



# Negative associations between aboveground and belowground biodiversity were primarily driven by specific microbial groups mediated by abiotic factors

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## Abstract

**Background and aims** Despite increasing evidence of strong relationships between plants and soil microbial communities, most studies on this topic have been controlled experimental studies at small spatial and temporal scales.

**Methods** In this study, we examined the relationships between tree communities and soil microbial communities by examining 1,287 soil samples collected from a 20-ha subtropical forest plot using high-throughput sequencing.

**Results** We found a negative association between above- and belowground biodiversity, primarily driven by the interactions between tree communities and six specific soil microbial genera (*Bryobacter*, *ADurb.Bin063-1*, *Russula*, *Archaeorhizomyces*,

*Tolypocladium*, and *Trichoderma*). These interactions were mediated by abiotic factors, particularly metal elements, which were positively correlated with the relative abundance of these specific microbial groups but negatively correlated with tree richness. Random forest analysis revealed that *Archaeorhizomyces* was most strongly correlated to the total basal area of evergreen and deciduous trees. Additionally, structural equation modeling indicated that the indirect impact of abiotic factors on *Archaeorhizomyces* was mediated by the total basal area of trees.

**Conclusion** Overall, our results provide robust observational evidence for the intricate relationship between tree diversity and soil microbial communities at a large scale, revealing that specific microbial genera and abiotic factors, particularly metal elements, play crucial roles in regulating this relationship. Effective management of these interactions is essential for maintaining ecosystem function and resilience in subtropical forests.

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**Keywords** Aboveground–belowground interaction · Community structure · Deciduous tree · Evergreen tree · Forest ecosystem

## Introduction

Forested ecosystems, which encompass over 30% of the global land surface, are home to more than 3 trillion individual trees across over 73,000 tree species

(Crowther et al. 2015; Gatti et al. 2022). These vital systems not only harbor significant terrestrial biodiversity (FAO and UNEP 2020) but also sequester substantial amounts of atmospheric carbon (Pan et al. 2011), serving as essential buffers against climate change (Bonan 2008; O'Connor et al. 2021). Within the soil of these forests, microbes—particularly bacteria and fungi—form the invisible majority, playing a pivotal role in shaping plant productivity and diversity (van der Heijden et al. 2008; Wei et al. 2019). By controlling key biogeochemical processes, soil microbial communities are instrumental in maintaining the multifunctionality of forest ecosystems (Delgado-Baquerizo et al. 2016; van der Heijden et al. 2008; Wardle et al. 2004; Wagg et al. 2014). Consequently, considerable effort has been dedicated to elucidating the intricate relationships between trees and soil microbes (Rivest et al. 2019; Wan et al. 2022). The covariation patterns between tree and microbial communities reveal the interconnectedness of aboveground and belowground components of terrestrial ecosystems, as well as the potential structural mechanisms that underpin both tree and microbial communities (Barberán et al. 2015; Li et al. 2015). However, findings have been inconsistent, with both positive (Chen et al. 2019; Gao et al. 2013; Hiiesalu et al. 2017; Peay et al. 2013; Strukelj et al. 2021) and negative (Wan et al. 2022) linkages reported, underscoring the strong context dependence of these relationships between tree species and soil microbial communities (Tedersoo et al. 2016).

The diversity and composition of tree communities are affected by a variety of environmental factors, including topography, soil chemistry, spatial processes (e.g., dispersal limitation), and stochastic factors (e.g., tree death and recruitment; Baldeck et al. 2013; De Cáceres et al. 2012). Such variability in tree species diversity can, in turn, significantly impact microbial diversity (Rivest et al. 2019) and community composition (Barberán et al. 2015; Khlifa et al. 2017; Schappe et al. 2017; Wan et al. 2022). In a reciprocal manner, microbial diversity and abundance are profoundly shaped by trees, which act as hosts, modify the soil environment, and supply organic matter through litter, root exudates, and fine root turnover (Georgiou et al. 2017; Khlifa et al. 2017; Lange et al. 2015; Ma and Chen 2018; Prescott and Grayston 2013; van der Heijden et al. 2008; Wardle 2006). Higher levels of tree

diversity, along with increased substrate and habitat heterogeneity, are known to foster greater microbial diversity (Gao et al. 2013; Hiiesalu et al. 2017; Singavarapu et al. 2022).

The identity of tree species (e.g., deciduous and evergreen trees based on functional traits; Martin-Guay et al. 2021) can significantly influence the types of microbes present in the soil. Fungi, for instance, often exhibit host preferences that dominate their relationships with trees (Tedersoo et al. 2010; Wang et al. 2019). For example, plant pathogens and symbionts (e.g., arbuscular mycorrhizal fungi, AMF, and ectomycorrhizal fungi, EMF) are significantly linked with tree species as hosts (i.e., host trees select specific plant pathogens and symbionts; in turn, specific host trees are selected by plant pathogens and symbionts) (Li et al. 2021; Tedersoo et al. 2010; Toju et al. 2013; Yang et al. 2019). Deciduous and evergreen trees may coexist in regions with similar climatic conditions but differ in functional traits, such as shade tolerance and photosynthetic product accumulation (Jin et al. 2018; Zhang et al. 2021). Deciduous trees typically have higher leaf litter nutrient concentrations and decomposition rates than evergreen trees (Cornelissen 1996; Freschet et al. 2012; Givnish 2002; Rawat et al. 2020), while evergreen trees are often favored in nutrient-poor habitats (Balocchi et al. 2010). According to nutrient transfer theory, deciduous species in mixtures with evergreens can promote the activity and abundance of soil microorganisms involved in decomposition processes and accelerate litter decomposition from evergreen trees (Hättenschwiler et al. 2005). The associations between microbes and tree communities and their potential moderating effects may be contingent upon the physiological and ecological characteristics of the trees. However, the dominant microbial groups within tree assemblages and the nuances of their relationships with tree identity remain subjects of ongoing research.

In our study, we examined a 20-ha stem-mapped subtropical forest plot, rich in ecological detail, to examine the associations between trees and soil microbes and to identify the microbial groups that dominated these relationships. Furthermore, we determined the microbial group that was most strongly correlated with evergreen and deciduous trees and tested its responses to abiotic factors.

## Materials and methods

### Study site and collection of data on the tree community

This study was conducted at the Tiantong National Field Observation Station for Forest Ecosystems (29°48' N, 121°47' E), which is a representative subtropical evergreen broadleaved forest in Zhejiang Province, East China. The forest plot was established in 2008 as part of the Forest Global Earth Observatory network (<https://forestgeo.si.edu/>) and covered a total area of 20 ha (500 m × 400 m) (Qiao et al. 2020). Topographic data (elevation, slope, and convexity) for the plot were collected and converted into topographic data for each sampling point using the Kriging interpolation method (Oliver and Webster 1990).

