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Fungal community reveals less dispersal limitation and potentially more connected network than that of bacteria in bamboo forest soils

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Abstract

A central aim of this microbial ecology research was to investigate the mechanisms shaping the assembly of soil microbial communities. Despite the importance of bacterial and fungal mediation of carbon cycling in forest ecosystems, knowledge concerning their distribution patterns and underlying mechanisms remains insufficient. Here, soils were sampled from six bamboo forests across the main planting area of Moso bamboo in southern China. The bacterial and fungal diversities were assessed by sequencing 16S rRNA and ITS gene amplicons, respectively, with an Illumina MiSeq. Based on structural equation modelling, dispersal limitation had strongest impact on bacterial beta diversity, while the mean annual precipitation had a smaller impact by directly or indirectly mediating the soil organic carbon density. However, only the mean annual temperature and precipitation played direct roles in fungal beta diversity. Moreover, the co-occurrence network analyses revealed a possibly much higher network connectivity in the fungal network than in the bacteria. With less dispersal limitation, stronger environmental selection and a potentially more connected network, the fungal community had more important roles in the soil carbon metabolisms in bamboo forests. Fungal beta diversity and the clustering coefficient explained approximately 14.4% and 6.1% of the variation in the carbon metabolic profiles among sites, respectively, but that of bacteria only explained approximately 1.7% and 1.8%, respectively. This study explored soil microbial spatial patterns along with the underlying mechanisms of dispersal limitation, selection and connectivity of ecological networks, thus providing novel insights into the study of the distinct functional traits of different microbial taxa.

KEYWORDS
carbon metabolism, dispersal limitation, fungi, network, spatial patterns

1 | INTRODUCTION

Among the main ecological processes that underlie the assembly of communities, dispersal and selection are two principle forces, although drift and diversification also play important roles. According to Vellend's conceptual synthesis of community ecology (Vellend, 2010), dispersal refers to the movement of organisms across space; selection represents the changes in community structure caused by deterministic fitness differences between taxa; drift reflects stochastic changes in the relative abundances of different taxa; diversification produces new genetic variation. There is increasing awareness that all of these processes operate in combination to assemble the

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community; however, their relative importance varies across different spatial scales (Martiny, Eisen, Penn, Allisona, & Horner-Devine, 2011; Wang et al., 2015) and habitat types (Wang et al., 2013, 2017). Recently, evidence has shown that the relative importance of the individual drivers of microbial community assembly also varies between different taxa (Brown & Jumpponen, 2014). On the one hand, dispersal ability can vary among microbial taxa due to deterministic traits, such as morphological features and habitat specificity (Hanson, Fuhrman, Horner-Devine, & Martiny, 2012). A modelling study indicated a very low probability of passive dispersal for microbes >20 μm in diameter between continents (Wilkinson, Koumoutsaris, Mitchell, & Bey, 2012). On the other hand, different ranges of physiologies of taxonomic groups also resulted in differences between the strength of selection (Schmidt, Nemergut, Darcy, & Lynch, 2014). A recent publication has suggested that the community of bacteria and fungi follow contrasting assembly trajectories along a chronosequence in retreating glacier soils, and a greater fraction of fungal operational taxonomic units (OTUs) displayed nonrandom patterns of occurrence compared with bacterial OTUs (Brown & Jumpponen, 2014). Ma et al. (2017) also revealed that soil bacteria and fungi had different biogeographic patterns and environmental filters along continental scales, implying their different community assembly mechanisms and ecological functions. Although distinct assembly trajectories were highlighted for soil bacteria and fungi, the underlying ecological processes and their relative importance remain major challenges.

A distance decay relationship (the community similarity declines with increasing geographic distance) can be used to evaluate the importance of these ecological processes because selection and dispersal could significantly affect this pattern. Although many studies have reported the spatial patterns of bacterial and fungal communities under similar environmental conditions, less attention has been paid to their dispersal potential. Some studies have asserted that free-living microorganisms, all of which have body sizes less than approximately 1 mm, do not experience passive dispersal limitations (Fenchel & Finlay, 2004; Finlay, 2002). However, Schmidt et al. (2014) speculated that bacteria are less likely to be dispersal limited than fungi due their body size differences. Thus, the dispersal capabilities of different taxa remain poorly understood. Distance decay relationships can also result from environmental differences through selection. Abiotic factors, such as soil properties (Zinger et al., 2011), climate (Martiny et al., 2011) and land use (Jesus, Marsh, Tiedje, & Moreira, 2009), are well-described environmental factors that determine bacterial and fungal assemblage. Additionally, recent surveys in forests also revealed that plant identity, such as plant species composition, is of great importance in predicting soil bacterial and fungal communities, mainly through the effects of plants on the food supply, physical microhabitats and environmental conditions (Prober et al., 2015).

Compared to abiotic factors, much less is known about how biotic interactions shape microbial communities. Interactions among microorganisms, both within and among groups, cause complexity in community structure through symbioses, parasitism, competition or predation (Schmitt et al., 2012; Steele et al., 2011). Network analysis-based approaches have been increasingly used to explore potential biotic interactions, including uncultured microorganisms in different systems (Eiler, Heinrich, & Bertilsson, 2012; de Menezes et al., 2015). The topological properties of the network (e.g., complexity and modularity) likely indicate the stability of the community or its functional diversity (Coux, Rader, Bartomeus, & Tylianakis, 2016; Dickie, Cooper, Bufford, Hulme, & Bates, 2017). However, very few attempts have been made to link co-occurrence network patterns with the variation in community structure or function at large spatial scales (Barberan, Bates, Casamayor, & Fierer, 2012; Durrer et al., 2017). Thus, with a variety of abiotic factors and complicated biotic interactions, similar environmental conditions across broad spatial scales can be a valuable material for studying the different ecological processes that shape community assembly and the difference in dispersal potential among taxonomic groups, such as bacteria and fungi.

The extensively planted bamboo forests in southern China with a large area provide a good resource to study the soil microbial assemblage at regional scales. With an aggressive rhizome system and fast-growing shoots, bamboo forests are noted for their essential role as carbon sinks in China, storing approximately 611.2 TgC in total, with 75% of that in the soil (Li et al., 2015). Bacteria and fungi are involved in a variety of processes that influence soil carbon sequestration in terrestrial ecosystems, such as the degradation and transformation of organic material (Falkowski, Fenchel, & Delong, 2008). Fungi are especially important in the decomposition of recalcitrant soil carbon (Courty et al., 2010), and bacteria are the primary decomposers of simple carbohydrates, organic acids and amino acids (Myers, Zak, White, & Peacock, 2001). A previous study showed that bamboo invasion shifted the community structure from a bacteria-dominated to a fungal-dominated microbial community, resulting in a functional change that caused more decomposition of the refractory lignin of the bamboo litter in soils (Chang & Chiu, 2015). This result indicated the ecological function of fungal communities in bamboo ecosystems are potentially more important compared to bacteria. In addition, there is increasing awareness that the spatial patterning of soil microbes may have important aboveground consequences, such as in plant community structure and ecosystem functioning (Ettema & Wardle, 2002; Green et al., 2004). Thus, more knowledge about soil microbial distribution patterns and the underlying mechanisms is required for the current understanding and future predictions of bamboo forest ecosystem functioning.

