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RESEARCH ARTICLE

Dryland soil mycobiome response to long-term precipitation variability depends on host type

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Abstract

1. Climate change is projected to cause shifts in precipitation regimes globally, leading to intensified periods of precipitation and droughts. Most studies that have explored the influence of changing precipitation regimes on ecosystems have focused on changes in mean annual precipitation, rather than the variance around the mean. Soil fungi are ubiquitous organisms that drive ecosystem processes, but it is unknown how they respond to long-term increased interannual precipitation variability.
2. Here, we investigated the influence of long-term increased precipitation variability and host type on soil fungal diversity and community composition in a dryland ecosystem. We collected 300 soil samples from two time points and different host type substrate types at a long-term precipitation variability experiment at the Jornada Long Term Ecological Research site. Next, we used amplicon sequencing to characterize soil fungal communities.
3. Soil fungal alpha diversity and community composition were strongly affected by host type and sampling year, and increased precipitation variability caused a modest, statistically insignificant, decrease in soil fungal evenness. Furthermore, results from our structural equational model showed that the decrease in grass-associated soil fungal richness was likely an indirect result of host decline in response to increased precipitation variability.
4. *Synthesis*. Our work demonstrates effects of increase in interannual precipitation variability on soil fungi, and that plant hosts play a key role in mediating soil fungal responses.

KEYWORDS
Bouteloua eriopoda, drylands, evenness, mycobiome, precipitation variability, *Prosopis glandulosa*, soil fungi

1 | INTRODUCTION

Drylands cover 40% of the Earth's terrestrial surface (Nielsen & Ball, 2015) and provide ecosystem services to more than 2.5 billion people (Prăvălie, 2016). Changes in precipitation regimes will lead to major consequences for organisms inhabiting drylands (Gherardi & Sala, 2019). It is critical to understand how these changes affect microbial taxa, because they are the most abundant soil organisms and rely heavily on moisture to interact with the environment, acquire resources and disperse (de Nijs et al., 2019; Tecon & Or, 2017). In addition, various soil micro-organisms respond differently to fluctuations in soil moisture (Schwinning & Sala, 2004). Fluctuations in soil moisture influence microbial growth rates, community composition and carbon use efficiency (Leizeaga et al., 2020). In ecosystems with low nutrient cycling and rainfall, soil fungi are significantly influenced by changes in precipitation regimes, whereas bacterial communities do not show significant changes (van der Heijden et al., 2008). Therefore, in drylands, the ramifications of changes in precipitation regimes on the mycological component of the soil microbiome (hereafter referred to as the mycobiome) are especially important.

Ecosystem responses to changes in environmental variables, such as precipitation, are not only subject to changes in means (Parmesan & Yohe, 2003), but also to how much the environmental variable of interest varies through time (Benedetti-Cecchi, 2003). For example, a species would be favoured by an increase in environmental variability if its growth rate follows a convex curve in response to an increase in an environmental variable. In this case, their growth rate increases more in response to favourable conditions than it decreases in response to unfavourable conditions. Conversely, if the species' growth rate decreases more during unfavourable conditions than it increases during favourable conditions (a concave stochastic population growth curve), overall population growth will decline when conditions become more variable (Lawson et al., 2015). Studies that alter variance while maintaining a constant mean are necessary to help us better understand the effects of environmental variance per se on dryland organisms.

The impact of directional change in mean precipitation on vegetation dynamics (Bradford et al., 2020) and microbial composition (Jansson & Hofmockel, 2020) is well documented. However, to our knowledge only one experimental study is published that explored the effects of increased interannual precipitation variability on plant productivity and community dynamics (Gherardi & Sala, 2015a, 2015b). They found that an increase in precipitation variability around a constant mean over 6 years led to a decrease in aboveground net primary productivity (ANPP) that was explained by a decrease in the dominant grass species and an increase in the dominant shrub species biomass. From the same experiment, the authors found that an increase in precipitation variability led to an increase in plant functional diversity, which in turn ameliorated its negative impact on plant productivity (Gherardi & Sala, 2015a). In an observational study, Adler et al. (2006) reported that increased interannual climate variability over three decades promoted the coexistence of three common grass species. However, they also argued that the impact of changes in precipitation variation, compared to changes in precipitation means, will have relatively small impacts on mean ANPP (Hsu et al., 2012). These findings demonstrate the importance of environmental variability to ANPP and vegetation community dynamics, but also highlight our lack of understanding of the mechanisms that underlie how ecosystems are responding to precipitation variability.

Compared to plants, there is a higher level of uncertainty about responses of soil micro-organisms to increased interannual precipitation variability. A few empirical studies have investigated the effects of intra-annual precipitation variability on soil microbial community composition and function. For example, Evans and Wallenstein (2014) found that soil microbes that were previously exposed to more frequent drying and rewetting in the field, responded differently—in community composition, respiration and microbial biomass—than soil microbes from ambient conditions after treated with drying and rewetting events in the laboratory over a 115-day period. In addition, Barnard et al. (2013) found that when soil microbial communities were desiccated and followed by immediate experimental rewetting, two dominant soil bacterial classes responded asymmetrically in relative abundance in a Mediterranean grassland. Lastly, in a rainfall manipulation experiment conducted on a variety of sites with climates ranging from arid to mesic, Franco et al. (2019) found that experimentally imposed drought and deluge events can change the composition of soil nematode communities, and that these changes depend on the historical mean annual precipitation at the site. Yet, current knowledge around microbial—and especially fungal—responses to precipitation variability at the interannual scale remains limited.

Plants and microbes form selective associations below-ground (Smith & Read, 2008; Wardle, 2004), which suggests that their responses to increased precipitation variability may depend on each other. Plant hosts are known to shape soil communities via variation in root traits, secretion of root exudates, by leaf litter inputs and also through physical effects by modifying its surrounding microclimate (Chen et al., 2021; Fitzpatrick et al., 2020; Semchenko et al., 2018; Somers et al., 2004). Previous work suggests that soil microbial community composition can be associated with plant community composition from local (de Vries et al., 2012) to intercontinental (Prober et al., 2015) scales. It is therefore important to investigate microbial response to increased interannual precipitation variability in the context of host type identity.

