

1. Introduction

Soil bacteria and fungi play a pivotal role in terrestrial carbon cycling (Bradford et al., 2019; Delgado-Baquerizo et al., 2018; Fierer, 2017). Considering their fast generation times, changes in community composition occur rapidly, within minutes, days, and even across years (Martiny et al., 2017). Such dynamics imply that such strong background variability (e.g., temporal variation) could have major implications for environmental change, particularly in the wake of climate change (Jansson and Hofmockel, 2019; Matulich et al., 2015). Although numerous studies have evaluated the impacts of climate change on the soil microbial communities (Bahram et al., 2018; Koltz et al., 2018), the findings are largely inconsistent and only a few studies have focused on the integrated effects of precipitation and warming on soil microbial communities (Zhang et al., 2017b; Zhang et al., 2017c). For example, in a California annual grassland, soil microbial communities exhibited strong responses to changing precipitation trends (Barnard et al., 2015); however, in the Angelo Coast Range Reserve in Mendocino County (California), soil microbial communities only exhibited weak responses to changes in rainfall (Cruz-Martinez et al., 2009). In alpine grasslands of the Qinghai-Tibetan Plateau, Zhang et al. (2016) observed that rainfall rather than warming could greatly influence soil microbial diversity (Zhang et al., 2016). In addition, in a semi-arid grassland, soil microbial communities responded positively to warming (Nie et al., 2013), while in the Great Plain Apiaries (near Norman, OK), warming did not influence soil microbial community structure in clipped subplots (Zhang et al., 2005). Furthermore, studies have reported that interactions between changes in moisture and temperature conditions could influence plant community structure (Yang et al., 2011), in addition to interannual climate variability (Adler et al., 2006; Cleland et al., 2004). Such changes in climate could in turn influence the microbial community structure indirectly through shifts in the compositions of above-ground plant communities. Consequently, it is critical to investigate the interactive effects of precipitation and temperature on soil microbial community structure annually.

Soil is a complex ecosystem hosting innumerable biotic-biotic and biotic-abiotic interactions, which influence physiochemical and nutrition cycling activities (Delgado-Baquerizo et al., 2018). Therefore, soil microbial communities do not persist in isolation and will interact and establish complex ecological networks with the numerous factors in the ecosystems (Faust and Raes, 2012). In 2009, Hegland et al. (2009) observed that climate warming could influence plant-pollinator interactions (Hegland et al., 2009). Since then, numerous studies have reported diverse impacts of climate warming on soil microbial interactions (Faust et al., 2015; Guo et al., 2018; Zhang et al., 2018). For instance, based on molecular ecology clustering methods, more nodes were observed in soil microbe ecological networks under warming conditions (177 nodes) than under environments not experiencing warming (152 nodes) (Deng et al., 2012), suggesting that warming enhanced the complexity of such ecological networks. In addition, some studies have reported that shifting precipitation trends could influence soil microbial ecological networks and assembly (Ma et al., 2018; Wang et al., 2018; Xiao et al., 2018). In a Chinese subtropical forest, soil fungal diversity and co-occurrence networks were more sensitive to shifts in the seasonality of precipitation than the bacterial networks (He et al., 2017). However, our understanding of the interactive effects of precipitation and temperature on soil microbial networks remains poor.

Our planet has warmed by approximately 0.6 °C over the past century (Climate Change, 2001) and changes in precipitation regimes are not uniform across space and time (Walther et al., 2002). Consider the Tibetan Plateau. It is the highest (4000 m on average), youngest (2.4×10^8 years), and largest (2.0×10^6 km²) plateau in the world, and the region is experiencing a two-fold rate of increase in warming compared to the global average warming rate (0.2 °C per decade over the past 50 years) (Chen et al., 2013). Therefore, the ecosystem is particularly vulnerable to the effects of climate change. Extensive evidence

