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The contrasting roles of fungal and bacterial diversity and composition in shaping the multifunctionality of rhizosphere and bulk soils across large-scale bamboo forests

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Abstract

Soil microbes regulate nutrient cycling, organic matter decomposition, and other processes, thereby maintaining soil multifunctionality (SMF). However, the relationship between microbial characteristics and soil multifunctionality has primarily been studied in bulk soils, with less attention to rhizosphere soils. Moreover, this relationship remains unclear within a single forest type across large scales. In this study, we selected six sites across the distribution range of moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz.) in China to quantify the relationship between microbial communities and soil multifunctionality in both rhizosphere and bulk soil, and to evaluate how abiotic factors influence this relationship. Our results showed that microbial diversity was negatively correlated with SMF, while the key microbial drivers (bacteria or fungi) of SMF varied between soil compartments (i.e., rhizosphere and bulk soil). Soil variables influenced SMF in bulk soils by affecting bacterial diversity and fungal composition, whereas in rhizosphere soils, soil variables influenced SMF primarily by affecting fungal diversity and composition, suggesting that different characteristics of bacterial and fungal communities drive SMF. Climatic factors exert a more significant influence on the multifunctionality of rhizosphere soils compared to bulk soils. Considering the intricate interplay between plants and soil microbes, our study highlights the importance of integrating SMF and microbial community structure within distinct soil compartments.

Keywords Driving factors, Microbial composition, Microbial diversity, Moso bamboo, Soil compartment, Soil multifunctionality

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Introduction

Soil multifunctionality (SMF), a comprehensive indicator of the soil's ability to simultaneously deliver multiple functions, contributes to the assessment of forest ecosystem functioning and regional sustainable development [1]. Notably, soil microbes play a paramount role in biogeochemical cycling and maintaining a multitude of soil functions, such as carbon sequestration and nitrogen mineralization [2, 3]. Changes in soil communities and the loss of diversity threaten soil multifunctionality and sustainability [4, 5]. However, bacteria and fungi exhibit differences in nutrient acquisition and organic matter decomposition, which may lead to varying degrees of their impact on soil multifunctionality [6]. Furthermore, due to the strong influence of root secretions and root activity, microbial community characteristics differ significantly between rhizosphere and bulk soils, potentially resulting in compartment-specific variations in the relationship between microbial characteristics and soil multifunctionality.

Previous studies on microbial characteristics-soil multifunctionality relationships have mainly focused on bulk soils [7–9]. For instance, Han et al. found that bacterial rather than fungal diversity drives bulk soil multifunctionality in subtropical forest ecosystems, and that bacterial diversity was negatively correlated with bulk soil multifunctionality [10]. Fungal rather than bacterial richness was positively correlated with bulk soil multifunctionality in boreal forest ecosystems [11]. Moreover, climatic factors can also influence the driving effect of microbial diversity on soil multifunctionality, directly by modulating the effect of soil properties on microbial diversity [12, 13], indicating that the role of climatic factors in the relationship between microbes and soil multifunctionality cannot be ignored [14]. For example, precipitation-induced changes in soil pH determine microbial gene abundance, which in turn affects bulk soil multifunctionality [15].

The zone surrounding plant root growth (rhizosphere) is an essential hotspot for plant water and nutrient uptake, rhizosphere deposition, microbial activity and plant-soil-microbe interactions [16, 17]. Previous studies on the relationship between microbes and soil multifunctionality concentrated on bulk soils, ignoring the fact that the existence of rhizosphere effects may lead to unexpected results [2, 13, 18]. A study of six dominant tree species in mountain ecosystem revealed a negative correlation between soil bacterial diversity and rhizosphere soil multifunctionality. In contrast, fungal diversity did not exhibit a significant relationship [19]. In fact, this relationship in rhizosphere soils remains poorly understood, particularly when based on pairwise comparisons with bulk soils. Specifically, climate change may lead to significant variations in soil microbial diversity and community composition at the rhizosphere-bulk interface by affecting plant root secretion fractions/rates, soil moisture, and nutrient availability [20, 21].

Bamboo is a woody, clonal plant with a wide distribution, high economic value, invasive capacity, and "explosive" growth characteristics [22]. In this study, we evaluated how microbial characteristics, climate, and soil factors predict soil multifunctionality at the rhizosphere-bulk interface in 24 sample plots from the main habitat area of moso bamboo forests in subtropical China. Our research focuses on the relationship between soil multifunctionality and microbial characteristics in relation to environmental drivers in moso bamboo forests. We hypothesize that: (1) A decrease in soil microbial diversity and a simplification of soil community composition will impair multiple ecosystem functions, and that microbial diversity and composition will jointly drive soil multifunctionality (H1); and (2) Due to distinct growth strategies, resistance, and resilience exhibited by bacteria and fungi, their relationships with soil multifunctionality will be inconsistent (H2). We also hypothesize that environmental factors will significantly influence the microbial diversity/composition-soil multifunctionality relationships (H3). Furthermore, due to the rhizosphere effect, rhizosphere and bulk soil microbial communities will exhibit dissimilarity, and the patterns driving soil multifunctionality will differ distinctly between rhizosphere and bulk soil microenvironments (H4).

Materials and methods

Study site

We sampled soil samples at six study sites (Changning, Xinyang, Anji, Taojiang, Conghua, Longmen) over an extensive area (> 1,600,000 km^2) in the main distribution areas of moso bamboo forest in subtropical China (N23°38'06"–31°49'14" and E105°01'13"–119°36'35") during the growing season of 2019 (Figure S1). To minimize the potential effects of human disturbances (e.g. logging, fertilizer, under forest economy) on soil community, natural bamboo forests as object of this study. According to the Chinese soil classification system, the soil types included yellow-red soil, red soil, yellow soil and yellow-brown soil. For each of the sites, we complied climate data from WorldClim v2 (https://www.worldclim.org/data/worldclim21.html). The sites ranged in MAT from 14.21 to 20.20 °C, in MAP from 91.00 to 151.00 cm, and in elevation from 252 to 877 m (Table S1).