Here, we tested two hypotheses: (i) soil free-living bacteria and fungi may experience similar dispersal limitation and (ii) bacterial and fungal communities have similar dispersal limitations, but their spatial and co-occurrence patterns—and associated function—may respond to different environmental filters. To address these hypotheses, we used next-generation sequencing technology to analyse 18 soil samples from six representative pure bamboo forests in southern China across temperature and precipitation gradients. The soil samples belong to Ferric Acrisols in the FAO classification system which derived from Quaternary red clay and have similar edaphic

properties. We analysed the direct and indirect relationships between environmental factors, microbial spatial patterns, network property and carbon metabolic profiles to reveal the effects of abiotic and biotic factors on soil microbial community assemblies and carbon metabolisms at the regional scale. Our results indicate a distance decay pattern for the bacterial community, which is mainly controlled by dispersal limitation, but no significant pattern for the fungal community, which is driven by the mean annual temperature and precipitation. Moreover, the fungal network has a potentially much higher connectivity than the bacterial network. These ecological features of the bacterial and fungal communities might consequently affect carbon metabolism in the bamboo forest soils.

2 | MATERIALS AND METHODS

2.1 | Sampling and site characteristics

The study area is located in southern China between 113°1′ and 118°18′E latitude and 25°40′ and 30°19′N longitude and is the predominant cultivation area of Moso bamboo (*Phyllostachys pubescens* Mazel ex Houz.) in China. The climate in the region is classified as Cfa (humid subtropical climate) based on Köppen's classification. The mean annual temperature (MAT) in the region ranges from 16.4 to 19.3°C, and the mean annual precipitation (MAP) ranges from 1452 to 1930 mm (Table S1).

To determine the effects of geographic and environmental distance on the soil bacterial and fungal beta diversities in bamboo forests, six Moso bamboo forests were selected from different sites, including Lin'an (LA), Quzhou (QZ), Jian'ou (JO), Changting (CT), Zixi (ZX) and Hengyang (HY) in southern China (Figure 1a). The geographic distance ranges from 141 to 767 km. It is notable that there is no other tree species in these bamboo forests, only with some ferns and few dwarf shrubs. The stand density of the bamboo forests ranged between 3,367 and 3,989 stems/ha, with a mean bamboo stem diameter of 10–11 cm. All six bamboo forests were extensively managed in a similar way, without fertilization. The soil of the study area is classified as Ultisol according to the United States Department of Agriculture (USDA) soil taxonomy. A central sampling plot was established in the middle of each stand wherever possible to exclude the edge effects. Vertically along the slope, a second plot was set at a 76 m distance from the central plot, and a third one was set horizontally along the contour at a distance of 36 m from the central plot, as shown in Figure 1b. At each plot, 10 soil cores (5 cm diameter) from the upper 10 cm of the soil were collected in a circle of 1 m diameter and combined into a single bulk sample. The litter layer was not included in the soil sampling. All bulk samples were placed in a sterile plastic bag and divided into two subsamples within 48 hr. One subsample was kept at 4°C for measuring soil properties, and the other was stored at −80°C for microbial community analysis. All soil sampling was performed in April 2013.

Soil pH was determined with a glass electrode at a 2.5:1 water:-soil ratio. Soil organic carbon (SOC) density was calculated by summing the product of the soil organic carbon content and the soil bulk density in four layers of the soil profile (0–10, 10–20, 20–40 and 40–60 cm) (Chen, Zhang, Zhang, Booth, & He, 2009). The results were reported by Ji, Zhuang, Zhang, Sun, and Gui (2013). The soil pH ranged from 4.0 to 4.4, and the SOC densities ranged from 85.1 to 114.2 tC per hm^2 among sites (Table S1).

2.2 | DNA extraction and PCR amplification

Soil DNA was extracted from 0.6 g of well-mixed soil for each sample using the FastDNA Spin Kit for Soil (MP Biomedicals, Santa Ana, CA, USA) according to the manufacturer's instructions. The extracted DNA quality was determined using a NanoDrop 2000 (Thermo Fisher Scientific, Wilmington, DE, USA) according to the 260/280 nm and 260/230 nm absorbance ratios. All DNA was stored at −80°C.

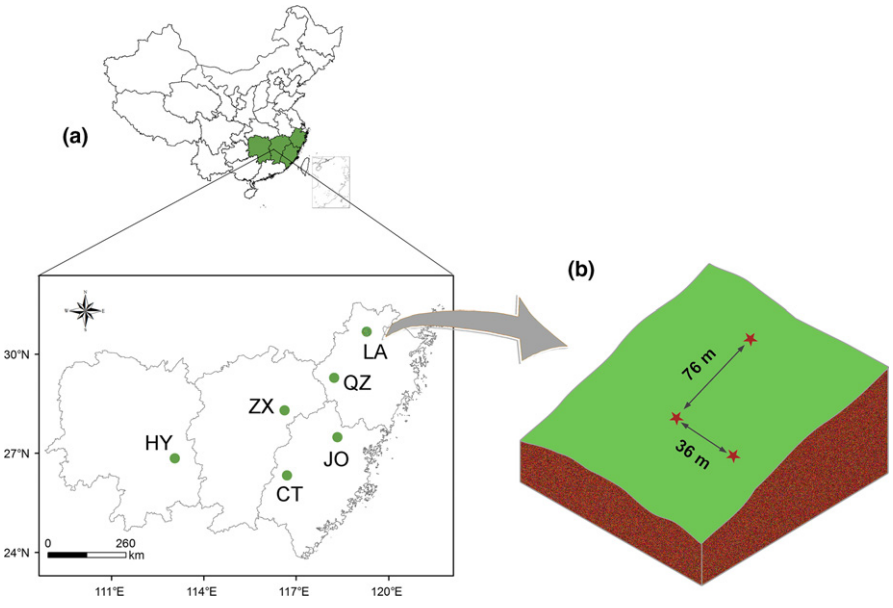

FIGURE 1 Sampling map showing six bamboo forest sites in southern China (a) and the sampling strategy at each site (b) [Colour figure can be viewed at wileyonlinelibrary.com]

For bacterial analyses, the V3–V4 region of the 16S rRNA gene was amplified using the 338F (ACTCCTACGGGAGGCAGCA) and 806R (GGACTACHVGGGTWTCTAAT) primer pair (Lee, Barbier, Bottos, McDonald, & Cary, 2012). For fungal analyses, internal transcribed spacer 1 (ITS1) region of the ribosomal RNA gene was amplified with primers ITS1-1737F (GGAAGTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC) (Degnan & Ochman, 2012). Both forward and reverse primers were tagged with adapter, pad and linker sequencing. A unique barcode was added to the reverse primer to permit the multiplexing of samples. The PCR amplification was performed using an ABI GeneAmp® 9700 (ABI, Foster City, CA, USA) with a 20 μl reaction system containing 4 μl of 5× FastPfu Buffer, 0.8 μl of each primer (5 μM), 2 μl of 2.5 mM dNTPs, 10 ng template DNA and 0.4 μl FastPfu Polymerase. The PCR protocol for bacteria consisted of an initial predenaturation step at 95°C for 3 min, 28 cycles of 30 s at 94°C, 30 s at 55°C and 45 s at 72°C, and a final 10-min extension at 72°C. The PCR protocol for fungi consisted of an initial predenaturation step at 95°C for 3 min, 35 cycles of 30 s at 95°C, 30 s at 59.3°C and 45 s at 72°C, and a final 10 min extension at 72°C. Three PCRs were conducted for each sample, and they were combined together after the PCR amplification. The PCR products were subjected to electrophoresis using 2.0% agarose gel. The band of the correct size was excised and purified using an AxyPrep DNA Gel Extraction Kit (Axygen Scientific, Union City, CA, USA) and quantified with QuantiFluor™-ST (Promega, Madison, WI, USA). All samples were pooled together with an equal molar amount from each sample for MiSeq sequencing.