shows that plant diversity and communities could be altered annually under simulated climate change conditions (Matulich et al., 2015), and water availability is the primary limiting factor in arid and semiarid areas (Niu et al., 2008). Ecologists have previously reported on the effects of interannual climate variability on aboveground plant diversity and community structure (Adler et al., 2006). Recently, some studies have investigated the influence of temporal variability on the microbial diversity and structure. For example, stream bacterioplankton communities could vary across seasons (Portillo et al., 2012), while soil fungal communities changed over time in a meadow habitat (Oja et al., 2014). When investigating the soil microbial communities in northward and southward soil transplants, Liang et al. (2015) observed a strong effect of temporal variation. Similarly, in a semiarid grassland, Liu et al. (2009) observed that interannual variations in soil respiration and microbial biomass were correlated positively with interannual fluctuations in precipitation (Liu et al., 2009). The studies above concluded that the influence of temporal variability on the soil microbial community structure was potentially attributable to seasonal temperature change or variable annual precipitation. Nevertheless, the effects of interannual climate variability on the soil microbial structure require further investigation. Here, we investigate how warming, altered precipitation (simulated experiment), and interannual climate variability (mean annual precipitation [MAP] and mean annual temperature [MAT]) influence soil microbial diversity and community structure under simulated conditions, and if the potential impacts would extend to the associated ecological networks in the soil. In the Tibetan Plateau, considerable temperature fluctuations are observed throughout the day (Maximum daily temperature: 8.9 °C; Minimum daily temperature: -7.5 °C). We assume that the influence of the disturbance on the soil microorganisms due to a 1.6 °C increase in temperature may not exceed the influence of the effect of the disturbance associated with the considerable diurnal and seasonal temperature variations on the soil microbes. To test our hypothesis, we selected the Haibei Alpine Grassland Ecosystem Research Station, which is located at the northeast of Tibetan Plateau, as an experimental site to study the effect of warming and precipitation (over 4 years, years 1, 2, and 4) on the soil microbial community.

2. Method and materials

2.1. Site description and soil sampling

The warming and precipitation experiments were performed at the Haibei Alpine Grassland Ecosystem Research Station (37°30'N, 101°12'E, 3200 m), which is to the northeast of the Tibetan Plateau. The local climate is a typical plateau continental climate and the average annual temperature ranges from -0.81 °C to -1.82 °C (maximum 7.3 °C, minimum -23.6 °C), while annual precipitation ranges from 350.6 mm to 501.3 mm (Wang et al., 2014). Soil at the station is classified as a Cambisol (IUSS Working Group WRB, 2007).

The well-replicated simulated climate change experiment established on July 2011 consisted of 36 plots (6 treatments × 6 replicates), each measuring 2 m × 2 m, and was based on a random block design (each treatment had six replicates, every replicate was a block, and the blocks were distributed randomly). In our study, to prevent the platform from being strongly disturbed, we selected four replicates from each treatment. Consequently, we tested 24 soil samples in each year. The treatment factors were warming and altered precipitation, including controls (CK), decreased precipitation (DP; -50%), increased precipitation (IP; +50%), warming (W; +2 °C), warming with decreased precipitation (W × DP), and warming with increased precipitation (W × IP). For detailed information on how warming and altered precipitation were achieved, please see Zhang et al.'s study (Zhang et al., 2017a). Briefly, to evenly heat the surface soil, two parallel infrared heaters (1000 × 22 mm) hang 1.5 m above the ground in each warmed plot. To collect the precipitation, four transparent resin polycarbonate channels, which covered approximately 50% of the plot area, were set

up above the heaters in the decreased precipitation plots. And the collected rain was added to the increased precipitation plots.

Soil samples (four replicates) were collected in each treatment in 2012, 2013 and 2015. To ensure consistency, all the soils were collected during growing seasons around mid-July. In each plot, five 0–5-cm soil cores (four vertices and one center) were drilled and then mixed to obtain one sample. Subsequently, the samples were transported to the laboratory on ice and stored at -20°C . The sampling yielded 24 soil samples (6 treatments \times 6 replicates) for each year and 72 soil samples in total.

Soil DNA extraction was performed according to the instruction manual of the Fast DNA R SPIN Kit for soil (MP Biomedicals, Santa Ana, CA, USA). Subsequently, soil DNA was quantified using a Nano Drop ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA) and stored at -20°C .

