



The structure of bacteria–fungi bipartite networks along elevational gradients in contrasting climates

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Abstract

Climate change is altering species distribution and modifying interactions in microbial communities. Understanding microbial community structure and their interactions is crucial to interpreting ecosystem responses to climate change. Here, we examined the assemblages of stream bacteria and fungi, and the associations between the two groups along elevational gradients in two regions with contrasting precipitation and temperature, that is the Galong and Qilian mountains of the Tibetan Plateau. In the wetter and warmer region, the species richness significantly increased and decreased with elevation for bacteria and fungi, respectively, while were nonsignificant in the drier and colder region. Their bipartite network structure was also different by showing significant increases in connectance and nestedness towards higher elevations only in the wetter and warmer region. In addition, these correlation network structure generally exhibited similar positive association with species richness in the wetter and warmer region and the drier and colder region. In the wetter and warmer region, climatic change along elevation was more important in determining connectance and nestedness, whereas microbial species richness exerted a stronger influence on network structure and robustness in the drier and colder region. These findings indicate substantial forthcoming changes in microbial diversity and network structure in warming climates, especially in wetter and warmer regions on Earth, advancing the understanding of microbial bipartite interactions' response to climate change.

KEYWORDS

association, bacteria and fungi, bipartite networks, connectance, elevation, robustness

1 | INTRODUCTION

Global climate change is one of the most profound anthropogenic disturbances, posing a threat to species persistence and ecosystem functions around the globe (Pereira et al., 2010). Species in natural communities are not isolated but interact with each other in a myriad of ways and form complex ecological networks that shape and maintain the structure of biodiversity and ecological functions (Ho et al., 2022; Thompson et al., 2012). Interaction networks account for both species occurrence and their interactions (Reiss et al., 2009;

Schleuning et al., 2015) and characterize communities comprising multiple trophic levels (Pellissier et al., 2018). Therefore, it is crucial to estimate the climate change effects on biodiversity and ecological networks to understand the shifts in ecosystem functioning under changing climate conditions, such as climate warming (Bardgett et al., 2008). Despite numerous insights have been revealed how climate warming can alter species richness and community composition, little is known about whether and how it impacts the correlation networks in communities (Toju et al., 2017; Yuan et al., 2021). In addition, understanding the response of correlation networks to

critical biotic and abiotic drivers under climate warming remains a relevant and cutting-edge topic for future exploration.

Studying shifts in biological communities and their associations along environmental gradients facilitates our understanding of how community assembly responds to changing climate and environment. Elevation gradients capture compressed and orderly climate variation under which biotic interactions can be evaluated (Chen et al., 2022; McCain, 2009; Morris et al., 2015), providing great opportunities for estimating climate change-driven dynamics (Rasman et al., 2014; Wang et al., 2022). Network analysis has recently been widely applied in microbial ecology to unravel the interplay or co-occurrence patterns along geographic gradients (Ma et al., 2016). For instance, the network complexity of soil bacterial and fungal communities significantly declines along elevational gradients on the Tibetan Plateau (Chen et al., 2022). Moreover, soil fungal connectivity decreases along elevational gradients on Mt. Norikura, Japan, and it is found that climate is the dominant factor regulating the co-occurrence patterns (Yang et al., 2021). For microorganisms, most investigations focussed on one-mode networks to decipher co-occurrence associations within microbial communities, including intraspecific and interspecific associations (Mikhailov et al., 2019). However, few studies have specifically disentangled complex associations between two different microbial groups. Microbial groups exhibit intricate interconnections, with prior research uncovering complicated associations between bacteria and fungi, such as positive associations caused by synergistic interaction (Meidute et al., 2008; Miransari, 2011) and negative associations arising from niche overlap between certain bacterial and fungal groups (Rousk et al., 2008). Although associations between two different microbial groups are arguably essential biological interactions associating virtually every species in ecological cycles (Alric et al., 2020), our knowledge of how correlation networks between different microbial groups respond to the changing climate remains limited.

Bipartite networks provide us with new insights into the interactions between two groups of organisms, and the direct interactions within each group are not considered (Bennett et al., 2018; Dormann et al., 2009). Recently, co-occurrence networks are increasingly used to generate bipartite networks between microbial taxonomic groups such as fungi and prokaryotes (Zhou et al., 2021), and between microbial communities and dissolved organic matter (Hu et al., 2022). With the co-occurrence network approach, structure properties, such as nestedness, modularity and connectance, could be quantified (Dormann et al., 2009). Recent studies suggest that the variation in the bipartite network structure along environmental gradients is strongly related to species richness (Grass et al., 2018; Ho et al., 2022; Martín González et al., 2015). Ecological bipartite networks generally show a nested or a modular structure (Fortuna et al., 2010; Kondoh et al., 2010). In strongly nested networks, specialist species tend to interact with subsets of the species that interact with more generalist species (Bascompte et al., 2003). There is an expectation of increased correlation network nestedness due to the preferential attachment of rare species interacting with abundant generalists (Bascompte et al., 2006). In highly modular networks,

species within a module tend to exhibit strong interactions, whereas inter-module interactions remain weak (Fortuna et al., 2010; Olesen et al., 2007). For instance, the modularity can increase with a higher number of interacting species in plant-pollinator networks (Olesen et al., 2007). Lower species richness may decrease specialization at a network level (Martín González et al., 2015), and then result in a greater degree of connectance (Plowman et al., 2017). In addition, species richness and such network structure can all affect the robustness of bipartite networks towards species losses because they mediate how species respond to extinctions (Bellay et al., 2020; Grass et al., 2018). Higher species richness and modularity may enhance or destabilize network robustness (Fornoff et al., 2019; Martín González et al., 2015; Neff et al., 2021; Thebault & Fontaine, 2010). Ecological networks with high connectance and nestedness tend to be more robust (Neff et al., 2021; Vanbergen et al., 2017) by delaying the sensitivity to species loss (Dunne et al., 2002) or minimizing competition (Bastolla et al., 2009). However, the bipartite networks for microbes remain understudied, and it is unclear whether the microbial bipartite network structure responds similarly to microbial species richness.

The ongoing climate change will increase global temperatures and create more variable precipitation patterns in most regions (IPCC, 2023). As temperature and precipitation levels fluctuate, the corresponding changes are not only reflected in the microbial communities and their interactions within a single group (de Vries et al., 2018; Pescador et al., 2022) but also have the potential to reorganize correlation networks of interactions between co-existing microbial taxa (Zhou et al., 2011). For instance, simulated warming induces variation in the hierarchical bipartite network structure of soil microbial groups, and result in common response of microbial taxa to similar environmental variables (Zhou et al., 2021). Freshwater ecosystems are likely to be among the most vulnerable systems to climatic change, providing an important model system for studying the responses and feedback mechanisms of microbial communities to climate warming (Wiens, 2016). Changes in precipitation and temperature can trigger substantial physical disturbance in stream ecosystems, giving rise to fluvial floods or hydrological droughts, as well as increased water temperature or nutrient concentrations, ultimately disturbing aquatic biota and their biotic interactions (Sabater & Tockner, 2010; Stevenson & Sabater, 2010). Ecological constraints can shape distinctive correlation networks in diverse climates or environments (Ho et al., 2022; Neff et al., 2021), and it is thus important to study how aquatic microbial biodiversity and correlation network structure respond to environmental gradients in contrasting climatic conditions.

Here, we compared the elevational patterns of species richness and bipartite network structure for stream biofilm bacteria and fungi in two different climates. The two regions are located in the southeast (Galongla Mountain) and northeast (Qilian Mountains) of the Tibetan Plateau, and are characterized by contrasting climates, that is wetter and warmer climate, and drier and colder climate, respectively. We further investigated the relationships of microbial diversity to their bipartite network structure and robustness, and

assessed the main drivers of network structure and robustness in the two regions. We aimed to address three questions: (1) How do microbial species richness and their bipartite network structure vary along elevational gradients in the contrasting climatic conditions described above? (2) How is microbial network structure related with their species richness in two contrasting climatic conditions? (3) How do elevation, environmental variables and species richness jointly influence microbial network structure in the two mountains?

