University of Calfiornia

SANTA BARBARA

Soil fungal community richness and diversity are highest in arid environments along a climatic space-for-time substitution

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by

An Thanh Bui

Committee in charge:

Professor Holly Moeller, co-chair

Professor Hillary McCauley, co-chair

Professor Carla D'Antonio

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The thesis of An Thanh Bui is approved.

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Professor Carla D'Antonio

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Professor Hillary McCauley, co-chair

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Professor Holly Moeller, co-chair

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DEDICATION

To Mẹ and Ba, for everything.

ABSTRACT

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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 along the climatic gradient than the whole fungal community. Lastly, an examination of functional traits for ectomycorrhizae, 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.

Introduction

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

While changes in climate can impact fungal community composition (Andrew et al., 2016; Classen et al., 2015; Peay et al., 2017), the direction and strength of these effects are variable across systems (Compant, Van Der Heijden, & Sessitsch, 2010; Rillig, Treseder, & Allen, 2002) especially when considering the different effects on functional groups (i.e. saprotrophs, symbiotrophs, and pathotrophs) and species guilds (e.g. ectomycorrhizae, arbuscular mycorrhizae) (Asemaninejad, Thorn, Branfireun, & Lindo, 2018; Geml et al., 2015; Mohan et al., 2014). 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., 2015; Aguilar-Trigueros, Powell, Anderson, Antonovics, & Rillig, 2014; Crowther et al., 2014;

Koide, Fernandez, & 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, Egger, Massicotte, & Green, 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 mutualist species – 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 & Read, 2008). This mutualism plays a major role in ecosystem function, as mycorrhizae can provide almost half of a tree's organic nitrogen budget (Zhang, Yuan, Liu, & Yin, 2019) and contribute the bulk of new carbon into soil (Zhang et al., 2018). Additionally, mycorrhizal groups (i.e. arbuscular mycorrhizae and ectomycorrhizae) differ in the amount of carbon they input to soil (Averill, Turner, & Finzi, 2014) and their respective nitrogen and phosphorus benefits to their hosts (Teste, Jones, & Dickie, 2019). Therefore, understanding changes in mycorrhizal communities in particular can provide insight into changing ecosystem functions in the future (van der Heijden, Martin, Selosse, & Sanders, 2015).

Given that mycorrhizas 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 (Adair & Douglas, 2017; Lebeis, 2015; Peiffer et al., 2013); 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 climatic gradients within a single host species than the entire species pool (Nuccio et al., 2016).

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. While mycorrhizal mutualists may remain similar in composition, changes in relative abundance of functional traits or species could conserve host function (Eduardo, Florencia, Nicolás, & József, 2018; Yan et al., 2018). Thus, by filtering membership of the fungal community (Kiers, Rousseau, West, & Denlson, 2003), host trees may maintain mycorrhizal mutualism function across drastically different climates, thereby preserving ecosystem function. 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 1) quantify changes in fungal community composition, 2) test the effects of host association on these shifts, and 3) measure turnover in relative abundance of fungal 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, & 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, Snyder, Sloan, Zavaleta, & Fulfrost, 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 climate gradients and there are distinct shifts in climatic conditions 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 gradients, soils in dry sites tend to be nutrient-poor compared to wet sites (Delgado-Baquerizo et al., 2013; Jiao, Shi, Han, & Yuan, 2016; Talmon, Sternberg, & Grünzweig, 2011); therefore, arid environments will likely support fewer fungal species than their mesic counterparts (Maestre et al., 2015). Next, we ask how host association may drive convergence of fungal communities, and hypothesize that communities of host-associated symbionts are more similar to each other than to free-living

communities across the climate gradient. Potential fungal partners are likely filtered by their hosts based on efficacy of nutrient acquisition given carbon costs (Dickie, 2007; Powell & Rillig, 2018; Vályi, Mardhiah, Rillig, & Hempel, 2016), and we expect host selectivity to override the filtering effects of climate. Lastly, we ask how 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. In this case, we explore the functional traits of ectomycorrhizal fungi and predict that functional traits considered adaptive for stressful environments will be found in higher abundance in arid compared to mesic sites (Moeller, Peay, & 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, Figure 1). April represents the full leaf out period for the main host plant species, as well as peak growth for most understory plants.

