



## Contrasting relationships between plant-soil microbial diversity are driven by geographic and experimental precipitation changes



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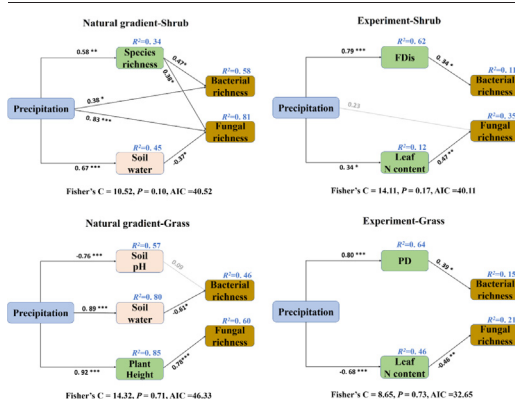
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### HIGHLIGHTS

- Precipitation changes strongly affect soil microbe diversity in deserts and steppes.
- Precipitation effects on soil microbe diversity were mediated by vegetation or soil properties.
- Precipitation changes can modify plant biodiversity attribute effects on soil microbial diversity.
- The short-term response of soil fungal diversity to precipitation changes mirrors long-term shifts in space.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

Editor: Zhaozhong Feng

#### Keywords:

Functional diversity  
Manipulative experiment  
Natural gradient  
Phylogenetic diversity  
Species diversity  
Soil bacteria and fungi

### ABSTRACT

Soil microbe diversity plays a key role in dryland ecosystem function under global climate change, yet little is known about how plant-soil microbe relationships respond to climate change. Altered precipitation patterns strongly shape plant community composition in deserts and steppes, but little research has demonstrated whether plant biodiversity attributes mediate the response of soil microbial diversity to long- and short-term precipitation changes. Here we used a comparative study to explore how altered precipitation along the natural and experimental gradients affected associations of soil bacterial and fungal diversity with plant biodiversity attributes (species, functional, and phylogenetic diversity) and soil properties in desert-shrub and steppe-grass communities. We found that along both gradients, increasing precipitation increased soil bacterial and fungal richness in the desert and soil fungal richness in the steppe. Soil bacterial richness in the steppe was also increased by increasing precipitation in the experiment but was decreased along the natural gradient. Plant biodiversity and soil properties explained the variations in soil bacterial and fungal richness from 43 % to 96 % along the natural gradient and from 19 to 46 % in the experiment. Overall, precipitation effects on soil bacterial or fungal richness were mediated by plant biodiversity attributes (species richness and plant height) or soil properties (soil water content) along the natural gradient but were mediated by plant biodiversity attributes (functional or phylogenetic diversity) in the experiment. These results suggest that different mechanisms are responsible for the responses of soil bacterial and fungal diversity to long- and short-term precipitation changes. Long-

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<http://dx.doi.org/10.1016/j.scitotenv.2022.160654>

Received 20 September 2022; Received in revised form 11 November 2022; Accepted 29 November 2022

Available online 5 December 2022

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and short-term precipitation changes may modify plant biodiversity attribute effects on soil microbial diversity in deserts and steppes, highlighting the importance of precipitation changes in shaping relationships between plant and soil microbial diversity in water-limited areas.

## 1. Introduction

Climate changes induced by anthropogenic activity are considered as the main driver of biodiversity loss in terrestrial ecosystems (Harrison et al., 2015; Maestre et al., 2015; Li et al., 2019), and their interrelationships are important to shape humanity's future (Chapin and Díaz, 2020). Soil microbial diversity losses driven by climate change will likely reduce multiple ecosystem functions and services, including soil carbon storage, biogeochemistry, biomass and food production (Crowther et al., 2019; Liang et al., 2019; Hu et al., 2021). Desert and grassland are two of the largest terrestrial ecosystems on Earth (De Deyn et al., 2008), and grassland degradation, shrub encroachment and state transitions between desert and grassland can alter ecosystem functions and services, thus further affecting the sustainable development of regions (Reynolds et al., 2007). Desert-grassland transitions are occurring globally and are primarily determined by changes in precipitation regimes (Gao and Reynolds, 2003; Petrie et al., 2015; Zuo et al., 2021). However, how precipitation changes affect soil microbial diversity in deserts and grasslands remains poorly understood. Therefore, exploring the underlying mechanisms of soil microbial diversity response to precipitation changes in deserts and grasslands is crucial for management guidance aimed at biodiversity conservation and ecosystem restoration under climatic change.

A growing number of studies have explored the effects of precipitation change, vegetation structure and soil properties on soil microbial diversity, while the underlying mechanisms vary with ecosystem types and spatial and temporal scales (de Vries et al., 2012; Delgado-Baquerizo et al., 2018; Wang et al., 2020; Yang et al., 2021; Wang et al., 2022). Observational studies across geographical gradients have shown that changes in precipitation amount affect soil microbial diversity by altering soil pH at regional and global scales (Yao et al., 2017; Zhou et al., 2020), soil nitrogen (N) content in subalpine meadows (Luo et al., 2020), plant diversity in temperate steppes (Wang et al., 2022), and functional traits in grasslands (de Vries et al., 2012) and deserts (Wang et al., 2020). In contrast, local-scale experimental studies in manipulations have shown that short-term precipitation changes affect soil microbial diversity by altering plant richness in grasslands (Fahey et al., 2020), and soil water content and pH in wet meadows (Yang et al., 2021). Despite this increasing effort to explore the underlying mechanisms of the soil microbial diversity response to precipitation changes, there is no consensus on how long- and short-term precipitation changes affect soil microbial diversity. Therefore, it is necessary to incorporate field observational and experimental studies to understand how altered precipitation regimes affect soil microbial diversity.