2 | MATERIALS AND METHODS

2.1 | Study area and field sampling

We sampled stream water and biofilm along elevational gradients on Galongla (MT) Mountain in July 2018, and on Qilian (QL) Mountain in September 2018, both situated in eastern Tibetan Plateau, China (Figure S1). In Galongla Mountain, 86 representing independent small streams were sampled (29°23′–30°03′ N, 92°19′–96°20′ E), while 79 sites along three larger stony streams were collected on Qilian Mountain (38°10′–39°56′ N, 97°57′–100°44′ E). The two regions have significantly contrasting climates. The climate on Galongla Mountains is wetter and warmer, with mean annual precipitation ranging among sites from 289 to 2412 mm (mean 897 mm) and mean annual temperatures varying from –0.7 to 20.1°C (mean 9.3°C). In Qilian Mountain, the climate is drier and colder, with mean annual precipitation of 100–364 mm (mean 232 mm), and mean annual temperatures of –6.1 to 7.4°C (mean 2.4°C). We chose this sampling design because smaller streams are dry and cannot be sampled in Qilian Mountain. Due to simplicity, the Galongla Mountain is referred to as the ‘wetter and warmer’ region and the Qilian Mountain as the ‘drier and colder’ region throughout the remaining of this chapter.

Tibetan Plateau is one of the world's biodiversity hotspots, where the vegetation distribution is sensitive to climate. In the Galongla Mountain, a full range of vegetation types is distributed along the elevational gradient. The vegetation varies from tropical monsoon rain forest, subtropical evergreen broadleaved forests, subtropical evergreen and semi-evergreen broadleaved forests, frigid-temperate coniferous forests to frigid shrub meadows with increasing elevation (Hu et al., 2020). However, Qilian Mountain presents a unique shift in vegetation, transitioning from scattered xerophytic plants in gobi-sand desert zone, desert steppe, alpine steppe, alpine shrub and finally alpine meadow along the elevational gradient (Zhao et al., 2017).

We followed the same protocols for sampling as shown in the previous literature (Wang et al., 2011). Briefly, we divided each sampling site into five or 10 cross sections, depending on the stream width. Ten stones were randomly selected from riffle or run habitats along these sections. Biofilm on stones was scraped for subsamples from a predefined area of 9 cm² using a sterilized sponge (for bacteria and fungi). At each site, the subsamples were combined into a composite sample, and then were frozen at –18°C immediately after

the sampling. Water samples were also preserved at –18°C until the chemical analyses in the laboratory. We obtained a total of 165 composite biofilms samples and 165 water samples along elevational gradients on the two mountains.

2.2 | Physicochemical variables

Several environmental variables of streams were measured in situ. The longitude, latitude and elevation were recorded using a portable GPS device. Water temperature, conductivity, pH and shading (% canopy cover) were measured at each site. Stream depth, width and current velocity were measured at 10 random locations along the transects. Ten stones submerged in water were randomly collected, and their stone length (*L*), width (*W*) and height (*H*) were measured to estimated stone size using the formula: $\log_{10}(L \times W \times H)$. The exposure of collected stones to sunlight varied depending on whether they were found in shady or sunny locations. Stone size ranged from 2.68 to 3.73 cm³_{log₁₀} in the wetter and warmer region (mean 3.20_{log₁₀} cm³), and from 2.91 to 4.34 cm³_{log₁₀} in the drier and colder region (mean 3.67 cm³_{log₁₀}).

We measured total phosphorus by ammonium molybdate spectrophotometric method and total nitrogen was assessed using alkaline potassium persulfate oxidation-UV spectrophotometric method. Nitrogen oxides (NO_x[–] – N), nitrite (NO₂[–] – N), ammonium (NH₄⁺ – N) and phosphate (PO₄^{3–} – P) were measured using a continuous flow analyzer (Skalar SA 1000, Breda, The Netherlands).

2.3 | Bacterial and fungal communities

Bacterial and fungal analyses were performed following previous studies (Wang et al., 2017). We extracted genomic DNA from biofilm using the MoBio PowerSoil DNA Isolation Kit (MoBio, Carlsbad, USA). For bacteria, 16S rRNA genes were amplified in triplicate using universal primers [515F, 5′-GTGCCAGCMGCCGCGGTAA-3′ and 806R, 5′-GGACTACHVGGGTWTCTAAT-3′] targeting the V4 hypervariable region (Peiffer et al., 2013). An amplicon of fungal ITS2 region was targeted using the primers: gITS7F, 5′-GTGARTCATCGARTCTTTG-3′ and ITS4R, 5′-TCCTCCGCTTATTGATATGC-3′ (Ihrmark et al., 2012). The polymerase chain reaction (PCR) amplification were performed using 1 μL of Phanta Max Super-Fidelity DNA Polymerase (Vazyme), 25 μL of 2× Phanta Max Buffer, 1 μL of dNTP Mix (10 μM each), 2 μL of forward primer, 2 μL of reverse primer, 1 μL of template DNA (20–30 ng/μL), and ddH₂O (fill the system to 50 μL). The thermal cycle conditions for bacterial 16S rRNA gene were as follows: 95°C for 3 min, 30 cycles of 95°C for 10s, 60°C for 10s, 72°C for 45s and a final extension at 72°C for 5 min. Fungal thermal cycle conditions were as follows: 95°C for 3 min, 35 cycles of 95°C for 10s, 52°C for 10s, 72°C for 45s and a final extension at 72°C for 5 min. We normalized the PCR products from triplicate reactions at equal molality and then sequenced them through the Miseq PE300/NovaSeq PE250 (Illumina, USA)

(Caporaso et al., 2011, 2012). Negative controls were included for all DNA extraction and PCRs throughout the experiment.

The sequence processing was achieved in QIIME v1.9.1 (Caporaso, Kuczynski, et al., 2010). In brief, we merged paired-end reads using FLASH (V1.2.72) (Magoč & Salzberg, 2011), and cleaned these sequences in vsearch 2.7.1 (Rognes et al., 2016). Sequences were demultiplexed using MID tags and primers, and then quality filtering on the raw tags was performed to remove any mismatch to MID tags of primers. We utilized UCHIME against ChimeraSlayer reference database in the Broad Microbiome Utilities to removed Chimeras (Haas et al., 2011). The forward and reverse sequences were combined and clustered to operational taxonomic units (OTUs) at 97% similarity using the seed-based UCLUST algorithm (Edgar, 2010). Representative sequences from each OTU were aligned to the Greengenes imputed core reference alignment (DeSantis et al., 2006) using PyNAST (Caporaso, Bittinger, et al., 2010), and further was identified taxonomically using the RDP classifier (Wang et al., 2007). For bacteria, chloroplast and archaeal sequences were finally removed. Fungal sequences were taxonomically identified by BLASTN queries against the UNITE database version 8.0 (Nilsson et al., 2019).

To avoid the effects of variations in abundance or sampling intensity on empirical biodiversity, the bacterial and fungal sequences were rarefied at 61,000 and 33,100 sequences, respectively (Figure S2).