2.3 | MiSeq sequencing and sequence analysis

MiSeq sequencing was carried out on an Illumina MiSeq (PE250) platform (Illumina, San Diego, CA, USA) by Shanghai Majorbio Bio-Pharm Biotechnology Co., Ltd. (Shanghai, China). The samples were prepared for sequencing using a TruSeq DNA kit according to the manufacturer's instructions. The purified mixture was diluted, denatured, rediluted, mixed with PhiX (equal to 30% of the final DNA amount) and then submitted to an Illumina Miseq system for sequencing with the Reagent Kit v2 2 × 250 bp as described in the manufacturer's manual.

After sequencing, raw sequences were selected based on sequence length, quality, primer and tag using the Trimmomatic and FLASH program. We eliminated low-quality sequences using the following criteria: (i) raw reads were shorter than 150 nucleotides, (ii) reads were truncated at any site receiving an average quality score <20 over a 50-bp sliding window, discarding the truncated reads that were shorter than 50 bp, (iii) exact barcode matching, two nucleotide mismatch in primer matching, reads containing ambiguous characters were removed and (iv) only sequences that overlap longer than 10 bp were assembled according to their overlap sequence. Reads that could not be assembled were discarded. The clean sequences were then subjected to chimera detection using the Uchime algorithm (Edgar, Haas, Clemente, Quince, & Knight, 2011). Operational taxonomic units (OTUs) were classified at the 97% similarity level using USEARCH (version 7.1), and the taxonomic assignment of OTUs was performed by the Ribosomal Database Project classifier (Wang, Garrity, Tiedje, & Cole, 2007) with a minimal 70% confidence score. For the 16S data, the taxonomic assignment was performed using the SILVA RELEASE 119 database (Quast et al., 2013); for the ITS, the UNITE version 6.0 database (Koljalg et al., 2013) was used. There was a very small portion of archaeal sequences obtained (accounting for 0.46%–8.9%), and we removed them as described by Zhang, Shao, and Ye (2012). To minimize the impact of read count variation from different samples, we rarefied all samples based on the smallest sequence numbers (18,159 sequences for bacteria and 9,166 for fungi per sample).

2.4 | Microbial carbon metabolic profiles

Carbon metabolic profiles of the soil microbial community were measured with BIOLOG 96-well Eco-Microplates (Biolog Inc., USA), with 31 different carbon sources and three replicates in each microplate. The carbon sources include carbohydrates, carboxylic acids, polymers, amino acids, amines and phenolic acid. Soil microorganisms were extracted as follows: 5 g soil (dry weight equivalent) was added to 45 ml sterile 0.85% (w/v) saline solution (Zak, Willig, Moorhead, & Wildman, 1994). The mixture was shaken for 30 min at 90 rpm and then left to stand for 30 min. Then, 1 ml supernatant was diluted to 20 ml with sterile saline solution. Soil suspensions (150 μl) were dispensed into each of the 96 wells, and the plates were then incubated at 25°C in the dark for 7 days. Colour development (reflecting carbon utilization) in the wells was followed by absorbance measurements at 590 nm every 12 hr. For the posterior analysis, absorbance at a single time point (108 hr) was used, when the asymptote was reached.

2.5 | Data analysis

Alpha diversity, the OTU richness and Shannon diversity of both bacterial and fungal communities were calculated for each individual sample. Beta diversity (community similarity, S_{com}) was estimated based on both bacterial and fungal OTU tables using the Bray–Curtis index, resulting in 135 data points among the sites (pairwise sample comparisons). We also visualized the bacterial and fungal community assemblages at different sites using nonmetric multidimensional scaling (NMDS) (Fig. S1c-d) and estimated by a permutation analysis of variance (PERMANOVA). We used the normalized optical density data obtained from the Eco-Microplates to analyse the microbial metabolic profiles. The similarity matrices were built using the Bray–Curtis index. All these analyses were conducted in R 3.2.1 (https://www.r-project.org/) with the VEGAN package (Dixon, 2003).

To estimate the slope of the distance decay relationship, a linear regression of the ln-transformed data of community similarity was plotted against the geographic distance according to Nekola and White (Nekola & White, 1999) as follows: $\ln(S_{com}) = \text{constant} - \beta \times \ln(D)$, where S_{com} is the community similarity, D is the geographic distance

and β is the slope of distance decay relationship. The significance of the distance decay slope was tested with 1000 Monte Carlo permutations of the residuals under the full regression model.

To investigate the relationship between microbial beta diversity and environmental distance (pairwise sample comparisons), we first applied a Pearson correlation analysis in SPSS 20.0 (SPSS, Inc., Chicago, IL). The environmental factors included geographic distance, soil properties (i.e., pH and SOC density) and climatic factors (i.e., MAT and MAP). To include the nonlinear relationships and multivariate interactions, we conducted a random forest classification analysis to estimate the important predictors to both bacterial and fungal beta diversities among the following variables: geographic distance, soil pH, SOC density, MAT and MAP. Random forest is a new classification and regression approach that modifies standard classification and regression tree methods using bootstrap samples of the training data and random feature selection in tree selection (Liaw & Wiener, 2002). The random forest analysis evaluated the importance of each predictor by looking at how much the mean square error (MSE) increased when the data for that predictor was permuted randomly while others remain unchanged. We conducted these analyses with the RANDOMFOREST package (Liaw & Wiener, 2002) for R, and we also assessed the significance of both the model and each predictor with the RFUTILITIES (Evans & Murphy, 2016) and RFPERMUTE (Archer, 2016) packages, respectively. We also evaluated the importance of all environmental factors and microbial beta diversity in the soil carbon metabolic profiles with a random forest analysis following the same protocols.