Functional diversity defined by a single-trait (community-weighted trait means) and multi-trait indices (e. g. functional dispersion, FDis), reflecting the functional composition of plant community and niche differentiation, is a good predictor of plant community responses to precipitation changes (Diaz et al., 2007; Butterfield and Suding, 2013; Conti and Diaz, 2013; Zuo et al., 2021). Phylogenetic diversity (PD) is increasingly regarded as a better indicator of biodiversity than taxon counting (Flynn et al., 2011; Miller et al., 2018), which reflects biological trait evolution and functional strategies in the face of environmental changes (Le Bagousse-Pinguet et al., 2019; Liang et al., 2019). The previous studies have shown that plant functional traits can strongly affect soil microbial diversity via their effects on the quality and quantity of resource input from litter decompositions and root exudates (Delgado-Baquerizo et al., 2018; Fahey et al., 2020; Wang et al., 2020). Soil microbial diversity can be affected by leaf N content in grassland (de Vries et al., 2012) and desert (Wang et al., 2020), leaf dry matter content and the leaf C: N ratio in subtropical forests (Pei et al., 2016), and specific leaf area (SLA) in forests

and grasslands (Delgado-Baquerizo et al., 2018). A drier climate can lead to a decline in plant PD in grasslands (Li et al., 2019) and FDis in deserts (Zuo et al., 2021), and their decline has been proven to strongly affect ecosystem function and stability (Flynn et al., 2011; Cadotte et al., 2012; Le Bagousse-Pinguet et al., 2019). However, whether precipitation-driven changes in FDis and PD in plant community can affect soil microbial diversity remains largely unknown in deserts and grasslands. Thus, to fill this knowledge gap, it is crucial to explicitly assess how the associations of species, functional or phylogenetic diversity in plant community with soil microbial diversity vary with precipitation changes.

Here, based on comparative observations along the natural and experimental precipitation gradients, we examined how long-term precipitation changes and short-term (three-year) precipitation manipulation, plant biodiversity attributes and soil properties affect soil bacterial and fungal diversity in desert-shrub and steppe-grass communities in Inner Mongolia, China (Table S1 and Fig. S1). In this paper, we ask the following three questions: 1) Do soil bacterial and fungal diversity respond similarly to a natural precipitation gradient as they do to an experimental precipitation gradient? 2) Do the responses of soil bacterial and fungal diversity to long- and short-term precipitation changes vary with plant community type? and 3) Whether the regulatory factors affecting soil microbial diversity in deserts and steppes are the same between natural and experimental gradients? We hypothesized that 1) soil bacterial and fungal diversity would demonstrate different responses to long- and short-term precipitation changes due to the differences in their adaptive strategies (Boer et al., 2005; Yang et al., 2021); (2) long-term precipitation changes across space would affect soil microbial diversity by altering plant biodiversity attributes (Delgado-Baquerizo et al., 2018; Wang et al., 2020; Wang et al., 2022) or soil properties (Fierer and Jackson, 2006; Maestre et al., 2015; Zhou et al., 2020; Yang et al., 2021) in deserts and steppes; and (3) short-term precipitation changes in experiments would affect soil microbial diversity by altering plant biodiversity attributes in shrub- and grass-communities (Fahey et al., 2020).

## 2. Methods

### 2.1. Study area and experimental design

We collected data from a comparative study of the responses of shrub- and grass-dominated communities to altered precipitation along the natural and experimental gradients. The field observations were conducted along an increasing precipitation gradient from desert to steppe in Inner Mongolia. This area spans 1050 km with a latitudinal range from 40°38'N to 42°06'N and a longitudinal range from 100°59'E to 113°13'E (Table S1). The mean annual precipitation in this area ranges from 37 to 260 mm, and the mean annual temperature ranges from 2.5 to 8.6 °C. We selected 39 sites along a natural precipitation gradient across the desert-steppe area, in which 22 sites with precipitation ranging from 37 to 151 mm were dominated by typical desert shrubs and 17 sites with precipitation ranging from 151 to 260 mm were dominated by perennial grasses (Fig. S1). At each site, we randomly chose three 20 × 30 m plots and set up one 5 × 5 m subplot and 1 × 1 m quadrat in each plot for the measurement of shrub and herbaceous plants. In total, there were 66 subplots and 117 quadrats for the field survey of shrub and herbaceous plant communities along the natural precipitation gradient, respectively.

The short-term experiment of manipulative precipitation was conducted at the Urat Desert-Grassland Research Station (106°58'E, 41°25'N). The Urat region with a mean annual precipitation of 151 mm was located in the transitional zone between desert and steppe. Two typical

plant communities dominated by desert shrub (*Reaumuria soongorica*) and steppe grass (*Stipa glareosa*) can coexist in this region. In August 2015, the precipitation manipulative experiment was separately established in the shrub and grass communities at the same location with a spacing of 600 m. We used the equipment of rainout shelters with a drip irrigation system to determine the precipitation increase and reduction (Zhang et al., 2019; Zuo et al., 2021). In each community, we arranged 18 rainfall shelters ( $4 \times 4$  m) with V-shaped clear strips at different densities to reduce 20 %, 40 % and 60 % of incoming annual rainfall (Fig. S2), according to the frequency and intensity of long-term precipitation change in this area (Zhang et al., 2019). At the same time, increased precipitation treatments of 20 %, 40 % and 60 % were imposed by using the drip irrigation system with small-hole pipes connected to the gutters of rainfall shelters (Fig. S2). We also set up the 6 replicated control plots with natural precipitation. The experimental precipitation gradient ranging from 60 mm ( $-60$  %) to 240 mm ( $+60$  %) can match the precipitation changes from desert to steppe in the field observations (Fig. S3). In each community, we set up a randomized block design experiment with 6 blocks and seven precipitation treatments. There was at least 3 m distance between blocks and a 0.6 m space between the decreased and increased rainfall plots. In each plot, a subplot of  $3.5 \times 3.5$  m and a  $1 \times 1$  m quadrat were set up for the measurement of shrub and herbaceous plants. In Total, there were 84 sampling subplots and quadrats within the two plant communities.

## 2.2. Vegetation survey and soil sampling

We carried out a field vegetation survey and soil sampling in August 2018. We counted species richness in each plot, recorded the individual number of shrub or herbaceous species and estimated the cover of each species in each subplot or quadrat. A mixed soil sample for chemical and microbial analyses was collected from five random cores (0–10 cm) using a soil auger (3 cm diameter) at each field site or in each experimental plot. Additionally, we collected five soil cores to measure the soil water content. Each mixed soil sample was sieved through a 2.0-mm sieve and then stored separately in two sterilized plastic bags. One bag was kept in a refrigerator at  $-4$  °C for DNA extraction and sequencing, and the other bag was air-dried for soil chemical property analyses.