2.4 | Bipartite network construction

To study the potential association between bacteria and fungi, we constructed bipartite networks with co-occurrence network analysis. In bacteria–fungi networks, bacterial species are only connected to fungal species, the direct associations within bacteria or fungi are not explicitly considered. The correlation network is inferred by the absolute value of positive and negative coefficients from correlations analyses. Positive associations could represent main cooperative behaviours, such as syntrophic and mutualistic interactions (Meidute et al., 2008; Miransari, 2011). Negative associations likely indicate most competition for limiting resources and niche overlap (Berry & Widder, 2014; Rousk et al., 2008). First, bacterial and fungal OTUs were merged into a single table, retaining only those that occurred in more than half of the samples to minimize errors in the correlation calculations. Second, the pairwise correlation of bacteria and fungi was calculated based on Sparse Correlations for Compositional data method (Friedman & Alm, 2012). To exclude weak associations, we applied a threshold value of $|\rho|=0.30$ in bipartite networks and obtained their absolute values. These values were then multiplied by 10,000 and rounded to integers. Finally, a separate sub-network was calculated for each sample by choosing bacterial and fungal OTUs in each sample based on community compositions.

For each network, we calculated five metrics to measure network structure and robustness: (i) Connectance was estimated by determining the realized proportion of potential links (Tylianakis

et al., 2007); (ii) nestedness was assessed using the “weighted NODF” index, which ranges from not nested (0) to perfectly nested (100) (Almeida-Neto & Ulrich, 2011); (iii) modularity was calculated using the Beckett algorithm, reflecting the tendency of a network to form modules (Beckett, 2016); and (iv) robustness was assessed by the secondary extinction curve approach (Memmott et al., 2004). In this study, robustness measures the extent of extinction in the remaining group following extinctions of randomly selected species at both levels. (v) specialization was quantified using the standardized Shannon index H'_2 , which takes into account the interaction frequency and strength between the two network parties (Bluthgen et al., 2006). Higher H'_2 values suggest greater specialization, while lower values imply a high level of generalization.

We employed a null modelling approach (Grass et al., 2018; Thebault & Fontaine, 2010) to directly compare these correlation network metrics across elevation. The five network metrics were standardized by computing their z-scores (Dormann & Strauss, 2014):

$$Z_s = (s_{\text{observed}} - \overline{s_{\text{null}}}) / \sigma_{s_{\text{null}}}$$

where $\overline{s_{\text{null}}}$ and $\sigma_{s_{\text{null}}}$ were the mean and standard deviation of the null distribution of s (s_{null}), respectively. For each network, we generated 100 randomized null networks (s_{null}) using the *swap.web* algorithm. These network metrics were computed using bipartite package in R (Dormann et al., 2009).

2.5 | Statistical analyses

To investigate the elevational species richness patterns, we applied linear and quadratic models, selecting the model with a better goodness of fit using the lower value of Akaike information criterion (AIC) (Yamaoka et al., 1978). This analysis was performed using the R package stats V 4.2.2.

To explore the associations between bacterial and fungal communities, we used Procrustes analysis based on NMDS coordinates for each community (Gower, 1975; Hurley & Cattell, 1962). The significance was evaluated through 999 permutations (Peres-Neto & Jackson, 2001). This analysis was performed using vegan V2.6-4 package in R (Dixon, 2003).

For bacteria–fungi associations, we further used linear and quadratic models to examine the relationships between four network metrics and elevation. The better model was selected based on the lower value of AIC (Yamaoka et al., 1978). We compared the significant differences of these network metrics between the two regions using Wilcoxon signed-rank test (Woolson, 2007). This analysis was performed using the R package rstatix V 0.7.2.

We tested the relationships of bacterial and fungal richness with the four network metrics using linear or quadratic models, which was selected based on the lower value of AIC (Yamaoka et al., 1978).

We finally used structural equation models (SEM) to assess the direct and indirect effects of elevation, environmental variables and species richness on network structure and robustness (Grace

et al., 2012). The hypothesized underlying structure of causal links was established based on the literature (Grass et al., 2018; Morrison et al., 2020; Ren et al., 2023) and is shown in Supplementary information (Figure S11). We used z-score transformation for all predictors before modelling. A composite variable, representing the combined effect of other environmental variables, was used (Grace et al., 2016) and is presented in Table S1. The model is translated into regression equations and all the hypothesized links were examined with AIC and overall model fit statistics (Grace et al., 2010). The final model was selected based on the lowest AIC value among models with a non-significant χ^2 test ($p > .05$), low standardized root mean squared residual (< 0.05) and high comparative fit index (> 0.95) (Tables S2 and S3). SEMs were performed with lavaan V.0.6-15 package in R (Rosseel, 2012).

3 | RESULTS

After filtering of sequences, a total 5,191,927 and 4,758,562 reads were obtained from pyrosequencing for bacteria in the wetter and warmer region and the drier and colder region, respectively. For fungi, 2,834,809 and 2,612,648 reads were retained in the contrasting regions. Altogether, 117,827 bacterial OTUs and 29,901 fungal OTUs were analysed in the wetter and warmer region, while 115,576 bacterial OTUs and 12,044 fungal OTUs were studied from the drier and colder region.

Bacterial and fungal richness increased and decreased significantly along elevational gradients in the wetter and warmer region, respectively, while they did not vary significantly with elevation in the drier and colder region ($p < .01$; Figure 1a,b). Notably, fungal richness was higher in the wetter and warmer region than in the drier and colder region ($p < .01$, Figure S3), but such the pattern was not found for bacteria. In the wetter and warmer region, bacterial and fungal richness were highly correlated with elevation and water temperature ($p < .001$, Figure 2). In addition, bacterial and fungal richness showed negative and positive correlations with water speed, $\text{NO}_2^- - \text{N}$, $\text{PO}_4^{3-} - \text{P}$ and $\text{NH}_4^+ - \text{N}$ content, respectively ($p < .01$). However, in the drier and colder region, bacterial richness had significantly negative correlations with shading, TN, $\text{PO}_4^{3-} - \text{P}$ and $\text{NH}_4^+ - \text{N}$ content ($p < .01$, Figure 2). $\text{NH}_4^+ - \text{N}$ content and electrical conductivity were negatively correlated with fungal richness.

For bacterial and fungal communities, the Bray–Curtis dissimilarity across the whole elevational gradient significantly increased with elevational distances in both regions (Figure S4, $p < .001$). These community dissimilarities also significantly increased with spatial distance in each region (Figure S5, $p < .001$). These results suggest that bacterial and fungal communities are spatially structured. Furthermore, bacterial community was strongly associated with fungal community according to Procrustes analysis in both regions ($p = .001$; Figure 1c,d). Compositional differences (M^2) between bacteria and fungi were similar in the wetter and warmer region ($M^2 = 0.47$) and the drier and colder region ($M^2 = 0.54$, Figure S6). There were striking effects of elevation to their association, for instance, compositional

differences between bacteria and fungi showed U-shaped patterns with increasing elevation ($p < .01$, Figure S6).

Network structure and robustness of bacteria–fungi bipartite networks varied significantly in the two regions (Figure 3). The connectance and nestedness both increased significantly along elevational gradients in the wetter and warmer region ($p < .001$), while they showed no such pattern in the drier and colder region ($p = .43$ and $.31$). Modularity and robustness were not, or only very weakly, associated with elevation in the two regions. In the wetter and warmer region, network modularity was significantly higher and robustness lower than in the drier and colder region ($p < .001$; Figure 3c,d).

Bacterial richness was positively correlated with the connectance and nestedness in both regions, except for the relationship between bacterial richness and connectance in the wetter and warmer region ($p < .01$; Figure 4a,b,e,f). Fungal richness was negatively correlated with connectance and nestedness in the wetter and warmer region, respectively, but strongly positive correlations were observed in the drier and colder region. In the two regions, connectance and nestedness generally showed positive relationships with the whole microbial richness (Figure S7). Similarly, the modularity was positively correlated with bacterial and fungal richness in both regions ($p < .01$). However, network robustness only decreased significantly with bacterial richness in the drier and colder region, and it was unrelated to fungal richness in both regions.