Soil sampling and analyses

At each site, we established four 20 × 20 m plots, and the distance between any two plots was more than 1000 m. The selected plots had similar habitats, including slope and aspect, and information such as geographic location was recorded. Rhizosphere and bulk soil samples were collected from the topsoil (0–10 cm) of moso bamboo. Rhizosphere soil, defined as the soil tightly adjacent to the fine root surface, was collected by brushing down soil from the roots using a sterile, soft-bristled brush. Bulk soil was collected by lightly shaking soil from the fine roots [15, 23, 24]. For rhizosphere soil, 6 replicates were collected per plot. For bulk soil, samples from every 3 bamboo plants were mixed into one sample, resulting in 2 mixed samples per plot. In total, 144 rhizosphere soil samples and 48 bulk soil samples were collected. Notably, we also considered the factor of bamboo age, but there was no significant difference between ages, probably resulting from its special whip-root system, and thus their data were pooled for the analysis. Soil was homogenized and manually screened in the field, then the samples were stored in self-sealed bags immediately transported to the laboratory under 4 °C, the fresh soil samples drying naturally and subsample stored in a -80 °C refrigerator.

Soil pH was analyzed by a pH meter (PHS-3 C, INESA Inc., China). Soil water content (WC) was determined by thermo-gravimetric method. Soil total carbon and total nitrogen were determined using an elemental analyzer (Costech ECS 4024 CHNSO, Picarro, California, U.S.A.). Soil total phosphorus, ammonia nitrogen and nitrate nitrogen were measured with an automatic chemical analyzer (Smartchem 4024, AMS Group, Italy). Soil DNA concentration was determined using a Nanodrop (NANODROP 2000, Thermo SCIENTIFIC). Here, we assessed soil multifunctionality using averaging method, soil multifunctionality using several variables that provide a balanced and comprehensive evaluation of soil nutrient cycling, microbial biomass, organic matter decomposition and sequestration: total C, nitrate, ammonium, total N, total P, DNA concentration [2, 12]. In this study, we used DNA concentration as an indicator to estimate microbial biomass [25]. Subsequently, each variable was standardized using Z-score transformation, and the mean of the resulting standardized values was used as the multifunctionality indicator [15].

Soil biodiversity analysis

DNA was extracted using the MO BIO Soil DNA Extraction Kit (MO BIO Laboratories, Carlsbad, CA, USA), and its purity and concentration of DNA were detected using agarose gel electrophoresis and Nanodrop 2000. The diversity of bacteria and fungi in soil was analyzed using high-throughput sequencing, by targeting the V4-V5 region of 16 S rRNA in bacteria and the internal transcribed spacer 2 region in fungi. Bacterial primers were 515 F (5’-GTGCCAGCMGCCGCGGTAA-3’) and 909R (5’-CCCCGYCAATTCMTTTRAGT-3’), fungal primers were ITS4 (5’-TCCTCCGCTTATTGATATGC-3’) and gITS7F (5’-GTGARTCATCGARTCTTTTT) [26, 27]. The PCR amplification conditions were: for bacteria, initial denaturation at 94 °C for 3 min, followed by 30 cycles (94 °C for 40 s, 56 °C for 60 s, and 72 °C for 60 s) and a final extension at 72 °C for 10 min; for fungi, initial denaturation at 94 °C for 5 min, followed by 34 cycles (94 °C for 30 s, 56 °C for 30 s, and 68 °C for 45 s) and a final extension at 72 °C for 10 min. Library construction was performed using the TruSeq® DNA PCR-Free Sample Preparation Kit and sequenced on an Illumina® MiSeq platform.

FASTQ data was processed using QIIME2 v. 2023.2, including sequence quality control, denoising and chimera removal, to obtain the Amplicon Sequence Variant (ASV). Briefly, adaptor sequences and any resulting short reads were removed using CUTADAPT [28, 29]. After plotting read-quality scores (https://view.qiime2.org), sequences were trimmed at a quality score threshold of 28. Bacteria and fungi were truncated at 180 bp and 190 bp, respectively. Chimeras were removed during the Divisive Amplicon Denoizing Algorithm pipeline (DADA2) denoising process. Using Silva v138 (https://www.arb-silva.de/) and UNITE v9.0 (http://unite.ut.ee/) as reference databases for bacterial and fungal annotations, respectively. ASVs not assigned at the domain level or assigned to chloroplasts and mitochondria were removed from the final ASV table. Rarefaction was performed at 10,688, 7000 reads per sample for bacteria and fungi, respectively, during ASV filtering and homogenization.

Statistical analyses

Mixed models were used to compare the effects of compartment and site on soil microbial community diversity. Bray-curtis distance, non-metric multidimensional scaling (NMDS), and permutational multivariate analysis of variance (PERMANOVA) were performed to analyze differences in microbial community composition. These analyses were conducted using the “rcompanion” and “vegan” packages. The “statnet” and “circlize” packages were used to plot microbial community composition at the phylum level. Linear discriminant analysis effect size (LEfSe) in the “microeco” package was used to identify microbial taxa more dominant in different compartments, based on a $P < 0.01$ from the Wilcox test and LDA score > 3.5. Linear Mixed Models (LMMs) were performed to test the relationship between microbial diversity and soil multifunctionality, with plots nested with site as random effect. Given the large sampling area and soil heterogeneity, the influence of climate and soil properties on this relationship was also considered. The LMMs were conducted using the “lme4”, “ggeffects”, and “MuMIn” packages.

Then, the direct and indirect causal relationships between soil variables, microbial (bacterial and fungal) diversity/composition and multifunctionality were constructed using structural equation modelling (SEM) for bulk and rhizosphere soils, respectively. Also, the goodness of fit (GOF) index is greater than 0.6 to ensure the degree of model fit. Random forest (RF) analysis was conducted to identify key taxa (in the phylum-level) driving soil multifunctionality in bulk and rhizosphere soils, respectively. The SEM and RF analysis were performed using "plspm" "randomForest" package, respectively. The metabolic potential of bacterial communities was predicted by PICRUSt2, with STAMP used to analyze differences in KEGG energy metabolism in different compartments. Fungal functional diversity was predicted by Fungaltraits, and the proportion of fungal functional groups in different compartments was visualized using histograms. All data processing was done in QIIME2 v. 2023.2 and R v4.3.2.

