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Environmental adaptation is stronger for abundant rather than rare microorganisms in wetland soils from the Qinghai-Tibet Plateau

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Abstract

Disentangling the biogeographic patterns of rare and abundant microbes is essential in order to understand the generation and maintenance of microbial diversity with respect to the functions they provide. However, little is known about ecological assembly processes and environmental adaptation of rare and abundant microbes across large spatial-scale wetlands. Using Illumina sequencing and multiple statistical analyses, we characterized the taxonomic and phylogenetic diversity of rare and abundant bacteria and fungi in Qinghai-Tibet Plateau wetland soils. Abundant microbial taxa exhibited broader environmental thresholds and stronger phylogenetic signals for ecological traits than rare ones. By contrast, rare taxa showed higher sensitivity to environmental changes and closer phylogenetic clustering than abundant ones. The null model analysis revealed that dispersal limitation belonging to stochastic process dominated community assemblies of abundant bacteria, and rare and abundant fungi, while variable selection belonging to deterministic process governed community assembly of rare bacteria. Neutral model analysis and variation partitioning analysis further confirmed that abundant microbes were less environmentally constrained. Soil ammonia nitrogen was the crucial factor in mediating the balance between stochasticity and determinism of both rare and abundant microbes. Abundant microbes may have better environmental adaptation potential and are less dispersed by environmental changes than rare ones. Our findings extend knowledge of the adaptation of rare and abundant microbes to ongoing environmental change and could facilitate prediction of biodiversity loss caused probably by climate change and human activity in the Qinghai-Tibet Plateau wetlands.

KEYWORDS
biogeographic pattern, environmental thresholds, microbial diversity, phylogenetic signals, stochasticity versus determinism

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1 | INTRODUCTION

Wetlands, regarded as the kidneys of the Earth, are important ecosystems for biodiversity, providing food, regulating climate, and purifying water (An et al., 2019; Martins et al., 2018). However, global wetlands are facing many ecological and environmental problems (e.g., biodiversity loss, reclamation, and water pollution) due to climate change and anthropogenic disturbance (Gauci et al., 2004; Price et al., 2019; Wang et al., 2018). Microorganisms in wetland soils are one of the largest world reservoirs of biodiversity and drive numerous ecological processes in terrestrial ecosystems (Louca et al., 2018; Shi et al., 2018; Wagg et al., 2014). Specifically, bacteria and fungi are responsible for the turnover and cycling of important elements, including carbon, nitrogen, and phosphorus (Ge et al., 2012; Luo et al., 2018; Wan, Hao, et al., 2021). In addition, soil microbial diversity (α- and β-diversity) has been shown to be closely correlated with multiple ecosystem functions, such as primary production and climate regulation (Luo et al., 2018; Wagg et al., 2014). Therefore, understanding microbial diversity can be beneficial for evaluating the health and functions of wetland ecosystems.

Deciphering the fundamental mechanisms for generating and maintaining microbial diversity is a core objective in community ecology, and some interesting patterns have been discovered. For instance, An et al. (2019) found that low α-diversity of bacterial communities in coastal wetlands was caused not only by salinity, but also by other environmental factors (e.g., altitude and temperature). In addition, microbial β-diversity varies along environmental gradients (e.g., pH and salinity) (Rath et al., 2019; Rousk et al., 2010). Many ecological theories that attempt to explain diversity-environment interconnections mainly consider species interaction models (e.g., competition and cooperation) and its in situ resource (e.g., space and nutrient availability) (Ghoul & Mitri, 2016; Jiao et al., 2020). Heterogeneity in substrate preference and environmental stress adaptations of microorganisms results in differences in microbial growth and biomass yield (Rath et al., 2019; Rousk et al., 2010; Zhalnina et al., 2018). This can lead to a skewed abundance distribution in a local microbial community, with relatively few dominant and a large number of rare species (alternatively known as a "rare biosphere") (Ji et al., 2020; Jia et al., 2018; Jiao & Lu, 2020a). Previous studies have reported that rare and abundant species often show different distribution patterns and functional traits (Chen et al., 2020; Jiao & Lu, 2020b; Liang et al., 2020). Consequently, disentangling the biogeography and community assembly of rare and abundant microbial taxa is essential for understanding microbe-driven ecosystem processes and functions.

Recent studies have described the biogeography of rare and abundant microbial taxa in various environments (Ji et al., 2020; Jiao & Lu, 2020a), with both geospatial effects and environmental factors (e.g., temperature, pH and conductivity) influencing soil microbial diversity (Hou et al., 2020; Ji et al., 2020; Jiao & Lu, 2020a). For instance, local physicochemical properties have greater effects on community compositions of both rare and abundant bacteria compared to geospatial factors (Ji et al., 2020). However, most studies investigate the biogeography of rare and abundant bacterial communities in agricultural soils (Kurm et al., 2019; Hou et al., 2020; Jiao & Lu, 2020a; Liang et al., 2020), and little is known about environmental adaptation and community assembly processes of rare and abundant bacterial and fungal taxa in natural wetlands.

Environmental filtering is an important determinant in shaping species distribution patterns and affecting abundance (Bahram et al., 2018; Jiao et al., 2019; Kivlin et al., 2014). The relative abundance of a rare or abundant taxon is the result of a tradeoff between its growth and death rates (Ratzke et al., 2018). Rare and abundant microbial taxa show diverse responses to environmental change (Kurm et al., 2019; Liang et al., 2020). Environmental thresholds of species reveal changes in taxa distributions along an environmental gradient over space or time (Baker & King, 2010). For example, environmental thresholds of arbuscular mycorrhizal fungi in European grassland were estimated using the accumulated values of change points of all the species in a given microbial community (Ceulemans et al., 2019). Procurable environmental thresholds rarely integrate the abundance, occurrence, and directionality of microbial responses at the species level, and few studies based on standardized phylogenetic and molecular evolutionary analysis of natural sites on a large spatial scale (Jiao & Lu, 2020a). Additionally, the responses of microbes to environmental change exhibit phylogenetic conservatism, and in this case microbes are not distributed randomly across the tree of life (Isobe et al., 2019; Martiny et al., 2015). For example, ectomycorrhizal fungi of the *Craterellus* genus show strong conservatism of a positive response to nitrogen deposition, while *Cortinarius*, *Tricholoma*, *Piloderma*, and *Suillus* spp. exhibit strong conservatism of consistently negative responses to nitrogen deposition (Lilleskov et al., 2011). Therefore, understanding the phylogenetic patterns of microbial response traits provides predictions for microbial biogeography and their responses to environmental change, and for changes in biodiversity-driven ecosystem multifunctioning (Goberna & Verdú, 2016, 2018; Jiao & Lu, 2020a; Wagg et al., 2014). Environmental breadth can reflect species niche breadth, and phylogenetic signals provide predictions for microbial evolutionary adaptation in response to environmental change (Gao et al., 2020; Martiny et al., 2015). However, environmental breadths and phylogenetic signals of both bacterial and fungal communities to ongoing environmental change, especially abundant and rare taxa, have not been evaluated in wetlands of high elevation geographic regions.