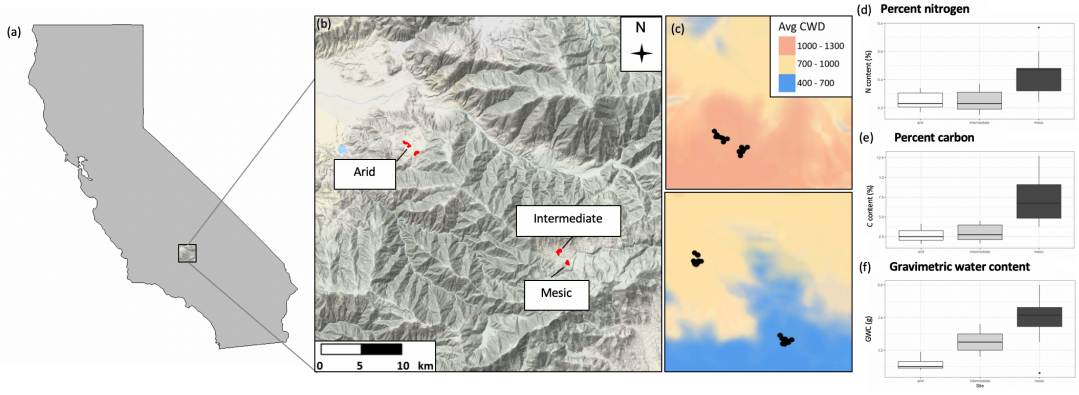

Figure 1. Sampling sites at Tejon Ranch. Tejon Ranch is in south-central California (a). Sampling sites are shown with each dot representing the geographic location of a sampled

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 percent nitrogen, carbon, and gravimetric water content differ between sites (d-f).

The mountain range is characterized by diverse oak woodland habitats (Davis & Sweet, 2012), with valley oaks (*Quercus lobata*) distributed widely across elevations between 1000 and 6000 feet. The Tehachapi mountain range experiences a Mediterranean climate and is representative of California oak woodland ecosystems; therefore, Tejon is an especially fitting site to examine the effects of climate on community composition and diversity patterns broadly applicable to these particular systems (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000; Sala et al., 2000).

We utilized existing experimental sites at Tejon, which build on pre-existing climate grids spanning approximately 33,000 hectares across the elevational gradient (Davis & Sweet, 2012; McCullough et al., 2016). These include three sites ("mesic", "intermediate", "arid") selected to roughly represent present, near-future, and far-future climate scenarios for this region of California, with a mean increase of approximately 2 °C and a climate water deficit (CWD) of approximately 200 mm H_2O between consecutive sites. 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 and precipitation, but also due to differences in soil water holding capacity (McCullough et al 2016). Soils at all three sampling sites are granite-derived coarse-loamy Haploxerolls (Soil Survey Staff, 2019). 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.

To characterize the host-associated fungal community, we sampled soil cores from valley oaks at each site. When possible, we sampled trees at least 10m from another tree. We removed any large (>2 cm) pieces of plant litter that lay atop the soil and took two soil cores 5cm wide and 10cm deep from the base of the tree. Soils were kept on ice until transport back to the lab. Soil samples were homogenized prior to all downstream processing and filtered through sieves of apertures of 2mm and 5.6mm to remove any remaining pieces of plant litter. From a random subset of samples (n = 23) representing all three sites, we measured soil percent nitrogen, percent carbon, phosphorus, organic matter (OM), total exchange capacity (TEC), ppm NO_3, and ppm NH_4 (Brookside Laboratories, New Bremen, Ohio, Supplemental 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.

Laboratory methods

Fungal community DNA extraction and sequencing

0.25g soil was extracted from each sample, and fungal DNA was extracted using the DNEasy Powersoil Kit (Qiagen). Extracted DNA was amplified using PCR with forward primer ITS1F-KYO1 and ITS2-KYO1 (Toju, Tanabe, Yamamoto, & Sato, 2012) using the following thermocycler protocol: 3 min @ 95°C, 0:30 sec @ 95°C + 0:30 sec @ 47°C +

0:30 @ 72°C 35x, 5 min @ 72°C, ∞ @ 4°C. Each sample was given a unique pair of forward and reverse barcodes, ligated on using the following thermocycler protocol: 3 min @ 95°C, 0:30 sec @ 95°C + 0:30 sec @ 55°C + 0:30 @ 72°C 10x, 5 min @ 72°C, ∞ @ 4°C. Samples were cleaned using AMPure XP beads and diluted to 4 nM. Samples were pooled and sequenced using the Illumina MiSeq platform at University of California Santa Barbara Biological Nanostructures Lab.