Results

Microbial diversity, composition and soil multifunctionality

Site and compartment significantly interacted to affect the alpha diversity of soil microorganisms. The alpha diversity of microbes in bulk soils was higher than that in rhizosphere soils (Fig. 1a and c). The NMDS analyses showed significant separation of microbial communities by site and compartment (Fig. 1b and d). This is also supported by the results of PERMANOVA, showing that compartment, site and their interactions had significant effects on microbial community structure ($P < 0.01$). The bacterial phyla Pseudomonadota, Acidobacteriota, and Actinomycetota, as well as the fungal phylum Ascomycota, were dominant in both rhizosphere and bulk soils (Figure S2). In addition, both rhizosphere and bulk soils had clearly dominant taxa. Rhizosphere soil was enriched in Chloroflexi (Ktedonobacteria), Planctomycetota (Planctomycetes, Gemmatales), Gemmatimonadota (Gemmatimonadetes), Acidobacteriota (Acidobacteriae, Subgroup_2), and Ascomycota (Dothideomycetes, Venturiales, Sordariales, Chaetothyriales, Helotiales). Bulk soil, on the other hand, was enriched in Pseudomonadota (Gammaproteobacteria, Burkholderiales, Enterobacterales, Rhizobiales), Ascomycota (Eurotiomycetes, Saccharomycetes), Mucoromycota (Mucoromycetes), and Basidiomycota (Umbelopsidomycetes, Tremellales) (Fig. 2).

Compared with bulk soils, rhizosphere soils had higher values of physicochemical properties (Table S2). The phenomenon that rhizosphere soils had higher multifunctionality than bulk soils was not static, and the

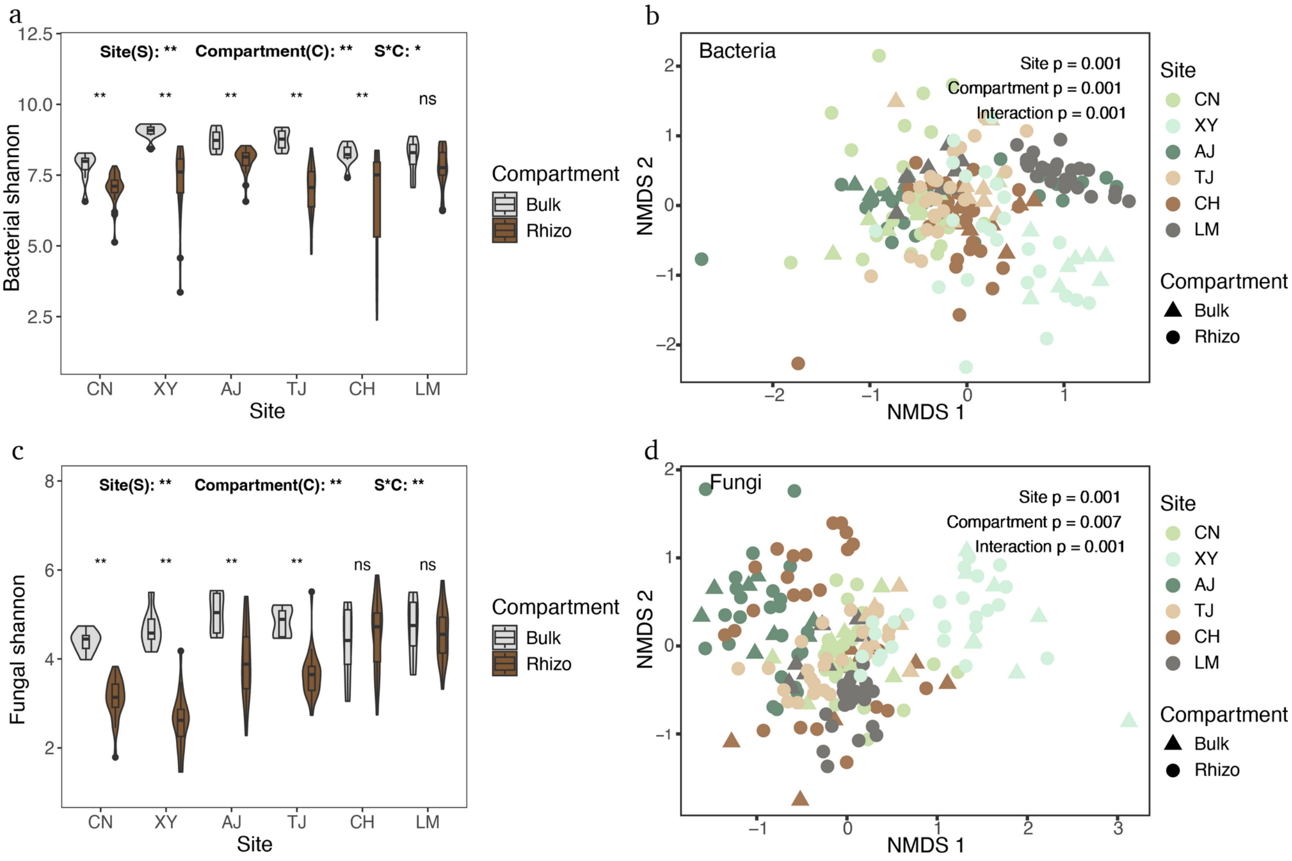

Fig. 1 Effects of site and compartment on soil microbial alpha (**a**, **c**) and beta (**b**, **d**) diversity in moso bamboo forests. Site abbreviations: CN Changning, XY Xinyang, AJ Anji, TJ Taojiang, CH Conghua, LM Longmen. Bulk: bulk soil, Rhizo: rhizosphere soil. '**' $P < 0.01$, '*' $P < 0.05$