In this study, we explored the temporal dynamics of soil fungal communities associated with different plant hosts exposed to increased precipitation variability in a dryland ecosystem. We sampled soil fungi from an ongoing field experiment that simulates increased interannual precipitation variability using rainout shelters diverting 50% and 80% of ambient precipitation from drought to irrigation plots, alternated annually (Gherardi & Sala, 2013). Using data from soil fungi characterized in this field experiment, we asked: (1) How does precipitation variability influence soil fungal diversity, community and functional guild composition? And do these effects differ between two sampling years with contrasting ambient growing

season precipitation? (2) Does precipitation variability affect fungal diversity directly, or indirectly through shifts in plant species composition? We expected to see differences in soil fungal richness, evenness, community and functional guild composition among host types. In addition, as short-term drying and rewetting is known to cause a decrease in fungal richness, but not evenness (Meisner et al., 2018), we expected that soil fungal diversity would be lower in soils treated with increased precipitation variability relative to soils sampled from ambient precipitation. We predicted that increased precipitation variability would cause shifts in soil fungal community composition and subsequently changes in functional composition. Finally, we expected that the effect of experimentally increased precipitation variability on fungal communities will differ between 2013 and 2019 due to contrasting ambient growing season precipitation levels (Figure 1) and differences in above-ground vegetation cover and composition.

2 | MATERIALS AND METHODS

2.1 | Study system

We explored the response of soil fungal taxa in a field experiment investigating increased precipitation variability as outlined in Gherardi and Sala (2015a). The field experiment is located at the Jornada Basin Long-Term Ecological Research Site (32.5°N, 106.8°W, 1188 m a.s.l.) in New Mexico, United States. The site is on a sand sheet formation where vegetation is co-dominated by *Bouteloua eriopoda*, a perennial C_4 grass, and *Prosopis glandulosa*, a leguminous shrub. The climate is warm, with wide diurnal fluctuations, low relative humidity and highly variable annual precipitation. The average maximum temperatures are recorded in June at 36°C, whereas the average minimum temperature in the coldest month of January is 13°C. The majority of precipitation occurs during the growing season from May to September (McMahon & Wagner, 1985), and the mean ambient growing season precipitation at the site throughout our data collection period (2009–2019) was 160 mm. The period preceding the first sample set (2009–2013; see Section 2.3) had a mean ambient growing season precipitation of 129 mm, whereas the period between the first and second set of samples (2014–2019) averaged 187 mm (Figure 1).

2.2 | Field experimental design

Gherardi and Sala (2015a) started alternating rainfall interception and irrigation in 2009 (ongoing) to simulate increased precipitation variability and study its effects on above-ground vegetation dynamics of two dominant plant species at the site. To experimentally increase precipitation variability, plots experience alternating years

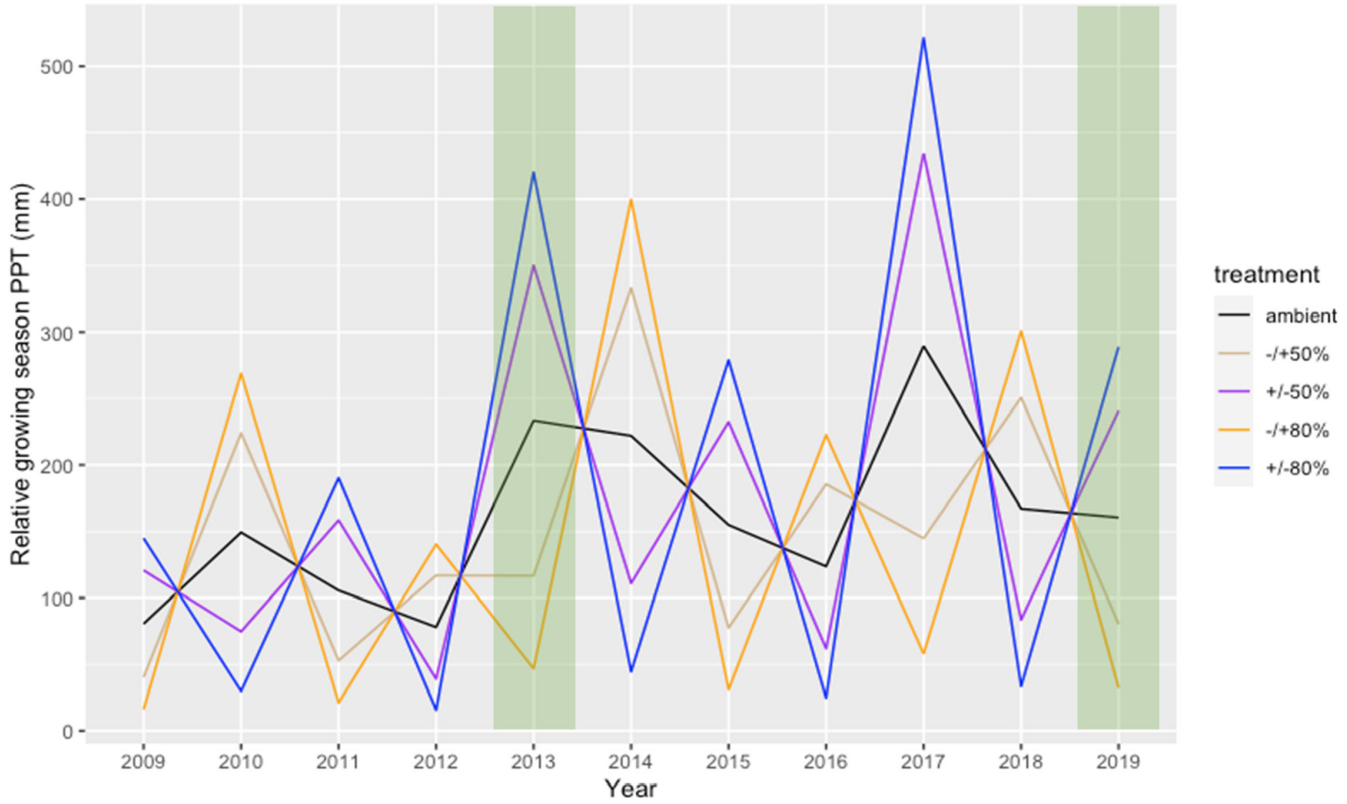


FIGURE 1 Growing season precipitation from 2009 to 2019. Different line colours and types indicate precipitation manipulations: Ambient, −/+50%, +/−50%, −/+80%, +/−80%. 50% and 80% treatments are relative to ambient growing season precipitation, and switched between rainfall interception and irrigation each year.

of 50% or 80% precipitation addition versus exclusion. Exclusion and addition treatments are switched every spring prior to the growing season, with rainout shelters collecting either 50% or 80% of the incoming rainfall from exclusion plots and diverting it to irrigation plots (Figure 1). Ambient rainfall plots represent controls for the field experiment. The experiment contains 10 replicates of five levels of interannual precipitation variability (ambient, +/−50%, −/+50%, +/−80%, −/+80%), totalling 50 plots. Each plot is 2.5 by 2.5 m, with the edges trenched down to 60 cm in the soil and lined with 6-ml PVC film to prevent lateral movement of water and roots throughout plots. See Gherardi and Sala (2015a) for experimental design details and references Gherardi and Sala (2013) and Yahdjian and Sala (2002) for detailed descriptions of methods.