Bioinformatics pipeline and data analysis

Sequence processing

Forward and reverse reads obtained through Illumina sequencing were merged, filtered, and clustered into operational taxonomic units (OTUs, serving as a proxy for species) by 97% similarity using USEARCH11 (Edgar, 2010). OTUs were assigned taxonomy using BLAST on the University of California Santa Barbara Knot Computing Cluster. Taxonomy for each OTU was determined using MEGAN (Huson et al., 2016). All fungal taxonomic paths were extracted, and all OTUs were filtered against this list in QIIME (Caporaso et al., 2010). An abundance-scaled OTU table was obtained using cumulative sum scaling (Paulson, Colin Stine, Bravo, & Pop, 2013).

Community convergence

Adapting techniques developed to characterize stable isotopic niche space (Layman, Arrington, Montaña, & Post, 2007), community convergence was calculated by dividing the Euclidean distance between a community and its site centroid by the distance between site centroids on a pairwise basis (Supplemental Figure 1A), with the expectation that as communities start to converge, this ratio decreases. We repeated this analysis on 1000

bootstrapped ordinations in which OTUs were downsampled to control for differences in OTU number between groups for ectomycorrhizae, arbuscular mycorrhizae (AMF), symbiotrophs, and the whole fungal community.

Functional trait characterization

OTUs were assigned trophic modes and guilds using FUNGuild (Nguyen et al., 2016, Table 1).

Table 1. Fungal trophic modes and guilds as assigned using FUNGuild.

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

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 2) was gathered for each ectomycorrhizal OTU using DEEMY (Agerer & Rambold, 2004) and the Ectomycorrhizal Descriptions Database (British Columbia Ectomycorrhizal Research Network, 2009).

Table 2. 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)

While exact species matches in either database were rare, coarse traits relevant to foraging type are similar at the genus level (Agerer, 2001; Moeller et al., 2014) – thus, OTUs were assigned functional traits if there existed genus-level matches in either trait database.

Statistical methods

All analyses were performed using R version 3.5.1. We determined if soil characteristics differed by site using one-way analysis of variance (ANOVA). Shannon diversity, species richness, and community dissimilarity were calculated using *vegan* (Oksanen et al., 2019). We determined if community composition differed between sites with PerMANOVA using the adonis() function. Differences in the proportion of functional traits across all three sites was assessed using chi-square goodness-of-fit. Data and R code for all analyses is available in a public repository on Github (https://github.com/an-bui/fungal-community-data).

Results

Soil characteristics

Soil percent nitrogen, percent carbon, phosphorus, organic matter (OM), total exchange capacity (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 2). 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 2).

Fungal community composition

From Illumina MiSeq sequencing, over 17 million reads were obtained with 2422 unique OTUs. After filtering the dataset further for OTUs successfully assigned to functional groups, we were left with 1563 OTUs (63%) for downstream analyses. Of 1563 fungal OTUs, 554 were symbiotrophs, 1022 were saprotrophs, and 555 were pathotrophs; 414 OTUs were classified in one or more trophic mode. Of the 294 identified mycorrhizal OTUs – a subset of symbiotrophs – 92 OTUs were ectomycorrhizal, 192 were arbuscular, and 10 were ericoid.

Mean fungal OTU richness per tree was highest in arid sites and lowest in mesic sites (Figure 1A, one-way ANOVA, $F(2, 51) = 63.68$, $p < 0.001$). Mean fungal Shannon diversity was also highest in arid sites and lowest in mesic sites (Figure 1B, one-way ANOVA, $F(2, 51) = 82.09$, $p < 0.001$).