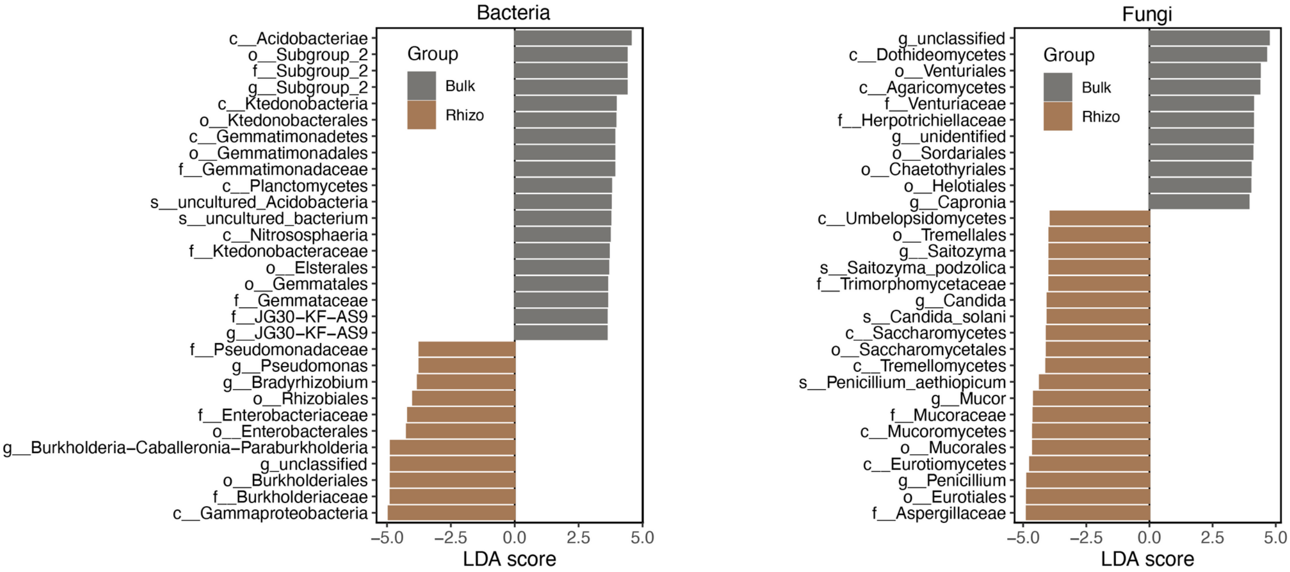

Fig. 2 Dominant microbial taxa in rhizosphere and bulk soils identified by LEfSe (from Phylum to Genus). left: bacteria, right: fungi. Bulk: bulk soil, Rhizo: rhizosphere soil

multifunctionality of rhizosphere soils at the southern edge of the moso bamboo distribution (CH and LM) was significantly less than that of bulk soils. Overall, soil physicochemical properties and multifunctionality were higher in the northwestern region (CN) and lower in the southeastern edge (Table S2).

Correlation between microbial diversity/composition and soil multifunctionality

The alpha diversity of microbes was negatively correlated with SMF (Figs. 3 and 4). In rhizosphere soils, fungal alpha diversity was significantly negatively correlated with SMF, and bacterial richness was significantly negatively correlated with SMF (Fig. 3a, b). In bulk soils, bacterial alpha diversity was significantly negatively correlated with SMF, and fungal richness was significantly negatively correlated with SMF (Fig. 3c, d). Interestingly, fungal alpha diversity was correlated more strongly with SMF than bacterial in rhizosphere soils did; and bacteria alpha diversity dominated SMF changes in bulk soils. Fungal beta diversity was significantly positively correlated with SMF in both bulk and rhizosphere soils, while bacteria did not show an obvious trend (Fig. 4a, b).

Microbial and soil multifunctionality in relation to environmental factors

Climatic variables were significantly negatively correlated with SMF (Fig. 5). Mean annual temperature (MAT) was negatively correlated with SMF in rhizosphere soil, and mean annual precipitation (MAP) was negatively correlated with SMF in both rhizosphere and bulk soil. Compared with bulk soils, climatic factors had a more drastic effect on the multifunctionality of rhizosphere soils. Soil variables (pH and WC) were significantly correlated with SMF (Figure S3). WC was positively correlated with SMF in bulk soil, while pH was negatively correlated with SMF in both rhizosphere and bulk soil. Compared with rhizosphere soil, soil variables had a more drastic effect on the multifunctionality of bulk soil.

Structural equation modeling indicated that microbial diversity and composition are important predictors of soil multifunctionality (Fig. 6). Soil variables were significantly correlated with soil multifunctionality by mediating changes in microbial diversity, and this relationship was significantly affected by soil compartments. In bulk soils, soil variables (pH and WC) altered soil multifunctionality by altering bacterial diversity, whereas in rhizosphere soil, soil variables affected soil multifunctionality by shifting fungal diversity (Fig. 6a, b). It is worth noting that soil variables affect soil multifunctionality by altering fungal community composition rather than bacterial community composition in the rhizosphere, while affecting both bacterial and fungal community composition in bulk soil (Fig. 6c, d). In addition, fungal community composition was positively correlated with soil multifunctionality in both rhizosphere and bulk soils.

However, the contribution of microbial taxa to soil multifunctionality was not always equivalent. To answer the question of which microbial taxa are key predictors of soil multifunctionality, the importance of microbial taxa for soil multifunctionality was evaluated by randomized forests (Fig. 7). Rare phyla (indicated as other in the chord diagram) were more predictive of soil multifunctionality than dominant phyla, except for unclassified, the top three rare phyla predicting soil multifunctionality in rhizosphere soils were WPS-2, Methylomirabilota,