We used structural equation modelling (SEM) (Grace, 2006) to evaluate the direct and indirect relationships between geographic distance, environmental factors (significantly indices based on Random forest analysis), microbial beta diversity, network properties and the carbon metabolic profile. An a priori model was usually constructed based on a literature review, and our knowledge of how these predictors are related (Fig. S3). Data manipulation was required before modelling. We examined the distributions of all of our endogenous variables and tested their normality. Non-normally distributed data were ln-transformed to improve normality. After the data manipulation, we parameterized our model using our data set and tested its overall goodness of fit. Here, we used the chi-square test (the model has a good fit when $p > .05$), the goodness of fit index (GFI; the model has a good fit when GFI >0.9) and the root mean square error of approximation (RMSEA; the model has a good fit when RMSEA <0.05 and $p > .05$) (Schermelleh-Engel & Moosbrugger, 2003). As some of the introduced variables were not normally distributed even after the transformations, we confirmed the fit of the model with the Bollen–Stine bootstrap test (the model has a good fit when the bootstrap $p > .10$). The a priori model attained acceptable fit for both bacterial and fungal models, and thus no post hoc alterations were conducted. With reasonable model fit, we interpreted the path coefficients of the models and the associated p-values. Additionally, we calculated the standardized total effects (by summing all direct and indirect pathways between the two variables) of geographic distance, MAT, MAP and SOC density on microbial beta diversity. All the SEM analyses were conducted using IBM® SPSS® AMOS 20.0 (AMOS IBM USA).

Intrakingdom interaction networks for soil bacteria and fungi were constructed separately to show the different topological features with Co-occurrence Network inference (CoNet). CoNet is a robust ensemble-based network inference tool designed to detect nonrandom patterns of microbial co-occurrence using multiple correlation and similarity measures (Faust et al., 2012). The OTUs were filtered by setting six as the minimum occurrence across 18 samples. Then, we selected four methods to evaluate pairwise associations among OTUs: Pearson, Spearman, Bray–Curtis and Kullback–Leibler correlation methods. Initial thresholds for all four measures were selected to retrieve 1,000 positive and 1,000 negative edges. For each measure and edge, 1,000 renormalized permutation and 1,000 bootstrap scores were generated to alleviate compositionality bias. The measure-specific p-value was computed first and then merged with Brown's method (Brown, 1975). Edges with merged p-values below .05 were kept after multiple testing using the Benjamini–Hochberg procedure (Benjamini & Hochberg, 1995). The final network was obtained after the permutations as the null distribution and the bootstraps as the random distribution. The co-occurrence networks were visualized with CYTOSCAPE 3.4.0, and network topological parameters were analysed using Network Analyzer (Assenov, Ramírez, Schelhorn, Lengauer, & Albrecht, 2008). To compare the network properties of bacterial and fungal communities, we extracted subnetworks for each soil sample from the original co-occurrence network by keeping OTUs associated with specific samples. Network density and clustering coefficient for these subnetworks were also calculated. Clustering coefficient was used in the SEM as an indicator of network connectivity.

3 | RESULTS

3.1 | Alpha and beta diversities of bacteria and fungi

After quality filtering, the high-quality reads were clustered into 1,974 and 1,756 different OTUs for bacteria and fungi, respectively. For bacteria, Acidobacteria was the dominant phylum at all sites, followed by Proteobacteria and Chloroflexi, as shown in Fig. S1a. For fungi, Ascomycota was the dominant phylum at sites LA, QZ, ZX and HY. At sites JO and CT, Basidiomycota was the dominant phylum (Fig. S1b). Bacterial alpha diversity (both OTU richness and Shannon diversity index) only showed a significant difference between sites QZ and JO (Table S2). Although the fungal OTU richness among sites was quite different, with the highest value at ZX (404.0 ± 40.0) and the lowest at LA (204.7 ± 46.8), there were no significant differences among these sites in terms of fungal Shannon diversity.

The overall patterns of bacterial and fungal community compositions were visualized using NMDS ordination based on the Bray–Curtis index at the OTU level, as shown in Fig. S1c,d. Both bacterial and fungal community similarities among sites were significantly different (PERMANOVA, bacteria: pseudo-$F = 2.1$, $p < .01$; fungi: pseudo-

$F = 1.5$, $p < .01$). Additionally, samples from JO, ZX and CT were clustered corresponding to their geographic location, especially for the bacterial community. To understand the potential relationship between geographic distance and microbial community similarity, the distance decay relationship was estimated based on linear regression with ln-transformed microbial community similarity and geographic distance (Figure 2). Bacterial community similarity significantly decreased with increasing geographic distance ($\beta = 0.17$, $p < .001$). Bacterial taxonomic divisions also displayed significant distance decay relationships, as shown in Fig. S2a–f; that is, Proteobacteria ($\beta = 0.18$, $p < .001$), Acidobacteria ($\beta = 0.12$, $p < .001$), Actinobacteria ($\beta = 0.16$, $p < .001$), Verrucomicrobia ($\beta = 0.17$, $p = .013$) and Planctomycetes ($\beta = 0.41$, $p < .001$). The strong relationships between community similarity and geographic distance still remained after controlling for the environmental factors (Table S3). In contrast, no significant relationship was found between fungal community similarity and geographic distance ($p = .32$). The fungal distance decay relationships in different taxonomic divisions were also not statistically significant, as shown in Fig. S2g–i.

3.2 | Potential important predictors of microbial beta diversity

To examine the relationships between bacterial and fungal community similarities and environmental factors, we conducted a Pearson correlation analysis, as shown in Table S4 ($n = 135$). The results showed that bacterial community similarity was related to the differences in SOC density ($r = .20$, $p = .02$). Fungal community similarity was related to MAP ($r = -.22$, $p = .009$) and MAT ($r = -.20$, $p = .02$) differences. To investigate the potential important predictors of microbial beta diversity, we conducted random forest modelling with geographic distance, MAP, MAT, soil pH and SOC density (Figure 3). Models for bacterial and fungal beta diversities were both significant at the 0.01 level with 5,000 trees. The model indicated that the most important predictor of bacterial beta diversity was geographic distance, followed by SOC density, MAP and MAT. For the fungal beta diversity, MAP was most important predictor, followed by MAT, geographic distance and SOC density. Soil pH was not significant indicator for neither bacterial nor fungal beta diversity; thus, we removed soil pH in the following analyses.

3.3 | The direct and indirect effects of geographic and environmental distance on microbial beta diversity

We used SEM to identify the potential direct and indirect effects of geographic and environmental distance on bacterial and fungal beta diversities, which was used widely in other terrestrial ecosystems (Delgado-Baquerizo et al., 2016; García-Palacios, Maestre, Kattge, & Wall, 2013). The final models fitted both the bacterial (Figure 4a) and fungal beta diversity (Figure 4b) data sets. Geographic distance was the most significant parameter directly influencing bacterial beta diversity ($r = -.60$, standardized coefficient). MAP directly ($r = .24$) and indirectly through mediating SOC densities ($r = -.28$) affected the bacterial beta diversity. SOC densities also directly influenced the bacterial beta diversity ($r = .19$). MAT had poor direct impacts on bacterial beta diversity. Overall, geographic distance, MAP and SOC densities were important in impacting bacterial beta diversity, as indicated by the standardized total effects based on the SEM analyses (Table 1).