Tree distribution was determined using tree species counts from July to October 2010, 2015, and 2020. Data from the most recent 2020 inventory were used as those best matched the time of soil microbial collection and analysis (2018). The tree data were collected using standardized methods (Condit 1998). All stems with a diameter at breast height (DBH) ≥ 1.0 cm (at 1.3 m above ground) were measured, tagged, and identified to the species level. Detailed information about the tree species is presented in Table S1. For the analyses, tree richness and assemblages (i.e., abundance and total basal area) were determined at four neighborhood scales (i.e., within circles with radii of 5, 10, 15, and 20 m around the corresponding soil sampling site). Briefly, all tree species were first divided into deciduous and evergreen trees based on their functional characteristics, and the total number of individuals at a given neighborhood level was considered as tree abundance. The total basal area of all trees (calculated for each tree as  $\pi \times (\text{DBH}/2)^2$ ; Bettinger et al. 2017) at each neighborhood scale was summed and used as an indicator of total biomass present.

### Soil sampling

Soil sampling was carried out according to the process reported by Wu et al. (2023). Briefly, after removing the surface litter and organic layer, we took four soil cores from the mineral layer (0–10 cm

depth) using a soil auger with a 10-cm inner diameter within 0.5 m around each selected sampling point to form a composite sample. In total, 1,287 soil samples were collected around all selected sampling points (Fig. S1). Each soil sample was passed through a sterilized 2-mm sieve to remove visible stones and roots and was then divided into three subsamples. One subsample was stored at –80 °C before DNA extraction for molecular analyses. The second sample was stored at 4 °C for the analysis of ammonium (NH<sub>4</sub><sup>+</sup>-N) and nitrate (NO<sub>3</sub><sup>-</sup>-N), which were extracted with 1 M KCl and measured using a continuous flow analyzer. The third subsample was air-dried, and other properties, including pH, soil moisture (SM), organic carbon (OC), total nitrogen (TN), total phosphorus (TP), available phosphorus (AP), available potassium (AK), aluminum (Al), calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), and zinc (Zn), were measured using the methods described in the supplementary file (Supplementary Methods).

### Soil microbial DNA extraction and polymerase chain reaction (PCR) amplification

DNA was extracted from 0.5 g of soil per sample using a MagPure Soil DNA KF Kit (Magigene Biotechnology Co., Ltd. Guangzhou, China) according to the manufacturer's instructions. DNA quality was assessed using 1% agarose gels, and its concentration and purity were determined using a NanoDrop One (Thermo Fisher Scientific, Waltham, MA, USA). For bacterial analyses, the V4–V5 hypervariable regions of the 16 S rRNA gene were sequenced using the universal primers 515 F (5'-GTGCCAGCMGCCGCG GTAA-3') and 907R (5'-CCGTC AATTCMTTTRAG TTT-3'). For fungal analyses, PCR amplification of the second internal transcribed spacer (ITS2) barcode region was performed using the primers ITS3 (5'-GCATCGATGAAGAACGCAGC-3') and ITS4 (5'-TCCTCCGCTTA TTGATATGC-3'). The primers were synthesized by Invitrogen (Carlsbad, CA, USA). For amplification, a mixture of 25 µL 2× of Premix Taq (Takara Biotechnology (Dalian) Co. Ltd., China), 1 µL of each primer (10 µM), 20 µL nuclease-free water and 3 µL DNA template (20 ng/µL) in a volume of 50 µL was used. Samples were then amplified on a Bio-Rad S1000 thermal cycler (Bio-Rad Laboratory, Hercules, CA, USA) with the

following settings: 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, elongation at 72 °C for 30 s, and final extension at 72 °C for 10 min. The PCR product length and concentration were determined using 1% agarose gel electrophoresis. The PCR products were mixed in equidensity ratios according to GeneTools Analysis (v.4.3.5, SynGene). The PCR products were purified using an EZNA<sup>®</sup> Gel Extraction Kit (Omega BioTek, Norcross, GA, USA). Sequencing libraries were generated using the NEBNext<sup>®</sup> Ultra<sup>™</sup> DNA Library Prep Kit for Illumina<sup>®</sup> (New England Biolabs, Ipswich, MA, USA) following the manufacturer's protocol.

### Sequence data processing

The DNA samples were sequenced using an Illumina HiSeq 2500 platform (Guangdong Magigene Biotechnology Co., Ltd. Guangzhou, China). Raw FASTQ files were demultiplexed, quality-filtered using Trimmomatic (Bolger et al. 2014), and merged using FLASH (Magoc and Salzberg 2011) with the following criteria: (i) reads containing N, with a quality score < 20 and a sequence length < 100-base pair (bp) were filtered; (ii) sequences with an overlap > 10 bp were merged according to their overlapping sequences. The maximum allowable error ratio of the overlapping region was 0.1, and reads that could not be assembled were discarded; (iii) sequences were assigned to each sample according to the barcodes and primers using the Mothur software (Schloss et al. 2009). The barcode allowed two deviations, with three as the maximum number of mismatches. The barcodes and primers were then removed, and high-quality clean tags were obtained (Bokulich et al. 2013). Operational taxonomic units (OTUs) with a 97% similarity cutoff were clustered using the USEARCH software (Edgar 2010), and singleton OTUs and chimeric sequences were removed. The taxonomy of each bacterial sequence was assigned using the SILVA database (<https://www.arb-silva.de/>), and that of each fungal sequence was assigned using the UNITE database (<http://unite.ut.ee/index.php>). The sequences of all samples were rarefied according to the minimum sequence number (11,155 for bacteria and 24,400 for fungi) to correct for differences in sequencing depth. Before rarefaction, there were

26,972 bacterial and 31,520 fungal OTUs in total; after rarefaction, 24,367 bacterial and 29,838 fungal OTUs were obtained. After deleting the OTUs with sequence numbers less than 20 across all samples (Jiao and Lu 2020), 8,373 bacterial and 11,961 fungal OTUs were obtained. Each identified fungal OTU was assigned to putative AMF, EMF, plant pathogens, or saprotrophic fungi with a confidence level of “highly probable” or “probable” using the FUNGuild database (Nguyen et al. 2016; <http://www.stbates.org/guilds/app.php>).