The SEM models showed that elevation and other environmental variables affected species richness in bacteria–fungi networks, leading to cascading effects on network structure and eventual robustness (Figure 5). For species richness, elevation had significant positive and negative direct effects on bacterial and fungal richness in the wetter and warmer region, respectively, but had no or weak direct effects on them in the drier and colder region. In turn, other environmental variables were the main determinants of bacterial richness in the drier and colder region. In the contrasting climatic conditions, we found that elevation, the richness of bacteria and fungi showed different effects on bacteria–fungi network structure and robustness. For connectance and nestedness, elevation was the dominant driver for connectance and nestedness in the wetter and warmer region, with total mean effects of 0.46 and 0.47, respectively (Figure 5; Figure S12). In the drier and colder region, however, fungal richness had even larger effect size on connectance and nestedness than elevation (Figure 5; Figure S12). Fungal richness showed direct effects on connectance, and mainly had indirect influence on nestedness via the interaction with connectance. In contrast, fungal and bacterial richness were the main determinants of network modularity in the two regions, respectively, with mean standardized effect sizes of 0.66 and 0.84 (Figures 4 and 5). Elevation mainly had indirect influence on modularity via fungal richness and connectance in the wetter and warmer region, while there was only a weak negative direct effect of elevation on modularity in the drier and colder region (Figure 5). For robustness, only other environmental variables had a positive direct effect in the wetter and warmer region, whereas bacterial and fungal richness showed strongly negative and positive

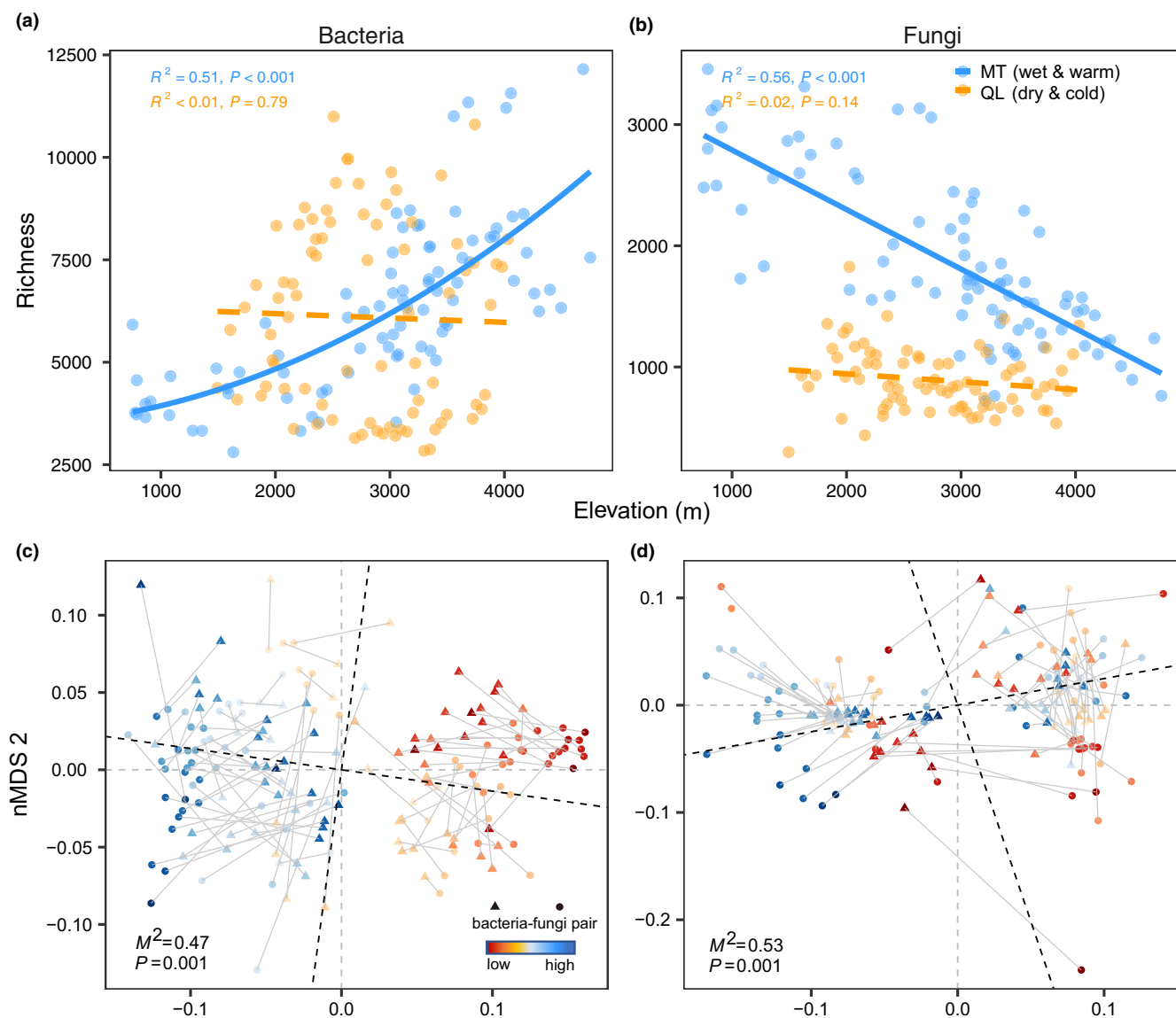


FIGURE 1 Species richness of stream bacteria and fungi and their associations along elevational gradients. The upper panels show elevational species richness patterns for bacteria (a) and fungi (b) in the wetter and warmer region (blue lines) and the drier and colder (yellow lines) region. The trends with elevations were modelled with both linear and quadratic models. The better model was selected based on the lower value of Akaike's information criterion. Statistically significant trends of models are shown as solid lines, while dotted lines indicate non-significant relationships. The lower panels illustrate the congruence between bacterial and fungal compositions along elevational gradients in the wetter and warmer (c) and drier and colder (d) regions using Procrustes analysis. The NMDS plots the position of bacterial and fungal communities that have been optimized based on Procrustes analysis. Each line with circle and triangle ends connects to a single community of bacteria and fungi, respectively, and circle and triangle ends are coloured by elevation (blue and red ends, with lower elevations in more red colours and higher elevations in more blue colours) in the two regions. The significance was assessed using a permutation-based approach with 999 permutations. M^2 , the sum of squared distances between matched data points after the transformation. [Colour figure can be viewed at wileyonlinelibrary.com]

direct effects of -0.32 and 0.26 in the drier and colder region, respectively.

4 | DISCUSSION

Understanding how climate warming affects microbes and their correlation networks is a critical issue in climate change research. To the best of our knowledge, this is the first study to reveal

relationships of bacteria–fungi bipartite network structure to elevation and species richness in microbes. We investigated the variation in microbial biodiversity and their bipartite network structure corresponding to changes in elevation in two regions with comparatively contrasting climates. Specifically, bacterial and fungal richness, their network connectance and modularity varied significantly along elevational gradients only in the wetter and warmer region, but such the pattern was not found in the drier and colder region. In the wetter and warmer region, climate could alter