Climatic factors played an important role in shaping the fungal beta diversity (Figure 3b). MAP was the most significant factor directly influencing the fungal beta diversity ($r = .28$), and it had an indirect effect through SOC densities. There was also a weaker and significant relationship between MAT and fungal beta diversity ($r = -.18$). Geographic distance and SOC densities had poor direct impacts on fungal beta diversity. According to the standardized total effects in Table 1, MAP and MAT were most important in impacting fungal beta diversity.

3.4 | Distinct co-occurrence patterns of soil bacteria and fungi

Distinct patterns were detected in the bacterial and fungal co-occurrence networks (Figure 5a,b). After quality filtering and OTU clustering at 97% identity, 1974 OTUs for bacteria across the 18 soil samples were used to detect the bacteria–bacteria interactions. The co-occurrence network of bacteria captured 536 associations (edges) among 465 OTUs (nodes), with 64.2% positive edges and 35.8% negative edges (Table 2). To assess the potential interactions among the main bacterial phyla (Figure 5c), the number of relationships

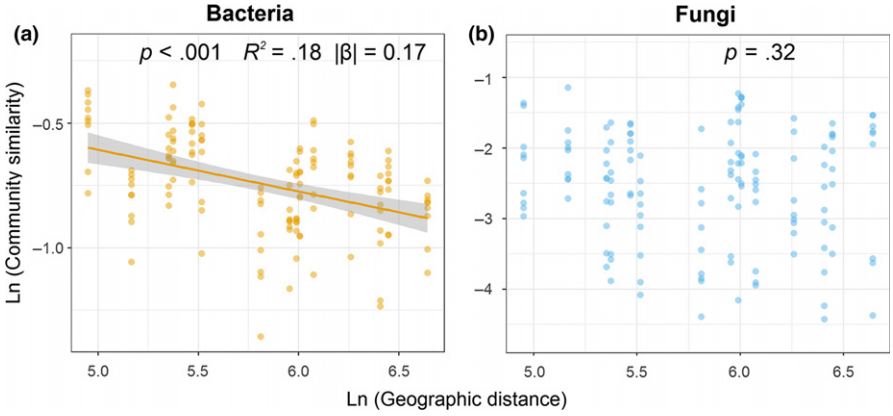

FIGURE 2 Relationships between soil bacterial (a) and fungal (b) community similarities and geographic distance based on Bray–Curtis similarity indices [Colour figure can be viewed at wileyonlinelibrary.com]

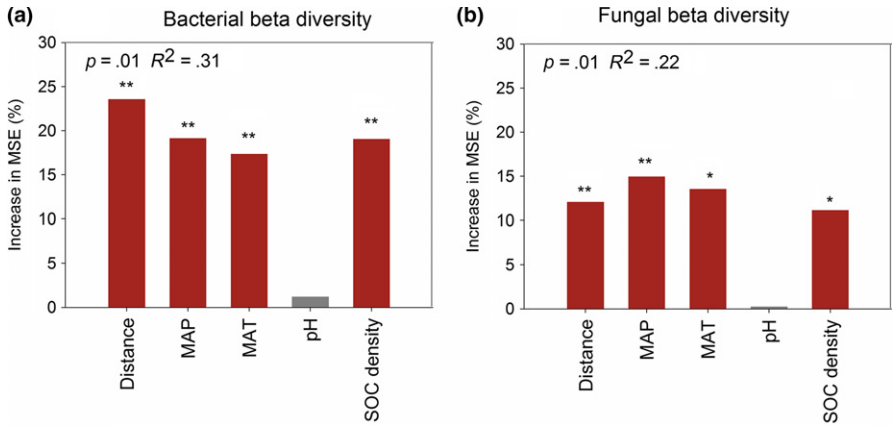

FIGURE 3 Mean predictor importance (% of increased mean square error) of environmental distance on soil bacterial (a) and fungal (b) beta diversities based on random forest analyses. Significance levels of each predictor are as follows: $^{*}p < .05$ and $^{**}p < .01$. Distance, geographic distance; MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon [Colour figure can be viewed at wileyonlinelibrary.com]

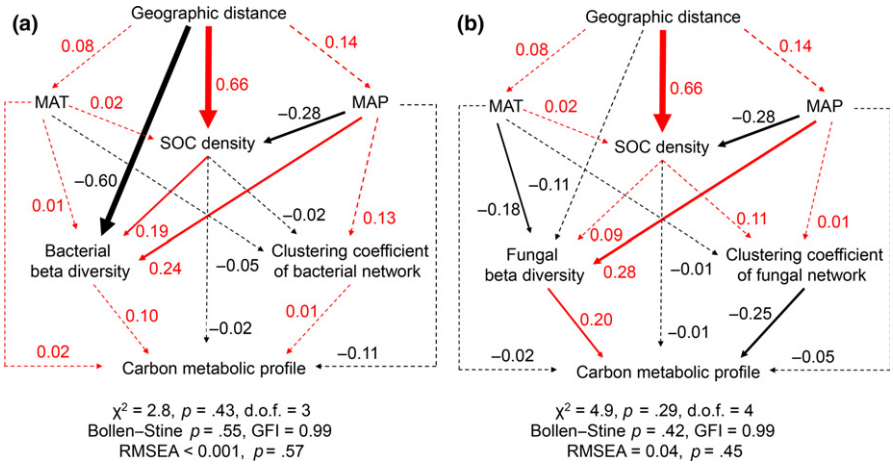

FIGURE 4 Direct and indirect effects of environmental distance on soil bacterial (a) and fungal (b) community assembly. Single-headed arrows represent causal relationships. Red and black arrows indicate positive and negative relationships, respectively. Dotted arrows represent nonsignificant paths ($p > .05$). Numbers adjacent to arrows are standardized path coefficients. The path widths are scaled proportionally to the path coefficient. MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Standardized regression weights of direct (*D*), indirect (*I*) and total (*T*) effects of environmental factors on microbial beta diversity in bamboo forest soil

Bacterial beta diversity				Fungal beta diversity			
	D	*I*	*T*		*D*	*I*	*T*
Ln (Distance)	−0.60***	0.15	−0.45	Ln (Distance)	−0.11	0.08	−0.03
Ln (MAP)	0.24**	−0.05	0.19	Ln (MAP)	0.28**	−0.03	0.25
Ln (MAT)	0.003	0.003	0.006	Ln (MAT)	−0.18*	0.00	−0.18
Ln (SOC density)	0.19*	0.01	0.20	Ln (SOC density)	0.09	0.00	0.09

Distance, geographic distance; MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon.
$^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

between nodes for each phylum pair was counted. Proteobacteria tended to be positively associated with members of Actinobacteria but negatively associated with Planctomycetes and Chloroflexi. Acidobacteria were mainly positively related to Planctomycetes (15 positive associations of a total of 19 associations) and Actinobacteria (four negative associations of a total of four associations). We also identified the fungi–fungi interactions among 1756 fungal OTUs. The network captured 1052 associations (85.3% positive edges and 14.7% negative edges) among 225 OTUs (Table 2). The results of the potential interactions among the main fungal classes showed a dominance of positive associations between fungal classes (Figure 5d).