2.3 | Soil sampling

We collected samples within each of the 50 plots described above underneath bare (unvegetated) soil, a grass individual (*Bouteloua eriopoda*) and a shrub individual (*Prosopis glandulosa*) in July 2013 and 2019, resulting in three samples per plot per year, and 300 samples total (3 host types × 2 years × 5 precipitation variation levels × 10 replications). Soil samples were collected with soil corers and trowels to 5 cm depth from the surface within the soil rooting zone of the focal plant. We sprayed equipment down with 10% bleach between samples to minimize contamination. Samples were stored on ice in a cooler in the field and transferred to storage a −20°C freezer until August 2019, when they were transported to the University of Georgia and stored at −80°C for downstream applications.

2.4 | DNA extraction and sequencing

To characterize soil fungal communities, we subsampled 250 mg of soil from each sample and extracted total genomic DNA using the QIAGEN Dneasy® PowerSoil Pro Kit®, following the manufacturer's protocol (QIAGEN). Prior to DNA extraction, we performed tissue lysis with a Spex® Genogrinder® at 1500 rpm for 10 min. We quantified DNA spectrophotometrically using a Nanodrop One/One© (ND2000; NanoDrop Technologies). Genomic DNA was stored at −20°C prior to library preparation and sequencing.

We characterized fungi with high-throughput sequencing to detect the variation in marker gene differences. To target fungal taxa, we amplified the ITS2 region using primers fITS7 (5′-GTGARTCATCGAATCTTG-3′; Ihrmark et al., 2012), and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′; White et al., 1990), augmented with multiplexing barcodes. Samples were sequenced on two runs of an Illumina MiSeq instrument (300PE V3 chemistry). Library preparation and DNA sequencing was conducted at the Georgia Genomics and Bioinformatics Core (GGBC) at the University of Georgia in Athens, GA. Raw paired-end sequence data are available at the Sequence Read Archive (SRA) at the National Center for Biotechnology Information (NCBI) under BioProject PRJNA884111.

2.5 | Bioinformatic processing

Forward and reverse reads were paired, merged and quality filtered with USEARCH (http://drive5.com/usearch/; Edgar, 2010, 2013). Sequences were then processed using Mothur (Schloss et al., 2009) to remove sequencing adapters, primers and chimeras. Combined reads were clustered into operational taxonomic units (OTUs) at 97% identity using the K-nearest algorithm (Wang et al., 2007), which we classified against the UNITE (Version 8.0) reference database (Nilsson et al., 2019). All nonfungal reads were excluded from the analysis. The total dataset included 1308 unique fungal OTUs with 10,370,208 total sequences. Due to uneven sequence depth, we rarefied samples to 3000 reads per sample for all downstream analyses. Samples with less than 3000 reads were excluded from the analysis (27 of 297) due to insufficient sequencing depth (Figure S1).

2.6 | Statistical analysis

All statistical analyses were performed in R (Version 1.2.1335, R Core Team, 2017) and conducted on the rarefied OTU abundance matrix. To evaluate the influence of increased precipitation variability on diversity metrics, we calculated the coefficient of variation of the amount of precipitation received for each variability treatment from 2009 to 2013 and from 2014 to 2019, such that precipitation variability can be analysed as a continuous variable (see Gherardi & Sala, 2015b). Thus, for the remainder of this paper, we refer to increased precipitation variability as the coefficient of variation (CV) of the amounts of growing season precipitation received for the five precipitation variability treatments calculated from the periods between 2009–2013 and 2014–2019 respectively. For the indicator species and functional guild composition analyses, we used increased precipitation variability as a categorical variable for three levels of increased precipitation variability: Control, medium (−/+50% and +/−50%) and high (−/+80% and +/−80%).

We analysed the influence of host type, precipitation variability and sampling year on soil fungal diversity using a linear mixed model (Bates et al., 2015) with Shannon's diversity index for each sample as a response variable, and host type, precipitation (CV), year and their interactions as fixed effects, and plot as a random intercept accounting for the repeated measures nature of the experiment. We included sampling year as a categorical variable in this and subsequent analyses to account for different ambient conditions between sampling years 2013 and 2019 (Figure 1). We performed post hoc multiple pairwise comparisons using the false discovery rate (fdr) method to correct *p*-values (package 'EMMEANS', Lenth, 2018). To further explain differences observed in Shannon diversity, we also separately analysed fungal richness (number of OTUs in each sample) and evenness (distribution of relative abundance with the Pielou's metric of evenness) using the same model structure and post hoc methods as above for Shannon diversity.

To investigate soil fungal community composition, we calculated Bray–Curtis dissimilarities among samples using the rarefied OTU abundance matrices. Using Bray–Curtis dissimilarity matrices,

we tested the effect of host type, precipitation variability and year on fungal community composition with a permutational analysis of variance (PERMANOVA) (function adonis in the 'VEGAN' package) (Dixon, 2003). We further identified soil taxa that were significant indicators of treatment groups using indicator species analysis (Dufrêne & Legendre, 1997) with the 'LABDSV' package. To visualize variation in fungal community composition, we performed nonmetric multidimensional scaling (NMDS) ordinations using Bray–Curtis dissimilarities. To assign functional guilds, or primary lifestyles to operational taxonomic units, we used only OTUs assigned to genus-level resolution (656 of 1308 OTUs) and assigned genera to functional identity using the FungalTrait database (Põlme et al., 2020).

To test whether soil fungal diversity responses were due to direct effects of increased precipitation variability or indirect effects via host type induced changes, we performed structural equational modelling (SEM) using the LAVAAN package (Rosseel, 2012). Our model incorporated the direct correlation between increased precipitation variability and soil fungal diversity, and the direct correlation between increased precipitation variability and percentage cover of the host type. The indirect path was modelled as the association between increased precipitation variability and soil fungal diversity, mediated through a change in percentage host type cover. Models were just-identified and therefore no general model fit was reported. We split up the OTU table by the three host types to investigate above-ground induced changes in each host-associated community type separately. We also modelled two different soil fungal responses: richness and evenness. We specifically modelled richness and evenness as separate responses—as opposed to only modelling Shannon Diversity as a response. This led to a total of six (host type by fungal response) models evaluated.