2.2. Sequence processing

The raw paired-end reads were joined using FLASH (Magoc and Salzberg, 2011) and 2,668,345 raw joined reads obtained for bacteria and 3,709,151 raw joined reads obtained for fungi. The merged reads were analyzed using QIIME2 v2018.08 (<https://qiime2.org>) for sequence quality control and diversity estimation. Deblur (Amir et al., 2017) was used to perform quality control on the raw sequences individually to obtain a subsampled operational taxonomic unit (sub-OTU) table. As the quality was relatively low at the end of the reads, all the paired-end bacterial sequences were truncated at 350 bp and the fungal sequences were truncated at 150 bp. After filtering the low quality sequences, the q2-vsearch plugin was used to identify and filter chimeras. Sklearn-based taxonomy classifier was used for taxonomy assignment in the Greengenes database (13–8) (Second Genome Inc., San Francisco, CA, USA) for 16S and the UNITE database (17–12 release) (<http://unite.ut.ee>) for ITS at 99% identity. A total of 12,041 16s rRNA and 18,200 ITS gene high-quality sequences were selected randomly for fungal and microbial diversity analyses.

2.3. Data analysis

Three-way Analysis of Variance (ANOVA) was used to evaluate the effects of warming, altered precipitation, and year on microbial sub-OTU, microbial community dissimilarity, and the relative abundances of bacterial phyla and fungal classes. The normality of the response variables was tested using the Shapiro–Wilk test. If the null hypothesis was rejected, square root transformation was applied before ANOVA testing.

Both abundance-based Bray–Curtis distance and presence–absence based Jaccard distance were calculated to reveal potential microbial compositional variation between treatments. PERMANOVA analysis was used to evaluate the effects of warming, altered precipitation, and year on the compositional variations. Cross-domain interaction networks were constructed using the SpiecEasi package in R (Kurtz et al., 2015) and the sparCC function of the SpiecEasi package was used to calculate the correlation between each sub-OTU. To reduce artificial correlation, the sub-OTUs with a frequency lower than 50% and sparCC correlation values less or equal to 0.3 were removed from the network. The undirected network graphs were visualized using gephi (<https://gephi.org/>). Topology features of a network were analyzed using functions of the igraph package in R. Node degree was used to evaluate the network sparsity and a lower degree indicated a sparser network (Tipton et al., 2018). Natural connectivity of a complex network was applied to reveal the robustness of a network (Wu et al., 2010). Box-plots and line plots were illustrated using the ggplot2 package in R.

To determine the influence of interannual climate variability (represented by MAT and MAP) on the soil bacterial and fungal communities, three-way ANOVA was used to test the effects of treatments, MAP, and MAT on the soil microbial community structure.

3. Results

3.1. Soil microbial community composition

We characterized 7007 bacterial and 2368 fungal species-level OTUs (sOTUs) using a 99% sequence similarity cutoff from 2,668,345 and 3,709,151 high quality reads, respectively. Most of the bacterial sOTUs were classified as Proteobacteria (32%), Actinobacteria (30%), Acidobacteria (13%), or Planctomycetes (5.9%), with Chloroflexi (6.4%) and Bacteroidetes (5.1%) at the phylum level (Table S1). The majority of the fungal sOTUs were classified as Agaricomycetes (18%), Leotiomycetes (9.6%) or Sordariomycetes (9.6%), followed by Mortierellomycetes (6.6%) and Dothideomycetes (4.7%) at class level (Table S2).

3.2. Effects of treatments and temporal variations on the number of soil microbial sOTUs

According to the results of the three-way ANOVA, year influenced the number of soil bacterial sOTUs significantly ($F = 10.46$, $P < 0.001$, Table 1), and precipitation influenced the number of soil fungal sOTUs significantly ($F = 4.55$, $P < 0.001$, Table 1). Both the number