### Co-occurrence network analysis

An integrated OTU table of both bacterial and fungal OTUs was used to construct a network to visualize the cross-trophic interactions between bacteria and fungi. This was done using a log-transformed Pearson correlation matrix that was constructed by the Molecular Ecological Network Analysis Pipeline (MENAP; <http://ieg4.rccc.ou.edu/mena/login.cgi>; Deng et al. 2012; Zhou et al. 2010; Zhou et al. 2011). Only the OTUs detected in more than 644 replicates (half of the 1287 soil samples) were used for network construction to ensure correlation reliability for network analysis. In ecological count data, a large portion of the sequencing data is made of zeros. Zero-value matching of two taxa produces a false strong correlation. A conventional way to deal with this problem is to remove taxa that occur in a few samples to avoid spurious correlations (Faust 2021). Although removing rare OTUs could destroy the network structure, a high rate of false positive results would be more destructive (Weiss et al. 2016). Molecular ecological networks (MENs) were constructed by setting appropriate  $St$  following the random matrix theory (RMT). The RMT-based approach is a reliable, sensitive, and robust tool for analyzing high-throughput genomics data for modular network identification (Deng et al. 2012; Shi et al. 2016). In each molecular ecological network, nodes represented the OTUs, and edges denoted the correlations between one OTU and another. Modules were detected using the greedy modularity optimization method because this method is more effective and sensitive at separating a complex network into modules compared to other methods, such as the short random walk, leading eigenvector of the community matrix, and simulated annealing

methods (Deng et al. 2012; Shi et al. 2016). The module eigengene E (the first principal component (PC1) of modules) of the top three modules for the integrated network was calculated to examine the correlations between modules and abiotic factors (Ma et al. 2020). The network was visualized with Cytoscape (version 3.8.2).

### Statistical analyses

The *corr.test* function of the *psych* R package was used to detect the relationships between microbial richness and tree richness (Revelle 2022). Correlations between microbial richness and tree assemblages were analyzed using the *mantel.test* function of the *linkET* package in R (Huang 2021). Here, only species richness was used as a measure of microbial biodiversity as it was significantly correlated with the other diversity indices (Fig. S2; Spearman's  $|r| > 0.55$  for bacteria and  $> 0.66$  for fungi).

We generated a NMDS ordination of tree community based on the Bray–Curtis dissimilarity matrix, and then used the *ordisurf* function within the *vegan* package (Oksanen et al. 2022) to fit the abiotic variables to tree community ordination using generalized additive models (GAMs; Sweeney et al. 2021). These models fitted the abiotic variables as a smooth response surface over the tree community ordination accounting for both NMDS axes.

We calculated the Spearman correlation between abiotic and biotic factors in R using the *psych* package (Revelle 2022) to estimate the importance of specific abiotic factors on the relative abundance of individual microbial genera. We also built multiple linear regression models of abundance as a function of edaphic and topographic (slope, elevation, convexity) predictors. All abiotic variables were first standardized (mean=0, SD=1). To find the most parsimonious model, we started with a global model that included all predictors and compared all possible subset models using the *stepAIC* function from the *MASS* R package (Venables and Ripley 2002). The model with the lowest Akaike Information Criterion was selected as the top-ranked model (Burnham and Anderson 2002). To quantify the explained variation for each of the predictors retained in the top-ranked model, we used variance decomposition implemented with the *relaimpo* package (Grömping 2006).

Regression models were fitted by using the *lm* function of the *stats* R package (Field et al. 2012).

To identify the major microbial predictors of the total basal area of deciduous and evergreen trees, we used random forest models, implemented with the *randomForest* package (Liaw and Wiene 2002). The contribution of each function was quantified as the percentage increase in mean squared error (MSE) of out-of-bag predictions when that function was removed, implemented with the *rfPermute* package (Archer 2022), where higher increases in MSE implied more important taxon (Breiman 2001; Jiao et al. 2018).

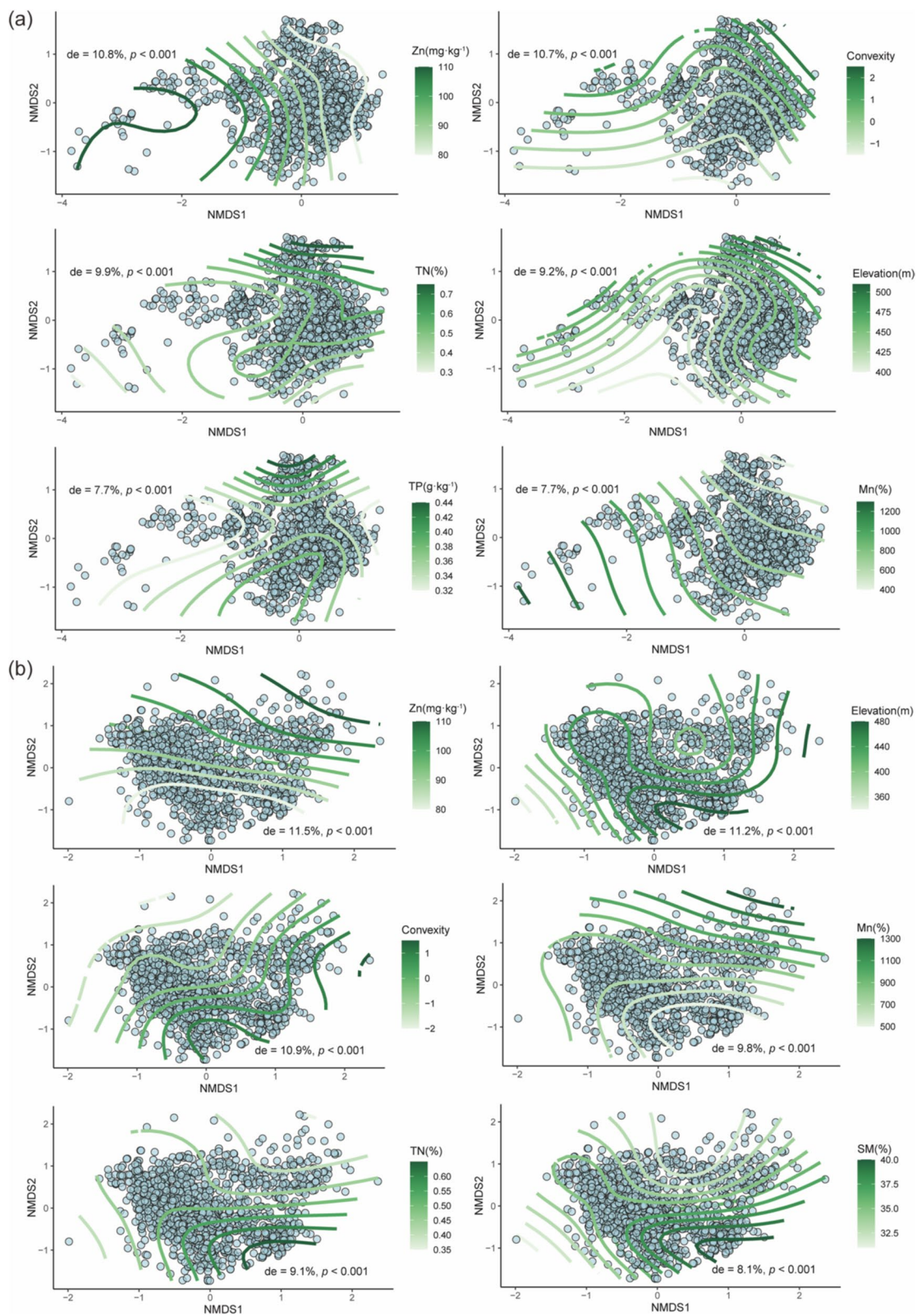
We then depicted hypothesized direct and indirect effects of abiotic factors and deciduous and evergreen trees on the strongest microbial predictor of tree total basal area by developing a causal path model, using the *lavaan* package (Rosseeel 2012). We used the *stepAIC* function from the R package *MASS* (Venables and Ripley 2002) to identify the parsimonious model for explaining variations in tree total basal area from a global model including all abiotic factors. For the path analysis, all predictors were standardized (mean=0, SD=1) to improve normality. Support for the causal path models was evaluated using the following criteria: non-significant Chi-square test ( $p > 0.05$ ), goodness-of-fit index  $> 0.90$ , and root mean square error of approximation  $< 0.08$  (Schermelleh-Engel et al. 2003). All analyses were performed in R version 4.2.1).