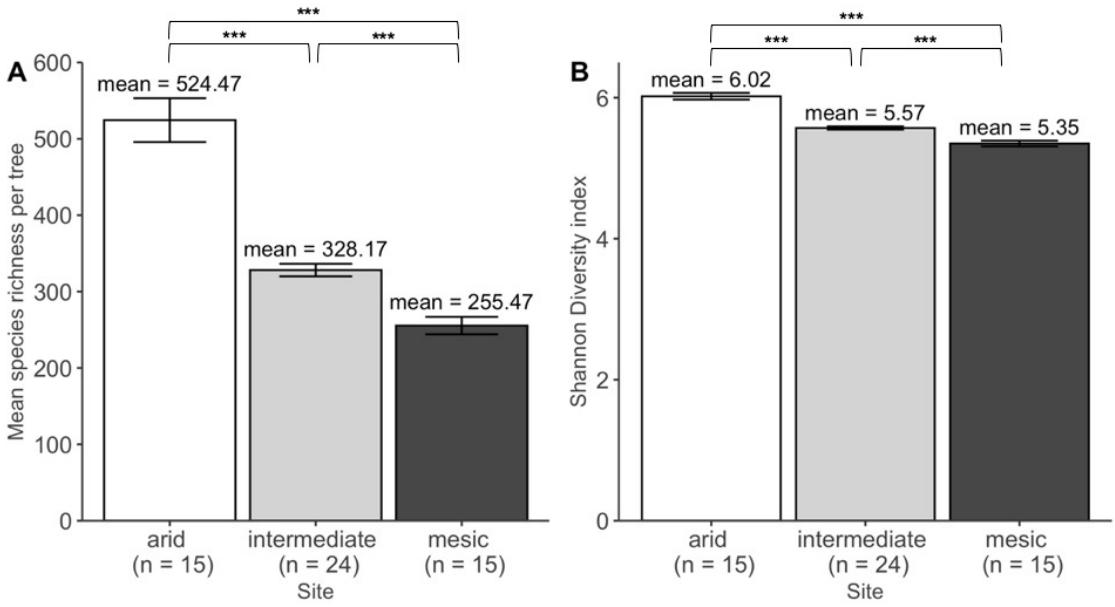

Figure 2. Fungal OTU richness and Shannon diversity. Mean fungal OTU richness and Shannon diversity was compared at three sites: arid, intermediate, and mesic. Bars indicate standard error. Mean richness was significantly different between sites, as was Shannon diversity. Asterisks indicate pairwise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

In addition to richness, fungal community composition also differed by site for all fungi (PerMANOVA, $F(2, 51) = 12.6$, $p = 0.001$, $a = 0.05$, Figure 2A) and for fungi grouped by guild (PerMANOVA, $F(2, 51)$ = symbiotrophs: 17.87, ectomycorrhizae = 10.52, AMF = 16.59, saprotrophs: 15.39, pathotrophs: 16.65 $p = 0.001$, , Figures 2B-D, Supplemental Figure 3A-B).