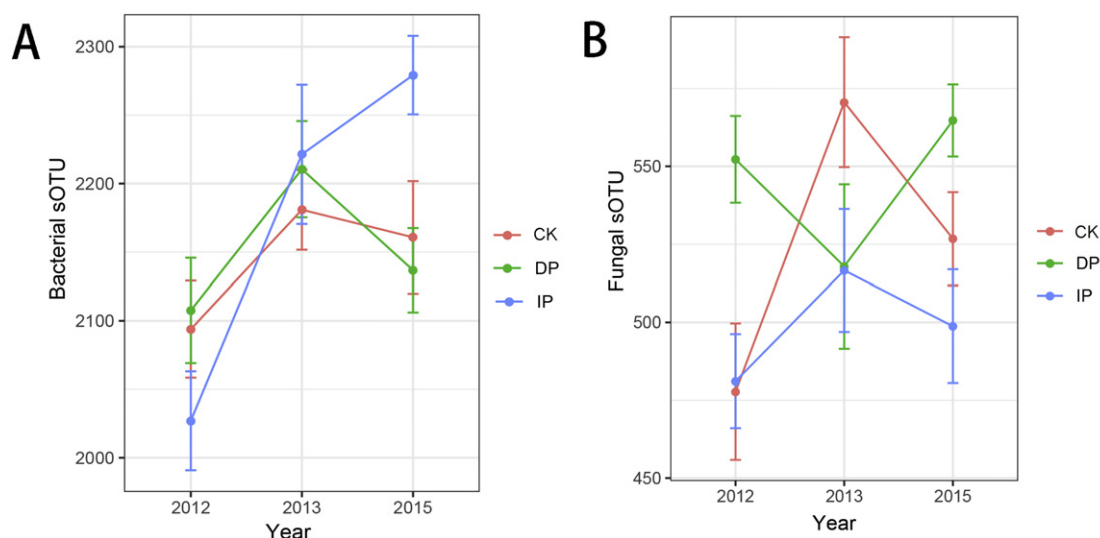


Fig. 1. Comparative analysis of the richness between the control, decreased precipitation and increased precipitation with the year. A: Bacterial richness. B: Fungal richness.

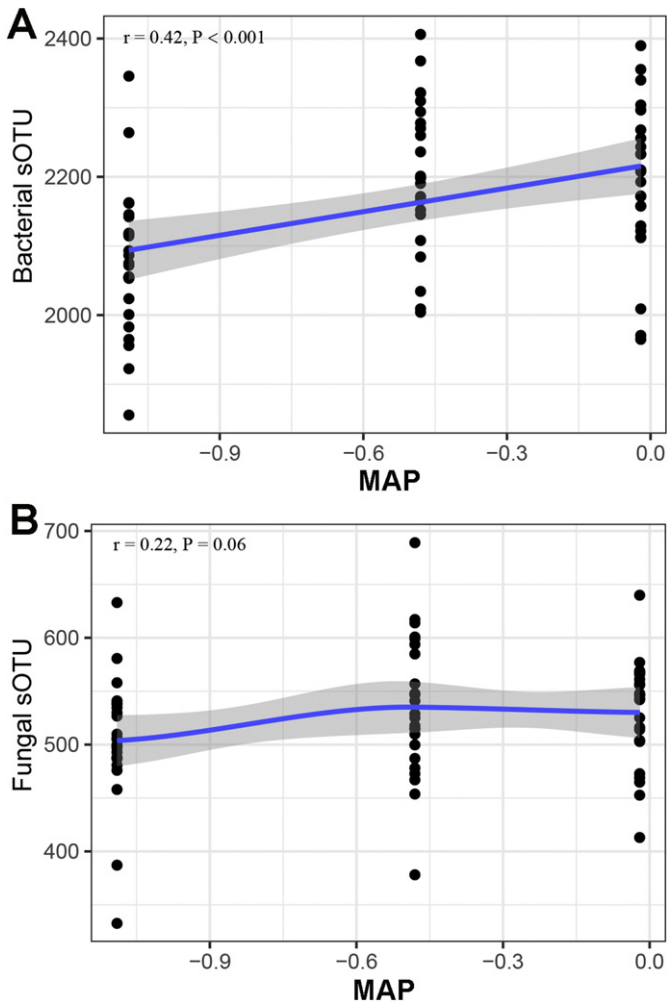


Fig. 2. Relationships between the number of bacterial sOTU (A), the number of fungal sOTU and mean annual precipitation (MAT).

of bacterial and fungal sOTUs were influenced significantly by the interactive effects of the precipitation treatments and year (Table 1). A comparative analysis revealed that the effect of year on soil microbial richness was greater than the effect of the precipitation treatments (Fig. 1). When we compared each treatment to the control within each year, only warming interacted with decreased precipitation (WDP), with significant effect on the number of fungal sOTUs (Table S3).

In our study, MAT and MAP represented interannual climate variability. To determine the influence of interannual climate variability on soil microbial sOTUs, a correlation analysis was conducted among

Table 1
Three-way ANOVA of the effect of warming, precipitation, year, warming × precipitation, warming × year, precipitation × year, and warming × precipitation × year on richness (number of sOTU) of bacteria and fungi. Bold means significant difference.