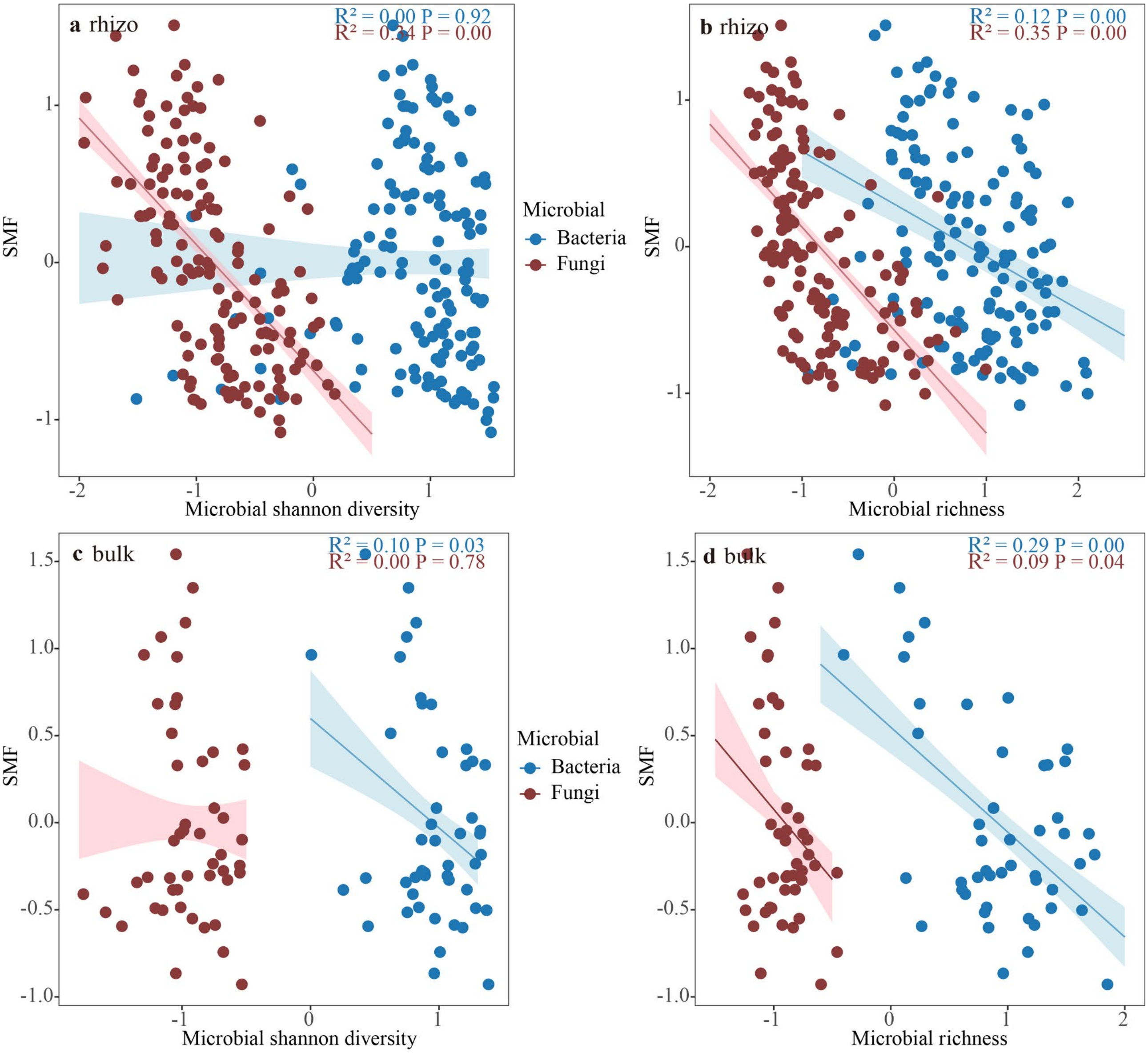

Fig. 3 Relationship between microbial alpha diversity and soil multifunctionality in different soil compartments of moso bamboo forests. Bulk: bulk soil, Rhizo: rhizosphere soil, SMF: soil multifunctionality. Solid lines indicate significant correlation

and NB1-j, and the top three rare phyla predicting soil multifunctionality in bulk soils were WPS-2, Myxococcota, and Planctomycetota, respectively, and the role of rare microbial taxa in maintaining the relationship of soil diversity and multifunctionality should not be ignored (Fig. 7). Consistent with the results of SEM, random forest results also showed that fungi were weaker predictors of multifunctionality in bulk soils than in rhizosphere soils.

Discussion

Bacterial diversity and fungal composition determine SMF in the bulk soil

Bacterial diversity, rather than fungal diversity, mediates the effects of environmental factors on bulk soil multifunctionality. The study showed that changes in fungal pathogen abundance may lead to the decoupling of fungal diversity from SMF by altering biodiversity and relationships between microbes (cooperation or competition) [30]. Generally, it is assumed that loss and simplification of microbial diversity can constrain soil multifunctionality. For instance, reduced microbial abundance may lead to inactivation of key functions and reduce the rate of generation of ecosystem multifunctionality [5, 9, 31].

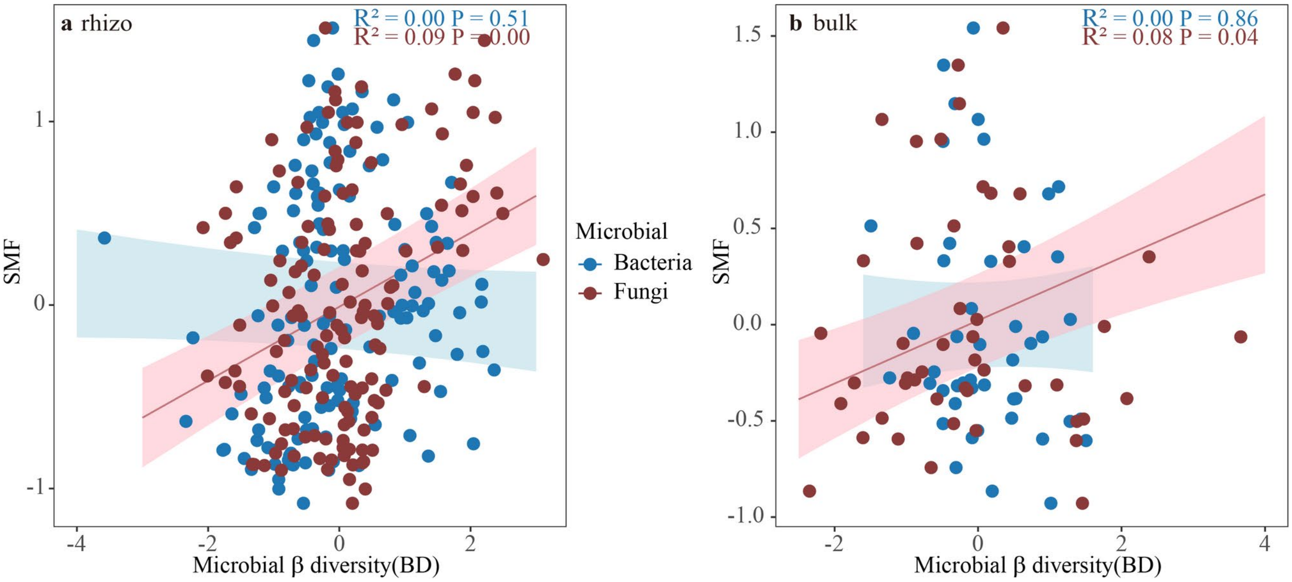

Fig. 4 Relationship between microbial beta diversity and soil multifunctionality in different soil compartments of moso bamboo forests. Bulk: bulk soil, Rhizo: rhizosphere soil, SMF: soil multifunctionality, BD: beta diversity. Solid lines indicate significant correlation