## 2.3. Soil microbial diversity

Soil total microbial genomic DNA was extracted from 0.5 g of defrosted soil samples using the Qiagen PowerSoil DNA KF Kit (Qiagen, Germany) according to the manufacturer's protocol. Five extracted DNAs from each natural site or each experimental plot were mixed as one target DNA for sequencing. The bacterial universal primer (515F-907R) (Yusoff et al., 2013) and the fungal universal primer (ITS1F-2043R) (Adams et al., 2013) were applied for PCR amplification targeting 16S rRNA and ITS rRNA of V4 genes, respectively. PCR products were purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, USA) and quantified using a Quantus Fluorometer (Promega, USA) according to the manufacturer's instructions. The purified amplicons were pooled in equimolar amounts and sequenced by the paired-end method at Majorbio Bio-Pharm Technology Co., Ltd. (Shanghai, China), according to the standard protocols. The raw reads were merged by FLASH (Magoc and Salzberg, 2011), demultiplexed into samples according to their barcodes, and subjected to multiple rounds of quality control. The high-quality chimaera-free sequences with high similarity ( $\geq 97$  %) were clustered and assigned to the same operational taxonomic unit (OTU) using UPARSE (Edgar, 2013). The representative sequences for each OTU were annotated and classified based on the Silva database (<http://www.arb-silva.de>) for bacteria and Unite database (<http://unite.ut.ee/index.php>) for fungi. ACE estimator of richness (abundance-based coverage estimator of species richness) is a common index which considers the abundance of the species present, the coverage of rare species and the proportion of all individuals in rare species (Chao and Lee, 1992). We separately calculated the ACE richness index as the measure of soil bacterial and fungal diversity (Bell et al., 2021; Qiu

et al., 2021). The relative proportions of major soil bacterial and fungal taxa in shrub- and grass- communities along a natural gradient and in the experiment are shown in Fig. S4.

## 2.4. Plant biodiversity attributes

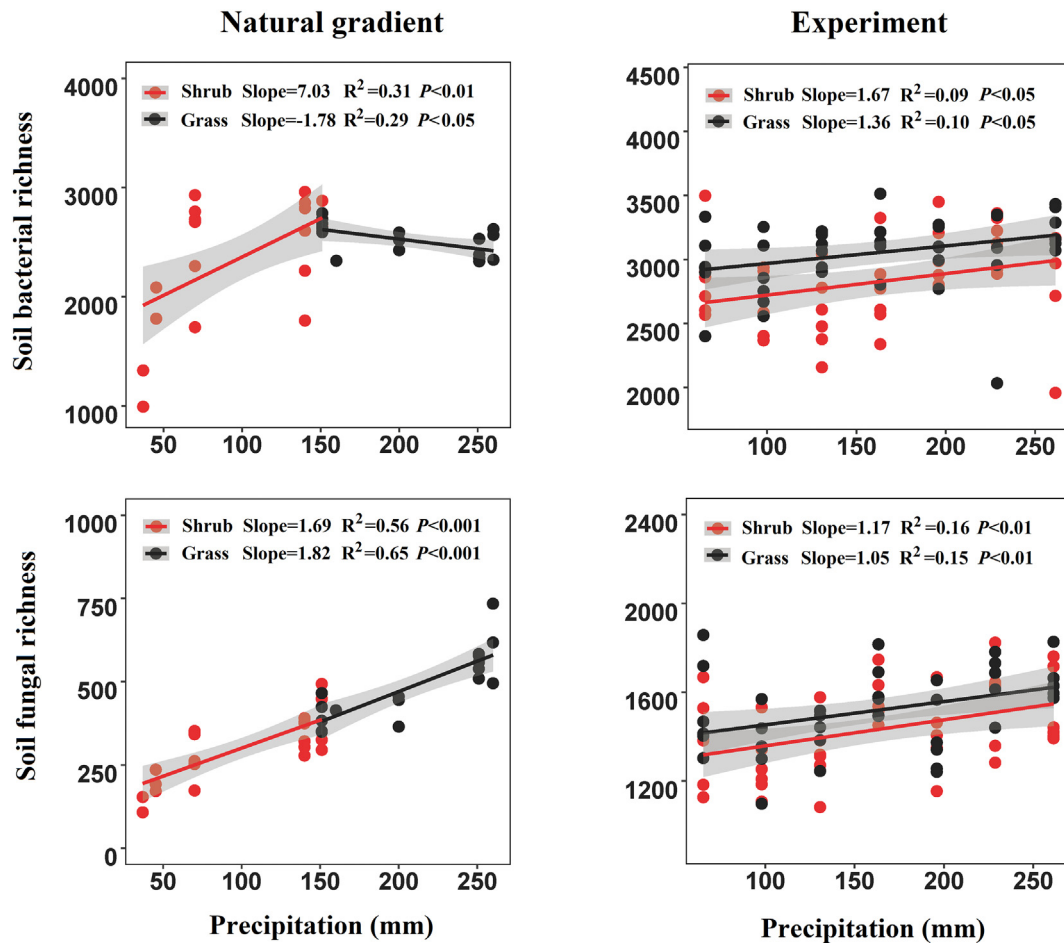
Based on the vegetation survey, we quantified the measurement of plant species diversity by species richness at each natural site and in each experimental plot. We quantified functional diversity measurement by the single trait index (community-weighted mean, CWM) and multi-trait index (functional dispersion, FDis) at each natural site and in each experimental plot (Valencia et al., 2015). We measured six functional traits associated with morphology, photosynthesis and reproductive ability (Valencia et al., 2015; Perez-Ramos et al., 2019; Zuo et al., 2021), including plant height, specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (LT), leaf carbon content (LCC) and leaf nitrogen content (LNC). We choose 10–15 healthy adults of each shrub or herbaceous species from each natural site and each plot in the experiment. We used standard methodologies to measure six functional traits of each species (Cornelissen et al., 2003). CWM reflecting the abundance-weighted average of trait values at the community-level was determined by multiplying the trait value of each species by its relative cover in the community (Violle et al., 2007; Conti and Díaz, 2013):  $CWM = \sum trait_i \times x_i$ , where  $trait_i$  is the relative biomass of the  $i$ -th species in the community and  $x_i$  is the trait value of  $i$ -th species. FDis reflecting the variation and divergence in multiple traits among species in a community was measured as the multiple trait dispersion within the functional volume of plant community (Laliberté and Legendre, 2010; Griffin-Nolan et al., 2019). The values of six functional traits were log-transformed to determine FDis to avoid scale effects (Casanoves et al., 2011). We used Faith's phylogenetic diversity (PD) as the measure of evolutionary history by defining the total branch length on a phylogenetic tree represented by a set of co-occurring plant species (Cadotte et al., 2012; Griffin-Nolan et al., 2019). We separately generated two phylogenetic trees along the natural and experimental gradients using the Phylomatic and Angiosperm Phylogeny Group's system on Phylomatic website (<http://www.phylodiversity.net>) by using all angiosperm species information in 39 sites and 84 plots, and then we determined the plant PD at each natural site and in each experimental plot using R software (Qian et al., 2014; Griffin-Nolan et al., 2019).