3 | RESULTS

3.1 | Influence of precipitation variability on soil fungal diversity, community and functional guild composition

Soil fungal Shannon diversity, richness and evenness all differed significantly among host types (Table 1, Figure 2). Soil fungal communities around grass roots had the highest Shannon

TABLE 1 Results of ANOVA on linear mixed models to assess how host type and increased precipitation variability influenced soil fungal Shannon diversity, species richness and evenness.

Factor	df	Chi^2	*p*
Response: Shannon diversity			
Precipitation CV	1	3.015	0.084
Host type	**2**	**16.937**	**<0.0001**
Year	1	0.545	0.461
Precipitation CV:Host type	2	0.445	0.642
Precipitation CV:Year	1	0.014	0.903
Host type:Year	**2**	**4.439**	**0.012**
Host type:Year:Precipitation CV	2	0.369	0.691
Residuals	256		
Response: Species richness			
Precipitation CV	1	0.503	0.478
Host type	**2**	**26.658**	**<0.0001**
Year	**1**	**43.791**	**<0.0001**
Precipitation CV:Host type	2	1.362	0.258
Precipitation CV:Year	1	0.390	0.533
Host type:Year	2	1.978	0.141
Host type:Year:Precipitation CV	2	0.393	0.675
Residuals	256		
Response: Species evenness			
Precipitation CV	1	3.469	0.064
Host type	**2**	**20.479**	**<0.0001**
Year	1	**12.732**	**<0.0001**
Precipitation CV:Host type	2	0.181	0.835
Precipitation CV:Year	1	0.003	0.959
Host type:Year	**2**	**5.328**	**0.005**
Host type:Year:Precipitation CV	2	0.387	0.679
Residuals	256		

Bold values indicate significant of $p < 0.05$.

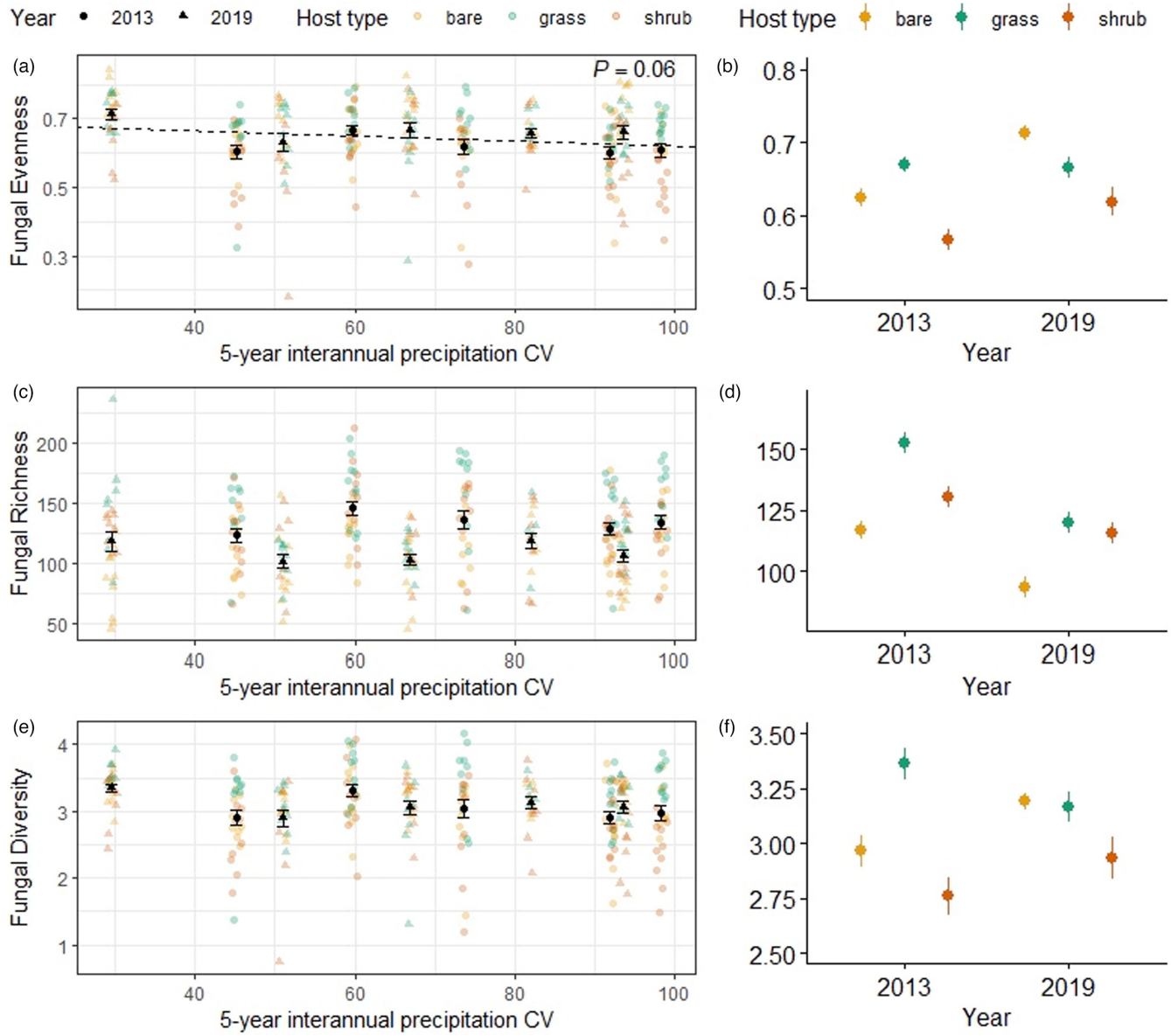


FIGURE 2 Effect of precipitation variability (CV) on soil fungal evenness (a), richness (b) and Shannon diversity (e). Points coloured by host type represent samples and are jittered along the *X*-axis to avoid overlapping. Black points show mean across all samples of each precipitation CV class. Panels on the right depict the effect of sampling year on fungal evenness (b), richness (d) and Shannon diversity (f).

diversity, followed by bare soil, then shrubs (Figure 2e; all post hoc pairwise comparisons $p < 0.05$). Soil fungal community evenness around shrub roots was significantly lower than grass and bare soil (Figure 2a). Contrasting to patterns observed in fungal evenness, soil fungal richness around grass roots was highest, followed by those around shrubs, and lastly bare soil (Figure 2c). While there were no directional effects of increased precipitation variability on soil fungal richness or diversity, we observed a 15% decrease in soil fungal evenness from control to the −/+80% variability treatment (Figure 2a). However, this trend was marginally significant ($p = 0.064$, Table 1). We found no significant effects of increased precipitation variability and host type on soil fungal alpha diversity. Fungal richness was lower in 2019 ($p < 0.0001$, Table 1, Figure 2d). In contrast, fungal evenness was higher in 2019 ($p < 0.0001$, Table 1, Figure 2b). Overall, the only difference in soil fungal Shannon diversity between years was in grass fungal communities, which was 5.8% lower in 2019 (Year: Substrate $p = 0.012$, Table 1, Figure 2e).