Community assembly, an important topic in microbial ecology, is considered to be influenced by both stochastic (e.g., dispersal limitation and homogenizing dispersal) and deterministic processes (e.g., variable selection and homogeneous selection) (Feng et al., 2018; Jiao et al., 2020; Stegen et al., 2013). Both stochastic and deterministic processes determine microbial communities and are considered to be obligatory in coupling microbial community structure with the ecosystem functions they supply (Feng et al., 2018; Xun et al., 2019). Abundant microbial taxa are limited by dispersion more than rare taxa in agricultural soils (Jiao & Lu, 2020a,2020b) and in inland freshwater ecosystems across China (Liu et al., 2015). In contrast, the dispersal of rare bacterial taxa is more limited than that of abundant bacterial taxa in three subtropical bays of China (Mo et al., 2018). The balance between stochastic and deterministic processes is regulated by environmental factors (Jiao et al., 2020; Logares et al., 2020; Tripathi et al., 2018). For instance, the divergence in soil pH and salinity can change the relative contributions of different ecological assembly processes in shaping bacterial communities (Jiao & Lu, 2020b; Shi et al., 2018; Tripathi et al., 2018; Zhang et al., 2020). However, it remains unclear whether similar environmental variables mediating the balance between stochasticity and determinism in community assemblies of rare and abundant microbes in wetlands.

The 36 wetlands in the Qinghai-Tibetan Plateau were chosen as our study areas. The mean annual temperature and mean annual precipitation of these wetlands are −4.49–17.62°C and 89–1,038 mm, respectively, and detailed terrain properties are described in Table S1. These wetlands have been largely protected from human activities. However, some factors including climate change might engender some unknown impacts on these wetlands. This situation caught our interest to predict and evaluate the responses of wetland ecosystems to environmental change, and in order to understand protection of wetlands by mitigating the impact of climate change in the future. In this study, we aimed to (a) assess the potential environmental thresholds and phylogenetic distributions of rare and abundant bacteria and fungi across diverse environmental gradients in wetlands across Qinghai-Tibetan Plateau, and (b) reveal the major environmental variables affecting the assembly of rare and abundant microbial subcommunities. In view of the low competition potential and growth rate of rare taxa (Campbell et al., 2011; Jousset et al., 2017), we hypothesized that rare microbial taxa would present relatively narrow environmental thresholds and relatively weak phylogenetic signals for traits compared with abundant microbial taxa. In addition, the ecological assembly processes dominating rare and abundant microbial subcommunities would be affected by different environmental variables.

2 | MATERIALS AND METHODS

2.1 | Soil collection and physicochemical properties

In July 2014, a total of 36 wetland sites across Qinghai-Tibetan Plateau (Figure S1), covering lacustrine, riverine, and palustrine locations, were selected for collection of experimental soils. Five soil cores (3 cm diameter and 10 cm depth) were collected randomly within each site using a hand corer and were then mixed thoroughly to form a composite sample. Approximately 10 g of soil from each soil sample was placed in a sterile tube and then immediately frozen in liquid nitrogen for subsequent DNA extraction. Other soils were stored at approximately 5°C in a portable refrigerator. The terrain properties of each site including longitude (Lon), latitude (Lat) and altitude (Alt) were recorded using a global positioning system (Unistrong). The plant richness (PR) and plant coverage (PC) were visually evaluated in the field by a 1 × 1 m grid frame. The mean annual temperature (MAT) and mean annual precipitation (MAP) were obtained from a national climate database (http://data.cma.cn).

Soil physicochemical properties including temperature (Tem), pH, electrical conductivity (EC), moisture (Moi), total carbon (TC), total phosphorus (TP), and ammonia nitrogen (NH_4) were measured, as described previously (Table S2; Liu et al., 2017).

2.2 | Molecular analyses

Soil total DNA from this set of samples was extracted in triplicates by using a FastDNA Spin Kit for Soil (MoBio) after the soil was lyophilized and ground. Unfortunately, we failed to extract total DNA from three soil samples. The 33 extracted DNA samples were further purified by removing humic substances and potential enzyme inhibitors using a Geneclean Spin Kit (QBiogene). DNA concentrations were determined using a NanoDrop 2000 Spectrophotometer (Thermo Fisher Scientific). All extracted DNA samples were stored at −80°C.

The V3-V4 region of the bacterial 16S rRNA gene was amplified by employing the primers 338F (5′-ACT CCT ACG GGA GGC AGC AG-3′) and 806R (5′-GGA CTA CHV GGG TWT CTA AT-3′) (Mori et al., 2013). The fungal internal transcribed spacer (ITS) region was amplified by applying the primers ITS1 (5′-CTT GGT CAT TTA GAG GAA GTA A-3′) and ITS2 (5′-GCT GCG TTC TTC ATC GAT GC-3′) (Buée et al., 2009). Each sample was amplified in triplicate in a 20 μl reaction under the following conditions: an initial denaturation at 95°C for 3 min, 30 cycles of 95°C for 30 s, 58°C for 30 s, and 72°C for 40 s, and then a final extension at 72°C for 10 min. The PCR products from each sample were pooled and purified by gel electrophoresis and extracted using an AxyPrep DNA Gel Extraction Kit (Axygen). Sequencing was performed on an Illumina MiSeq platform at Novogene Bioinformatics Technology Co., Ltd.

The raw reads were processed following the pipeline of QIIME (Caporaso et al., 2010). To minimize the impact of random-sequencing errors, we removed (a) sequences that did not exactly match primers and barcodes, (b) sequences with an average quality score <20, (c) sequences that contained ambiguous base calls, and (d) sequences with maximum homopolymers <10 bp. The purified sequences were clustered into operational taxonomic units (OTUs) at a 97% similarity level, with bacterial taxonomy assessed against the SILVA v128 reference and fungal taxonomy against UNITE v8.0 reference (Jiao et al., 2020). The OTUs with relative abundance <0.001% were filtered out.

2.3 | Data analysis

We removed OTUs that contained less than 20 reads to avoid random effects on the identification of rare taxa (Jiao & Lu, 2020a). Based on minimum number of sample sequences (Figure S2), 32,098 reads for bacteria (all sample sequences ranging from 32,098–33,599) and 24,513 reads for fungi (all sample sequences ranging from 24,513–31,491) were used to standardize the sequencing effort across samples. The rare and abundant OTUs were defined following recent reports (Campbell et al., 2011; Jiao & Lu, 2020a). Briefly, OTUs with relative abundances below 0.01% of the total sequences were designated as "rare", those with relative abundances above 0.1% were designated as "abundant", and the remaining OTUs (0.01%–0.1%) were defined as "intermediate".

The phylogenetic clustering reflects whether species cluster closer to the tips of the phylogeny (Kembel et al., 2010). To estimate the phylogenetic clustering of rare and abundant taxa, we calculated a standardized index using the mean nearest taxon distance (SES.MNTD) by means of the ses.mntd function in the picante package of R (Kembel et al., 2010). To evaluate the pairwise phylogenetic distance between communities, beta mean nearest taxon distance (βMNTD) was calculated using the comdistnt function. The distance-decay relationship was determined as the slope of an ordinary least-square between phylogenetic similarity (1-βMNTD) and geographical distance.