## 2.5. Precipitation and soil property parameters

Along the natural gradient, the mean annual precipitation data were obtained from 1985 to 2018 from the weather station near each field site. Precipitation data at sites away from the weather station were obtained from the Global Land Data Assimilation System (<https://disc.gsfc.nasa.gov/datasets?keywords=GLDAS>). The precipitation amount in each experimental plot was calculated as the percent increase or decrease from the mean annual precipitation from 2015 to 2018. Soil total C and N were measured by an automatic element analyser (Costech ECS 4010, Italy). Soil pH was measured in a 1:1 soil-water slurry using a pH probe. The soil water content (SWC) was obtained by the gravimetric method with oven drying at 105 °C for 24 h. The soil coarse sand and silt + clay contents were measured by the wet-sieving method with international and USDA classification systems.

## 2.6. Statistical analyses

Simple linear regression models were used to examine the relationships of plant biodiversity attributes, soil bacterial and fungal diversity and soil properties with mean annual precipitation changes along the natural gradient (Fig. 1 and Table S2). Linear mixed models with blocks included as a random effect were used to examine the relationships of plant biodiversity, soil bacterial and fungal diversity and soil properties with precipitation changes in the experiment (Fig. 1 and Table S2). These analyses were separately performed for the shrub and grass communities along the natural



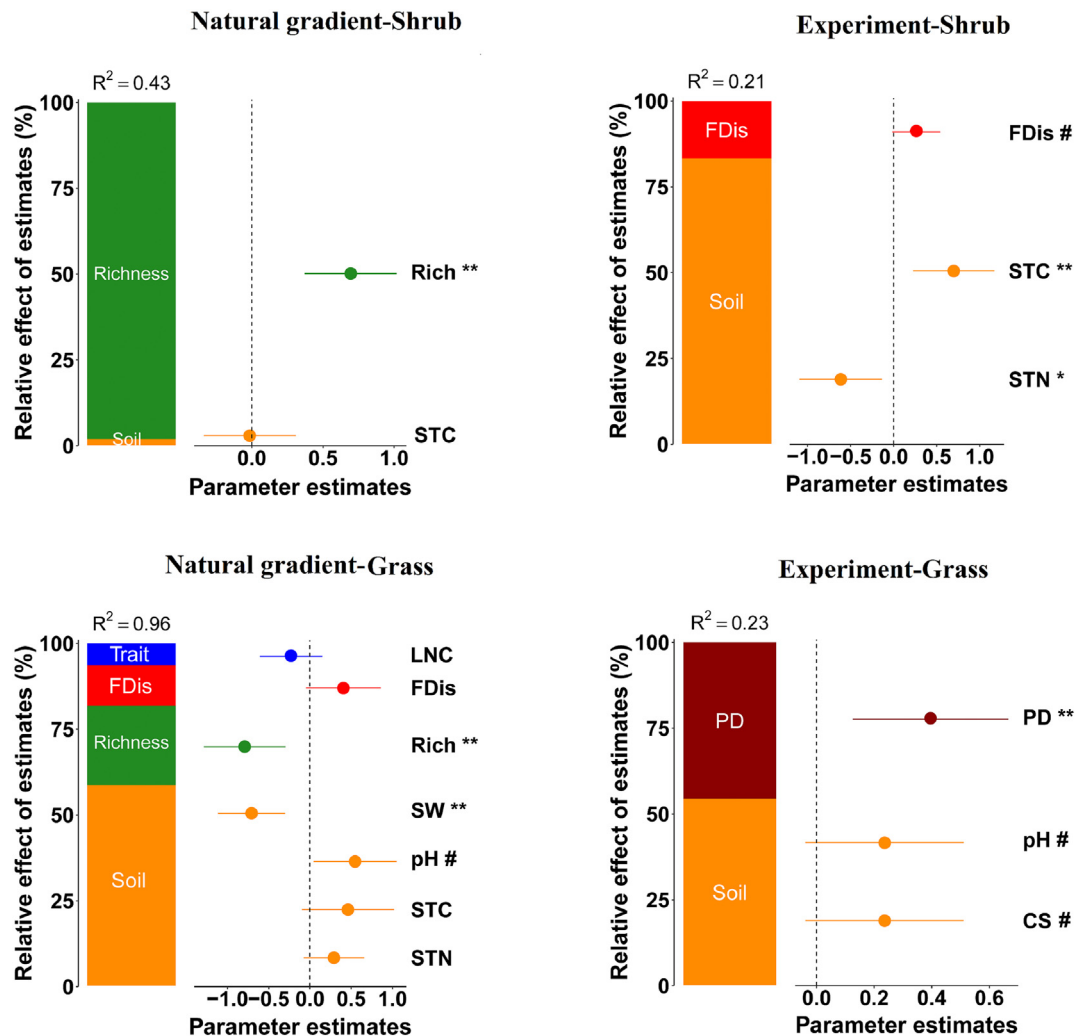
**Fig. 1.** Relationships of soil bacterial and fungal diversity with precipitation changes along a natural gradient and in the experiment. Shrub and grass communities are indicated by black and red dots, respectively. Shaded areas show the 95 % confidence interval of the fit.

gradient or in the experiment. Multiple stepwise regression analyses (MSRs) were used to examine which the variables in species richness, functional traits, FDis, PD and soil properties were significant predictors of soil bacterial and fungal diversity in the shrub and grass communities along the natural gradient or in the experiment (Table S3). Then, we established the full model using the vegetation and soil variables selected by MSRs. We further applied a model-averaging selection procedure based on Akaike's information criterion (AICc,  $\Delta AICc < 2$ ) to determine the best final set of predictors of soil bacterial and fungal diversity (Garcia-Palacios et al., 2018). We performed this procedure using the function 'dredge' in the R package MuMIn (Gross et al., 2017). When performing the 'dredge' procedure, there was the only model with AICc  $< 2$  in four MSRs (soil bacteria in desert, soil fungi in shrub community in experiment and soil bacteria and fungi in grass community in experiment) due to the few predicted variables (Table S3), we established the best final model using the variables selected by MSRs. To quantify the relative importance of vegetation and soil properties in predicting soil bacterial and fungal diversity, we calculated a percentage of absolute value of the parameter estimate in each predicted variable from their sum (Gross et al., 2017; Garcia-Palacios et al., 2018). We further calculated the relative effect of each vegetation or soil predictor in comparison with the effect of all predictors in the model.