Treatment	Df	Bacterial richness		Fungal richness	
		F	P	F	P
Warming	1	0.15	0.7	1.34	0.25
Precipitation	2	0.55	0.58	4.55	0.02
Year	2	10.46	<0.001	2.41	0.1
Warming × precipitation	2	0.78	0.46	1.36	0.27
Warming × year	2	0.69	0.51	0.45	0.64
Precipitation × year	4	2.55	0.05	3.13	0.02
Warming × precipitation × year	4	0.55	0.7	0.68	0.61

MAP, MAT, and number of microbial sOTUs. MAT was correlated significantly with bacterial sOTUs, while no factors were correlated with the fungal sOTUs significantly (Fig. 2, Table S4).

3.3. Influence of treatments and temporal variations on the soil microbial communities

Three-way ANOVA was used to test the effects of treatments and year on soil microbial community composition. The precipitation treatments and year had significant effects on the dissimilarity of bacterial and fungal communities (Table 2). In addition, warming had a significant effect on the Bray-Curtis distances of the fungal communities (Table 2). Furthermore, a comparative analysis revealed that the effect of annual variations on soil microbial communities was greater than the effects of precipitation treatments on soil microbial communities (Table 3). When we compared each treatment to the control within each year, DP influenced the dissimilarity in bacterial communities in 2012 and 2013 (Table S5).

According to the results, both MAP and MAT had significant effects on the bacterial and fungal community structure (Table 4).

When investigating the effect of treatments and annual variability in climate on the dominant bacterial and fungal phyla, we observed that the abundance of Acidobacteria, Actinobacteria, Chloroflexi, Gemmatimonadetes, Nitrospirae, Planctomycetes, Proteobacteria, Dothideomycetes, Mortierellomycetes, and Tremellomycetes were significantly affected by annual variation, while the precipitation treatments significantly influenced the abundance of Actinobacteria, Chloroflexi, Planctomycetes, Proteobacteria, and Tremellomycetes. In addition, the abundance of Sordariomycetes was influenced a great deal by an interaction between warming and year (Tables S6 and S7).

3.4. Effects of treatments and temporal variability on the associated soil microbial ecological networks

To determine the potential effects of treatments and temporal variability on soil microbial interactions, cross-domain interaction networks were constructed (Table 5). Generally, the topological feature values had no obvious differences among treatments. However, with regard to the modularity index, the values decreased along the years (Table 5), which implied that the clusters within the networks would be influenced by the annual climate variability. After assessing the role of each node within a module, we observed that the modular hubs and network hubs disappeared gradually along the years (Fig. 3), which confirmed that annual variability influenced module formation.

To determine the robustness of the microbial networks among the treatments and years, a natural connectivity analysis was carried out. According to the results, there were no obvious trends in the control treatment across the years (Fig. 4A). However, in the DP and IP treatments, contrasting trends were observed. Compared to 2012, the natural connectivity values increased sharply in 2013 and dramatically decreased in 2015 in the DP treatment. Conversely, the natural connectivity values decreased sharply in 2013 and increased dramatically in 2015 in the IP treatment (Fig. 4B). The results indicated a major effect of annual variability on the robustness of the soil microbial network. With regard to the effect of treatment on the robustness of the soil microbial network within each year, similar trends were observed in 2012 and 2015, where the robustness of the soil microbial networks in the control was the highest followed by in the IP and DP treatments. However, in 2013, both the control and DP had higher values than the IP.

4. Discussion

Climatic conditions (e.g., temperature and precipitation) and plant growth are vary highly seasonally or annually in the ecosystems (Bardgett and Wardle, 2010; Matulich et al., 2015). Consequently,

Table 2

PERMANOVA analysis of the effect of warming, precipitation, year, warming × precipitation, warming × year, precipitation × year and warming × precipitation × year on the dissimilarity of bacterial and fungal communities. Bold mean significant difference.