## Results

### Characteristics of tree species and soil microbial communities

Over the entire 20-ha forest dynamic plot, a total of 106,551 individual trees of 148 species with  $DBH \geq 1.0$  cm were recorded in the inventory of 2020. The average tree species richness was 13.18 ( $\pm 5.75$ ) for the 5 m radius around each sampling plot, 26.10 ( $\pm 7.74$ ) for the 10 m radius, 36.09 ( $\pm 8.14$ ) for the 15 m radius, and 44.46 ( $\pm 8.14$ ) for the 20 m radius. *Eurya loquaiana* (Theaceae, evergreen), *Litsea elongata* (Lauraceae, evergreen), and *Camellia fraterna* (Theaceae, evergreen) were the top three species with the most individuals ( $> 10^4$ ) in the plot. *Choerospondias axillaris* (Anacardiaceae, deciduous), *Lithocarpus harlandii*





◀**Fig. 1** Results from the generalized additive models fitting abiotic factors across the nonmetric multidimensional scaling (NMDS) ordination of tree assemblages. **(a)** Based on the tree abundance. **(b)** Based on the tree total basal area. Splines show the fit of the abiotic variables from high values (dark) to low values (light) over the ordination. The abiotic variables overlay indicates that tree community, as represented by the points on the NMDS, are associated with higher or lower predictor variables in line with the colored abiotic variables gradient. Nonlinear relationships between the abiotic variables and tree community are represented by curved splines. ‘de’ shows the deviance explained by the respective model. Only the top six strong determinants of tree community structure were shown

(Fagaceae, evergreen), and *Cyclobalanopsis sessilifolia* (Fagaceae, evergreen) were the three species with the largest total basal areas (Fig. S3). During 2010–2020, the total number of individuals increased by 14,004 during the first 5 years and decreased by 2,541 during the last 5 years (Fig. S3). Furthermore, the tree richness decreased from 154 (79 deciduous and 75 evergreen tree species) in 2010 to 148 (73 deciduous and 75 evergreen tree species) in 2020. Seven tree species disappeared, namely *Aralia echinocaulis*, *Buddleja lindleyana*, *Oreocnide frutescens*, *Photinia beauverdi-ana*, *Phyllanthus glaucus*, *Rhamnus crenata*, and *Trachycarpus fortune*, and the newly occurring tree species (*Machilus pauhoi*) was recorded (DBH < 1 of the first two inventories; Fig. S3). Most measured soil properties and topographic attributes (e.g., Zn, convexity, TN, elevation, TP, and Mn) were predictive of tree community composition, represented by the NMDS ordination of these communities (Fig. 1; Table S2). Zn was the strongest determinant of tree community structure, with Ca explaining a low amount of deviance within our models (Table S2).

For soil microbes, the bacterial communities were dominated by Proteobacteria with 2,688 OTUs and Acidobacteria with 997 OTUs (Fig. S4). Ascomycota in fungi was the most abundant fungal phylum across all samples with 5,622 OTUs. Moreover, 1,786 OTUs of saprotrophic fungi (14.93%), 442 OTUs of EMF (3.70%), 374 OTUs of plant pathogenic fungi (3.13%), and 306 OTUs of AMF (2.56%) were identified across all samples.