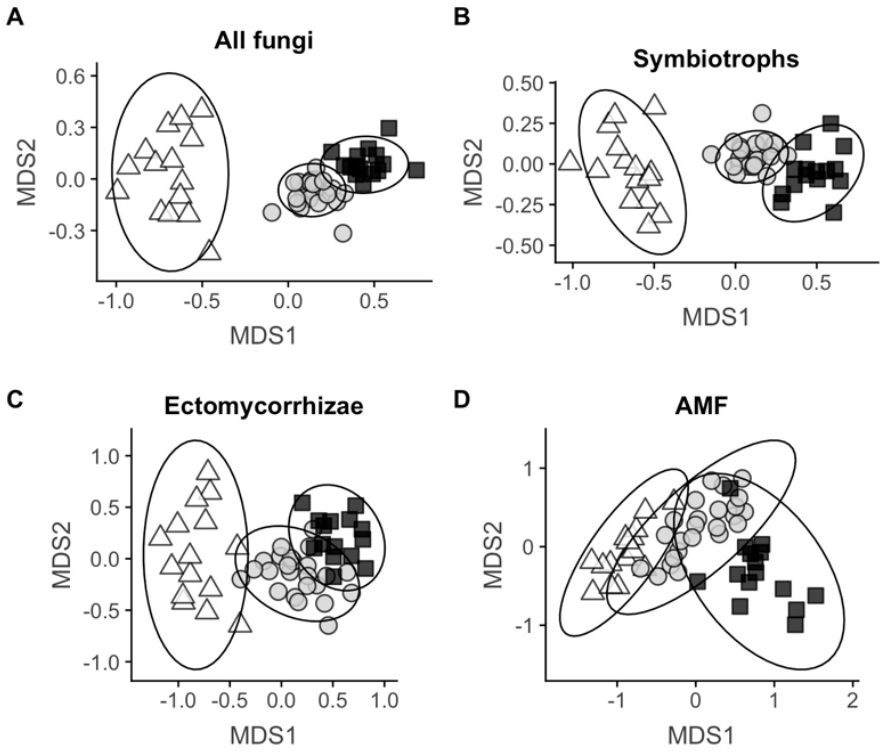

Figure 3. NMDS ordination of fungal communities by guild. Each point in the plot represents one host tree from arid (white triangles), intermediate (grey circles), and mesic (black squares) sites. The distance between points is proportional to the distance between fungal communities, measured by Bray-Curtis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

Community convergence

Increasing levels of host association appeared to drive community convergence: after downsampling to control for OTU number, ECM and AMF communities were more similar across sites than the total fungal community (Supplemental Figure 1B).

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. We assigned functional traits to each OTU and calculated the mean proportion of functional traits by site.

With regards to foraging distance, the proportion of short, medium, and long distance foragers was significantly different between sites (chi-square, \chi^2(4) = 198.31, p < 0.001, Figure 3A-C).

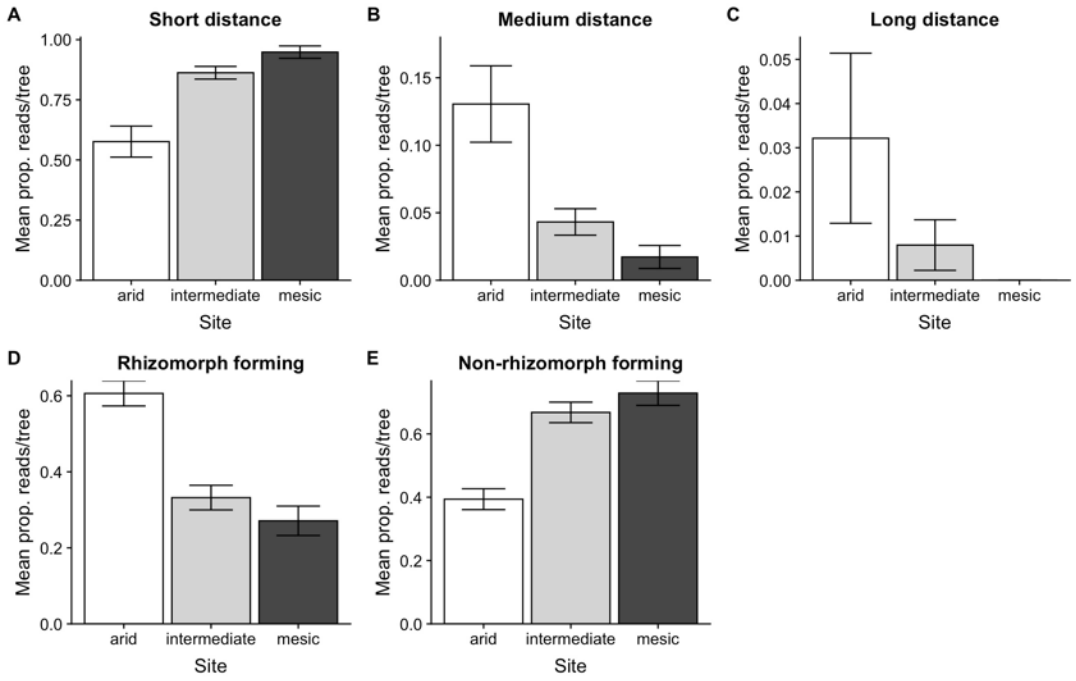

Figure 4. Ectomycorrhizal functional trait distribution across sites. Functional traits were assigned to OTUs, then mean proportion of reads of each OTU per trait were calculated. Bars indicate standard error.

With regards to rhizomorph formation, the proportion of rhizomorph formers and non-rhizomorph formers was significantly different between sites (chi-square, \chi^2(2) = 134.07, p < 0.001, Figure 3D-E).