Treatment	Df	Bacteria				Fungi			
		Bray-Curtis		Jaccard		Bray-Curtis		Jaccard	
		F	P	F	P	F	P	F	P
Warming	1	1.126	0.19	1.084	0.231	1.372	0.036	1.233	0.051
Precipitation	2	2.111	0.001	1.752	0.001	2.261	0.001	1.831	0.001
Year	2	3.357	0.001	2.661	0.001	2.673	0.001	2.038	0.001
Warming × precipitation	2	1.126	0.189	1.074	0.209	1.186	0.09	1.131	0.087
Warming × year	2	0.859	0.872	0.891	0.916	0.732	0.994	0.81	0.996
Precipitation × year	4	0.92	0.771	0.967	0.652	0.746	1	0.843	0.999
Warming × precipitation × year	4	0.738	1	0.814	1	0.766	0.999	0.836	0.997

belowground microbial communities could be influenced directly or indirectly by such factors (Zak et al., 2003). Based on a temporal variation perspective, we investigated the responses of bacterial and fungal community structure to two simulated climatic change events: warming and altered precipitation. According to our results, year had a strong effect on the soil bacterial and fungal community structure and the robustness of microbial ecological networks. In addition, the interannual fluctuations in MAP and MAT were correlated significantly with the interannual variability in soil bacterial and fungal community structure in the Tibetan Plateau grassland soils (Table 4). Consistently, we also observed that altered precipitation trends had considerable effects on soil microbial diversity and community structure. Many studies have reported that precipitation influences soil microbial diversity and community structure. For example, soil microbial communities in Chihuahuan desert grasslands exhibited significant responses to seasonally altered precipitation over seven years (Bell et al., 2014). The influence of precipitation on the soil microbial community structure could be associated directly with the close association between soil moisture, and microbial diversity and community structure (Sheik et al., 2011).

Altered precipitation trends and annual variability could influence not only microbial community structure but also the microbial co-occurrence relationships. Although the patterns of robustness of co-occurrence relationships in 2015 tended to recover to the previous trends observed in 2012, the response mechanisms of soil microbial communities to drought and precipitation could be different, as observed, for example, in the dramatic shift in 2013. Previous studies have reported that dry conditions could increase bacterial isolation and, in turn, decrease competition among species (Treves et al., 2003; Zhou et al., 2002). In addition, drought conditions could decrease soil nutrient availability (Fang and Zhang, 2018). Under poor nutrient conditions, competition would be more intense within a complex microbial community, and studies have demonstrated that competition among microbes could reinforce the robustness of networks (Foster and Bell, 2012; Coyte et al., 2015). In addition, under such conditions, the dominant species would be abundant and could outcompete less dominant species, which could weaken the robustness of the co-occurrence relationships among soil microbes.

Table 3

Analysis of the effect of the precipitation and year on the soil bacterial community and fungal community.

	Bacteria_Bray Curtis	Bacteria_Jaccard	Fungi_Bray Curtis	Fungi_Jaccard
Precipitation	0.407	0.61	0.66	0.632
Year	0.411	0.612	0.662	0.635
Wilcox test P value	0.006	0.045	0.571	<0.001

Conversely, an increase in precipitation would increase the abundance of nutrients in the soil (Tuttle and Salvucci, 2016). Therefore, competition among species would decrease, which would also lead to low robustness of co-occurrence relationships among soil microbes. However, with the extension of the rainfall period, precipitation would become a stress factor for the soil microbes. Therefore, species would compete with other species to survive under the stress environments, which would lead to relatively low levels of robustness of co-occurrence relationships within soil microbial communities.

In our study, warming did not influence soil microbial community structure significantly, while the bacterial and fungal community structures exhibited high responses to altered precipitation trends. Potentially because of the unique geographical location of the experimental station (high elevation ecosystem), the disturbance on the soil microorganisms occasioned by a 1.6 °C increase in temperature could not offset the influence of the considerable diurnal and seasonal temperature variations in the area (Table S8). Presumably, the soil microbial communities in the Tibetan Plateau have adapted to such large temperature differences throughout the day (Maximum daily temperature: 8.9 °C; Minimum daily temperature: -7.5 °C). In addition, under drought conditions (425.36–850.4 mm, annual mean precipitation: 582.1 mm), precipitation or soil moisture, rather than soil temperature, would have major effects on soil microbial community structure (Lin et al., 2016; Ochoa-Hueso et al., 2018). In 2018, Ladau et al. (2018) reported that the prevailing climate warming trend would increase microbial diversity over the following 50 years, and that current microbial diversity is strongly influenced by past climatic conditions and trends (Ladau et al., 2018). Therefore, climate change has a legacy effect on soil microbial community structure. This could be the reason for not witnessing obvious effects of warming on the soil microbial diversity and community structure in the present study.