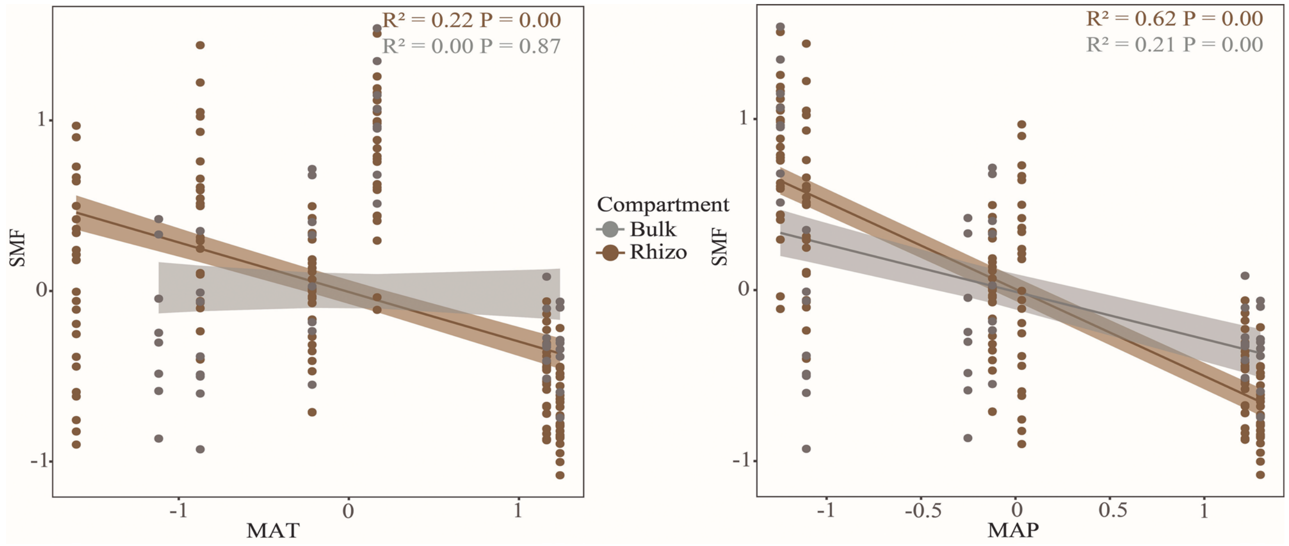

Fig. 5 Relationship between climate and soil multifunctionality in different compartments of moso bamboo forests. Bulk: bulk soil, Rhizo: rhizosphere soil, SMF: soil multifunctionality, MAT: mean annual temperature, MAP: mean annual precipitation. Solid lines indicate significant correlation

Interestingly, our study highlights an unexpected negative correlation between bacterial diversity and bulk soil multifunctionality (Fig. 3c, d). Notably, the effects of functional redundancy, metabolic pathways and requirements, and the complexity of microbial interactions may lead to a negative trend in microbial diversity and soil multifunctionality [10, 32, 33]. In this study, fungal rather than bacterial community composition significantly affected bulk soil multifunctionality (Fig. 6c), which supports our hypothesis H2. Compared to bacterial communities, fungal communities exhibit greater efficiency in decomposing complex organic compounds and acquire resources through their extensive hyphal networks, thereby significantly contributing to soil multifunctionality [15].

Except for biotic factors, abiotic factors also play a critical role in predicting bulk soil multifunctionality, and that climate may influence bulk soil multifunctionality by regulating soil properties, which supports our hypothesis H3, and is also revealed by previous studies [34]. We found that pH and WC affect soil multifunctionality by influencing bacterial community diversity and fungal composition, which is consistent with previous studies (Fig. 6a, c). For instance, soil moisture may affect soil