The analysis of network topological properties revealed that the fungal network had higher network density (how densely the network is populated with edges) and clustering coefficients (how well the nodes are connected with their immediate neighbours) than the

bacterial network (Table 2). For a meaningful comparison of network properties, 18 subnetworks were generated for both bacterial and fungal communities. The topological properties, that is network density and clustering coefficients, indicated a potentially more connected fungal network compared with bacteria (Fig. S4). Additionally, these features indicated that the fungi displayed small-world behaviour. In a small-world network, most OTUs are accessible to every other OTU through a relatively short path (Layeghifard, Hwang, & Guttman, 2017). The degrees for the bacterial network were distributed according to power-law distributions (Fig. S5), which indicated a scale-free network structure. A scale-free network indicates that a few OTUs have many associations with other OTUs, while most have few associations.

3.5 | Soil carbon metabolic profiles

The SEM results indicated significant effects of fungal beta diversity (r = .20) and cluster coefficient (r = −.25) on the soil carbon metabolic profile. However, bacterial beta diversity (r = .10) and cluster coefficient (r = .01) were weakly related with carbon metabolic profile. Based on the SEM results, neither climatic factors nor soil properties were directly related to the carbon metabolic profile. The random forest model also indicated that the beta diversity and cluster coefficient of fungi were the most important factors predicting the carbon metabolic profile in bamboo forests (Figure 6a). According to the random forest model, the mean square error (MSE) increased approximately 14.4% and 6.1% when removing the predictor of fungal beta diversity and cluster coefficient, respectively. However, removing the bacterial beta diversity and cluster coefficient only increased the MSE by approximately 1.7% and 1.8%, respectively. Among the three dominant fungal phyla, only the Ascomycota community similarity was significantly related to the carbon metabolic profile (r = .25, p = .004). Relationships between taxonomic abundances and carbon metabolic activities were also estimated to explore the potentially important microbial groups in carbon metabolism in bamboo forests (Figure 6b). The abundances of Chaetosphaeriales (Ascomycota), Helotiales (Ascomycota) and Mortierellales (Zygomycota) were positively related to the soil metabolism of amines. Agaricales (Basidiomycota) abundance was correlated with the soil metabolism of both amino acids and phenolic

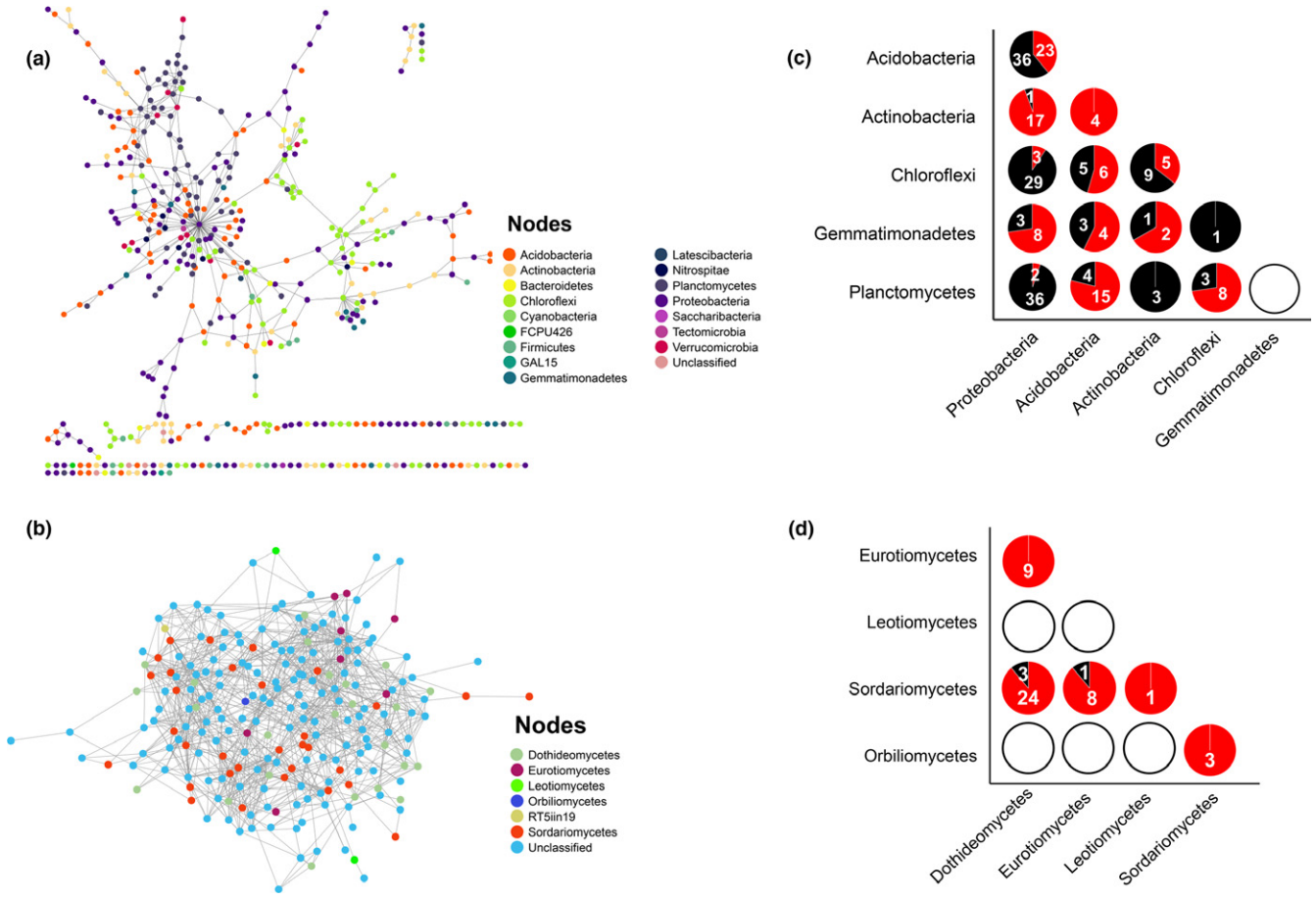

FIGURE 5 Overview of the co-occurrence networks for (a) bacterial and (b) fungal communities in bamboo forest soils and the number of associations among (c) bacterial phyla and (d) fungal classes. Each node represents an operational taxonomic unit (OTU). Node size is proportional to the relative abundance. Pie charts in c and d represent the relative abundance of positive and negative associations among bacterial phyla or fungal classes in the networks. Red circles: positive associations among the taxa; black circles: negative associations among the taxa; unfilled circles: no significant associations among the taxa [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Properties of bacterial and fungal co-occurrence networks in bamboo forest soils

Networks	Nodes	Edges			Network density	Clustering coefficient
		Total	Positive	Negative		
Bacteria	465	536	344 (64.2%)	192 (35.8%)	0.005	0.12
Fungi	225	1052	897 (85.3%)	155 (14.7%)	0.042	0.32