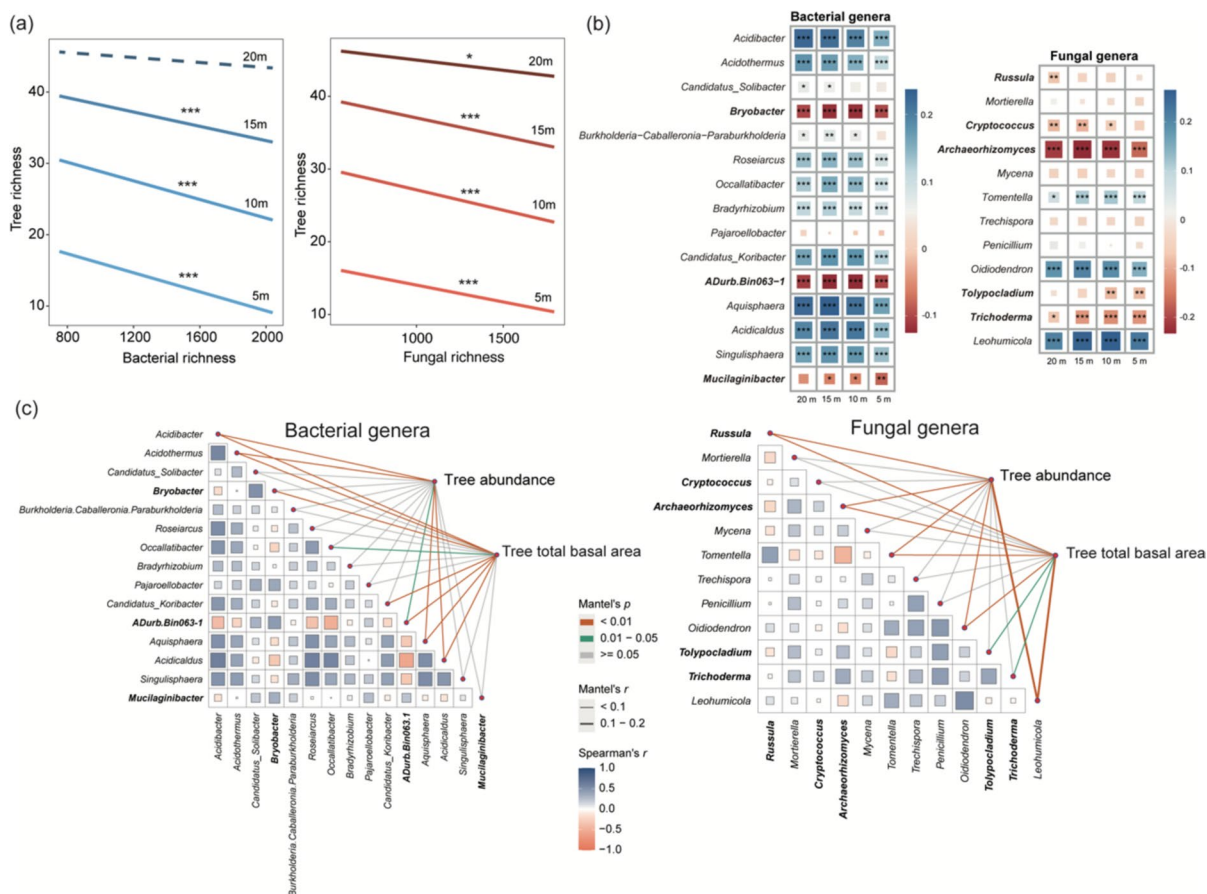
#### Relationships between tree assemblages and soil microbial communities

There were significant negative correlations between tree richness and microbial richness

(Fig. 2a). Specifically, the richness of three bacterial (i.e., *Bryobacter*, *ADurb.Bin063-1*, and *Mucilaginibacter*) and five fungal (i.e., *Russula*, *Cryptococcus*, *Archaeorhizomyces*, *Tolypocladium*, and *Trichoderma*) genera was significantly and negatively correlated with tree richness (Fig. 2b). Furthermore, bacterial genus *ADurb.Bin063-1* as well as fungal genera *Russula* and *Archaeorhizomyces* were significantly correlated with the tree assemblages, and bacterial genus *Bryobacter* as well as fungal genera *Tolypocladium* and *Trichoderma* were significantly correlated with the tree total basal area (Fig. 2c). Overall, these six specific soil microbial genera (*Bryobacter*, *ADurb.Bin063-1*, *Russula*, *Archaeorhizomyces*, *Tolypocladium*, and *Trichoderma*) dominated the negative associations between above- and belowground biodiversity.

#### Effects of abiotic factors on the relative abundance of the six specific genera

We first analyzed the impact of soil properties and topographic attributes on network modules by constructing an integrated network, which was clustered into three major interconnected modules (Fig. 3a). On the whole, the top three modules were positively correlated with pH, Mg, Mn, and Zn, while negatively correlated with OC, TN,  $\text{NH}_4^+\text{-N}$ , SM, and topographic attributes (Fig. 3b). Interestingly, the relationships between the relative abundance of the six specific genera and abiotic factors exhibited similar patterns to those between the major modules and abiotic factors (Fig. 3c; S5). Specifically, soil properties and topographic attributes were associated with the relative abundance of individual bacterial genus, explaining 46.76% of variation for *Bryobacter*, and 38.36% of variation for *ADurb.Bin063-1* (Fig. 3d). Across these two bacterial genera analyzed, pH, TN, Mg, and Mn were more influential than other factors, although the direction and magnitude of correlation varied within and among taxa (Fig. 3d). Abiotic factors were also correlated with specific fungal genera abundance but accounted for less variation (~4.14–5.71%, Fig. 3d). Notably, the direction of association with abundance for many influential edaphic factors were opposite for bacteria and fungi (especially AP and AI, Fig. 3c, e).



**Fig. 2** Relationships between microbial richness and tree communities. **(a)** Overall correlations between microbial richness and tree richness. **(b)** Correlations between microbial genus richness and tree richness. Only microbial genera with average relative abundance greater than 0.5% are shown. The color gradient on the right indicates Spearman's correlation coefficients, with more positive values (dark blue) indicating stronger positive correlations and more negative values (dark red) indicating stronger negative correlations. The  $p$  values

were adjusted by false discovery rate. Significance levels are as follows: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ . **(c)** Correlations between microbial genus richness and tree assemblages (tree abundance and total basal area) within a 20 m radius of the soil sampling site. Edge width corresponds to the Mantel's  $r$  value, and the edge color denotes the statistical significance. Pairwise correlations of these variables are shown with a color gradient denoting Spearman's correlation coefficient

Contributions of six specific genera to evergreen and deciduous trees

Random forest analysis revealed that the richness of *Archaeorhizomyces* was most strongly correlated to the total basal area of evergreen and deciduous trees (Fig. 4a). Our structural equation modeling results indicated that abiotic factors had a direct effect on the total basal area of trees, with certain soil properties (e.g., TN, TP, Al, and Cu) demonstrating contrasting effects

on the evergreen vs. deciduous trees (Fig. 4b; S6). Notably, the total basal area of evergreen trees negatively affected the richness of *Archaeorhizomyces* while deciduous trees positively affected that of *Archaeorhizomyces*, and abiotic factors also had strong direct effects on *Archaeorhizomyces* ( $R^2 = 0.35$ ; Fig. 4b). This resulted in an indirect causal pathway between abiotic factors and *Archaeorhizomyces* mediated by the total basal area of trees (Fig. 4b).