Environmental breadth was defined as the threshold value of rare or abundant taxa in response to environmental gradients and was measured using threshold indicator taxa analysis (TITAN) in the TITAN2 package of R (Baker & King, 2010). The sums of taxa scores for both bacterial and fungal OTUs were used to determine upper and lower thresholds of difference in the rare and abundant communities based on environmental variables. Additionally, we obtained potential trait information about both rare and abundant microbial taxa. Briefly, the ecological preferences for each OTU were determined by calculating Spearman correlations between environmental variables and relative abundances of microbial taxa (Oliverio et al., 2017). For example, the OTUs positively or negatively correlated with salinity were regarded as "high-salinity-preferred" or "low-salinity-preferred"; the OTUs positively or negatively correlated with pH were designated as "alkaline-preferred" and "acid-preferred". Subsequently, we applied Blomberg's *K* statistic to calculate the phylogenetic signals for the environmental preference of rare and abundant taxa (Goberna & Verdú, 2016; Jiao & Lu, 2020a; Oliverio et al., 2017). The Blomberg's *K* statistic is an approach describing a phylogenetic signal that compares the observed signal in a trait to the signal under a Brownian motion-based metric of trait evolution on a phylogeny (Blomberg et al., 2003). The *K* value was calculated by applying the multiPhylosignal function in the picante package of R, where *K* values higher than 1 imply strong phylogenetic signals and conservatism of traits, and *K* values closer to 0 denote a convergent or random pattern of evolution (Kembel et al., 2010).

The community assembly processes of rare and abundant microbial communities were evaluated by using variation partitioning analysis, null and neutral models (Ji et al., 2020; Jiao et al., 2020; Stegen et al., 2013; Wan, Liu, et al., 2021). The variation partitioning analysis can distinguish the pure effects of geospatial factors and environmental variables on microbial community composition (Ji et al., 2020; Shi et al., 2018). Pure environmental effects without a geospatial component denotes the effect of species sorting (deterministic process), while pure geospatial effects without an environmental variable represents the effect of dispersal limitation (Jiao et al., 2020). The null model analysis was conducted to calculate the relative contributions of four ecological processes, namely, homogeneous selection, variable selection, dispersal limitation, and homogenizing dispersal (Feng et al., 2018; Jiao & Lu, 2020a; Stegen et al., 2013; Tripathi et al., 2018). Briefly, null model-based Bray-Curtis-based Raup-Crick (RC_{bray}) and β-nearest taxon index (βNTI) were applied to calculate the differences in taxonomic and phylogenetic diversity using the picante package of R. If $\beta NTI < -2$ or $\beta NTI > 2$, deterministic processes govern the community assembly, with distinctly more (i.e., variable selection; $\beta NTI > 2$) and less (i.e., homogeneous selection; $\beta NTI < -2$) phylogenetic turnover than expected. Whereas if $|\beta NTI| < 2$, $RC_{bray} < -0.95$ and $RC_{bray} > 0.95$ denote the relative contribution of homogenizing dispersal and dispersal limitation, respectively. The $|\beta NTI| < 2$ and $|RC_{bray}| < 0.95$ were estimated as the influence of "undominated" assembly, namely, no single process drives variations in community structure (Feng et al., 2018; Jiao et al., 2020). The effects of environmental factors on microbial community assembly were evaluated using the Mantel test, where environmental factor dissimilarity was calculated using Euclidean distance matric. The linear regression between change in environmental variable and βNTI was generated based on ordinary least-squares. The neutral model was selected to further reveal the contribution of the stochastic process to the rare and abundant microbial community assembly by predicting the interconnection between species abundance distribution and species area (Zhou & Ning, 2017). In this model, the migration rate (*m*) was calculated using the stats4 and hmisc packages in R (Jiao et al., 2020). A lower value of *m* suggests that the microbial community is less influenced by neutral processes (Sloan et al., 2006).

3 | RESULTS

3.1 | General distribution patterns of rare and abundant subcommunities

After quality filtering and reads control, a total of 1,041,535 and 775,601 high-quality sequences were clustered into 4,443 OTUs for bacteria and 1,977 OTUs for fungi. Rare bacteria comprised 66.4% of the total bacterial richness, but their total relative abundance accounted for only 13.2% of the entire bacterial community. Conversely, a quite low proportion of 3.91% OTUs was identified as abundant bacteria, which occupied 47.9% of the entire bacterial community. Similarly, 61.9% and 7.4% OTUs were identified as rare and abundant fungi, and their relative abundances accounted for 5.9% and 76.5% of the total fungal community. Abundance-occupancy relationships demonstrated that both rare bacteria and fungi possessed stronger positive correlations than corresponding abundant bacteria and fungi (Figure 1a, b). 97.1% abundant bacteria and 54.4% abundant fungi occurred in more than 50% of the soil samples, while only 43.2% rare bacteria and 0.7% rare fungi existed in more than 50% of the soil samples. Across all the samples, the rare