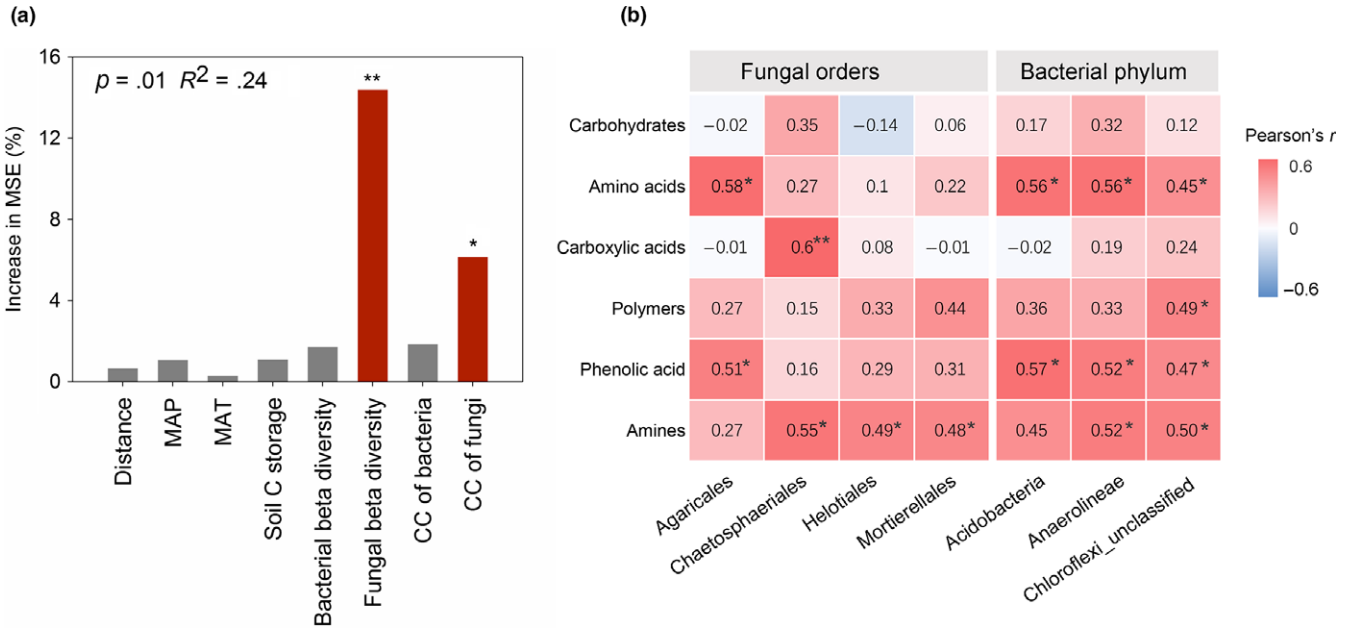

FIGURE 6 (a) Mean predictor importance (% of increased mean square error) of environmental distance and microbial community assembly on carbon metabolic profiles based on random forest analyses. Distance, geographic distance; MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; CC, clustering coefficient; (b) The correlations between taxonomic abundance and carbon metabolic activity of different substrates. Significance level of predictors is as follows: $^{*}p < .05$; $^{**}p < .01$ [Colour figure can be viewed at wileyonlinelibrary.com]

acid. We also found a significant relationship between Chaetosphaeriales abundance and the metabolism of carboxylic acids. The abundance of three bacterial phyla was also related to carbon metabolic activities.

4 | DISCUSSION

4.1 | Less dispersal limitation in the fungal community and the underlying mechanisms

A significant distance decay relationship was detected in the bacterial communities but not in the fungal communities in bamboo forest soils (Figure 2). The soil bacterial community compositions were quite different among locations at the regional scale (Fig. S1c). This variation was spatially autocorrelated, that is, the soil bacterial community similarity across bamboo forests declined significantly with geographic distance. However, we did not detect a distance decay relationship for fungi in bamboo forest soils. Distance effects are often attributed to historical processes, including drift and past selection, along with dispersal limitation (Hanson et al., 2012). The strong direct effect of geographic distance on the bacterial community similarity indicated the importance of dispersal limitation among all the evolutionary and ecological processes in shaping the bacterial diversity (Figure 4a). Although the 16S rRNA genes of the relatively common taxa are widely distributed, bacteria are dispersal limited even at local scales (Martiny et al., 2011). Compared with bacteria, less dispersal limitation was found in fungi based on the absence of distance decay patterns in both fungal communities and fungal taxa. However, two additional considerations will be important to draw the conclusion of less dispersal limitation for fungi. First, some unmeasured environmental factors may be strong controls on bacteria, such as soil nutrients N/P, or soil moisture (Flores-Rentería, Rincón, Valladares, & Curiel Yuste, 2016; Martiny et al., 2011), that may account for autocorrelated variation with geographic distance and drive the spatial pattern in bacterial communities. Second, the measured environmental factors in our study, especially MAP, MAT and SOC density, are all controls on the decomposition and may more strongly structure the fungal communities. Nevertheless, the different dispersal potential for soil bacteria and fungi requires further studies.

Distance decay patterns have been previously reported for soil fungal communities, for instance, in a meadow ecosystem (Schmidt et al., 2013) and natural forests (Davison et al., 2012). In addition to the relatively lower dispersal limitation in fungi, the selective effects of aboveground plants on the fungal community might also

lead to a pattern of less spatial heterogeneity among the fungi in this monoculture ecosystem. Soil fungal communities have been reported to show more tree specificity compared to those of bacteria (Urbanová, Šnajdr, & Baldrian, 2015), especially rhizospheric fungi (Mummey & Rillig, 2006). In fact, in addition to the highly documented root-symbiotic taxa, tree specificity is also exhibited by saprotrophic fungi (Urbanová et al., 2015). Based on our results, the plant specificity of soil fungi could be attributed to their important roles in the decompositional processes as supported by the Biolog analysis (Figures 4 and 6). The prevalent saprotrophic fungi (i.e., Ascomycota and Basidiomycota) were reported to have important roles in degrading refractory carbon (Courty et al., 2010). The physiological properties further suggested that the fungal communities might be more active in bamboo forests, where there is high concentration of lignin derived from bamboo litters. Additionally, it is notable that with lower diversity in fungal communities (Table S2), stochastic sampling effects may also contribute to the detection of their lesser heterogeneity compare with bacteria. Increasing sampling efforts and/or the number of sample replicates should be the effective ways to ameliorate the effect from stochastic sampling (Zhou et al., 2013). Thus, studies with a more extensive sampling effort are needed to confirm the distinct spatial patterns of soil bacterial and fungal communities in bamboo forest ecosystems at regional scales.