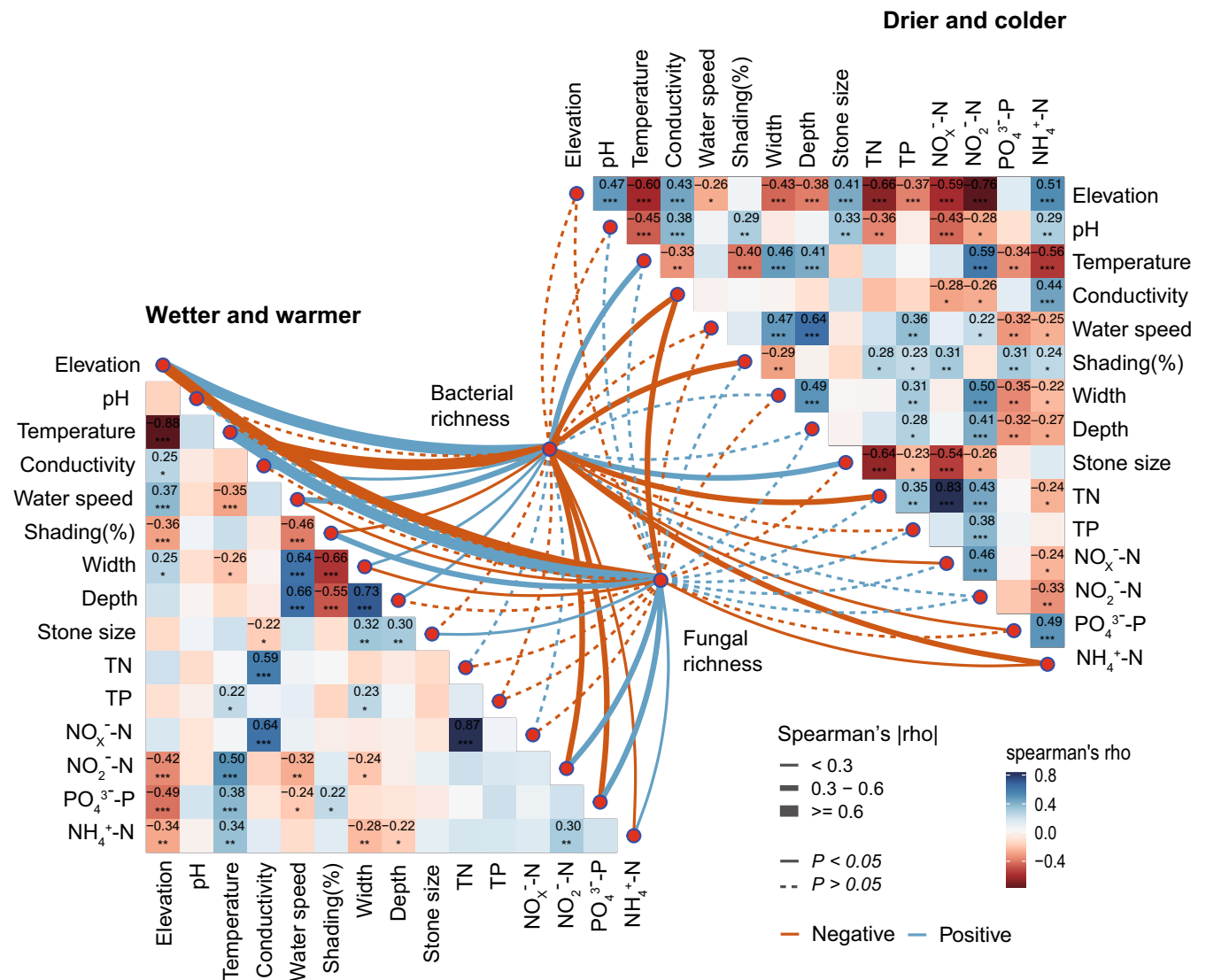


FIGURE 2 Correlations between environmental variables and microbial species richness. Edge width corresponds to the absolute value of the Spearman's correlation coefficient between microbial species richness and environmental variables. Different colours indicate correlation types. Solid and dotted lines represent significant and non-significant correlations, respectively. Pairwise comparisons of environmental factors are shown in the triangle, with a colour gradient denoting Spearman's correlation coefficient. *, $p < .05$; **, $p < .01$; ***, $p < .001$. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/mec.17442)]

network structure through changes in the number of interacting microbial species, whereas the cascading effects was weaker in the drier and colder region. In comparison with the wetter and warmer region, microbial species richness was more important in explaining network structure and robustness than elevation in the drier and colder region.

4.1 | Differences in microbial diversity along elevational gradients in contrasting climates

Our results revealed the significantly increased and decreased elevational patterns for bacterial and fungal richness in the wetter and warmer region, respectively. The elevation gradient is often used as a proxy of potential responses to climate change in ecological

research (Frei et al., 2014), and temperature was correlated strongly and negatively with elevation in our study (Figure 2). The contrasting patterns reveal that microbial richness is not solely driven by temperature, but by some local environmental factors (Wang et al., 2011). For fungi, the decreasing elevational diversity pattern indicates the temperature dependency of microbial diversity, which could be primarily explained by the metabolic theory of ecology (Wang et al., 2022; Zhou et al., 2016). Moreover, the geographic range trend of increasing generalist species (i.e. species that have larger range sizes) with increasing elevation is also thought to underlie decreasing elevational diversity patterns (Grytnes & McCain, 2007; McCain & Bracy Knight, 2013; Stevens, 1992). For bacteria, the increasing elevational richness pattern is in line with previous studies across alpine stream ecosystems in China and Spain (Wang et al., 2017). This could be explained by two mechanisms, that is temperature variation and