Discussion

In this study, we found significant differences in fungal community composition across three sites differing largely in local climate. Fungal species richness in arid sites was twice as high as mesic sites and diversity in arid sites was 1.5x that of mesic sites, suggesting a potential increase in diversity of fungal communities in future climate scenarios. Using a Euclidean distance-based metric, we also found that host association buffered fungal communities from change – fungal guilds which displayed strong host association (e.g. ectomycorrhizae and arbuscular mycorrhizae, Figure 3C-D) were more similar across the climate gradient than the fungal community as a whole (Figure 3A). Lastly, we examined a subset of species in our dataset for functional trait analysis: although ectomycorrhizal communities were more similar across the climate gradient 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 space-for-time substitution in our study provides insight into how patterns of fungal diversity may change with climate change. While some studies find that fungal OTU diversity and richness increases with nutrient availability and moisture (Peay et al., 2017), others show the opposite effect (Giauque & Hawkes, 2016; Newsham et al., 2016) and still others show no or inconsistent effects (Fierer et al., 2011; Hendershot, Read, Henning, Sanders, & Classen, 2017). Insights into the patterns of species richness and diversity we see in our study may be described by a working hypothesis in animal microbiome research, the Anna Karenina Principle (Zaneveld, McMinds, & Thurber, 2017). Based on the opening line of the eponymous novel by Leo Tolstoy, this hypothesis states that an unhealthy (i.e.

stressed) host may have a more diverse microbiome than its healthy counterparts (Zaneveld et al., 2017). Here, we find that tree hosts in arid sites support more diverse communities than those in mesic sites and that within-site variation is higher in arid sites than 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, suggesting the possibility of preserving major ecosystem functions performed by soil fungi.

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 their mutualist communities (i.e. mycorrhizal partners) 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 (Ji & Bever, 2016; Kiers et al., 2011). From a management perspective, this could have both benefits and costs to adapting management plans: action can be taken to mitigate functional loss of mutualists to conserve function of habitat-forming species, but sudden loss of hosts could imply complete loss of mutualist function as well.

Though host-associated communities remain similar to each other across a climatic gradient, we show that trait space shifts to more costly but higher performing fungi in arid environments. We were able to examine functional traits for ectomycorrhizae 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. For ectomycorrhizae, foraging distance and rhizomorph formation is 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 et al., 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.

Differences in community composition between host-associated and non-host-associated fungi across a climatic gradient 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 ectomycorrhizae and arbuscular mycorrhizae release tree photosynthetic products into soil in exchange for the acquisition of nitrogen and phosphorus (Rillig, 2004; Tedersoo & Smith, 2013), while saprotrophs do not rely on tree hosts but rather decompose dead plant tissue (Buée, de Boer, Martin, van Overbeek, & Jurkevitch, 2009), and pathotrophs consume living plant tissue.

Our results demonstrate that fungal community composition changes along a climatic gradient. 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 (Diffenbaugh, Swain, & Touma, 2015; Rapacciuolo et al., 2014), preserving ecosystem function in oak woodlands depends on understanding dynamics of oaks in future climate contexts (Kueppers et al., 2005; Mclaughlin & 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 a climatic gradient 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.

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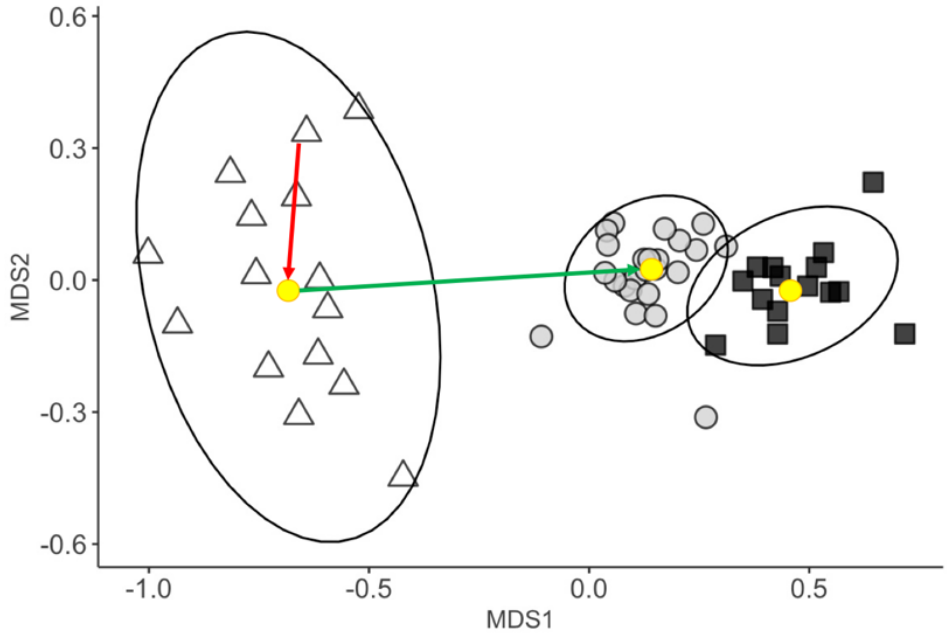
APPENDIX