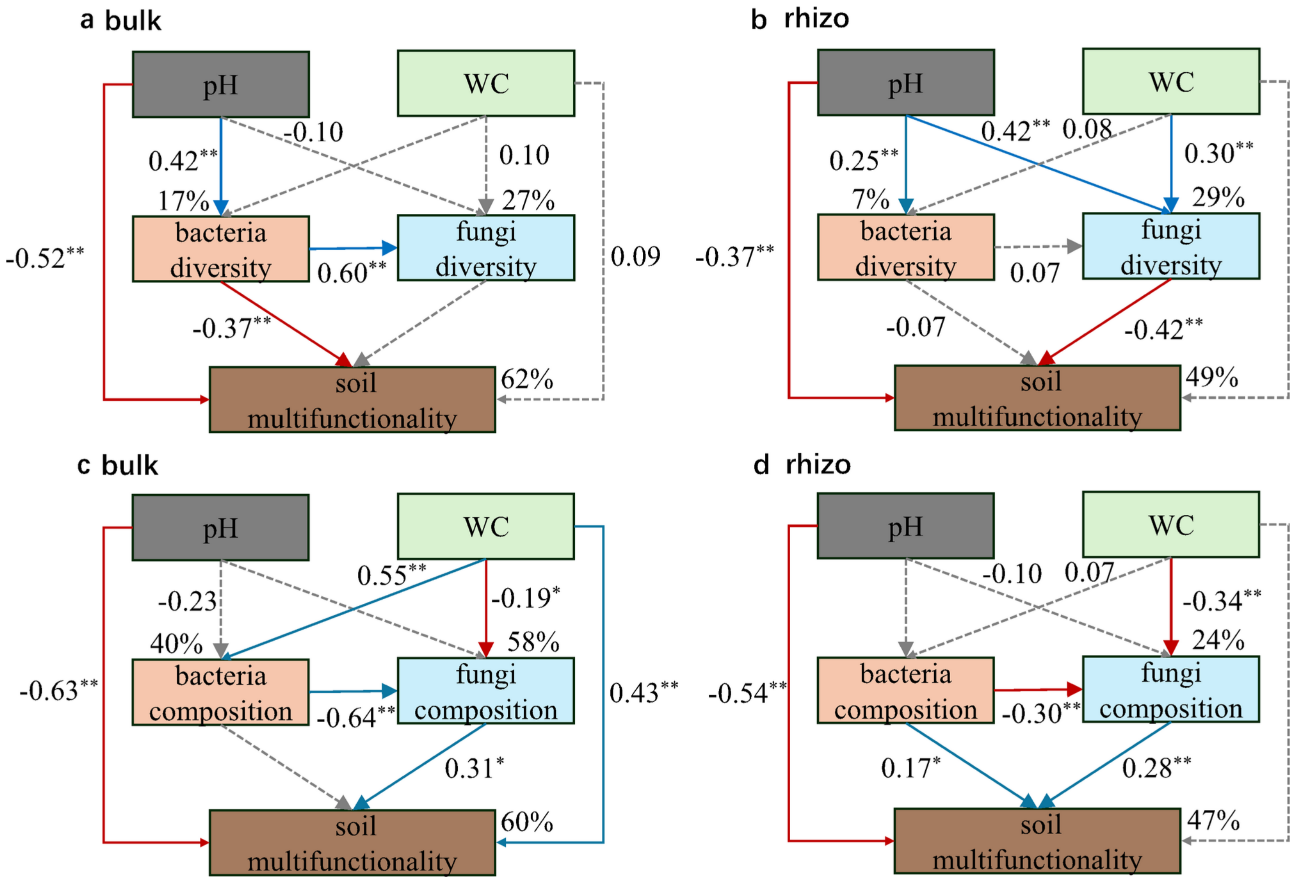

Fig. 6 Relationships between soil properties, microbial diversity (**a**, **b**) /composition (**c**, **d**) and soil multifunctionality in different compartments of moso bamboo forests. Bulk: bulk soil, Rhizo: rhizosphere soil, WC: water content. '**' represents $P < 0.01$, '*' represents $P < 0.05$. Red lines indicate negative correlation, and blue lines indicate positive correlation

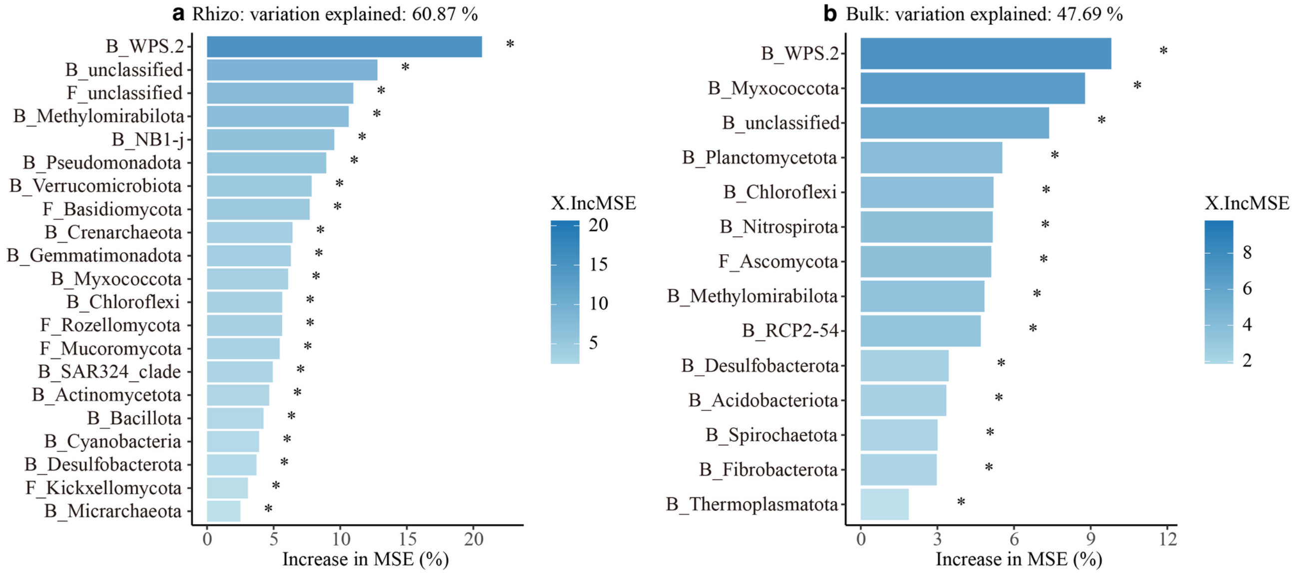

Fig. 7 Important microbial taxa were identified by randomized forests as potentially important predictors of soil multifunctionality. Bulk: bulk soil, Rhizo: rhizosphere soil. B-bacteria, F-fungi. '*' represents $P < 0.05$