We used the piecewise structural equation model (SEM) to quantify how precipitation changes affected soil bacterial and fungal richness via plant biodiversity attributes and soil properties (Lefcheck, 2016). Firstly, based on the best final set of predictors (Figs. 2 and 3), we conceived theoretical framework of initial null SEM including all possible pathways of the

direct and indirect relationships among precipitation changes, soil properties (pH, water, carbon, nitrogen, coarse sand and silt + clay content), plant biodiversity attributes (species, functional and phylogenetic diversity) and soil bacterial and fungal richness. Secondly, according to the key literature (Maestre et al., 2015; Yao et al., 2017; Wang et al., 2018a; Fahey et al., 2020), we hypothesized that precipitation changes could affect the predicted variables of soil properties and plant biodiversity attributes, as well as soil bacterial and fungal richness. Thirdly, we determined the influencing paths of predicted soil properties on plant biodiversity based on their correlations (Tables S4-S7). Finally, we separately constructed the initial full SEMs in the shrub and grass communities along the natural and experimental gradients (Fig. S5). To simplify the initial models, we removed nonsignificant pathways ( $P > 0.05$ ) with low path coefficients until the best-fitting SEM remained. The best fitting SEMs were determined using Fisher's C statistic with  $P > 0.05$  and a low AIC (Lefcheck, 2016).

We calculated functional diversity indices of CWM and FDis using the FDivsity and R package (Casanoves et al., 2011). Plant PD was calculated using the "picante" package in R software. We performed linear mixed-effects models using the "lme4" and "sjstats" packages, Pearson correlation analysis using the "corrplot" package, stepwise regression analyses using the "stats" package and SEMs using the "piecewiseSEM" package in R software. All variables of response and predictor were standardized before the analyses of multiple stepwise regression, MuMIn and piecewiseSEM using the Z-score to interpret parameter estimates on a comparable scale (Garcia-Palacios et al., 2018). The variables were log-transformed before Z-score standardization to meet the assumptions of the tests used. All statistical analyses were conducted in R software (R Core Team, 2020).



**Fig. 2.** Relative effects of vegetation and soil properties on soil bacterial diversity in the shrub and grass communities along a natural gradient and in the experiment. Averaged parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95 % confidence and relative importance of each predictor, expressed as the percentage of explained variance. Rich, richness; FDis, functional dispersion; PD, phylogenetic diversity; LT, Leaf thickness; LNC, leaf nitrogen content; STC, soil carbon content; STN, soil nitrogen content; C: N, Soil carbon: nitrogen; SW, Soil water content; CS, Soil coarse sand content. #  $\leq 0.10$ , \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