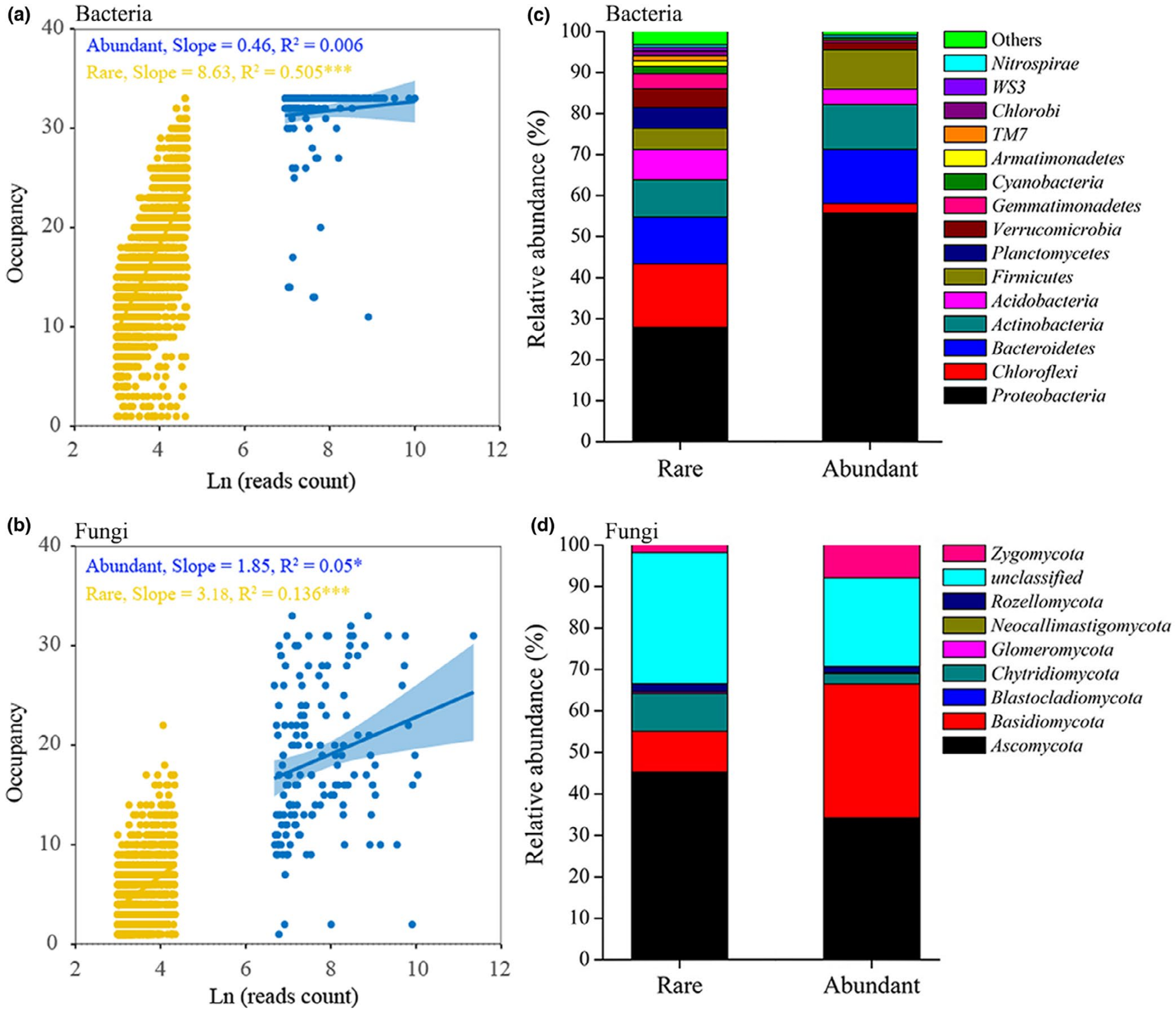

FIGURE 1 Abundance-occupancy relationships and taxonomic composition of rare and abundant microbial subcommunities. (a) and (b) Show the abundance-occupancy relationships of rare and abundant operational taxonomic units (OTUs). Occupancy is the number of samples an OTU is being detected from, and abundance is the number of reads. (c) and (d) Reflect the taxonomic composition of rare and abundant microbes at the phylum level. Asterisks denote significance (*p < .05; ***p < .001) [Colour figure can be viewed at wileyonlinelibrary.com]

bacterial subcommunity was dominated by *Proteobacteria* (27.8%) and *Chloroflexi* (15.5%), while the abundant bacterial subcommunity was dominated by *Proteobacteria* (55.7%) and *Bacteroidetes* (13.3%) (Figure 1c). In contrast, *Ascomycota* (45.2%) and unclassified fungi (31.6%) dominated in the rare fungal subcommunity, while *Ascomycota* (34.2%) and *Basidiomycota* (32.3%) were the dominant phyla in the abundant fungal subcommunity (Figure 1d). These results indicate that the rare and abundant bacteria and fungi showed distinct distribution patterns in the wetlands of the Qinghai-Tibet Plateau.

We evaluated both taxonomic and phylogenetic patterns for both rare and abundant microbial subcommunities in the Qinghai-Tibet Plateau wetlands (Figure 2). Although the distance-decay relationships of community similarity-geographical distance (Figure 2a) and phylogenetic similarity-geographical distance (Figure 2b) were significant (p < .05 and p < .001), the fitness values were relatively low (R^2 <.1), demonstrating weak decays of taxonomic and phylogenetic similarities with geographical distance. Significantly higher community distance was found in the rare bacteria compared with the abundant bacteria (Wilcoxon p < .001), while there was no remarkable difference in community distance between rare and abundant fungi (Wilcoxon p > .05) (Figure 2c). Similarly, noticeably higher phylogenetic distances for both rare bacterial and fungal subcommunities were higher than those of the corresponding abundant bacterial and fungal subcommunities (Wilcoxon p < .001) (Figure 2d). Shannon-Wiener indexes of rare bacteria and fungi were

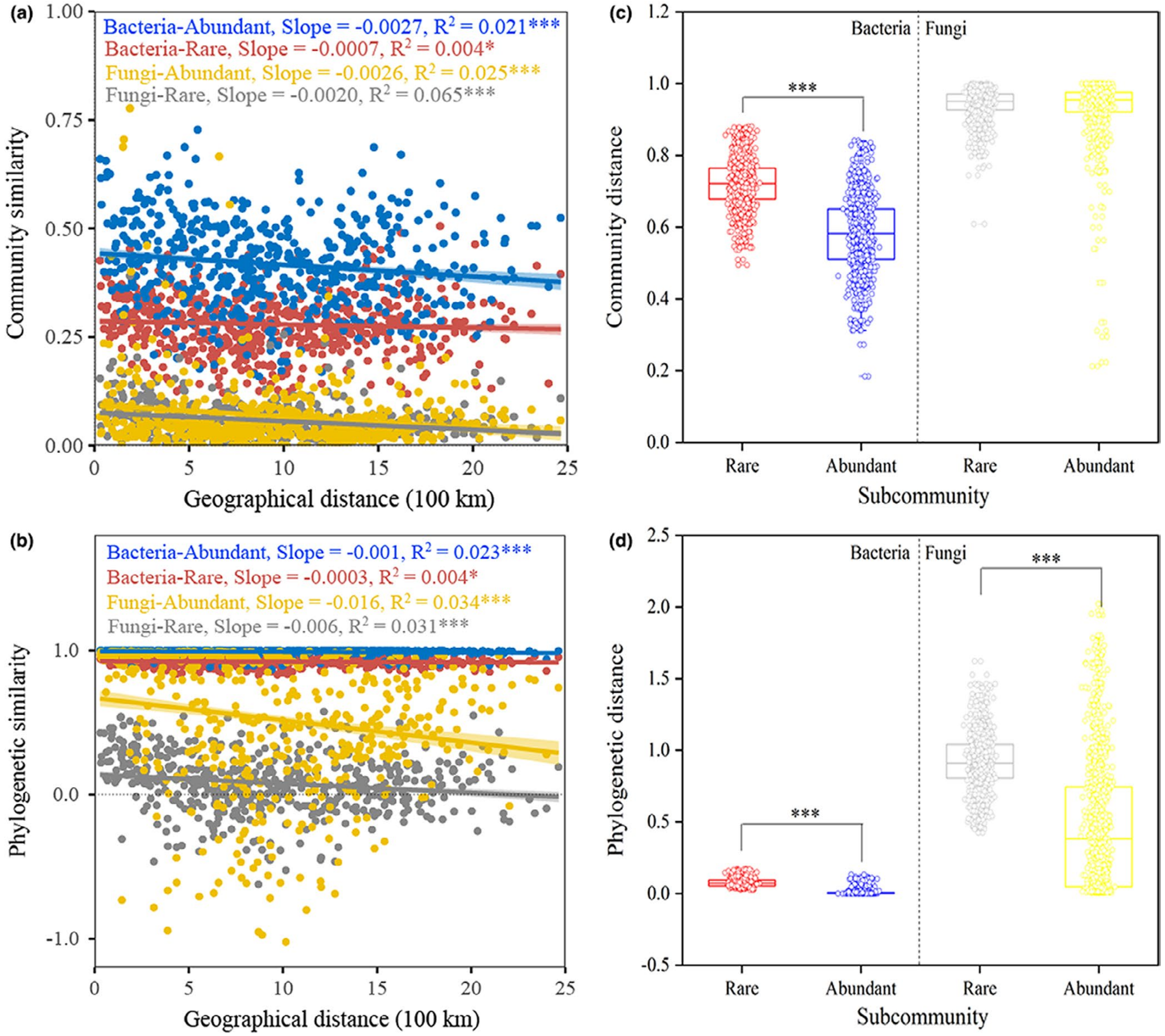

FIGURE 2 Patterns of rare and abundant microbial taxonomic and phylogenetic β-diversity. (a) Distance-decay curves of community similarity for rare and abundant microbial subcommunities. (b) Community distance based on Bray-Curtis dissimilarity between rare and abundant subcommunities. (c) Distance-decay curves of phylogenetic similarity for rare and abundant microbial subcommunities. (d) Phylogenetic distance based on βMNTD matrix between rare and abundant subcommunities. Asterisks denote significance (*$p < .05$; ***$p < .001$) [Colour figure can be viewed at wileyonlinelibrary.com]

significantly higher than those of corresponding abundant bacteria and fungi (Wilcoxon $p < .001$) (Figure S3). The mean values of SES.MNTD were noticeably higher for abundant rather than for rare microbial subcommunities (Figure S4). Additionally, significantly positive correlations between compositional dissimilarity and phylogenetic distance were observed in both rare and abundant bacterial and fungal subcommunities, and the correlations in rare bacterial and fungal subcommunities were much stronger than those for the corresponding abundant subcommunities (Figure 3). This might imply that the phylogenies of rare and abundant microbial subcommunities exhibited distinct sensitivities to environmental changes. We further found that environmental and geospatial variables exhibited different effects on community composition, and explained more variations in both abundant bacterial and fungal subcommunities than for corresponding rare bacterial and fungal subcommunities based on redundancy analysis (Figure S5).

