and phosphorus (Rillig 2004; Tedersoo and Smith 2013), while saprotrophs do not rely on tree hosts but rather decompose dead plant tissue (Buée *et al.* 2009), and pathotrophs consume living plant tissue. We focus on the responses of symbiotrophs, hypothesizing that host-associated species engaging in mutualisms would respond uniquely to climatically distinct conditions because their reliance on a host may buffer their responses to climate change. While our hypothesis was specific to mutualists, other host-associated species such as pathotrophs may also experience the same response and therefore be buffered from climate impacts by associating with plant hosts. However, our data demonstrate that their responses do not match with the convergence seen for mycorrhizal groups (Supplemental Figure 5); rather, their patterns of community composition are more similar to the whole fungal community than symbiotrophs. Therefore, we directed our attention from addressing questions regarding community convergence towards symbiotrophs.

An important consideration in our work, as in all next-generation approaches to quantifying fungal community composition, is the challenge of linking sequencing data (specifically, read counts) to actual abundance in the fungal community. In addition to potential asymmetries in extraction, amplification and sequencing across fungal taxa, fungi also differ in per-cell ITS copy number (Taylor *et al.* 2016). Thus, caution should be used when interpreting relative abundance results based on ITS amplicon numbers. However, two lines of evidence suggest that our findings are likely robust to these potential sources of bias. First, we observed strong site-based differentiation of our fungal communities, with turnover in a subset community membership (beta diversity) across arid, intermediate and mesic sites. Second, and relatedly, differences in community composition were significant when using either abundance-based (e.g. Bray–Curtis) or presence–absence based (e.g. Jaccard, Supplemental Figure 8) diversity metrics. Our work contributes important information on fungal community membership, which could assist in the assembly of relevant mock fungal communities for future studies of this nature.

The greater diversity of ground cover in our mesic site (Supplemental Figure 1) and physical distance may have impacted the composition of our fungal community. For example, a greater abundance of shrubs on mesic sites, compared to grasses and herbs on intermediate and arid sites, means that arbuscular mycorrhizal host abundance was greater on arid and intermediate sites. Additionally, while some part of the patterns we see across climatically distinct sites may be due to physical distance (i.e. dispersal limitation by fungal species), site effects appeared to be greater than those of distance or soil characteristics. Though samples that are close together are more similar, they do not necessarily have similar soil properties (Supplemental Figure 6); additionally, there was no effect of distance within sites on fungal community dissimilarity. We also found that site was the best predictor of fungal community composition over soil characteristics. Therefore, while distance may be a confounding factor in the patterns of composition and richness we see, we demonstrate that site—our proxy for climate—predicts these patterns best.

Our results demonstrate that fungal community composition changes across distinct climatic conditions that represent the climate future in California's oak woodlands. As parts of our planet continue to become warmer and drier, we can start to infer how ecosystem function may change following shifts in fungal community composition. In California, where the interaction of warming temperatures and variable precipitation is of particular concern (Rapacciuolo *et al.* 2014; Diffenbaugh, Swain and Touma 2015), preserving ecosystem function in oak woodlands depends on understanding dynamics of oaks in future climate contexts (Kueppers *et al.* 2005; Mclaughlin and Zavaleta 2012). While our observed shifts in fungal community composition potentially foreshadow changes in oak woodland ecosystem function, the increase in diversity we see in our system implies there may be more resilience in function than would be predicted by compositional shifts alone. Additionally, potential buffers against change exist via two pathways: first, oak–host association can drive compositional similarities across distinct climatic conditions and, second, shifts in relative abundances of functional traits can permit survival given a changing climate. However, we do not yet know how far such buffers will extend—further work explicitly linking changes in community composition and traits to observed function is needed to fully understand how ecosystem function as a result of fungal community turnover will change in the future.

AUTHORS' CONTRIBUTIONS

AB and HVM conceived the ideas and designed methodology. DO and HSY established the field site. AB, DO, MLB, KK and HVM collected data. AB analyzed the data and led the writing of the manuscript. All authors provided critical revisions of the manuscript and gave final approval for publication.

DATA AVAILABILITY

Data and R code for all analyses are available in a public repository on Github (https://zenodo.org/badge/latestdoi/221615362). Sequence data have been archived at the Sequence Read Archive supported by the National Center for Biotechnology Information with accession number PRJNA623934.

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SUPPLEMENTARY DATA

Supplementary data are available at *FEMSEC* online.

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