## Discussion

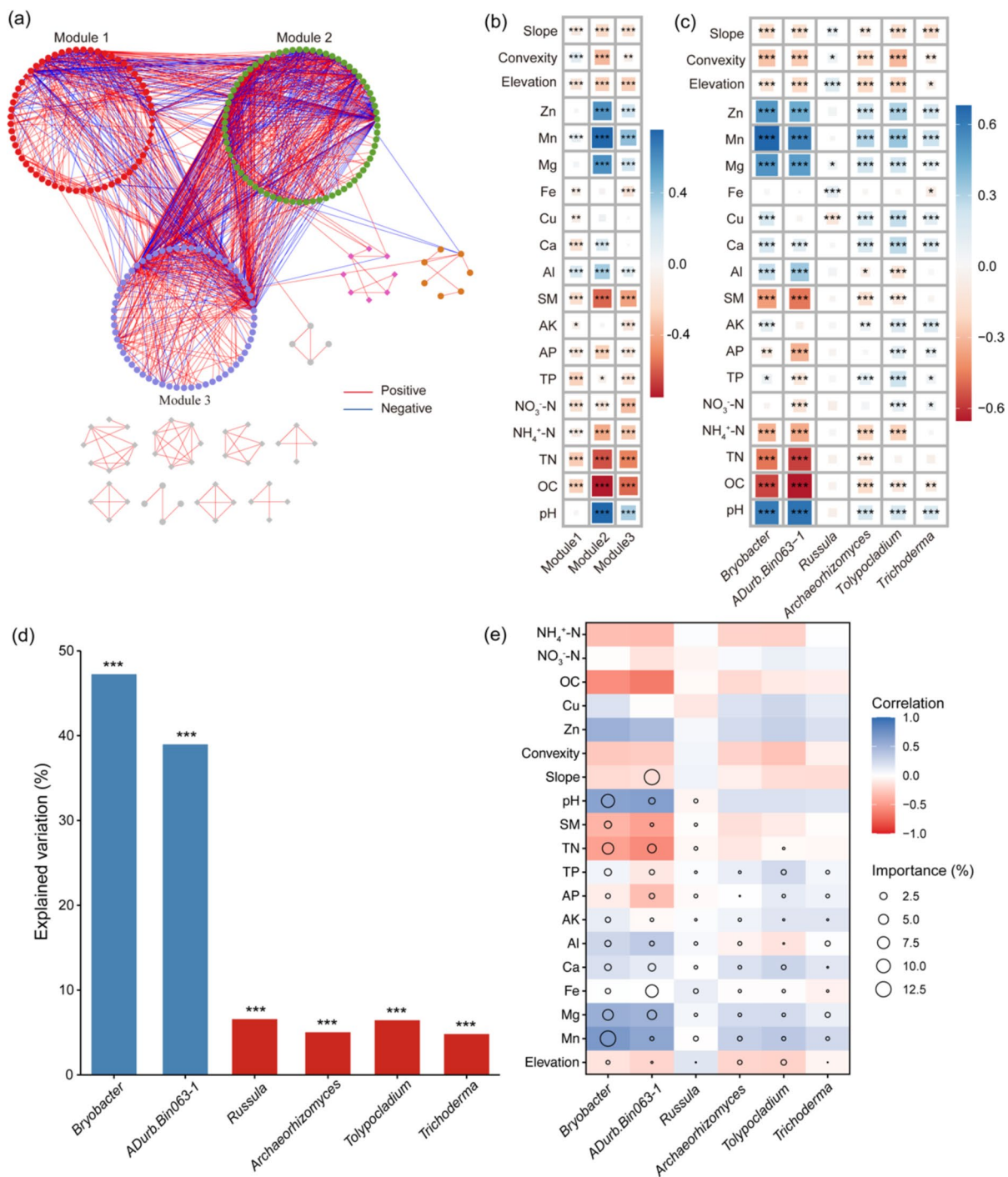
In this study, we conducted a thorough investigation into the profound interdependence of above- and belowground systems within a representative subtropical forest area. Utilizing comprehensive soil sampling coupled with detailed characterization of both microbial communities and tree assemblages, our study provides novel insights into the intricate interplay between above- and belowground biodiversity. While previous research has often examined these interactions in controlled experiments, we explored these relationships within a large-scale, naturally occurring system, revealing unique patterns and offering new perspectives on the factors shaping above- and belowground interactions.

Contrary to expectations from previous studies (Chen et al. 2019; Gao et al. 2013; Hiiesalu et al. 2017; Peay et al. 2013; Strukelj et al. 2021), we found a significant negative correlation between tree richness and soil microbial richness (Fig. 2a). Several ecological processes and theories might explain this negative correlation. One explanation is the resource competition theory, which suggests that as tree diversity increases, competition for belowground resources such as nutrients and water intensifies among tree species (Tilman 1982). Moreover, more competitive species generally utilize resources with greater efficiency under the framework of the selection effect (Fox 2005), and competition among trees can lead to a reduction in the allocation of resource to belowground biomass (Martin-Guay et al. 2019), particularly reducing carbon allocation to coarse root components with diameters greater than 10 cm (Men et al. 2023). Root-derived carbon constitutes the predominant (>60%) carbon source for forest soil microbes (Kramer et al. 2010). Total soil microbial biomass may markedly decline as tree species richness increases (Wan et al. 2022). Thus, intensified tree competition may reduce belowground carbon allocation and nutrient availability for microbial communities, ultimately decreasing microbial diversity. Additionally, the high diversity of tree species may promote the production of a wider array of allelochemicals or secondary metabolites, including phenolics, terpenoids, and alkaloids. These metabolites can impact soil microbial reproduction and activity, thereby potentially reducing soil microbial diversity (Berendsen et al. 2012; Reigosa et al. 2002;

Uhlik et al. 2013). Finally, varying litter quality and quantity resulting from diverse tree species can lead to heterogeneous decomposition environments that might favor only certain microbial groups adapted to specific decomposition processes, instead of supporting a rich microbial community (Hättenschwiler et al. 2005).

This unexpected pattern challenges the often-assumed positive relationship between tree species richness and soil microbial diversity. In particular, our findings suggest that the richness of specific microbial genera negatively correlates with tree richness (Fig. 2). Members of the *Russula* genus, which are pivotal plant root mutualists, particularly in forested ecosystems, function as EMF (Gao et al. 2015; Looney et al. 2020). This ectomycorrhizal association creates a close link between *Russula* and specific tree hosts (e.g., Fagaceae family) for nutrient exchange, which can lead to the competitive exclusion of other fungi (Peay et al. 2007). Additionally, *Trichoderma* fungi, renowned for their rapid mycelial growth and their adaptability to a range of environmental conditions (Yao et al. 2023), excel in outcompeting pathogenic fungi in the root zone, effectively preventing the spread of disease (Druzhinina et al. 2018). *Trichoderma* also actively absorbs essential nutrients for pathogen development, thereby creating a nutrient scarcity that hampers the growth and reproduction of harmful fungi (Bazghaleh et al. 2020). Nevertheless, pathogens have the potential to shape tree communities and enhance diversity by limiting the dominance of certain tree species through plant-soil feedback mechanisms (Bagchi et al. 2014; Liang et al. 2016). Consequently, the suppression of pathogens by *Trichoderma* may ultimately contribute to the dominance of some tree species and a potential reduction in overall diversity of tree species. These findings underscore the importance of considering specific taxa, rather than simply focusing on overall richness, when investigating above- and belowground interactions.