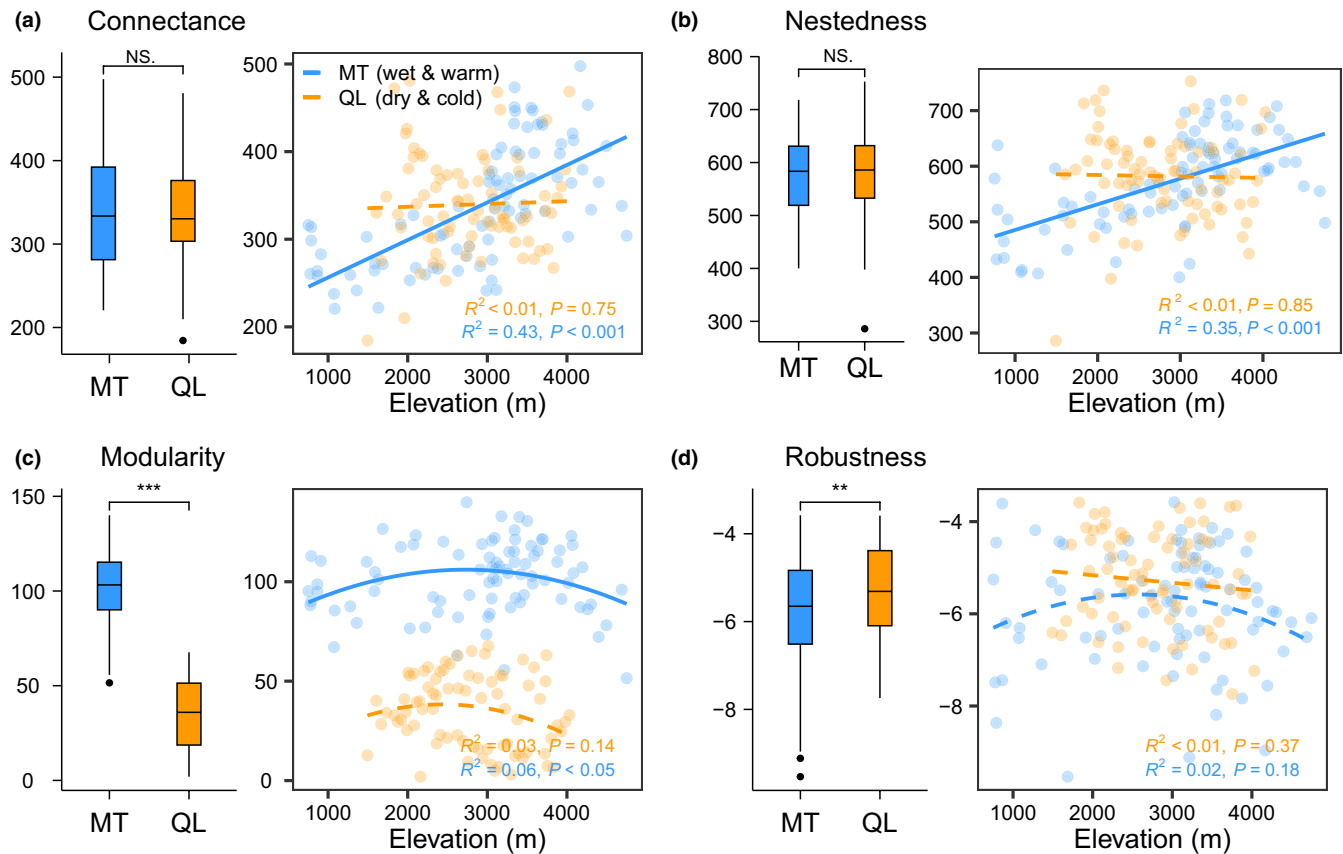


FIGURE 3 The structure and robustness of bacteria-fungi bipartite networks and their elevational patterns. These network indices are connectance (a), nestedness (b), modularity (c) and robustness (d). The boxes represent the 25th and 75th percentiles, the whiskers range from minimum to maximum values, and outliers are represented by dots. Statistical analysis used nonparametric Wilcoxon signed-rank paired test to compare the difference of network structure between the two regions (** $P < .001$, ** $P < .01$, NS, non-significant). The patterns along elevations were modelled with linear and quadratic models. The better model was selected based on the lower value of Akaike's information criterion. Statistically significant trends of models are shown as solid lines, while dotted lines indicate non-significant relationships. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/mec.17442)]

current abiotic conditions. Large temperature variation at high elevations may widen bacterial niches, and the increase of carbon supply with elevation may provide more energy to bacterial population growth, thereby promoting their richness (Adams et al., 2010; Wang et al., 2011). In streams systems, the stream flow speed or width both vary with elevation, and constrain the species existence (Ho et al., 2022; Kaelin & Altermatt, 2016). Bacterial richness was negatively related to water speed or width of the stream, while the positive relationship was observed for fungal richness (Figure 2), which may result in contrasting elevational patterns of species richness. Overall, the elevational species richness patterns likely reflect the effects of different underlying mechanisms for bacteria and fungi.

However, in the drier and colder region, the relationships between species richness and elevation were not statistically significant for bacteria and fungi. We found that total nitrogen and ammonium were the main environmental drivers of their species richness (Figure 2; Figure S10). The low precipitation level can lead to a decline in water level and increased nutrient levels of aquatic ecosystems in arid climates, which forces microbes to shift resource allocation and alter ecosystem function (Harris, 1981, Schimel

et al., 2007). In the drier and colder region, the elevational changes in microbial richness may be limited by other environmental factors or other biotic communities. For instance, the fauna and flora surrounding aquatic habitats may influence microbial communities (Wang et al., 2022). Unfortunately, we did not explore the variation in fauna and flora around aquatic habitats due to limitations in sampling resources. We encouraged future studies to incorporate these important variables for better explaining the observed patterns in microbial biodiversity.

Furthermore, fungal but not bacterial communities were generally more species rich in the wetter and warmer region than those in the drier and colder region. This result may suggest that fungal communities exhibit higher variability than bacterial communities across space (Kivlin & Hawkes, 2020). The divergence in temperature and water levels between the two regions may partially account for the higher fungal diversity in the wetter and warmer region. Organisms tend to have more active individual metabolic processes and a higher growth rate at higher temperature (Brown et al., 2004). Additionally, high water levels, often associated with high water flow speeds, may positively affect microbial diversity (de Oliveira & Margis, 2015).

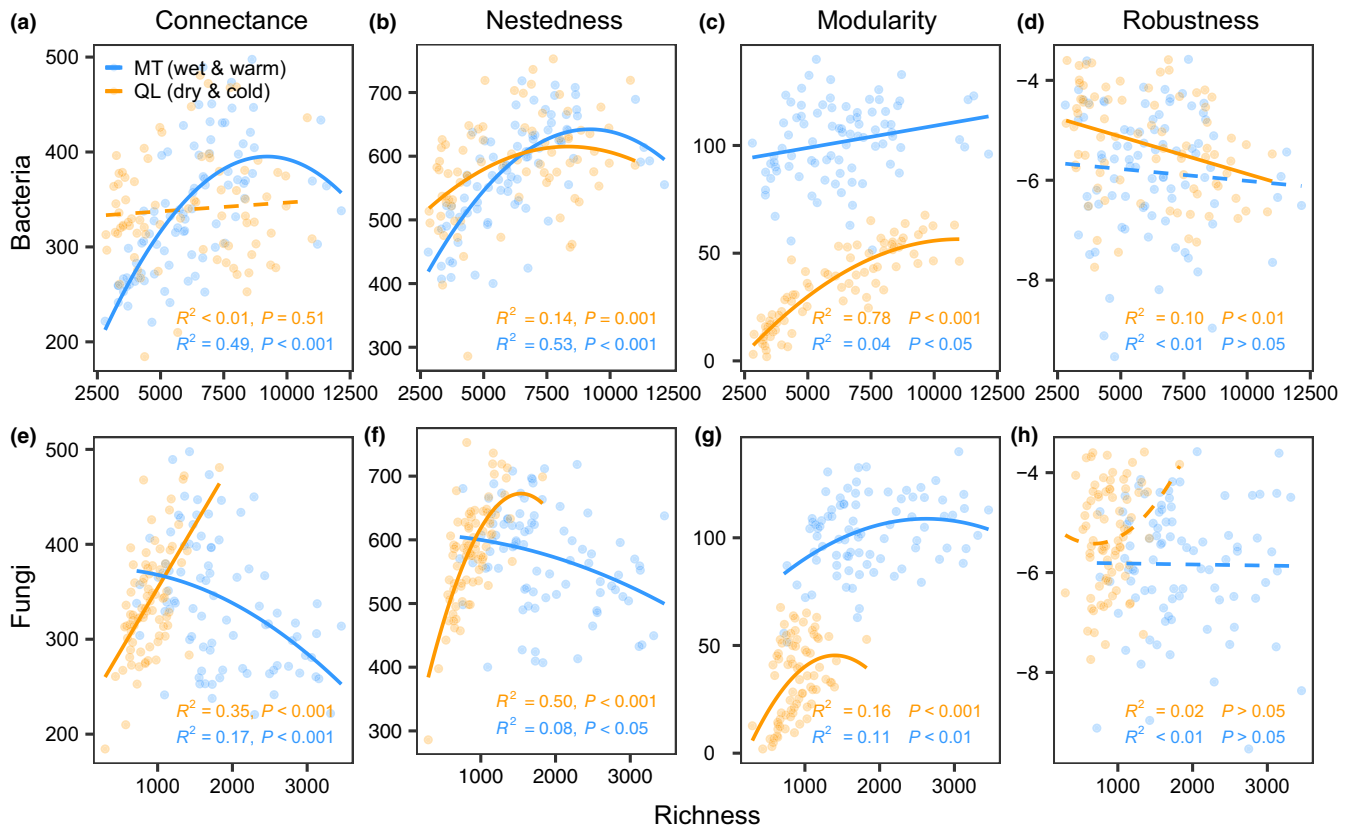


FIGURE 4 The associations of species richness with structure and robustness of bacteria-fungi bipartite networks. These network indices are connectance (a, e), nestedness (b, f), modularity (c, g) and robustness (d, h). The relationships were modelled with both linear and quadratic models. The better model was selected based on the lower value of Akaike's information criterion. Statistically significant trends of models are shown as solid lines, while dotted lines indicate non-significant relationships. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

4.2 | Differences in network structure and robustness along elevational gradients in contrasting climates

In addition to biodiversity, we also found distinct increases in network connectance and nestedness with increasing elevation in the wetter and warmer region, but not in the drier and colder region. The results suggest that bacteria-fungi networks change differently in their structure along elevation in contrasting climates. Connectance, representing the ratio of realized interaction out of all possible pairwise links, may vary due to environmental filtering or changes in how species interact (Pellissier et al., 2018), thereby influencing resistance to species loss (Dunne et al., 2002). In the wetter and warmer region, higher network connectance observed at higher elevations implies that ecological networks at high elevations may be less sensitive to secondary extinctions due to the increased probability of remaining partners per species (Dunne et al., 2002; Gilbert, 2009). Our result is in line with recent findings that higher temperature tend to decrease the connectance in stream food webs (O'Gorman et al., 2019). It is typically thought that the shifts in the prevalence of generalists or specialists can drive changes in correlation network structure (Brodie et al., 2014). In our study, network specialization, indicated by H'_2 , decreased along elevational gradients (Figure S8).