Although soil bacteria and fungi have quite different dispersal rates, environmental selection (especially based on climatic factors) significantly influenced both groups. Here, we measured only few environmental factors though important ones, including MAP, MAT and SOC density. In this case, we reported a stronger selection on fungal communities. Contemporary environmental selection has been reported to influence diversity patterns by altering the relative abundances of species (Hanson et al., 2012). In our study, higher SOC densities seemed to promote the abundance of several bacterial taxa, such as Actinobacteria, Candidate_division_TM7, Firmicutes, Gemmatimonadetes, TM6 and WCHB1-60 ($p < .05$, Table S5). MAP impacted their abundance positively or negatively. We also detected an indirect effect of the MAP on bacterial community assembly by altering the SOC densities according to the SEM analysis because precipitation will increase the soil moisture, which then intensifies the loss of carbon in the soil (Nielsen & Ball, 2015). The fungal community similarity also varied with the MAP and MAT. Both temperature and precipitation have been reported to impact the fungal community indirectly via their effects on plants and soil nutrients (Bahram, Polme, Koljalg, Zarre, & Tedersoo, 2012). Taken together, water–energy dynamics also play an important role in shaping microbial communities at regional scales. Although we evaluated the effects of dispersal and selection on microbial assembly, the caveat here is that other ecological processes (i.e., drift and diversification) might also be crucial in shaping the microbial geographic patterns. Meanwhile, with complex interactions among these assembly processes (Evans, Martiny, & Allison, 2017), a more comprehensive way of describing how these processes shape community assembly is required in further work (Zhou et al., 2014).

4.2 | Potentially more connected network of fungi than that of bacteria in bamboo forest soils

Microbe–microbe interactions have also been shown to influence microbial distributions and ecological functions (Barberan et al., 2012). With different dispersal abilities and selection strengths of bacteria and fungi in bamboo forest soils based on the results, we further evaluated the potential contributions of their network topological characteristics to the spatial assembly. In consistent with previous studies, soil bacterial and fungal communities in bamboo forest also exhibited scale-free and small-world characteristics as in other ecosystems (Jiang et al., 2017; Zhou et al., 2010). To date, few study compared the network properties between microbial groups as they always considered them a meta-community functioning in the environment. In our study, we aimed to discuss the potential reasons of distinct spatial patterns of two groups through understanding their intrakingdom interactions. Here, we reported that the bacterial network was potentially less connected than the fungal network in bamboo forest soils based on their topological properties. On the one hand, this is likely due to the high habitat variability covered by bacteria and the presence of fungi in restricted environments. On the other hand, a recent study suggested that the more connected network may contribute to the efficient carbon utilization (Morriën et al., 2017). Our results that fungi were more active in decompositional processes with a potentially more connected network further proved their finding. The co-occurrence networks of both bacteria and fungi indicate multiple potential microbe–microbe interactions in bamboo forest soil. For the bacterial network, positive associations between members of Proteobacteria and Actinobacteria as well as between members of Acidobacteria and Planctomycetes might indicate their interdependencies or consistent responses to similar environmental conditions (Eiler et al., 2012). An opposite result was described in agricultural soils, where Actinobacteria had a negative correlation with Proteobacteria (Durrer et al., 2017). This indicates that interaction patterns might vary among different habitats containing other indigenous groups. Co-occurrence networks also help to detect potentially competition relationships between bacterial groups, for example, between the members of Acidobacteria and Gemmatimonadetes as well as between Actinobacteria and Planctomycetes. However, for fungi, positive associations between taxonomic groups dominated the whole network, that is, the members of Sordariomycetes with Agaricomycetes, Dothideomycetes, Eurotiomycetes and Leotiomycetes (Figure 5d). Although we reported distinct co-occurrence networks of bacterial and fungal communities, these findings should be interpreted cautiously, as microbial diversity may influence network properties (Faust et al., 2015). Thus, further studies about how microbial diversity will influence their network properties are necessary. Despite these inadequacies, network analysis using an OTU-based approach represents a step forward in understanding microbial community assembly beyond conventional studies of microbial richness and abundance.

4.3 | Connectivity of microbial ecological features to carbon metabolism in bamboo forests

Soil bacteria and fungi are involved in the decomposition of most plant detritus in terrestrial ecosystems (Swift, Heal, & Anderson, 1979), forming the key step in carbon cycling by mediating the balance of carbon being respired as CO_2 into the atmosphere or stored in the soil. Our results showed that both fungi and bacteria are involved in utilizing a variety of carbon substrates in bamboo forest habitats, such as amines, phenolic acid, carboxylic acid, polymers and amino acids. However, the fungal community assembly better predicts metabolic profile similarities than bacteria in bamboo forest soils according to both SEM and random forest analyses. Fungi are known to have broader enzymatic capabilities (de Boer, Folman, Summerbell, & Boddy, 2005), slower biomass turnover rates (Rousk & Bååth, 2011) and potentially higher carbon use efficiency (Six, Frey, Thiet, & Batten, 2006) than bacteria. The essential role of soil fungi in carbon sequestration is always highlighted in forest ecosystems due to their ability to degrade complex substrates. These physiological differences enable fungi to play a more important role than bacteria in bamboo forests with abundant complex substrates. A recent study in bamboo forests described that the variation in soil fungal communities was closely related to changes in organic C forms (Li et al., 2017). In addition to their physiological differences, the ecological differences between fungi and bacteria might also contribute to their functional traits relevant to carbon metabolism. Our results showed that the fungal community revealed less dispersal limitation, stronger environmental selection and a possibly more highly connected and positively dominated network than bacteria. Based on these characteristics, fungi may have a relatively stable community composition at small scales and less heterogenous distribution at regional scales compared to bacteria. Fungi have previously been reported as being the most connected group among microbes (archaea, bacteria, fungi and arbuscular mycorrhizal fungi) in forest soils, which has been linked with their importance in food webs and SOC cycling (Creamer et al., 2016). This finding further demonstrated the importance of fungi in soil carbon cycling in bamboo forests in our study.

In summary, overall depictions of the spatial patterns, network structures and carbon metabolism-based functional traits of both bacterial and fungal communities in bamboo forest soils were provided in this study. We detected a significant distance decay relationship for bacteria but not for fungi. Both dispersal limitation and environmental selection contributed to the soil bacterial distribution pattern. However, the fungal community showed less dispersal limitation compared to the bacterial community. Environmental selection, especially caused by climatic factors, strongly influenced fungal community assembly. Moreover, there were distinct co-occurrence patterns in bacteria and fungi, with potentially higher connectivity and dominant positive associations in the fungal network. The significant effects of fungal beta diversity and clustering coefficient on the carbon metabolic profile indicated that the dispersal potential, environmental selection and network structure of microbial taxa likely contributed to their carbon metabolic-based functional traits. Additionally, the overall analysis and frameworks used in our study can also be applicable to other ecosystems to identify the significant environmental drivers and ecological processes in shaping the microbial assemblies which could be connected with their ecosystem functioning.

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AUTHOR CONTRIBUTION

B.S. and S.-Y.Z. conceived and designed the experiments; S.Z. and X.X. conducted the laboratory analysis; X.X. and Y.-T.L. performed the analyses and wrote the first draft of the manuscript, and all authors contributed substantially to revisions. X.X. and Y.-T.L. contributed equally to the study.

DATA ACCESSIBILITY

Raw sequence data for 16S rRNA and ITS gene amplicons were deposited under NCBI BioProject Accession No. PRJNA380749 and No. PRJNA380834, respectively. Environmental data and location information associated with the sequences in this article are archived in Dryad, https://doi.org/10.5061/dryad.33th5

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