These specific genera mentioned may occupy specialized ecological niches and possess environmental preferences that are not conducive to promoting higher tree diversity. Soil metal elements are primary predictors of the structure and function of soil microbial communities (Dai et al. 2023), aligning with findings from a prior study conducted in this forest plot (Wu et al. 2023). Our study revealed



that metal elements, particularly Zn, Mn, Mg, and Ca, had contrasting roles with specific microbial groups (positively) and tree communities (negatively) (Fig. 3c; S7). In the acidic soils of this study (pH: 2.79–5.79), the high solubility of Zn and Mn can lead

to excessive absorption by plants, resulting in toxic effects (DalCorso et al. 2014; Hansch and Mendel 2009). Elevated levels of soil Zn can cause nutritional imbalances that primarily affect root systems, ultimately hindering the growth of tree seedlings (Souza

◀**Fig. 3** Relationships between abiotic factors (soil and topographic factors) and microbial communities. **(a)** Co-occurrence patterns in the integrated network. Interconnected modules shown in circular layout for the composite bacterial–fungal network. Different colored nodes represent different modules in top three modules. Red and blue links indicate positive and negative correlations between nodes, respectively. **(b)** Correlations between the top three modules in the networks and soil environmental parameters. **(c)** Correlations between the relative abundance of six specific microbial genera and environmental parameters. The color gradient on the right indicates Spearman's correlation coefficients, with more positive values (dark blue) indicating stronger positive correlations and more negative values (dark red) indicating stronger negative correlations. The  $p$  values were adjusted by false discovery rate. Significance levels are as follows:  $***p < 0.001$ ,  $**p < 0.01$ ,  $*p < 0.05$ . **(d)** Contributions of abiotic factors to the differences in relative abundance of six specific microbial genera based on correlation and top-ranked regression models. We examined the correlations of these values with the differences in soil and topographic factors for each pairwise set of soil samples and identified the major predictors. The bar chart represents the total contributions of soil and topographic factors to explain microbial variation (calculated by multiple regression modeling). All of the models had a type 1 error  $< 0.001$ . **(e)** The importance of abiotic factors on six specific microbial genera. Circle size in the heatmap represents variable importance, and colors represent Spearman correlations

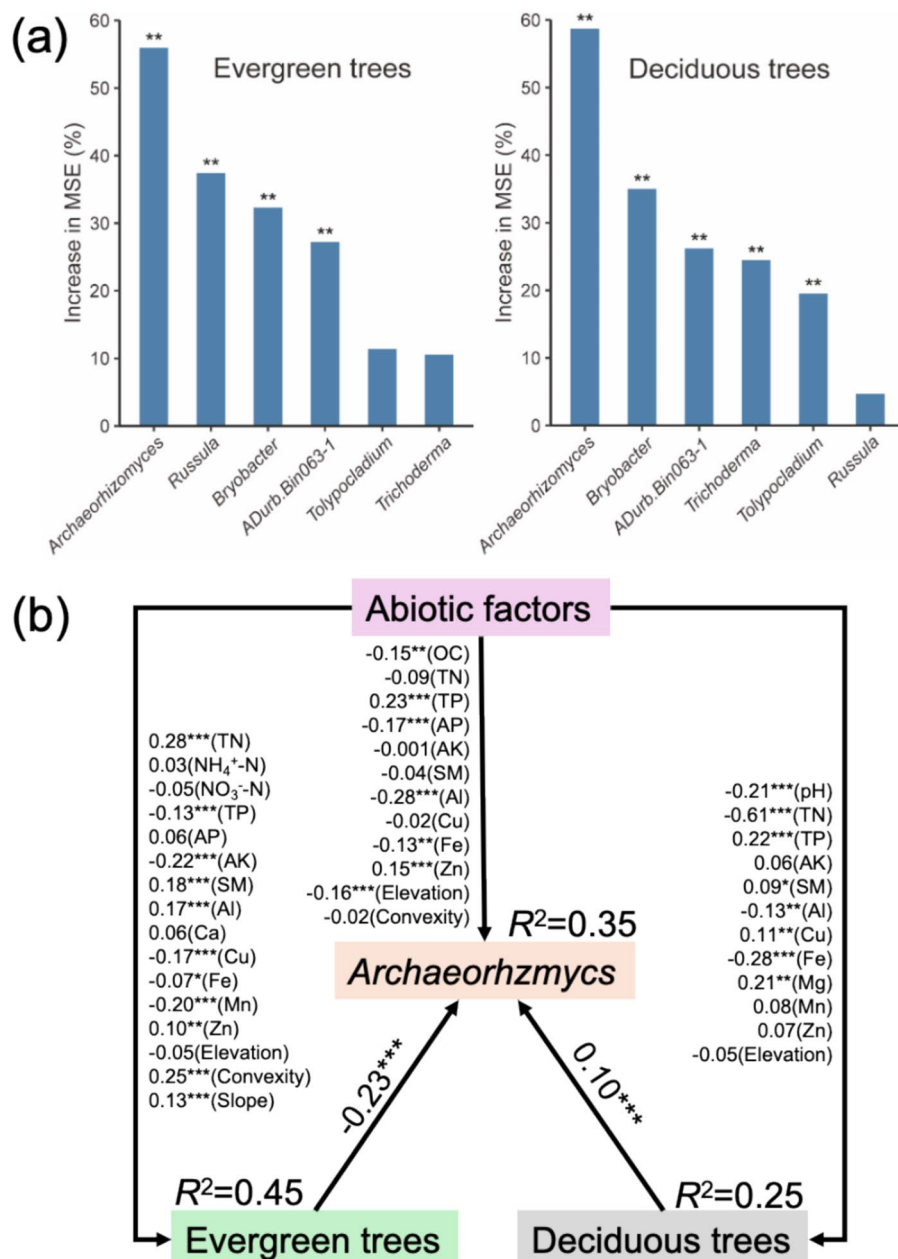
et al. 2020). Additionally,  $Mn^{2+}$  is significant in litter decomposition (Keiluweit et al. 2015). However, excess Mn can trigger the production of reactive oxygen species, causing oxidative damage to proteins and lipid peroxidation, as well as inducing deficiencies of Mg and Ca (DalCorso et al. 2014). Mg deficiency can impair chlorophyll synthesis, negatively impacting photosynthetic efficiency, and thereby restricting tree growth and development (Marschner 2012). Furthermore, Mg deficiency can diminish the plant's resistance to environmental stressors, leading to increased tree mortality rates and a decrease in overall tree diversity (Marschner 2012). A reduction in Ca concentration elevates the susceptibility of xylem tissue to fungal invasion, which exacerbates the dissolution of cell walls in conductive vessels, ultimately resulting in plant wilting (Hirschi 2004). Moreover, *Bryobacter*, an acid-tolerant and strictly aerobic organism, thrives in acidic soils (Dedysh et al. 2006; Wang et al. 2022b). The acidic conditions prevalent in the study plot create a favorable environment for *Bryobacter*, while simultaneously diminishing the diversity of aboveground communities due to an increase in  $H^+$  and  $Al^{3+}$  ion concentrations (Chen et al. 2013). Consequently, abiotic factors play

a crucial role in mediating the negative relationships observed between specific microbial groups and tree communities.