Decreased specialization at a network level may limit partner choice, thereby increasing the degree of connectance (Blüthgen et al., 2007; Plowman et al., 2017). However, this contrasts with the prior findings that revealed a prevalence of generalists in aquatic food webs with increasing temperatures (Barbosa & Siqueira, 2023). Higher nestedness is also associated with a increased climatic variability (Song et al., 2017), and the magnitude of which increases with elevation (Janzen, 1967; Stevens, 1992). Network nestedness theoretically expands the range of environmental conditions compatible with species coexistence (Rohr et al., 2014; Saavedra et al., 2016). Bacteria and fungi are efficient dispersers with high population densities, and demonstrate adaptability to varying climatic and environmental conditions with elevation (Fenchel & Finlay, 2004). Therefore, their distributions along elevations are anticipated to be affected by their physiological tolerances and preferences in relation to elevational temperature variation (Wang et al., 2022; Zhou et al., 2016). In the wetter and warmer region, the elevational patterns of network structure likely reflect the effect of climatic change with elevation on species distribution and community compositions.

However, in the drier and colder region, we found no effects of elevation on the connectance and nestedness of bacteria-fungi networks. This might correlate with our results that there was no significant relationship between network specialization and elevation

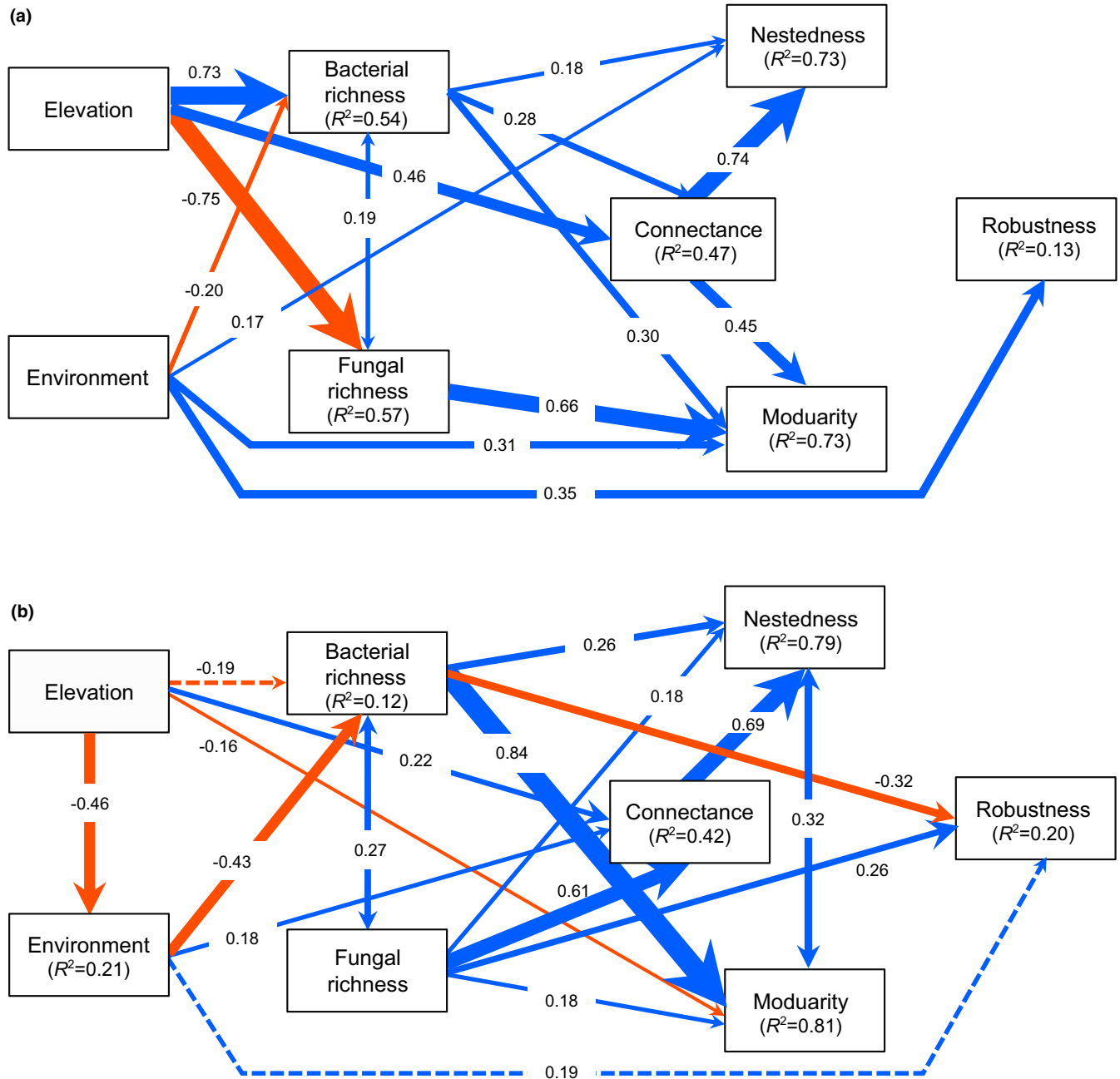


FIGURE 5 Structural equation models (SEMs) of the effects of elevation, other environmental variables, and species richness on the structure and robustness of bacteria-fungi bipartite networks. Best-fitting models illustrate the effects of predictor variables on bacteria-fungi hierarchical interactions in the wetter and warmer region (a) and the drier and colder (b) region, respectively. Squares represent measured variables and arrows represent the direction of hypothesized causal relationships among variables. Values along numbered paths are standardized partial regression coefficients. The width of each arrow is scaled to the absolute value of the standardized path coefficient. Positive paths in blue, negative in red, significant as solid, marginal-significant as dashed. R^2 denotes the proportion of variance explained for endogenous variables. All hypothesized pathways including in the SEMs before model simplification are shown in Figure S11. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

(Figure S8). The dilution of partners and potential resources of each species in the local biodiversity may provide a patchy environment, and lead to the absence of higher specialization at lower elevations (Dore et al., 2021). In addition, we found no discernible effect of elevation on modularity and robustness in either region, which is consistent with previous macroecological studies of plant-pollinator networks (Miller-Struttman & Galen, 2014; Ramos-Jiliberto

et al., 2010). The invariable modularity and robustness reflect the consistent resistance of communities to the harmful disturbances along elevational gradients, which is critical in the harsh environments associated with high elevations (Liu et al., 2021). Ecological networks exhibiting high levels of flexibility tend to be relatively robust to changing environmental conditions (Grass et al., 2018). For instance, species in ecological networks show high potential for

adaptive switches to persisting partners (Grass et al., 2018; Kaiser-Bunbury et al., 2010) and low sensitivity to the loss of their interaction partners (Schleuning et al., 2016). Overall, our findings suggest different elevation-dependent strategies for bacterial and fungal communities in contrasting climates. Climatic changes with elevation are likely to have a stronger impact on microbial bipartite networks and community compositions in the wetter and warmer region compared to the drier and colder region.