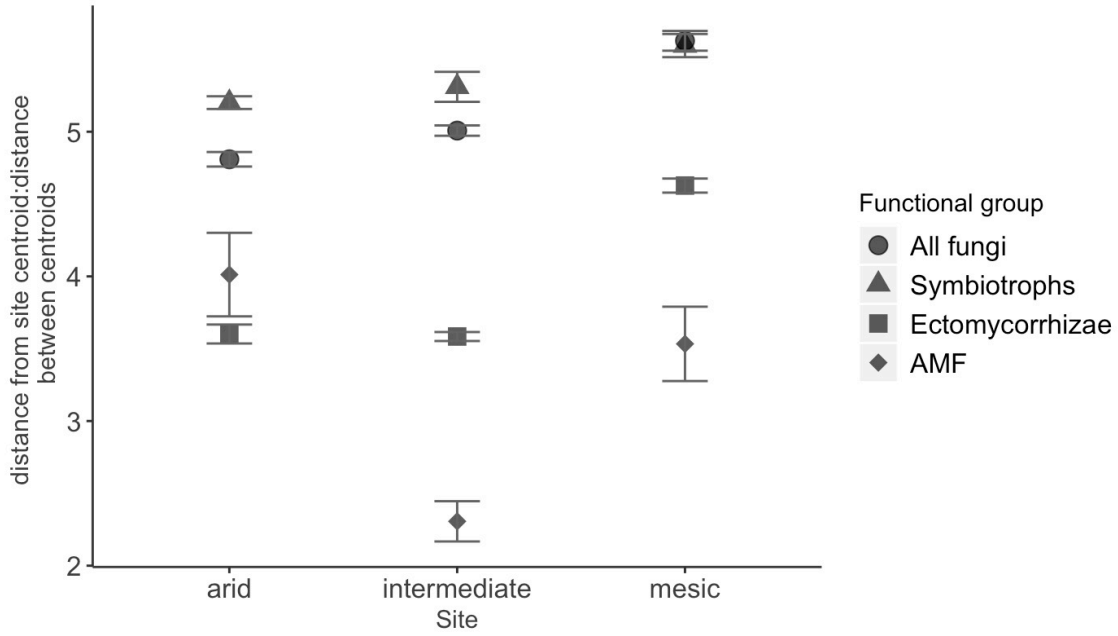
Supplemental Table 1. Methods of soil characteristic measurements.

Measurement	Method	Citation
Percent nitrogen	Combustion	(McGeehan & Naylor, 1988; Nelson & Sommers, 1996)
Percent carbon	Combustion	(McGeehan & Naylor, 1988; Nelson & Sommers, 1996)
Phosphorous	Bray II	(Bray & Kurtz, 1945)
Organic matter	Weight loss on ignition	(Schulte & Hopkins, 1996)
Total exchange capacity	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)