The majority of OTUs belonged to Ascomycota (83%) and Basidiomycota (10%) (Figure 3), whereas to Mortierellomycota, Glomeromycota (now grouped in the Zygomycota phylum), and Mucoromycota only comprised 3% of total OTUs. Ascomycota was dominated by Pleosporales (73%) where a smaller fraction of OTUs belonged to Sordariales (7%). Basidiomycota was represented by Agaricales (38%), Geastrales (20%), Cantharellales (15%), Filobasidiales (11%) and Tremellales (6%). Out of a total of 1308 OTUs, 365 were unique to 2013 and 131 were unique to 2019, while 809 OTUs were shared between 2013 and 2019.

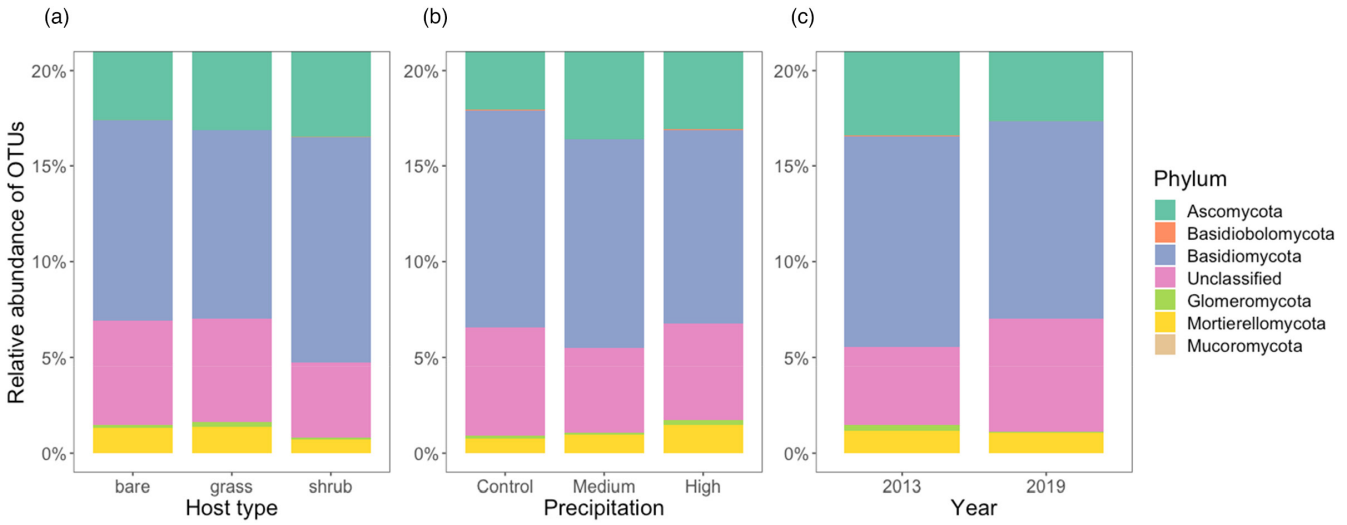
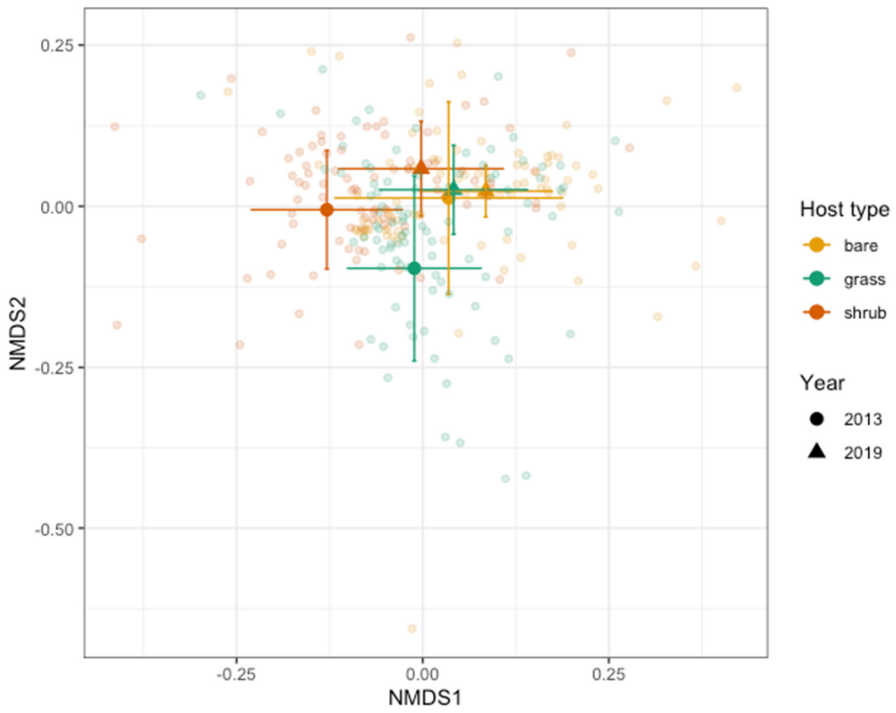


FIGURE 3 Relative abundance of soil fungal phyla with comparisons based on host type (a), precipitation variability (b) and year (c). Note truncation of *Y*-axis for visibility of less abundant phyla; the remaining truncated space correspond to Ascomycota for all bars.