The structure and robustness of bacteria–fungi networks varied significantly in contrasting climates. In the wetter and warmer region, the relatively high modularity was detected, which reflects clearer delimited or more specialized bacteria–fungi pairs within communities (Olesen et al., 2007). However, the relatively low network specialization was observed in the wetter and warmer region (Figure S8). It is important to note that high modularity does not, per se, entail specialization (Trøjelsgaard et al., 2013). Thus, the stronger modular structure in the wetter and warmer region might only suggest clearer delimitation of species within communities, that is, species interacts more frequently with subsets of available species within a community. Furthermore, modularity of ecological networks tends to prevail in regions with high precipitation (Dupont et al., 2009; Fortuna et al., 2010; Olesen et al., 2007; Trøjelsgaard et al., 2013). For instance, the relatively high modularity in hummingbird–plant networks have been observed in areas of high precipitation across the America (Martín González et al., 2015). In contrast, we observed more robust correlation network in the drier and colder region than in the wetter and warmer region, suggesting a relatively high tolerance of communities to species extinctions in the drier and colder region (Dunne et al., 2002). Higher modularity may initially buffer the perturbations across environments and provide higher network resilience, but it ultimately leads to community fragmentation and rapid species loss (Martín González et al., 2015; Stouffer & Bascompte, 2011; Thebault & Fontaine, 2010). High modularity can also increase the likelihood of secondary extinctions by reducing functional redundancy of individual species (Dalsgaard et al., 2013; Tylianakis et al., 2010).

4.3 | The relationships of microbial species richness to network structure and robustness

Species richness strongly influenced bacteria–fungi network structure. Higher bacterial and fungal richness generally promoted interaction connectance, nestedness and modularity in both regions. Increasing species richness in ecological networks can exponentially increase the number of potential links, leading to higher connectance (Kay & Schemske, 2004). Bacteria–fungi networks generally had fewer specialized interaction with increasing species richness (Figure S9). Species-rich communities may have promoted the interaction of generalist into networks, thus increasing network connectance (Blüthgen et al., 2007; Plowman et al., 2017). The degree of interaction asymmetry can potentially be broken by the high extinction risk of specialists, ultimately reducing the nestedness of

ecological networks, while generalists tend to shape a nested structure (Vázquez & Aizen, 2004). The increase in connectance and generalist with species richness tend to promote nestedness in ecological networks (Ho et al., 2022). Furthermore, higher bacterial and fungal richness can increase their network modularity by providing more species for interactions and intensifying interspecific competition (Krasnov et al., 2012; Martín González et al., 2015). Interestingly, there were no clear effects of bacterial and fungal richness on network robustness in either of the regions, except for a decrease in robustness associated with higher bacterial richness in the drier and colder region. This may reflect a consistent community stability with increasing species richness. Nevertheless, in the drier and colder region, species-rich bacterial communities are more prone to secondary extinctions than communities with a smaller number of species. The most plausible explanation for this is the heightened intensity of interspecific competition, which increases the risk of extinction (Kaneryd et al., 2012). Our study demonstrates that species richness supports greater microbiome complexity and associations between bacterial and fungal communities.

4.4 | The effects of elevation and microbial species richness on network structure and robustness

Elevation has been shown to be a major driver of network connectance and nestedness in the wetter and warmer region, while microbial richness played a more crucial role than elevation in shaping connectance and nestedness in the drier and colder region. In the wetter and warmer region, higher elevation is typically associated with colder temperatures, imposing harsher conditions for fungal communities (Figure 1). The increases in connectance and nestedness with elevation may be driven by reduced partner availability between bacteria and fungi, owing to decreased fungal species richness (Cheshire et al., 2021). This might require more bacterial generalists to connect with fungal species, which lead to higher nestedness. Our result is in line with recent findings that higher temperatures tend to decrease the connectance in stream food webs (O'Gorman et al., 2019). However, microbial biodiversity is likely to dominate network connectance and nestedness in drier and colder climates. This is in accordance with the generally strong association between species richness and network connectance and nestedness observed in macroecology (Blüthgen et al., 2008; Ren et al., 2023).

The divergent effects of elevation and species richness on network structure in the contrasting climates may arise from the difference of environmental conditions, species adaptation, or vegetation types. First, aquatic ecosystems in the wetter and warmer region may experience greater environmental stress compared to the drier and colder region, including strong temperature and precipitation fluctuations with elevation, and low nutrient level (Figures S15 and S16). Such enhanced environmental stress may increase the influence of elevation on bacteria–fungi network structure. Second, higher species adaptation in the wetter and warmer region may lead to stronger constraints of climate on potential associations between species

(Sonne et al., 2020). The lower seasonal variation in temperature at warmer latitudes may favour species with narrower physiological tolerance, leading to these species to develop more specialized habitat requirements (Janzen, 1967; McCain, 2009). In contrast, fewer climatic effects on microbial interactions are predicted in the drier and colder region, where species diversity is expected to strongly influence their potential associations. Third, changes in riparian vegetation can modify the availability of nutrients and energy in stream ecosystems, and further induces shifts in microbial communities and food webs (Gilling et al., 2013; Naiman & Decamps, 1997). The different vegetation types may lead to divergent effects of elevation and species richness on the network structure in the contrasting regions.

Microbial richness was the dominant factor affecting modularity in the two regions (Figure 4; Figures S13 and S14), while only showed direct effects on network robustness in the drier and colder region. Our findings are consistent with previous studies of bipartite networks that have emphasized the importance of species richness in determining modularity (Martín González et al., 2015). However, the impact of microbial richness on network robustness varies significantly among different microbial groups and ecological conditions. Elevation and network structure proved to be poor predictors of robustness in the two regions, as the lack of corresponding relationships of elevation and network structure to robustness (Figures 2 and 5). Such effects of species richness were further statistically supported by random forest analyses (Figures S13 and S14). Thus, our findings reveal that there were different constraints on bacteria-fungal network structure in contrasting climates, with microbial biodiversity showing stronger associations with network structure and robustness than elevation in the drier and colder region.

5 | CONCLUSION

In conclusion, bacterial and fungal species richness and their bipartite network structure responded differently to elevation in the contrasting climates. Bacterial and fungal richness, connectance and modularity of their bipartite networks varied significantly along elevational gradients only in the wetter and warmer region. This may reflect temperature change with elevation is likely have a greater impact on microbial diversity and their correlation networks in wetter and warmer climates than in drier and colder climates. As the associations between bacteria and fungi drive important ecosystem processes, the observed differences in the contrasting climates could reflect the outcome of both evolutionary and ecological function. The structure in bacteria-fungi bipartite networks generally exhibited a consistent increased association with their species richness in contrasting climates. Compared with the wetter and warmer region, species richness was found to play a stronger role in shaping network structure and robustness in the drier and colder region. Climate warming can threaten biodiversity and lead to shifts of potential interactions through triggering biological range shifts, which may be early signs of future extinction and ecosystem function debts (Grass et al., 2018; Haddad et al., 2015). A better understanding about the

response of microbial associations and their impact on ecosystem processes under climate change is urgently needed.

AUTHOR CONTRIBUTIONS

JW conceived the idea. JW, WZ, ML and JL performed the field experiments. JW, WZ generated the environmental and biological data. WZ performed the data analyses, with the contributions from JW and JS. WZ wrote the first draft of the manuscript. WZ, JW and JS finished the manuscript with the contributions from other co-authors. All authors approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw sequences were submitted to NODE with accession number (<https://www.biosino.org/node/project/detail/OEP004862>): OEP004862.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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