Given that various trees (e.g., evergreen vs. deciduous) foster distinct microbial communities through root exudates (Chandra et al. 2016), shifts in tree species composition can strongly impact soil microbial communities (Eisenhauer et al. 2017; Prescott and Grayston 2013). Moreover, shifts in tree species composition can also lead contextual changes that may impact microbial communities. For example, different tree species exhibit significant variations in litter chemical characteristics (Binkley and Giardina 1998), and the changing composition of tree species will influence soil fertility due to differences in litter quality which largely determines the rate of litter decomposition, subsequently affecting release of nutrients into the soil (Aponte et al. 2013; Norris et al. 2013). Tree species composition can also influence light transmittance through the canopy (Canham et al. 1994), thereby affecting the availability of light beneath the canopy (Forrester et al. 2017; Ligot et al. 2016).

Evergreen and deciduous trees exhibit several differences, such as leaf lifespan (Givnish 2002), fine root biomass (Liu et al. 2014), and nutrient acquisition strategies (Guo et al. 2020). Specifically, evergreen trees, with their longer leaf lifespans and greater fine root biomass (Gonzalez-Zurdo et al. 2016; Liu et al. 2014), contrast with deciduous trees, which are characterized by acquisitive strategies (Guo et al. 2020). These inherent differences fundamentally affect how each tree type responds to various abiotic factors in their environment, leading to divergent ecological impacts. In general, evergreen trees can have greater impacts on soil microbes via litter than deciduous trees (Augusto et al. 2002; Urbanová et al. 2015). For example, the acidic litter produced by certain evergreen conifers can induce the development of fungi-dominated soil ecosystems, creating an environment that supports specific microbial communities (van der Heijden et al. 2008). This phenomenon may explain why the impact of evergreen tree species on *Archaeorhizomyces*, which relies on host plants for nutrition (Rosling et al. 2011), is more pronounced compared to deciduous tree species (Fig. 4b). *Archaeorhizomyces* has the capacity to enhance the bioactive components in plants, bolster their resistance to stress, and prevent the onset of plant diseases (Zhang

**Fig. 4** Relationships between six specific genera and the total basal area of evergreen and deciduous trees. **(a)** Topmost influential soil microbial genera (based on richness) driving the total basal area of deciduous and evergreen trees. The accuracy importance measure is computed for each tree and averaged over the forest (1,000 trees). Percentage increases in the mean squared error (MSE) of variables are used to estimate the importance of these predictors, and higher MSE% values imply more important predictors. Significance levels are as follows: \*\* $p < 0.01$ , \* $p < 0.05$ . **(b)** Causal path models for direct and indirect effects of abiotic factors (soil properties and topographic attributes) and the total basal area of evergreen trees and deciduous trees on *Archaeorhizomyces* richness. Solid and dashed arrows indicate significant and non-significant relationships, respectively.  $R^2$  values denote the proportion of variance explained for each variable. \*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$



Chisq = 22.854 ( $P = 0.196$ ), GFI = 0.992, RMSEA = 0.014, df = 18

et al. 2020). Interestingly, there exists a significant positive correlation between deciduous tree species and *Archaeorhizomyces* with putative saprotrophic activity (Rosling et al. 2011). This correlation may stem from the fact that deciduous trees, through their acquisitive strategies, contribute more substantially to carbon accumulation in the mineral horizon compared to evergreen trees, which typically have conservative

strategies (Cotrufo et al. 2015). Additionally, the increased productivity of deciduous tree species promotes the variety of organic substrates entering the soil in the form of litter, thereby increasing the niches that can be occupied by heterotrophic fungi (Peay et al. 2013). In summary, the contrasting characteristics and strategies of evergreen and deciduous trees lead to differing impacts on *Archaeorhizomyces*,



which is most strongly correlated to the total basal area of evergreen and deciduous trees.

In our study, over 1,000 soil samples from a 20-ha stem-mapped subtropical forest with an extensive count of tree species were integrated, totaling more than 100,000 individuals with a DBH of 1 cm or greater. This wealth of data significantly enhances our predictive capabilities regarding forest development within contiguous natural ecosystems. Our analysis revealed that six prominent taxonomic groups, *Bryobacter*, *ADurb.Bin063-1*, *Russula*, *Archaeorhizomyces*, *Tolypocladium*, and *Trichoderma*, primarily dominated the negative associations between above- and belowground biodiversity. While a significant correlation was evident between microbial communities and tree assemblages, discerning definitive causality remains a challenge inherent in large-scale observational studies. Such limitations call for further exploration through targeted follow-up experiments. Inspired by the successful application of a limited number of key microbial taxa in agroecosystems (Fan et al. 2021; Wang et al. 2022a; Zheng et al. 2021), we can isolate those microbial taxa that demonstrate positive interactions with trees and exhibit antagonistic effects against other microbes dominating the negative associations between above- and belowground biodiversity (e.g., *Acidibacter*, *Aquisphaera*, *Acidicaldus*, and *Tomentella*). These isolated microbial taxa will be introduced into forest soils as inoculants (or biofertilizers), thereby allowing for the evaluation of their subsequent effects on tree growth and diversity. Consequently, it is expected that the resilience and functioning of natural forests may be promoted by regulating these key soil taxa.

The ongoing advancements in metagenomic methodologies promise to shed light on the intricate relationships between microbial functions and the dynamic shifts in tree populations over time, such as demographic rates across a decade. These methodological improvements will be instrumental in deepening our understanding of the complex interplay between trees and soil microbes in forest ecosystems. Particularly, in the context of climate change, investigating the alterations in the interdependence between above- and belowground systems in forests is a critical issue. Climate change has a potential to disrupt the symbiotic relationships between trees and fungi (Fernandez et al. 2023). Additionally, declines in soil microbial diversity induced by warming may

substantially impair the functioning of forest ecosystems (Delgado-Baquerizo et al. 2016; Guo 2022), thereby potentially posing a significant threat to forest health (Trumbore et al. 2015).

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**Data availability** The datasets generated during and analyzed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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