3.2 | Environmental responses of rare and abundant subcommunities

Differing correlations between environmental factors and relative abundances of the top 20 rare and abundant microbes were observed, and specific environmental factors determined the relative

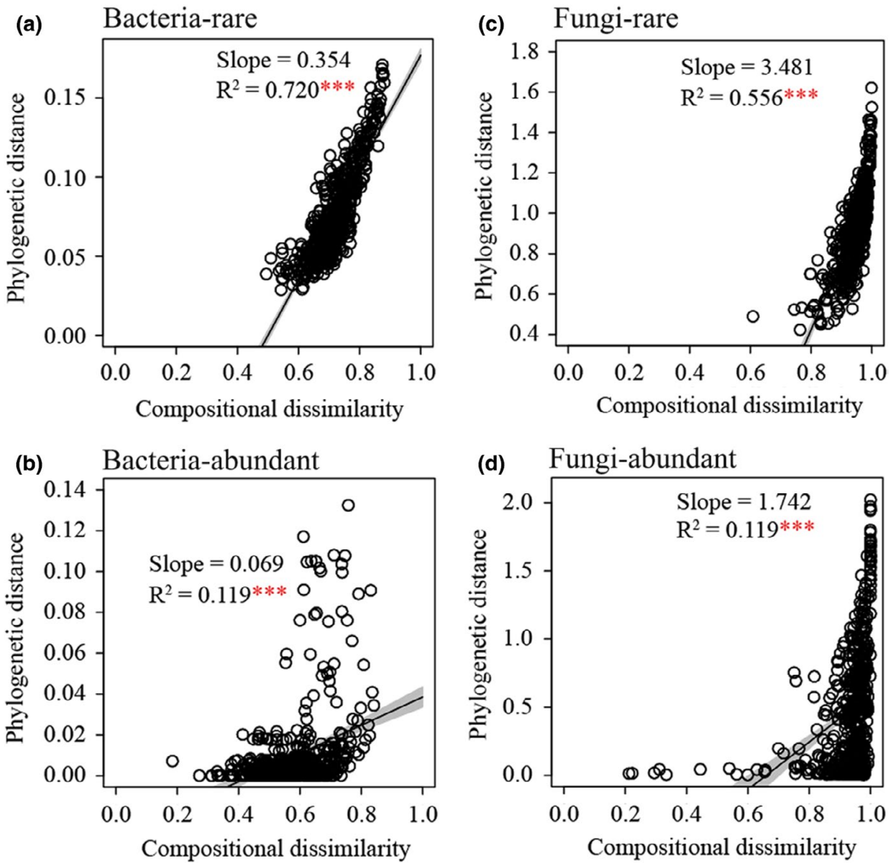

FIGURE 3 Relationships between phylogenetic distance and compositional dissimilarity of rare (a) and abundant (b) bacterial communities, rare (c) and abundant (d) fungal communities. Asterisks represent significance level (***$p < .001$) [Colour figure can be viewed at wileyonlinelibrary.com]

abundance of specific microbes (Figures S6, S7). For instance, longitude significantly affected the relative abundance of OUT_1088 belonging to the *Basidiomycota*. Environmental threshold analysis was used to explore the responses of rare and abundant microbial subcommunities to each of the environmental variables based on calculations of $z+$ and z^- (Figures S8–S10). Interestingly, the abundant bacterial subcommunity showed a broader range of environmental thresholds compared with the rare bacterial subcommunity for almost all the variables except for electrical conductivity (EC) (Figure 4a). Similarly, the abundant fungal subcommunity had a wider range of environmental thresholds than the rare fungal subcommunity, excluding pH (Figure 4b). The strength of the relationship between environmental preferences and microbial phylogeny was also calculated to determine whether ecological traits could be predictive in terms of phylogenetic diversity (Figure 4c, d). Blomberg's *K* statistic signified that the abundant bacterial and fungal subcommunities presented stronger phylogenetic signals for all environmental variables compared with the corresponding rare bacterial and fungal subcommunities (Figure 4c, d). Phylum-level taxonomy confirmed such observations (Figures S11, S12). For example, the abundance taxa of *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, and *Proteobacteria* exhibited stronger phylogenetic signals for all 14 environmental variables (Figure S11). The abundant taxa of *Ascomycota* (64.3%), *Basidiomycota* (100%), and *Chytridiomycota* (71.4%) presented stronger phylogenetic signals for more than 60% of the 14 environmental variables (Figure S12).

3.3 | Ecological community assembly processes in rare and abundant microbial subcommunities

The relative contributions of ecological processes differed in microbial subcommunities based on null model analysis (Figure S13). Dispersal limitation belonging to stochastic processes dominated in the abundant bacterial subcommunity, rare and abundant fungal subcommunities, with corresponding relative contributions of 72.5%, 75.8%, and 90.5%, respectively. Variable selection (69.9%) belonging to deterministic processes governed the rare bacterial subcommunity assembly. Homogenizing dispersal and homogeneous selection, belonging to homogenizing process, had little impact on both rare and abundant bacterial and fungal subcommunity assembly.

Mantel tests revealed that change in soil ammonia nitrogen (NH_4^+-N) was significantly correlated with βNTI of rare bacterial ($r = -.117$; $p < .001$), abundant bacterial ($r = -.072$; $p < .05$), rare fungal ($r = -.084$; $p < .01$), and abundant fungal ($r = -.139$; $p < .001$) subcommunities (Table 1). In addition, pairwise comparisons of βNTI values for rare and abundant microbial subcommunities were noticeably and negatively correlated with changes in soil ammonia nitrogen (Figure S14). This indicated that an increasing divergence in ammonia nitrogen resulted in an increase in stochasticity in rare bacterial community assembly, and decreases in stochasticity in the assemblies of both rare and abundant fungal subcommunities and abundant bacterial subcommunity. To further investigate the relationship between ammonia nitrogen and phylogenetic turnover (βNTI), soils were separated into subgroups based on