FIGURE 4 Centroids (mean ordination scores) with standard deviation (SD) bars of nonmetric multidimensional scaling for fungal communities of the whole dataset, coloured by host type. Sample-level data shown in faded colour



Soil fungal community composition differed significantly among host types (PERMANOVA $F_{2,256} = 7.36$, $p \leq 0.001$; Figure 4), but it only explained 5.2% of the total variation in community composition. All pairwise comparisons between different host types showed statistically significant difference in soil fungal community composition (Figure 4; all post hoc pairwise comparisons $p < 0.05$). Likewise, we observed a significant difference in soil fungal community composition between 2013 and 2019 (PERMANOVA $F_{1,256} = 17.577$, $p \leq 0.001$; Figure 4), but the main effect of year only explained 5.8% of the total variation in community composition. Precipitation variability also significantly altered soil fungal community composition (PERMANOVA $F_{1,256} = 2.77$, $p = 0.001$). However, increased precipitation variability only explained 1% of total variation in community composition and based on a visual assessment of the results, the separation in community composition by increased precipitation variability was weak. Finally, sampling year and host type significantly interacted to affect soil fungal composition (PERMANOVA $F_{2,256} = 2.82$, $p = 0.001$), with a stronger distinction among communities from different host types in 2013 (Figure 4).

To reveal taxa underlying differences in community composition, we calculated indicator values to identify OTUs that most strongly associated with different host types, years and

precipitation treatments (Table S1). We found 224 total significant indicator OTUs that distinguished among the three host types. Of these, the majority were Ascomycota, followed by Basidiomycota (Figure S2). The OTU with the highest indicator species scores for a host type was an unclassified species in the genus *Pleiochaeta*, which was an indicator for shrub-associated communities. Across the three host types, 63% of sequencing abundance of this *Pleiochaeta* OTU was in shrub-associated soil samples. Members in this genus are often plant pathogens to legumes (Marin-Felix et al., 2019), which includes *P. glandulosa*, the leguminous focal shrub in our study. *Mycocalicium victoria* was the best indicator OTU for grass-associated soil fungal communities, with 58% of its sequencing abundance recorded in soil samples from underneath grass. This taxa is a lichen forming fungi typically found in desert environments (Esslinger, 2018).

We found 79 significant indicator taxa that were specific in their association and abundance among precipitation variability treatments. The OTU with the highest indicator species scores in this comparison was an indicator for the control precipitation variability treatment which is an unidentified species that belongs to the *Ceratobasidiaceae*. Members in this family are most commonly plant pathogens but have also been found to play important ecological roles as nonmycorrhizal endophytes, ectomycorrhizal symbionts and soil saprotrophs (Veldre et al., 2013). The top indicator taxon for the moderate precipitation variability treatment was an unidentified member in the *Tulostoma* genus. Taxa within this genus are mostly soil saprotrophs (Tedersoo et al., 2014). For the high precipitation variability treatments, the taxa with the highest indicator value belonged to an unclassified member in the *Lasiosphaeriaceae*. Species in this family are dung saprotrophs that strongly associate with dung and decaying plant material (Fletcher, 2008).

To understand whether soil fungal functional composition shifted in response to increased precipitation variability and host type, we assigned OTUs from our rarefied dataset with genus-level resolution primary lifestyles or guilds, using the FungalTrait reference database (Põlme et al., 2020). Of 1308 total OTUs, 656 were classified to genus-level resolution and of these, 635 were assigned to a primary lifestyle. The majority of OTUs characterized were saprotrophs (82%), while pathogens (<15%) and mutualists (<5%) represented a small fraction of the dataset. There were no strong differences in the compositional change in functional types (Figure S3).

3.2 | Direct versus indirect host type-mediated response of soil fungal diversity to increased precipitation variability

Structural equational modelling results suggested that the relative importance of direct versus indirect effects of increased precipitation variability on soil fungi depended on host type (Table 2). For example, for soil fungi associated with grasses, we found no direct effects of increased precipitation variability on soil fungal richness. However, there was a strong negative association between percentage grass cover and increased precipitation variability, and a strong positive association between fungal richness and percentage grass cover. Combined, our results showed a significant negative *indirect* effect of precipitation variability on soil fungal richness (Figure 5a). For soil fungi associated with bare soils, we found a significant negative direct effect of precipitation variability on fungal evenness (Table 2). There was an additional positive correlation between fungal evenness and bare soil cover, but that was not influenced by precipitation variability (Table 2). We found no evidence of direct or indirect effects of precipitation variability on shrub-associated soil fungal communities (Figure 5c).

4 | DISCUSSION

Dryland soil fungal community response to increased interannual precipitation variability is an important and understudied topic that is critical to understanding how dryland ecosystems will respond to future climate scenarios. In this study, we showed that soil fungal communities associate strongly with host type-functional identity. We also showed that increased precipitation variability led to a subtle decrease in fungal evenness. We found that there was a decrease in soil fungal richness between 2013 and 2019 and provide evidence that this decrease was likely because of plant-mediated indirect effects on richness for grass-associated soil fungi.

4.1 | Soil fungal communities were most strongly determined by host type

Our results showed that soil fungal diversity, richness, evenness and community composition differed strongly by host type. We

TABLE 2 Results from SEM to evaluate the direct and indirect effects of increased precipitation variability on soil fungal richness and evenness

	Fungal richness					Fungal evenness				
	R^2	Direct effect	*p*	Indirect effect	*p*	R^2	Direct effect	*p*	Indirect effect	*p*
Grass	0.082	1.664	0.096	**−2.382**	**0.017**	0.008	−0.359	0.720	0.548	0.584
Shrubs	0.025	−0.861	0.389	−0.492	0.623	0.031	−1.676	0.094	0.103	0.916
Bare soil	0.141	1.637	0.102	0.773	0.440	0.140	**2.001**	**0.045**	−0.769	0.442

Bold values indicate significant of $p < 0.05$.