Table 4

Three-way ANOVA was used to test the effects of treatments, mean annual precipitation, and mean annual temperature on the soil microbial community composition.

	Df	Bacteria		Fungi	
		F	P	F	P
MAP	1	3.46	0.001	2.65	0.001
MAT	1	3.26	0.001	2.7	0.001
Warming	1	1.13	0.203	1.37	0.043
Precipitation	2	2.11	0.001	2.26	0.001
MAP * warming	1	0.91	0.6	0.73	0.949
MAT * warming	1	0.81	0.88	0.73	0.95
MAP * precipitation	2	0.91	0.702	0.75	0.987
MAT * precipitation	2	0.93	0.673	0.74	0.988
Warming * precipitation	2	1.13	0.143	1.19	0.096
MAP * warming * precipitation	2	0.8	0.955	0.83	0.91
MAT * warming * precipitation	2	0.68	1	0.7	0.997

Bold values mean P < 0.05

Table 5
Topological features of microbial networks in treatments (CK: control, DP: decreased precipitation, and IP: increased precipitation) in each year.

Year	Treatment	Node	Edge	Connectance	Transitivity	Average degree	Modularity
2012	CK	497	58,311	0.473	0.558	234.7	0.132
	DP	508	52,116	0.405	0.478	205.2	0.128
	IP	469	50,673	0.462	0.547	216.1	0.124
2013	CK	527	62,526	0.451	0.529	237.3	0.122
	DP	508	58,519	0.454	0.533	230.4	0.134
	IP	504	54,672	0.431	0.499	217	0.12
2015	CK	488	56,218	0.473	0.558	230.4	0.119
	DP	505	54,735	0.43	0.497	216.8	0.122
	IP	487	52,853	0.447	0.525	217.1	0.131

5. Conclusion

In conclusion, our results indicate that altered precipitation and temporal variation could alter soil bacterial and fungal diversity and community structure, with additional impacts on the robustness of co-occurrence relationships among microbes. In particular, interannual

climate variability in the form of MAP and MAT influenced the interannual variations in soil bacterial and fungal community structures considerably. The results of our longitudinal study offer novel insights into the responses of soil microbial communities to climate change.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.136794>.