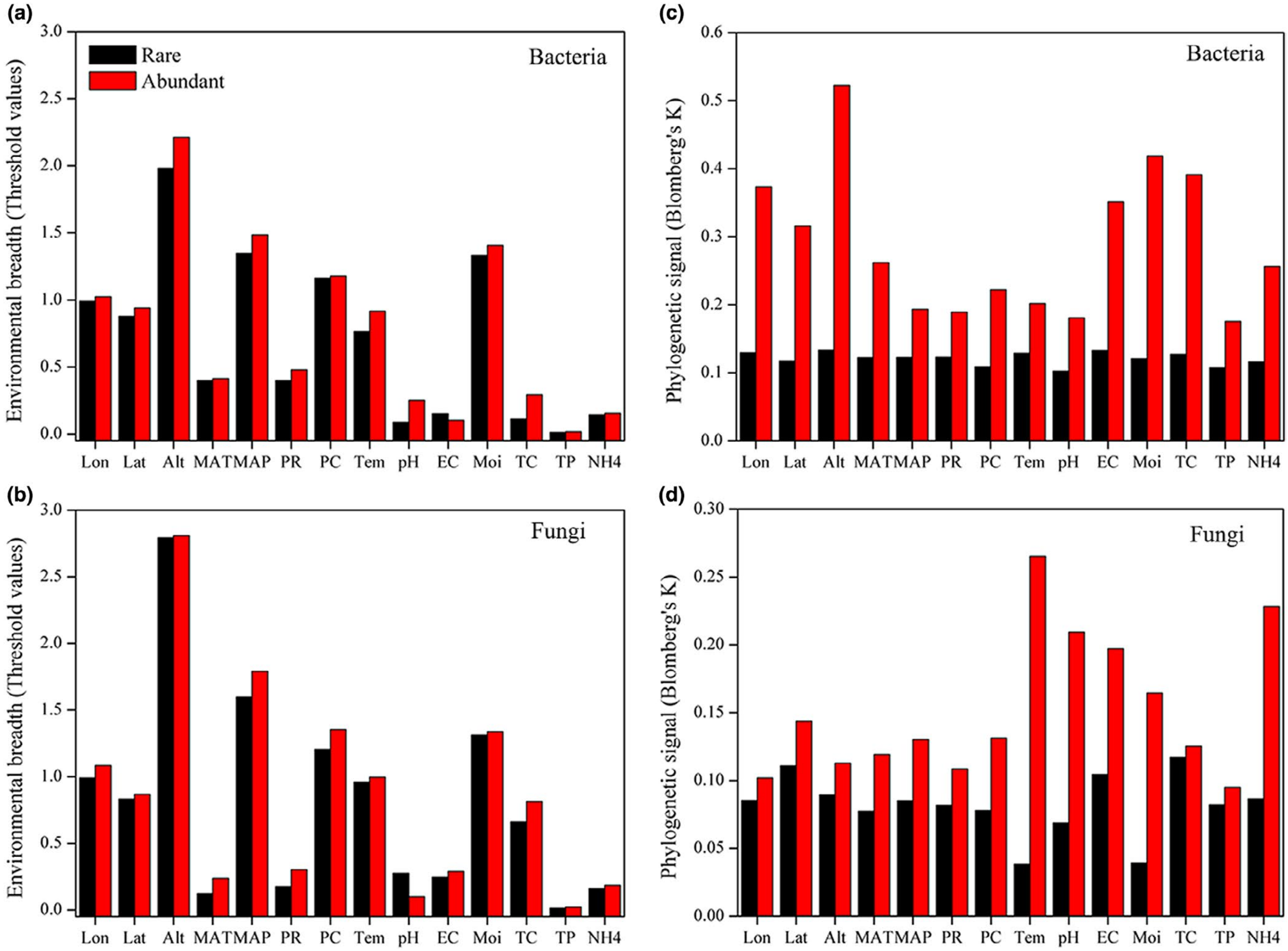

FIGURE 4 Environmental adaptation of rare and abundant microbial taxa in wetland soils. Environmental breadths of bacteria (a) and fungi (b) evaluated by the threshold values of rare and abundant taxa in response to environmental and geospatial factors were measured using TITAN. The threshold values in the figures were standardized using $\log_{10}$ (original threshold value +1). Phylogenetic signals of bacteria (c) and fungi (d) reflecting the trait conservatism for environmental preferences of the rare and abundant subcommunities were determined applying Blomberg's *K* statistic. The abbreviations of environmental factors are defined in Section 2 [Colour figure can be viewed at wileyonlinelibrary.com]

ammonia content. With increasing soil ammonia nitrogen, the relative contributions of stochasticity increased in the rare bacterial subcommunity and decreased in the abundant bacterial subcommunity, first decreased and then increased in the rare fungal subcommunity, and first increased and then declined in the abundant fungal subcommunity (Figure S15).

To make the community assembly of stochasticity more comparable, variation partitioning analysis and neutral analysis were also employed. The ratios of sorting/dispersal limitation were higher in rare bacterial and fungal subcommunities than that in the corresponding abundant bacterial and fungal subcommunities based on variation partitioning analysis (Figure 5a) and null model analysis (Figure 5b). These results suggested that the abundant microbial subcommunities were less environmentally constrained. Neutral model analysis further validated this finding with relatively higher *m* values in the abundant microbial subcommunities (Figure 5c).

4 | DISCUSSION

4.1 | Broader environmental adaptations of abundant microbial taxa

Environmental filtering governs microbial communities and in turn affects ecosystem function (Bahram et al., 2018; Feng et al., 2018; Li et al., 2018). Some studies have investigated the effects of environmental variables on the compositions of rare and abundant microbial communities (Hou et al., 2020; Jiao et al., 2017). We have attempted to provide insights into the responses of rare and abundant microbial subcommunities to ongoing environmental change. Here, the environmental adaptations of microbial subcommunities were clarified in two contexts: environmental breadth based on TITAN analysis (Baker & King, 2010; Jiao & Lu, 2020a) and the levels of phylogenetic signals to ecological preference based on Blomberg's *K* statistic (Goberna & Verdú, 2016).

TABLE 1 Mantel tests of environmental variables and geospatial factors against βNTI of rare and abundant microbial subcommunities

Property	Bacterial community		Fungal community	
	Rare	Abundant	Rare	Abundant
Lon	0.155***	−0.058	0.090**	0.119***
Lat	0.005	−0.080**	0.015	0.124***
Alt	−0.005	−0.226***	0.090**	0.043
MAT	−0.035	−0.183***	0.173***	0.007
MAP	−0.121***	−0.100***	0.081**	0.050
PR	−0.012	−0.038	−0.021	0.038
PC	0.045	−0.006	0.016	0.036
Tem	−0.120***	0.008	0.012	−0.018
pH	0.006	−0.101***	0.020	−0.038
EC	0.041	0.017	0.063*	0.049
Moisture	−0.013	0.047	−0.005	−0.017
TC	0.088**	0.061*	0.060	0.106***
TP	0.089**	0.082**	0.042	0.015
NH_4^+-N	−0.117***	−0.072*	−0.084**	−0.139***

Note: The abbreviations of environmental factors are defined in Section 2. Asterisks denote levels of significance (**p* < .05; ***p* < .01; ****p* < .001).