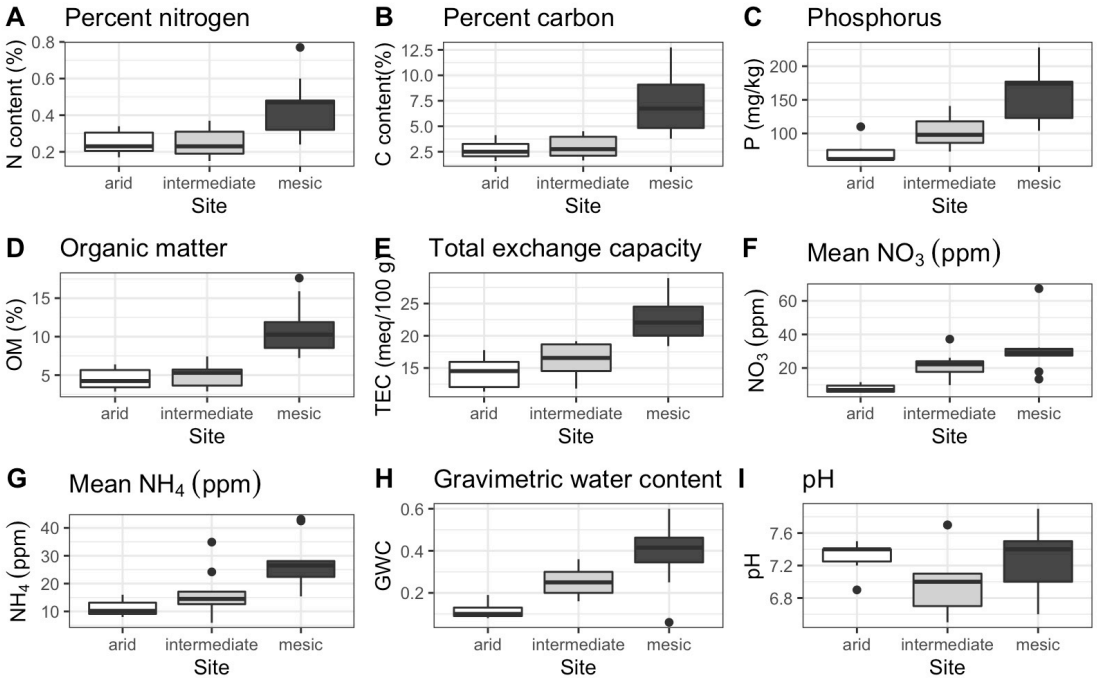


Supplemental Figure 1A. Graphical representation of community convergence calculation.
Each point represents a tree from an arid (white triangles), intermediate (grey circles), or mesic (black squares) site. Yellow circles represent site centroids. The red arrow represents Euclidean distance between an arid tree and its site centroid. The green arrow represents

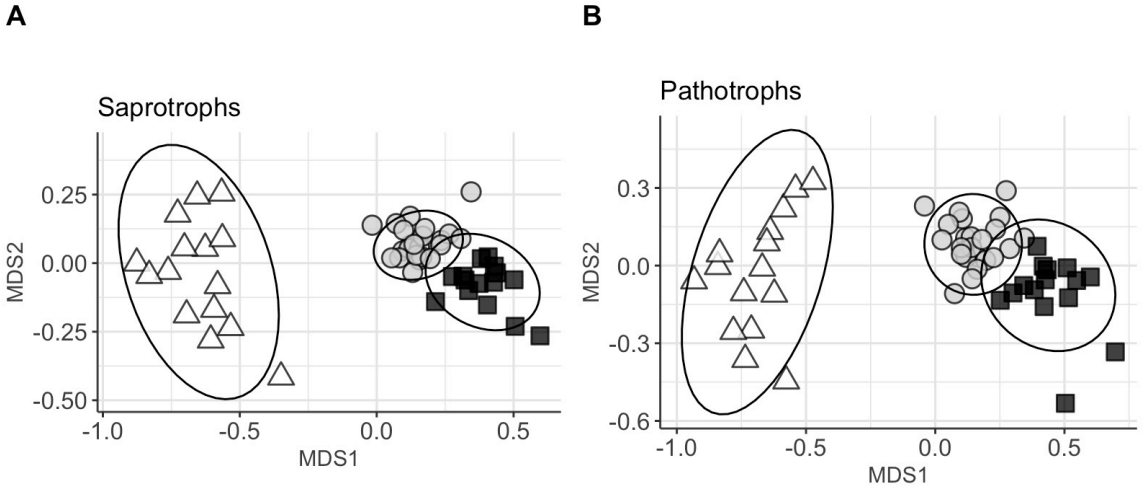
Euclidean distance between two site centroids. The community convergence statistic is the ratio of these two distances. As communites get closer, this ratio decreases.



Supplemental Figure 1B. Euclidean distance between tree and site centroid divided by distance between site centroids. As expected, the ratio between these two measurements decreases with more host-association.



Supplemental Figure 2. Edaphic characteristics of sample sites. Soil characteristics were measured for a subset of samples (n = 23).



Supplemental Figure 3. NMDS ordination of saprotrophs and pathotrophs. 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 both saprotrophs and pathotrophs, measured using PerMANOVA with a significance level of $p < 0.001$.