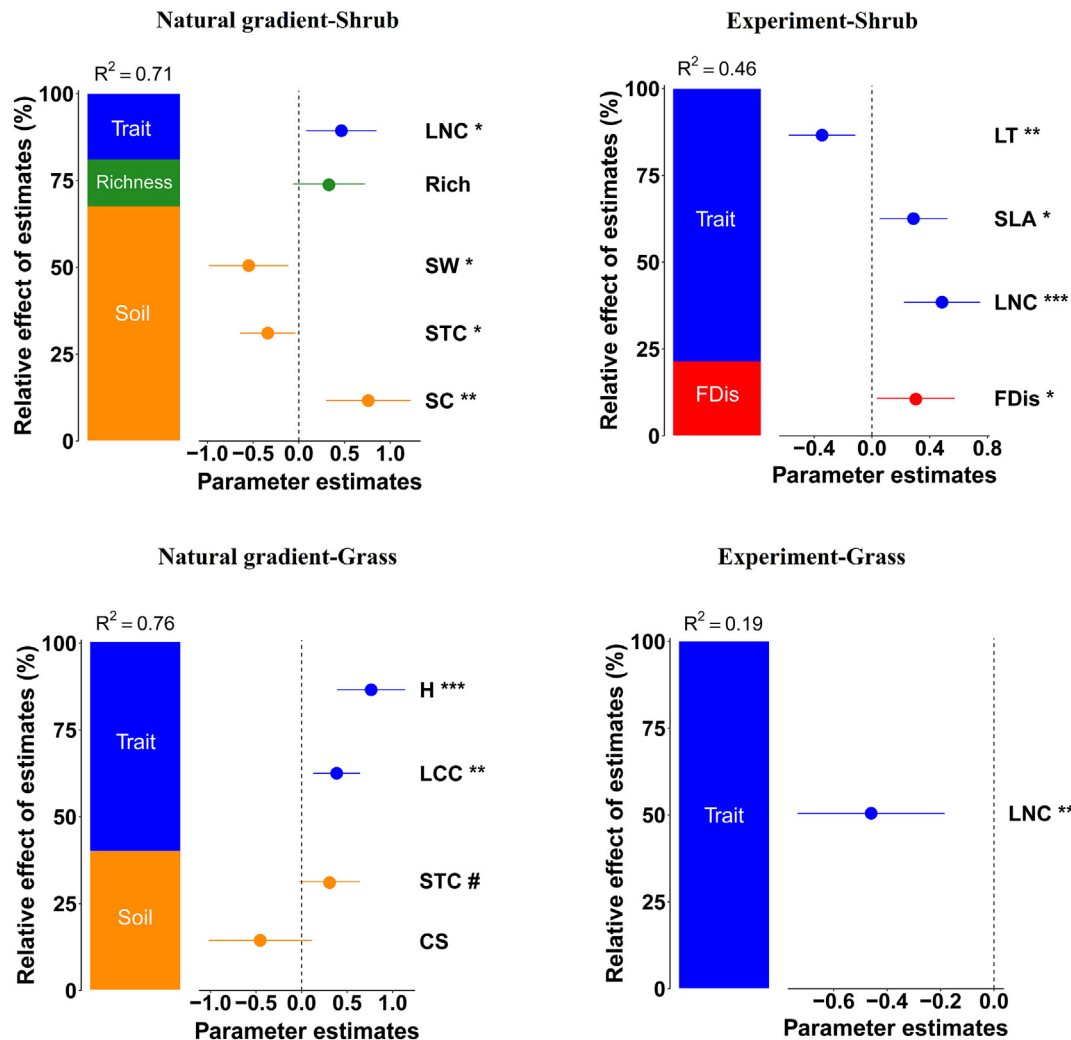
### 3. Results

The relative proportion of major soil bacterial and fungal taxa differed between the natural and experimental gradients (Fig. S4). Proteobacteria and Actinobacteria were the dominant bacterial phyla along the natural gradient, varying in relative abundance from 24.59 to 29.65 % and 20.89 to 21.57 % respectively. Actinobacteria was the dominant bacterial phylum in the experiment, varying in relative abundance from 87.68 to 88.56 %. The soil fungal community along the natural gradient was dominated by Ascomycota which varied in relative abundance from 32.95 to 40.05 %. Ascomycota and Basidiomycota were the dominant fungal phyla in the experiment, varying in relative abundance from 41.65 to 44.39 % and 43.93 to 48.18 % respectively. On the average, the datasets of OTUs were subsampled to 38,188 sequences for bacteria and 63,062 sequences for fungi along the natural gradient (Table S8). The rare taxa in soil bacteria and fungi accounted for 72.63 % and 78.48 % of the OTU number, while abundant taxa accounted for approximately 0.11 %–1.11 %, respectively. In contrast, the datasets of OTUs were subsampled to 76,644 sequences for bacteria and 78,935 sequences for fungi in experiment (Table S8). The rare taxa in soil bacteria and fungi accounted for 74.05 % and 60.19 % of the OTU number, while abundant taxa accounted for approximately 0.05 %–0.51 %, respectively. In experiment, precipitation treatment had a

significant effect on soil bacterial and fungal richness in shrub community and soil fungal richness in grass community ( $P < 0.01$ ), and had a marginal significant effect on soil bacterial richness in grass community ( $P < 0.10$ ).

Along the natural and experimental gradients, increasing precipitation increased soil bacterial and fungal richness in the shrub community, explaining 10–56 % of the variation (Fig. 1). In contrast, in the grass community, increasing precipitation also increased soil fungal richness along both gradients and soil bacterial richness in the experiment, explaining 10–65 % of the variation. However, increasing precipitation decreased soil bacterial richness along the natural gradient, explaining 29 % of the variation. When looking at the slope of the linear relationship between soil microbial richness and precipitation, soil bacterial and fungal richness were more sensitive to altered precipitation along the natural gradient than in the experiment (Fig. 1).

The associations of precipitation changes with plant biodiversity attributes and soil properties in the shrub and grass communities differed between natural and experiment gradient (Table S2). The best final models including vegetation and soil predictors could explain 43, 96, 71 and 76 % of the total variation observed in soil bacterial and fungal richness in the shrub and grass communities along the natural gradient, respectively (Figs. 2 and 3). By contrast, in experiment, the models that included vegetation and soil predictors explained 21, 23, 46 and 19 % of the total



**Fig. 3.** Relative effects of vegetation and soil properties on soil fungal diversity in the shrub and grass communities along a natural gradient and in the experiment. Averaged parameter estimates (standardized regression coefficients) of the model predictors are shown with their associated 95 % confidence and relative importance of each predictor, expressed as the percentage of explained variance. Rich, richness; FDis, functional dispersion; LT, Leaf thickness; LCC, leaf carbon content; LNC, leaf nitrogen content; STC, soil carbon content; SW, Soil water content; CS, Soil coarse sand content; SC, Soil silt + clay content. #  $\leq 0.10$ , \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

variation observed in soil bacterial and fungal richness in the shrub and grass communities, respectively.

The best fitting SEMs showed that along the natural gradient, increasing precipitation directly increased soil bacterial and fungal richness in the shrub community (Fig. 4, Table S9). Increasing precipitation indirectly increased soil bacterial and fungal richness in the shrub community by increasing plant species richness, and indirectly increased soil fungal richness in grass-community by increasing plant height, while it indirectly decreased soil fungal richness in the shrub community and soil bacterial richness in the grass community by increasing soil water content. In contrast, in the experiment, the positive effects of precipitation on soil bacterial and fungal richness were mediated by increasing FDis and leaf nitrogen content in the shrub community, respectively (Fig. 4, Table S9). In the grass community, precipitation indirectly increased soil bacterial richness by increasing plant PD, and indirectly increased soil fungal richness by decreasing leaf nitrogen content.

#### 4. Discussion

To our knowledge, our study is the first to compare the responses of soil bacterial and fungal diversity in deserts and steppes to precipitation changes between natural and experimental gradients. Along both gradients, soil bacterial and fungal richness showed significant shifts, supporting the

finding that precipitation change is the main driver in regulating soil microbial diversity in drylands (Maestre et al., 2015; Yao et al., 2017; Wang et al., 2018b). Consistent with our hypotheses, plant biodiversity attributes or soil properties play a key role in mediating the effects of precipitation change on soil microbial diversity at larger spatial scales, while plant biodiversity attributes are crucial in manipulative experiments. The contrasting relationships between plant and soil microbial diversity were shaped by long- and short-term precipitation changes, suggesting that precipitation change can also regulate the relationship between plant and soil microbial diversity in space and time (de Vries et al., 2012; Delgado-Baquerizo et al., 2018; Fahey et al., 2020). Our study further provides empirical evidence of strong direct links between plant and soil microbial diversity under climate change scenarios.

Our results indicate that long- and short-term precipitation changes have different effects on plant biodiversity attributes and soil properties in deserts and steppes. The positive associations of species richness and PD with increasing precipitation along both gradients (Table S2), which are consistent with the previous finding that altered precipitation drives species richness and evolutionary history in plant communities (Harrison et al., 2015; Li et al., 2019). Functional traits and diversity (e.g., plant height, leaf C and N contents, FDis) were altered by precipitation in the experiment. This finding is mainly because the plant community in desert-grassland transitional areas is sensitive to precipitation changes (Zuo