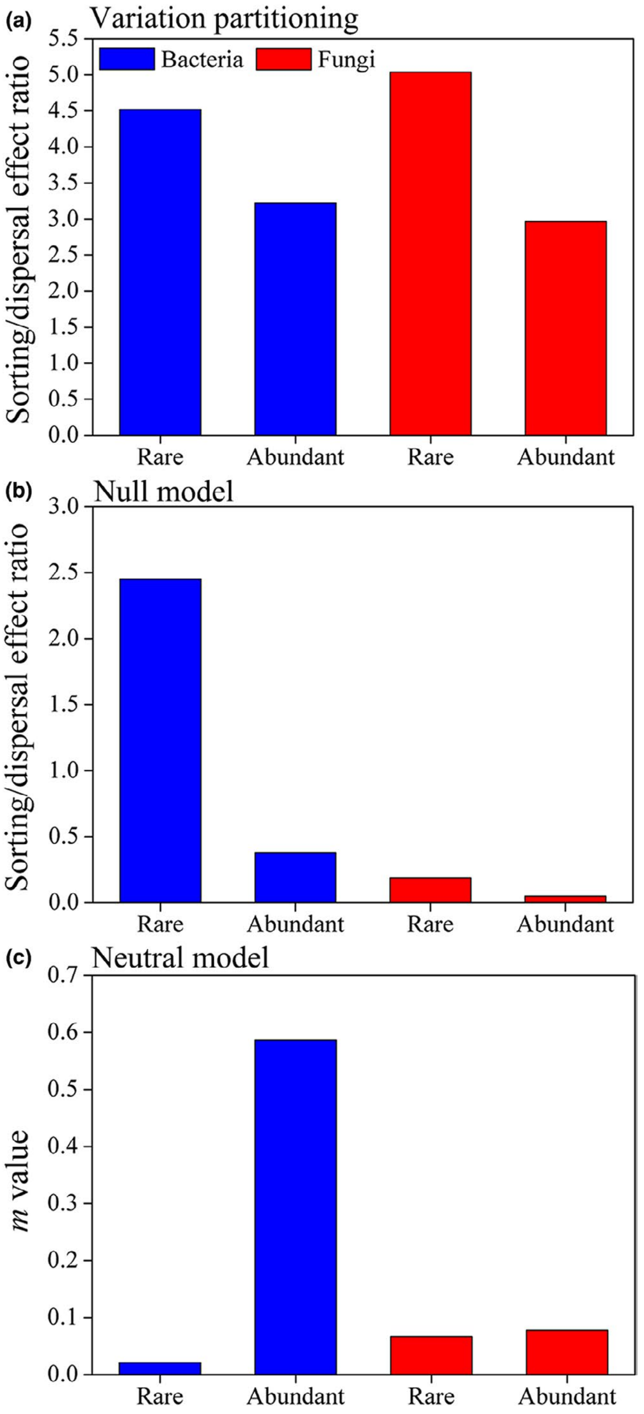

FIGURE 5 Community assembly patterns of rare and abundant microbial taxa using variation partitioning (a), null model (b), and neutral model (c) [Colour figure can be viewed at wileyonlinelibrary.com]

Firstly, we found that abundant bacterial and fungal subcommunities showed broader response thresholds to environmental factors than the corresponding rare bacterial and fungal subcommunities. These results are in line with the finding that the abundant fungal subcommunity exhibits higher environmental thresholds than rare fungal taxa in agricultural soils of China (Jiao & Lu, 2020a). This phenomenon might be due to the easier access and broader nutrient utilization potential of abundant microbial taxa compared with rare taxa (Jia et al., 2018; Zhalnina et al., 2018). Indeed, the abundant microbial taxa were omnipresent compared with rare microbial taxa across wetlands in Qinghai-Tibet Plateau, which is in accordance with previous findings (Ji et al., 2020; Jiao & Lu, 2020a; Mo et al., 2018), and could support the perspective described above. Rare bacterial and fungal taxa were not distributed evenly, and most taxa occurred only in a few soils. This might be attributed to the low growth rate and competition potential of rare microbial taxa, thus constraining in their environmental breadth (Jousset et al., 2017; Reveillaud et al., 2014). Our results emphasized that both abundant bacterial and fungal subcommunities had higher niche breadths, which reflected their adaptations to broader ranges of environmental gradients. Environmental threshold analysis based on TITAN has been reported in some biodiversity-related studies (Ceulemans et al., 2019; Jiao & Lu, 2020a; Steidinger et al., 2020). For instance, ectomycorrhizal fungal diversity in North American Pinaceae forests determines large effects on ectomycorrhizal fungi-associated biogeochemical cycles (Steidinger et al., 2020). The results of environmental breadths of microbes based on environmental threshold analysis are attractive, but are also controversially discussed regarding implications for the real field situation. Therefore, confirmatory experiments are needed when applying such statistical results to environmental policy.

Secondly, we observed that abundant bacterial and fungal taxa exhibited stronger phylogenetic signals for environmental preference compared with rare microbial taxa based on Blomberg's *K* statistic. The results are consistent with findings reported for Chinese agricultural soils (Jiao & Lu, 2020a) and grassland and forest soils across North America (Oliverio et al., 2017). Such findings might reveal that closely correlated species exhibit more similar ecological preferences across environmental gradients within the abundant microbial subcommunities. Prior studies have clarified that functional traits based on the ecological preferences of an organism depend on species evolutionary history (Graham & Fine, 2008; Saladin et al., 2019). For instance, traits of bacteria in four forest ecosystems are to a higher degree constrained by evolutionary history than environmental heterogeneity (e.g., temperature, precipitation, and dominant vegetation) (Morrissey et al., 2019). Additionally, the response traits of salinity and pH preferences for environmental microorganisms are found to be deeply conserved at phylogenetic level (Martiny et al., 2015), which might be related to the decisive roles of salinity and pH in shaping microbial biogeography (Griffiths et al., 2011; Jiao & Lu, 2020a; Shi et al., 2018; Zhang et al., 2020). In the present study, abundant microbial taxa exhibiting stronger phylogenetic signals for ecological preferences might reveal that abundant taxa possessed more phylogenetic niche conservatism with respect to the evolutionary history of environmental adaptation (Bennett et al., 2010). Interestingly, tighter connections (Figure 3, larger R^2 values) between compositional dissimilarity and phylogenetic distance were observed in rare rather than abundant microbial subcommunities. This phenomenon might be mainly attributed to the phylogenies of abundant microbial subcommunities being less sensitive to ongoing environmental change (Ji et al., 2020). The potential to maintain a community's phylogeny could reveal the capacity of the community to preserve the ecological niche (Miller et al., 2013; Pyron et al., 2015). Therefore, the decoupling between community composition and phylogenetic distance indicates that abundant bacteria and fungi are better in maintaining ecological niches than the corresponding rare bacteria and fungi. These findings might explain why abundant taxa have broader environmental breadths and distinct biogeographic patterns compared with rare microbial taxa. In summary, the results of environmental breadth and phylogenetic signal analyses show that rare and abundant bacterial and fungal subcommunities possessed distinct adaptations to various environmental conditions in wetlands across the Qinghai-Tibet Plateau.