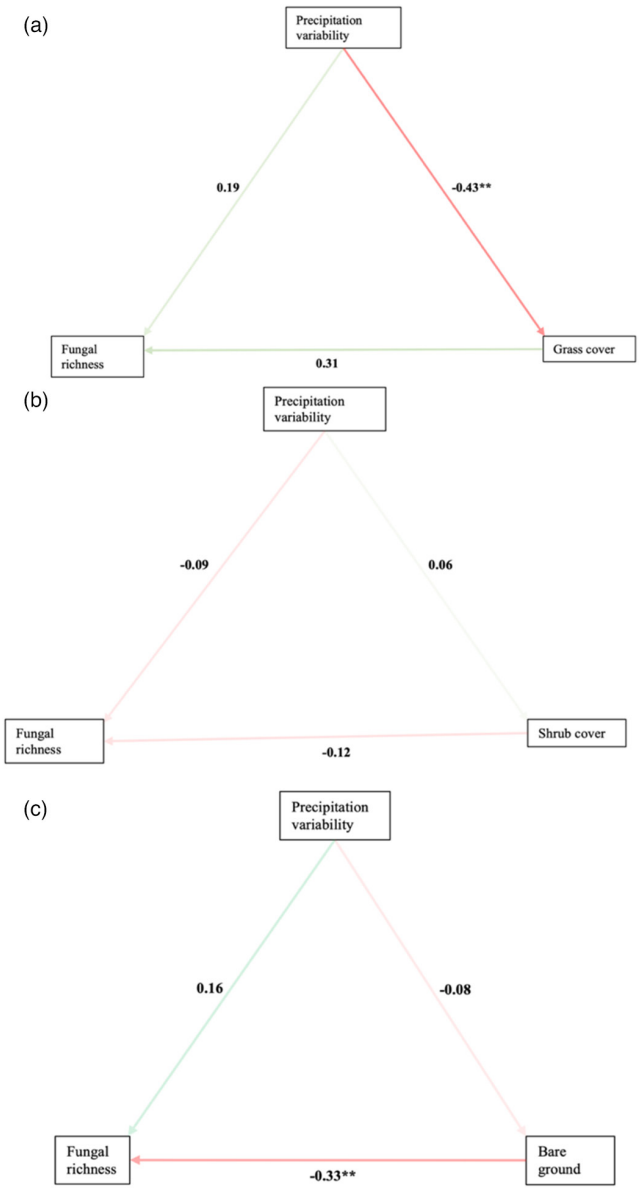


FIGURE 5 Diagram of the structural equational modelling results of direct and indirect effects of precipitation variability on (a) grass-associated soil fungal richness, (b) shrub-associated fungal richness and (c) bare soil-associated fungal richness. Green lines represent a positive correlation whereas red lines indicate a negative correlation between the two variables. Values above the lines depict fitted partial regression coefficients; statistically significant coefficients are starred.

observed higher soil fungal alpha diversity, richness and evenness associated with the dominant grass compared to associated with the dominant shrub. Overall, soil fungal Shannon diversity found under bare soil was low, yet still higher than the levels observed underneath shrubs. This resulted from a combination of higher soil fungal evenness and slightly lower richness in bare soils compared to under shrubs (Figure 2). There is ample evidence that soil microbes form unique associations with host types and therefore differ in community composition and diversity by host type (Fitzpatrick et al., 2020; Somers et al., 2004). Such host specificity is explained by variation in root morphological traits, variation in activity and chemical profiles of root exudates (Berg & Smalla, 2009; de Vries et al., 2012; Semchenko et al., 2018; Somers et al., 2004), and through physical variation in microclimate by host type identity (Chen et al., 2021; Fitzpatrick et al., 2020; Somers et al., 2004).

Results from the indicator species analysis shed light on specific taxa that underpinned host type associations of soil fungi. For example, an unidentified member in the genus *Pleochata* was a strong indicator for shrub-associated communities in our experiment. Fungi in this genus are often legume pathogens (Marin-Felix et al., 2019). The two top indicators of grass-associated soil fungal communities were lichen-forming fungi *Teichospora kingiae* and *Mycocalicium victoriae* (Esslinger, 2018; Tedersoo et al., 2014). Biological soil crusts (biocrusts) are photoautotrophic communities of lichens, fungi and cyanobacteria that coexist with plants and influence soil functioning, especially in drylands such as our study site (Zhang et al., 2006). Biocrusts can benefit plant communities in drylands by increasing soil water availability, soil organic matter, as well as inorganic N availability (DeFalco et al., 2001; Havrilla & Barger, 2018). Havrilla and Barger (2018) found that *Bouteloua eriopoda* survival in the Chihuahan Desert was 38% higher in lichen-dominated biocrusts versus bare soil and when biocrusts with lichens were removed, it significantly decreased *B. eriopoda* seedling performance. Our results are in accord with the pattern of a positive association between *B. eriopoda* and soils containing lichen-forming fungi that may create advantageous microhabitats such as biological soil crusts.

We found higher fungal richness in soil sampled underneath grasses and shrubs, than underneath bare soil. However, soil fungal Shannon diversity was lower in shrubs than in bare soil and grass due to significantly lower soil fungal evenness underneath shrubs than bare soil and grass. This finding is likely because *Prosopis glandulosa*, is a nitrogen-fixing legume. There is evidence that in temperate grasslands the size and activity of soil microbial communities is higher under low-fertility conditions than under high-fertility conditions regulated by consistent nitrogen (N) additions (Lovell et al., 1995). In experimental grassland ecosystems in Europe, Lange et al. (2014) and Bartelt-Ryser et al. (2005) found that the presence of legumes generally decreased the biomass of soil fungi. Others have found nitrogen-fixing bacteria associating with legumes can cause changes in its surrounding soil leading to nitrogen and phosphorous limitation that could contribute to a decrease in soil fungal biomass (Aerts & Chapin, 1999; Roscher et al., 2011). These changes in available soil nutrients surrounding legumes, compared to other plants, could create favourable conditions for fungi that are specifically adapted to nutrient stress. A recently published study from an experimental grassland in Europe, found that soil microbes differed in diversity and community composition by host type identity. Similarly to our results, they found that soil fungal richness and evenness increased in soil sampled underneath grasses, whereas soil fungal evenness decreased in soils sampled underneath legumes, compared to other host types (Schmid et al., 2021). Our results demonstrate that functional characteristic of dominant plants, such as nitrogen fixation, could

have a strong influence on soil fungal diversity and community composition. A complementary explanation is associated with the different distribution of root biomass in the soil profiled between grasses and shrubs (Jackson et al., 1996). Grasses have shallower root systems than shrubs and contribute most of their root litter and carbohydrate excretion into the top layers of the soil where fungi are located.

Soil fungi from our dataset were overwhelmingly dominated by saprotrophs. We observed more litter saprotrophs in soils sampled underneath grass and shrubs compared to bare soil (Figure S3). It is possible that our dataset contained more saprotrophs and fewer mutualists (such as arbuscular mycorrhizal fungi) due to our choice of the ITS2 target region (Öpik et al., 2010). However, previous work showed low occurrences of AMF in Chihuahuan desert grasslands (Chung, Jumpponen, et al., 2019; Porras-Alfaro et al., 2008). Our results suggest that while we found effects of host type on fungal taxonomic composition, how this impacts ecosystem functioning remains to be seen. Therefore, it is crucial to consider changes in both taxonomic and functional composition of microbial communities to fully understand the impacts of changes in precipitation amount and variability.