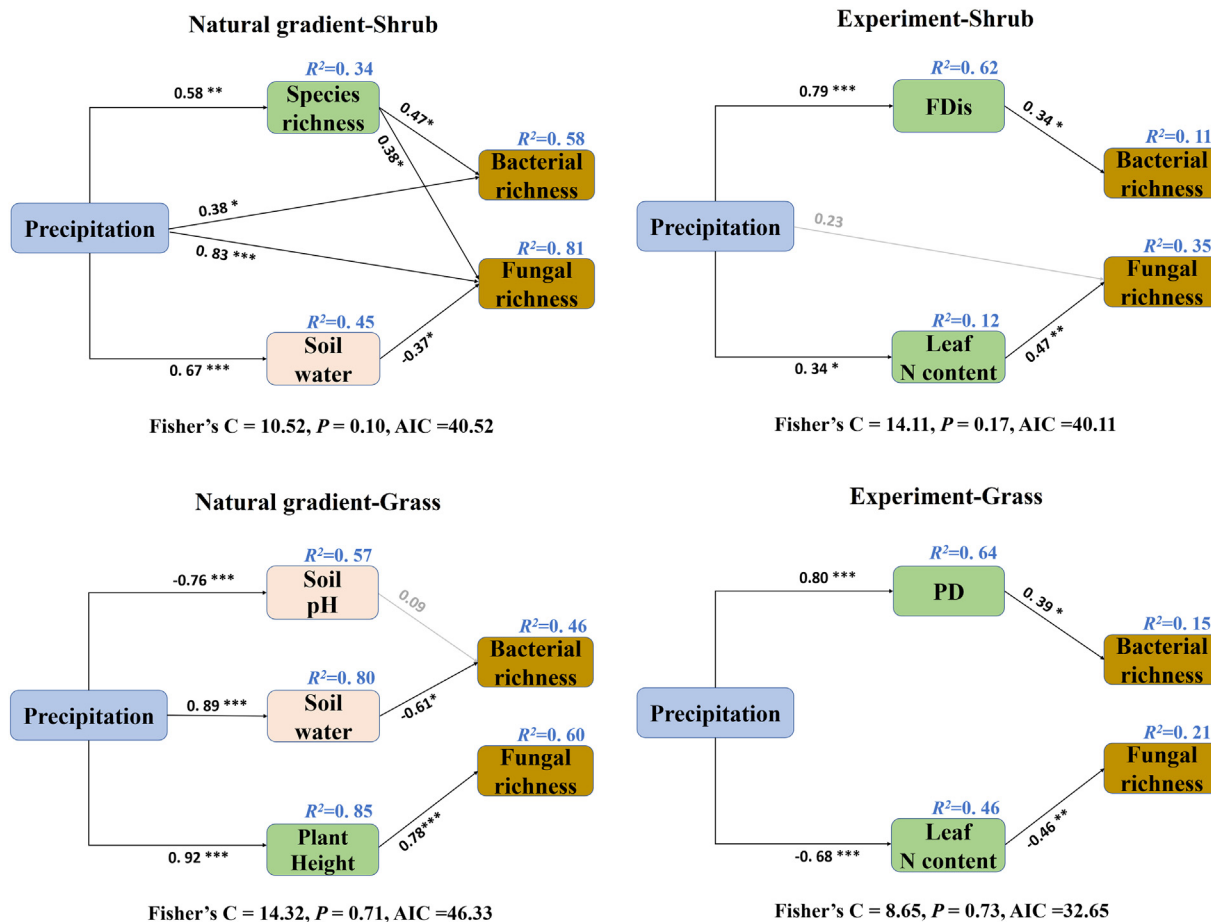


Fig. 4. Structural equation models depicting the direct and indirect effects of precipitation changes on soil bacterial and fungal diversity in the shrub and grass communities along a natural gradient and in the experiment. Standardized regression weights (along path) and total variance explained as a result of all predictors pointing to that variable (top right corner of rectangle). FDis, plant functional dispersion; PD, phylogenetic diversity. \*, \*\* and \*\*\* indicate statistically significant paths at  $P < 0.05$ ,  $P < 0.01$  and  $P < 0.001$ , respectively.

et al., 2021), and higher drought or precipitation treatments in experiments can lead to changes in plant traits (Nunes et al., 2017). In addition, increasing precipitation increased the soil water content along both gradients, supporting that soil water availability is largely regulated by precipitation in dryland regions (Gao and Reynolds, 2003; Bickel and Or, 2020). Along the natural gradient, increasing precipitation increased the soil N and silt + clay contents in the shrub community and the soil coarse sand and silt + clay contents in the grass community but decreased the soil pH in the grass community (Table S2) due to the effects of long-term precipitation on aboveground community production and plant inputs (Austin and Sala, 2002) and soil type changes (Yang et al., 2021). However, in the experiment, all soil properties except for the soil water content were unchanged with increasing precipitation.

Consistent with other studies (Fahey et al., 2020; Wang et al., 2022), plant species richness had a strong positive effect on both soil bacterial and fungal richness in deserts along the natural precipitation gradient, indicating that plant species richness played a significant role in determining the distribution pattern in soil microbial diversity in deserts. In addition, plant height, FDis, plant PD and leaf nitrogen were also important drivers affecting soil microbial diversity. In our study, we can't clearly reveal the mechanisms proposed for the effects of plant biodiversity attributes on soil microbial diversity. However, the underlying associations of soil microbial diversity with plant richness (Eisenhauer et al., 2010; Fahey et al., 2020) and functional traits and diversity (de Vries et al., 2012; Delgado-Baquerizo et al., 2018; Wang et al., 2020) have been reported in some observational and experimental studies, further providing support that the proposed associations are of general significance.

In fact, an increasing number of studies have shown the effects of plant biodiversity attributes on soil microbial diversity by altering the range and quality of resources and the microenvironment (Wardle, 2006; Eisenhauer et al., 2010; Joly et al., 2017; Delgado-Baquerizo et al., 2018). Highly diverse plant communities can produce higher variability in litter quality and promote higher resource diversity, thus affecting soil microbial composition and diversity (Paterson et al., 2007; Joly et al., 2017). Similarly, plant communities with high functional and phylogenetic diversity can produce high-quality litter mixtures and high niche differentiation, which can allow a more complementary use of resources for the soil microbe community, therefore increasing soil microbe richness and biomass (Xiao et al., 2020). Numerous studies have shown that functional trait reflecting plant life strategy is a major driver of plant community biomass, carbon and nitrogen processes (Conti and Díaz, 2013; Gross et al., 2017; Xiao et al., 2020). Plant functional traits (e.g., plant height and leaf nitrogen) reflecting species with rapid resource acquisition are associated with the quantity and quality of litter, thus significantly contributing to explaining soil microbial diversity (de Vries et al., 2012; Delgado-Baquerizo et al., 2018; Luo et al., 2021). The higher plants can increase plant community biomass, and the shade of higher plants can improve the microclimatic factors (e.g. soil temperature and humidity), thus increasing soil fungal richness in steppe (Zuo et al., 2016; Fahey et al., 2020). In contrast, in the short-term experiment, increasing precipitation-induced increase in plants with high leaf N content is likely to favour soil fungal richness in the shrub community, while the decrease in plants with low leaf N content is likely to favour soil fungal richness in the grass community. Such changes in plant compositions with high or low leaf N content in the shrub or grass community can regulate

the nitrogen release from litter decomposition, thus affecting soil fungal richness. Our results from observational and experimental studies further support that the complexity of plant biodiversity plays the primary role in affecting soil microbial diversity in drylands (de Vries et al., 2012; Fahey et al., 2020; Wang et al., 2022).