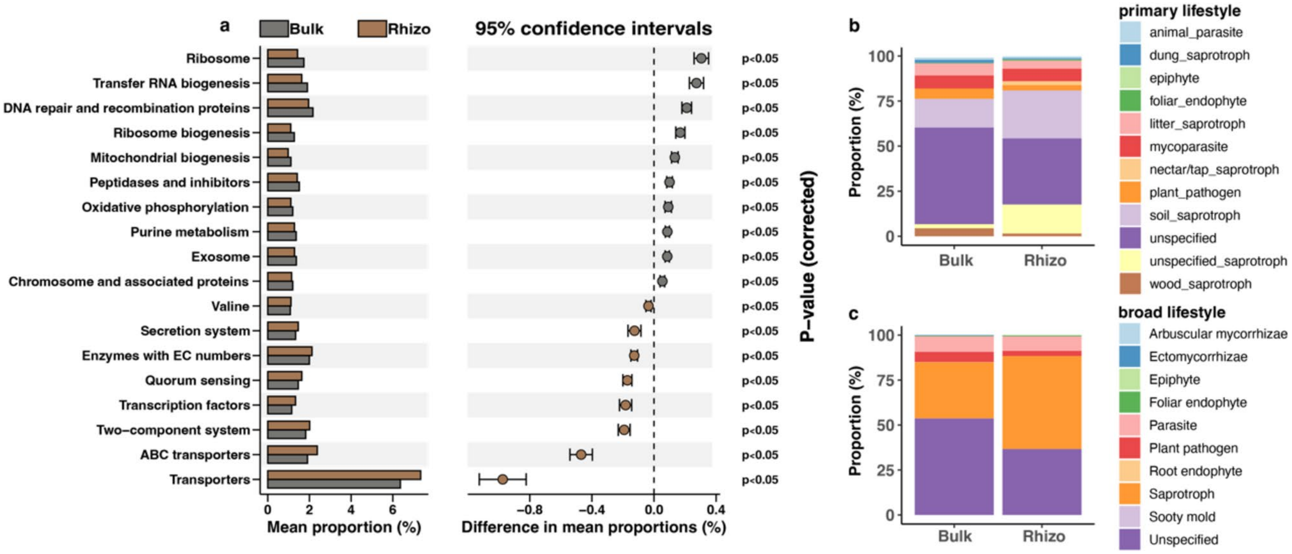

Fig. 8 Functional differences between rhizosphere and bulk soil microbes based on PICRUSt2 and Fungal traits. **a**: bacterial functions, **b** and **c**: fungal functions. Bulk: bulk soil, Rhizo: rhizosphere soil

multifunctionality by altering microbial activity, soluble substrate diffusion, and nutrient cycling processes [7, 35]. pH is a determinant factor influencing microbial diversity and community composition; Microbes that prefer acidic soils may affect soil function by modulating signal transduction, cell motility, secretion systems, and the ability of bacterial taxa to degrade complex compounds [7, 36].

Fungal diversity and composition jointly determine SMF in the rhizosphere soil

Consistent with our hypothesis H4, microbial diversity and composition-multifunctionality relationships in rhizosphere soils exhibit distinct response strategies compared to bulk soils. Specifically, fungal alpha diversity was significantly and negatively correlated with multifunctionality in rhizosphere soils (Figs. 3a, b), likely due to the influence of root secretions and metabolites [20]. Functional predictions indicated that metabolic pathways related to core metabolism and cell maintenance dominated in bulk soils, while metabolic pathways related to signaling, environmental sensing, and enzyme secretion dominated in rhizosphere soils. Rhizosphere soil had a higher proportion of saprotrophic fungi. The differentiation of bacterial metabolic pathways and fungal functional groups in these soil compartments may lead to distinct patterns of microbial characteristic-multifunctionality (Figs. 8). Additionally, plants recruit specific fungi (saprotroph) in the rhizosphere that suppress pathogens, and the overlapping niches of rhizosphere microbes may exacerbate competitive effects and produce opposite results [37, 38]. However, some studies have suggested thant niche differences between functional groups of fungi strengthen complementary effects and thus enhance soil multifunctionality [39, 40]. Importantly, fungal community composition was a critical predictor of soil multifunctionality in the rhizosphere, this result was confirmed by both SEM and random forests (Figs. 6d and 7a). However, some argue that due to issues such as primer mismatches, fragment length, and data processing methods, caution should be exercised when interpreting results regarding fungal diversity [41].

Similarly, abiotic factors influence the relationship microbial diversity/composition-soil multifunctionality in the rhizosphere (see our hypothesis H3). Rhizosphere soil multifunctionality is more sensitive to climate (MAP and MAT) than bulk soils, suggesting that more attention should be paid to the rhizosphere microenvironment in a changing world (Fig. 5). Evidence suggests that rhizosphere has higher soil multifunctionality than bulk soils, which can screen for specific groups of microbes and functional genes to accelerate nutrient cycling, plant growth and defense, etc [42]. However, our findings that rhizosphere have higher soil multifunctionality are not a static result (Table S2), and it is speculated that pathogen abundance, microbial competition, and inhibitory effects of secretions may reverse this situation.

Rare bacterial taxa cannot be ignored in driving soil multifunctionality

Random forest results indicate that both dominant and rare bacteria play critical roles in predicting soil multifunctionality processes, especially rare bacteria (Fig. 7). Some studies have suggested that microbes with different strategies can explain the mechanisms of soil multifunctionality changes, such as eutrophic bacteria have a greater effect on organic matter building than decomposition, while oligotrophic bacteria have the opposite effect [13, 43]. However, there is still ambiguity that not all taxa under a particular bacterial phylum exhibit absolute oligotrophy or eutrophication [44]. Interestingly, differences in microbial ecological niches may result in different contributions to soil multifunctionality, and rare taxa may contribute more to soil multifunctionality than dominant taxa, suggesting that rare taxa often play a disproportionate effect in biological processes [11, 45]. Conversely, some argue that most taxa have similar functions, and rare taxa may exist only as "insurance" and do not need to provide a function, and that taxa with irrelevant functions may be activated to provide indispensable functions under the appropriate conditions [46, 47]. Therefore, our results emphasize the importance of dominant and rare taxa for the maintenance of soil multifunctionality, and climate change resulting in shifts in these key taxa may alter the ecological service functions provided by soils.

Conclusion

We found that microbial community diversity was negatively correlated with soil multifunctionality in undisturbed bamboo forests, which may be a result of a balance between positive and negative microbial effects. Interestingly, microbial diversity and composition jointly drive soil multifunctionality. Environmental variables significantly influenced soil multifunctionality, and bacterial diversity and fungal composition significantly influenced multifunctionality in bulk soils, while fungal diversity and composition significantly influenced multifunctionality in rhizosphere soils. Moreover, our results emphasize that rare microbial flora play a disproportionate role in the multifunctionality of both rhizosphere and bulk soil. Our study highlights the different effects of soil compartments (rhizosphere vs. bulk soil) and taxa (dominant vs. rare taxa) on soil multifunctionality under climate change. We also suggest that further studies should focus on the microbial diversity-multifunctionality relationship across multiple dimensions and scales, because multitrophic levels constructed through food webs may contribute much more to multifunctionality than a single trophic level.

Supplementary Information

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Supplementary Material 1

Author contributions

WG designed and performed the experiments and wrote the manuscript, ML and LQ revised the manuscript.

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Data availability

All sequence data are deposited in the NCBI Sequence Read Archive under bioproject accession numbers PRJNA1223675 and PRJNA1224042.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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