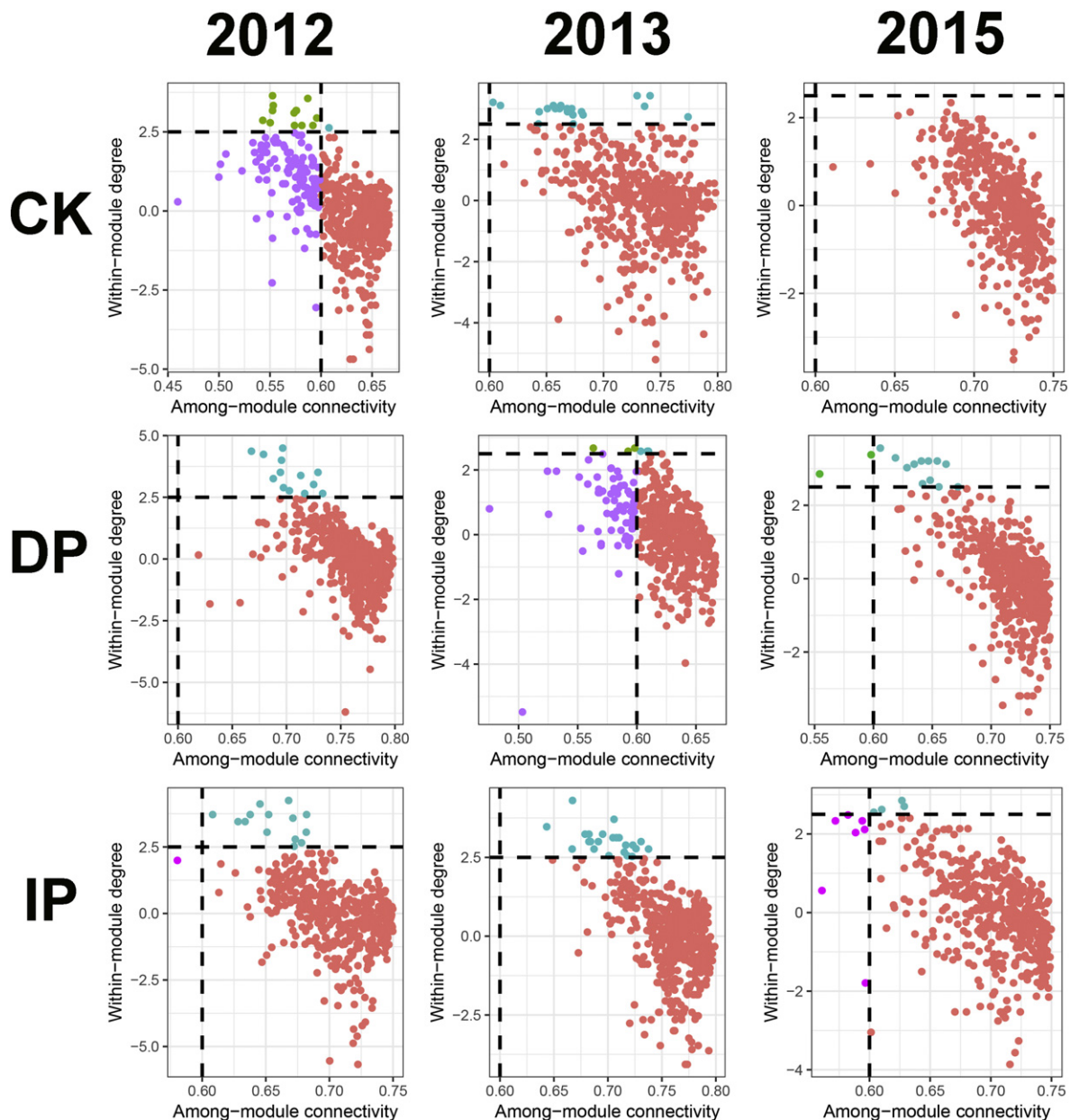


Fig. 3. The co-occurrence network roles of analysing module feature.

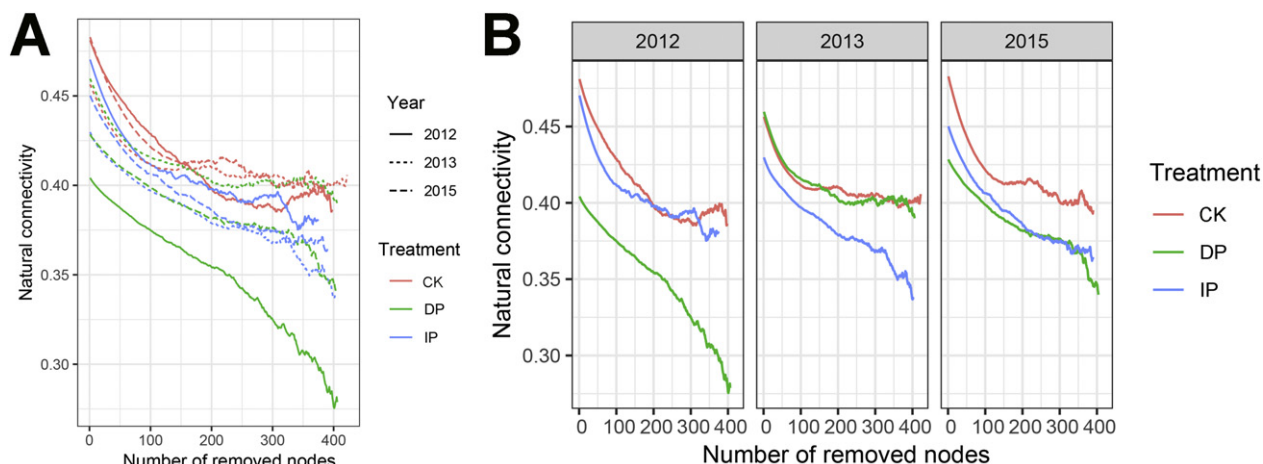


Fig. 4. The natural connectivity of microbial network by treatments and years (A), and by treatments (B) within each year.

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Data statement

Research data is not publicly available. Upon reasonable request, data can be shared by corresponding author Haiyan Chu.

Declaration of competing interest

The authors declare that they have no competing interests.

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