Soil properties contributed to determining the pattern of soil bacterial and fungal richness in the desert and steppe along the natural precipitation gradient (Figs. 2 and 3). In particular, the soil water content had a negative effect on the soil fungal richness in the desert and the soil bacterial richness in the steppe. This may be because soil water content is likely to constrain microbial community diversity by affecting soil properties and O<sub>2</sub> content (Na et al., 2019; Yang et al., 2021). Although there was a negative effect of the soil water content on the soil fungal richness in the desert, the soil fungal richness still increased with increasing precipitation gradient, which can be attributed to the positive effects of plant species richness and the soil silt + clay content overwhelming the negative effect of the soil water content (Fig. 3). In contrast, a previous study has shown that soil bacterial richness is higher at intermediate water contents due to the higher soil aqueous-phase connectedness (Bickel and Or, 2020), and high soil water may lead to a decrease in soil bacterial richness due to the disappearance of some species of bacteria (Yang et al., 2021). Additionally, in agreement with others studies (Fierer and Jackson, 2006; Yang et al., 2021), the decreasing soil pH could also contribute to decreasing soil bacterial richness in steppe along the natural precipitation gradient (Fig. 2). In our study, soil pH was negatively correlated with soil water content ( $r = -0.689$ ,  $P < 0.01$ , Table S6) in steppe, indicating that increasing soil water content induced by increasing precipitation led to the decrease in soil pH. Due to the death of some species of bacteria under high soil acidic stress, soil bacterial richness was decreased by the lower soil pH or acidic soils (Fierer and Jackson, 2006; Wang et al., 2018a).

Importantly, our results indicated that soil fungi had similar responses to precipitation changes along the natural and experimental gradients. Increasing precipitation increased soil fungal richness by altering plant biodiversity attributes along both gradients, which is consistent with the previous finding that plant diversity has significant linkages with soil fungal diversity due to the strong plant–fungi interactions (Wang et al., 2022). This is mainly because soil fungi can form symbiotic associations with diverse plants (van der Heijden et al., 2008) and decompose complex and recalcitrant molecules of plant litters (de Boer et al., 2005). However, soil bacterial diversity showed different responses to long- and short-term precipitation changes in grass communities due to the effects of changes in soil water content with soil pH (Barnard et al., 2013; Sorensen et al., 2013; Yang et al., 2021). Because of the diverse source of energy, carbon and reductive power, soil bacterial diversity can be affected by a wide range of biotic and abiotic factors (de Vries et al., 2012; Maestre et al., 2015; Wang et al., 2020). In natural ecosystems, soil bacteria are more sensitive to soil properties (e. g. soil water content and pH) than fungal community (Fierer and Jackson, 2006; Yao et al., 2017; Yang et al., 2021). Along the natural gradient, increasing precipitation-induced increases in plant richness had a positive effect on soil bacterial richness in barren and arid desert areas, while in agreement with a previous study in the same area (Yao et al., 2017), increasing soil water content with decreasing soil pH could decrease soil bacterial richness in steppe. In contrast, in experiments, precipitation-induced high plant functional and phylogenetic diversity can allow a more complementary use of resources for soil bacteria, therefore promoting soil bacterial richness. Notably, due to the complex effect of above- and below-ground interactions on nutrient acquisition and cycling (van der Heijden et al., 2008; Na et al., 2019; Fahey et al., 2020; Wang et al., 2022), the underlying mechanism of precipitation changes driving soil bacterial and fungal diversity varies with plant community types (e. g. shrub vs grass). It is likely that the changes in plant communities induced by altered precipitation become especially important for the nutrient maintenance and microclimatic conditions, thus having different consequences for soil microbial diversity in desert and steppe (Eisenhauer et al., 2010; Fahey et al., 2020; Wang et al., 2020). This calls for the necessary conservation strategies to promote biodiversity persistence under climate

change due to the importance of plant and soil microbial diversity in affecting ecosystem functions and processes in drylands (Le Bagousse-Pinguet et al., 2019; Hu et al., 2021).

## 5. Conclusions

Our synthesis of observational and experimental studies emphasizes the important role of plant biodiversity attributes in mediating the effects of precipitation on soil microbial diversity in desert and steppe ecosystems. Long- and short-term precipitation changes shaped different associations of soil bacterial and fungal richness with species, functional and phylogenetic diversity, thus providing deep insight into the nature of plant-microbe relationships with a changing climate. In particular, our results demonstrate a similar positive pattern and different mechanisms of soil fungal richness in response to long- and short-term precipitation changes, further enhancing our understanding of how climate change affects soil fungal communities in water-limited areas. The short-term response of soil fungal richness to manipulative precipitation changes can mirror long-term shifts at large spatial scales. Obviously, as some species in terrestrial ecosystems are facing loss with climate change, better prediction of the relationships between plants and microbes in the future will require a combined study from observations and experiments linking plant and microbe diversity to climate change.

## CRedit authorship contribution statement

X. Z. designed the research and analyzed the data; S.S., Y. H., S. Z., H. C., X. G. and X. L. helped to collect the field data and lab measurement. S. W., P. Y., M. C., X. M., H. Q., X. Z., W. H. and R. G. assisted with paper revision. The first draft was written by X. Z., S.W. and P. Y. contributed to the interpretation of data and the writing of the manuscript, and all authors contributed to the final version of the manuscript.

## Data availability

Data will be made available on request.

## Declaration of competing interest

All authors have approved the final article to publish and have no any conflict, depending on author's particular contribution for this paper.

## Acknowledgements

We thank the field help of members in Urat Desert-grassland Research Station. This study was supported by National Natural Science Foundation of China (42071140) and Second Tibetan Plateau Scientific Expedition and Research program (2019QZKK0305). We are very grateful to Dr. Julio Di Rienzo for the support of FDiversity software.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.160654>.

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