4.2 | Increased precipitation variability had weak direct effects on soil fungal communities

Increased precipitation variability affected soil fungal diversity with a modest decrease in fungal evenness and a reduction in dominance. This could be due to selection for stress-tolerant taxa that were underrepresented under control conditions. We did not observe a decrease in fungal richness like in previous drying and rewetting studies (Meisner et al., 2018). One reason is associated with our finding of *Pleosporales* being the most dominant order in our dataset. Many species in this order are dark septate endophytic (DSE) fungi, which are known to be able to withstand stress imposed by drought, UV radiation, heat and desiccation (Gostinčar et al., 2010; Ndinga-Muniania et al., 2021).

We expected to see differences in soil fungal community composition due to long-term precipitation variability selecting for taxa that are favoured more by periods of rain than they are hampered by periods of drought. Furthermore, we expected long-term drying and rewetting to select for taxa that are resilient and/or resistant to periods of extreme drought. We found that the effects of increased interannual precipitation variability on microbial diversity were idiosyncratic and context dependent. Furthermore, contrary to our expectations, we did not see any clear differences in soil fungal community composition with an increase in long-term precipitation variability. Increased precipitation variability also did not cause a reordering in fungal functional guilds. We based this expectation on previous work, showing that bacterial communities shifted towards moisture stress-tolerant taxa after being exposed to a decade of simulated extreme intra-annual precipitation events using rain-out shelters in a US tallgrass prairie (Evans & Wallenstein, 2014). However, others have found that in Californian semi-arid grasslands, soil fungal community composition did not respond to a dry summer typical of this ecosystem, followed by an experimental rewetting event (Barnard et al., 2013), which is more in line with our results.

One reason for the weaker response in soil microbial communities compared to plant community responses could be that of time-scale. Past work has shown that environmental variability on very short time-scales can greatly influence microbial community composition and function. For example, Blazewicz et al. (2020) found that bacterial growth and mortality responded to drying and rewetting within 3 h. Likewise, de Vries et al. (2018) found that extreme drought caused a slight shift in fungal community composition and an increase in fungal richness and evenness, but that fungal richness and evenness recovered to control levels only 1 week after rewetting soils. It could be that microbial community composition is more sensitive to these pulses in moisture conditions at the time-scales of weeks and days, and less so to interannual trends.

4.3 | Indirect effects of host type-mediated responses to increased precipitation variability are an important driver of fungal diversity

In our experiment, we observed a strong decrease in soil fungal richness in grass-associated soils from 2013 to 2019. Results from our SEM suggest that this decrease could be explained by the negative association between grass cover and long-term increased precipitation variability. Little research has been done on the interaction between precipitation variability and host type effects on soil microbes, but previous work shows that the effects of drought on soil microbial community dynamics depend on host type (de Vries et al., 2018; Lagueux et al., 2021; Veach et al., 2020). For example, in a climate-controlled greenhouse experiment, Veach et al. (2020) found that short-term drought-induced plant physiological changes caused shifts in soil microbial diversity, even after a period of rewetting. In grassland mesocosms, experimental drought caused a shift in plant community composition, which was strongly associated with shifts in bacterial community composition and network structure, although to a lesser extent with fungal networks and communities (de Vries et al., 2018). In grassland ecosystems throughout the central United States, host type and ecosystem type were the two dominant factors driving root-associated fungal diversity, community composition and root colonization in response to drought (Lagueux et al., 2021). Finally, ectomycorrhizal soil fungal richness has been shown to have a positive association with the area of its habitat (Peay et al., 2007). We found that different host types have distinct fungal communities and of these host types, grass cover is decreasing in area, with a corresponding decrease in soil fungal richness. Our SEM results add a novel dimension to past work to demonstrate that soil fungal community response to increased precipitation variability is mediated by host type and that soil microbial community response to moisture stress is host dependent.

Climate change is projected to cause shifts in vegetation community dynamics in drylands, often resulting in increased shrub cover and decreased grass cover, leading to declines in ANPP and plant biodiversity (Briggs et al., 2007; Ratajczak et al., 2012; Van Auken, 2009). At this site, experimental increases in interannual precipitation variability are causing a decline in grass cover. Since grasses constituted the highest percentage cover at the beginning of this experiment, the indirect effects of grass-mediated responses to increased precipitation variability will likely have the most profound impact on soil fungal gamma diversity in this ecosystem. We therefore expect to see a projected decrease in overall fungal richness mediated by a decrease in grass cover in response to increased precipitation variability at this site. This reduction in fungal richness could have important consequences for biogeochemical cycling, feedbacks between soil microbiota and plant population and community dynamics, and the ability of this ecosystem to buffer future ecosystem responses to global change (Chung, Collins, et al., 2019; Maestre et al., 2012).

Our findings highlight the nuanced relationships between different diversity metrics that are integral to understanding how soil fungi associated with different plant hosts respond to long-term increases in precipitation variability. We found that soil fungi differed most strongly in diversity and composition according to host type, and that long-term increased precipitation variability had a negative direct effect on soil fungal evenness, and stronger negative indirect effects on soil fungal richness mediated by change in grass cover. Our results suggest that long-term soil fungal community responses to precipitation variability are likely to be mediated by host type association and changes in above-ground dynamics. We hypothesize that direct effects of precipitation variability (drying and wetting cycles) on fungal composition will be seen at short time-scales while the indirect effects through changes in plant-species composition will be observed in the longer time-scales that are the focus of this study. To better understand how ecosystems are responding to climate change, there is an urgent need to conduct more experiments that alter environmental variances around a constant mean under field-realistic conditions. Future experiments should include more frequent sampling to account for asymmetric time-scales in plant and microbial responses, and supplement amplicon sequencing techniques with culture-based and/or plant–soil feedback experiments to investigate the significance of changes in soil fungal diversity and community composition on population, community and ecosystem dynamics.

AUTHOR CONTRIBUTIONS

Laureano A. Gherardi and Osvaldo E. Sala designed the original field experiment, and all authors designed the current study. Laureano A. Gherardi and Osvaldo E. Sala led field sample and data collection, and Nicolas Louw and Y. Anny Chung led the bench work and bioinformatics analyses. Nicolas Louw led the writing of the manuscript, with substantial input from Y. Anny Chung, Laureano A. Gherardi and Osvaldo E. Sala.

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CONFLICT OF INTEREST

Y. Anny Chung is an Associate Editor of Journal of Ecology but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data deposited in the EDI repository https://doi.org/10.6073/pasta/7f47439df0e09f1dcc6f0da77d5cc558 (Louw et al., 2022).

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SUPPORTING INFORMATION

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