4.2 | Different assembly processes dominating rare and abundant subcommunities

Here, the stochastic process (i.e., dispersal limitation) dominated in the abundant bacterial subcommunity and the rare and abundant fungal subcommunities, while the deterministic process (i.e., variable selection) was dominant in the rare bacterial subcommunity. These results agree with previous findings in that community assemblies of abundant fungi are mainly affected by dispersal limitation (Jiao & Lu, 2020a,2020b), while differing from the findings that homogeneous selection determined community assemblies of rare bacteria and fungi (Jiao & Lu, 2020a, 2020b) and abundant bacteria (Hou et al., 2020). These inconsistencies might be due to differences in habitat characteristics and geography (Shi et al., 2018). It has been reported that stochasticity increases with higher nutrient condition, while determinism seems to be more related to low nutrient conditions (Chase, 2010; Zhou et al., 2014). The divergences in community assembly processes of rare and abundant bacteria and fungi might be also because of environmental heterogeneity in general and the capability of different taxa to adapt to environmental changes (Morrissey et al., 2019; Palomo et al., 2018). In addition, some discrepancies might be due to the differences in cell size and lifestyle of bacteria and fungi (Zinger et al., 2019). Both bacteria and fungi have different cell sizes, and cell size has often been regarded as an important factor in affecting the dispersal potential of organisms (Bailey et al., 2018; Zinger et al., 2019). Due to the effects of cell size for bacteria and fungi, dispersal abilities and metabolic activities may affect the adequacy of stochasticity or determinism for explaining their community composition (Gao et al., 2020; Xun et al., 2019; Zinger et al., 2019). Despite this, our findings still support previous studies reporting that abundant microbial taxa were more limited by dispersion than rare taxa in agricultural soils (Jiao & Lu, 2020a,2020b) and inland freshwater ecosystems (Liu et al., 2015). The variation partitioning analysis and neutral model analysis further validate that abundant taxa are less environmentally constrained in this and other studies (Jiao & Lu, 2020a; Xue et al., 2018). Additionally, the phylogenetic clustering represented by the SES.MNTD value was more distinct in rare microbial subcommunities in our work as reported in other studies (Fan et al., 2017; Xue et al., 2018). A previous study has reported that environmental filtering could mediate phylogenetic clustering in a bacterial community (Huber et al., 2020).

Previously published literature has revealed that organic matter, pH, available sulphur, and salinity are crucial factors affecting bacterial community assembly processes in soils collected from many different environments (Feng et al., 2018; Jiao & Lu, 2020b; Logares et al., 2020; Zhang et al., 2020). Based on pairwise community comparison using a null model, we observed that the βNTI of both rare and abundant bacterial and fungal subcommunities was more closely correlated with soil ammonia nitrogen than other factors. This suggests that soil ammonia nitrogen is the crucial factor adjusting the balance between stochastic and deterministic processes for both rare and abundant microbial subcommunities in the Qinghai-Tibet Plateau wetlands.

The key role of soil ammonia nitrogen in governing both rare and abundant bacterial and fungal community assembly processes might be partially attributed to the functions of nitrogenous nutrients and the physicochemical characteristics of bacteria and fungi (Zhong et al., 2020). Ammonia nitrogen is an important nutrient for plant and microbial growth (Blázquez et al., 2017), and plays an important role in regulating soil nitrogen cycling and nitrogen-cycling-related microbial communities (Ma et al., 2020; Xiao et al., 2020). Moreover, ammonia nitrogen is closely correlated with soil bulk density, which in turn affects gas diffusion (e.g., oxygen and carbon dioxide) and microbial activity (Pan et al., 2018). We therefore conjecture that soil ammonia might affect microbial community assembly via two pathways: (a) Directly influencing microbial

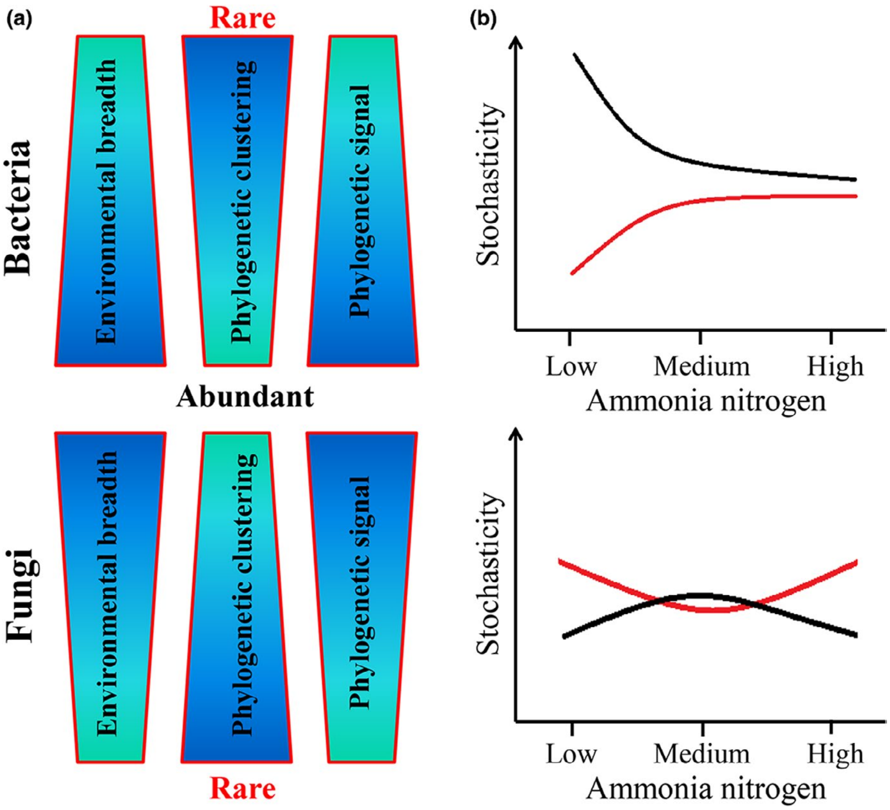

FIGURE 6 Conceptual models revealing environmental adaptation (a) and stochastic processes (b) in the assembly of rare and abundant microbial subcommunities under the influence of soil ammonia nitrogen. The red and black lines denote rare and abundant microorganisms, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

metabolism and growth, and (b) indirectly shaping soil bulk density. Considering the coupling of microbial nitrogen cycling with carbon, phosphorus, and sulphur cycling (Liang et al., 2015; Slate et al., 2019), other nutrients (e.g., available phosphorus, organic matter, and available sulphur) might also partially mediate the balance between stochastic and deterministic processes. Future work will investigate more environmental variables in determining community assembly processes.

Ultimately, we have constructed a conceptual paradigm to describe the environmental adaptation and ecological community assembly processes of rare and abundant bacteria and fungi in wetland soils from the Qinghai-Tibet Plateau (Figure 6). Abundant bacterial and fungal subcommunities exhibited broader environmental breadths and stronger phylogenetic signals of ecological preference than corresponding rare bacterial and fungal subcommunities. Rare microbial subcommunities exhibited closer phylogenetic clustering than abundant microbial subcommunities. Deterministic processes dominated in the rare bacterial subcommunity, while stochastic processes governed abundant bacterial subcommunity, and rare and abundant fungal subcommunities. Soil ammonia was a crucial factor in shaping the balance between community assembly processes of rare and abundant microbial subcommunities, showing distinct changes in stochasticity with higher ammonia content.

In conclusion, to our knowledge, this is the first study demonstrating that abundant microbial taxa show better environmental adaptation than rare microbial taxa in wetland soils from the Qinghai-Tibet Plateau. Soil ammonia nitrogen plays a critical role in influencing the community assemblies of both abundant and rare microorganisms. Our findings are of significance for understanding the maintenance of microbial diversity and predicting microbial responses to environmental perturbation caused by climate change and human activities in the Qinghai-Tibet Plateau.

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

Y.Y. and W.L. designed the whole experiment and collected the soil samples. Y.Y., W.L., W.Y., and W.W. conducted all experiments. W.W. analysed the data and wrote the manuscript. Y.Y., W.L., G.M.G., L.Y., and J.G. revised the manuscript, and W.L. submitted the manuscript.

DATA AVAILABILITY STATEMENT

The MiSeq raw sequencing data have been deposited in the NCBI Short Read Archive database under accession number PRJNA657692 for bacteria and PRJNA657715 for fungi.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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