



## Proportion of mycorrhiza-associated trees mediates community assemblages of soil fungi but not of bacteria

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### ABSTRACT

Recent studies have shown that mycorrhizal trees can greatly influence soil microbial communities, which in turn play important roles in the function of forest ecosystems. However, there is lack of understanding how the composition of trees with different mycorrhizal types affects soil microbial communities. Here, we collected 1606 soil samples from a 25-ha subtropical forest plot to investigate how the proportion of arbuscular mycorrhizal (AM) versus ectomycorrhizal (EcM) trees mediated soil microbial assemblages. Results showed the alpha diversities of both soil fungal and bacterial communities were significantly positively correlated with the ratio of AM/EcM trees. The AM/EcM tree ratio was important to the fungal community assembly, whereas soil pH was key to the bacterial communities. The increase in the AM/EcM tree ratio decreased the importance of stochastic forces in assembling fungal communities, while it had no significant effect on the bacterial communities. The differential importance of the AM/EcM tree ratio to fungal and bacterial communities highlights the role of mycorrhiza-associated tree composition in regulating soil microbial communities. This finding suggests that forests with different AM/EcM tree ratios would have different soil microbial communities, potentially leading to differences in soil nutrient cycling and in return different tree diversity and forest productivity.

### 1. Introduction

Trees are often found to form symbiotic associations with different types of mycorrhizal fungi (Bennett et al., 2017; van der Heijden et al., 2015; Zhong et al., 2021), with arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) trees being the two major types (Brundrett and Tedersoo, 2018; Soudzilovskaia et al., 2020; Wang and Qiu, 2006). These symbiotic associations underscore the importance of tree diversity and composition for soil microbial (fungal and bacterial) communities (Barberán et al., 2015; Laforest-Lapointe et al., 2016; Prober et al., 2015) and the functional roles they play (Heděnc et al., 2020; Singarvarapu et al., 2022). However, there is a limited understanding of how the proportion of trees associated with different mycorrhizal types (i.e., AM versus EcM tree ratio) structures soil microbial communities in forest ecosystems.

Although more tree species are associated with AM than EcM fungi in nature (Brundrett, 2009), the latter constitute approximately 60% of all tree stems on the Earth (Steidinger et al., 2019) and some EcM trees (e.g., those belonging to Fagaceae and Pinaceae) form monodominant forests (Corrales et al., 2016). Generally, forests dominated by AM-associated trees tend to have an inorganic nutrient economy due to rapid litter decomposition and increased rates of carbon and nitrogen mineralization, whereas forests dominated by EcM-associated trees select an organic nutrient economy due to poor litter decomposition and slower turnover of carbon and nitrogen (Phillips et al., 2013). Consequently, Phillips et al. (2013) referred to this framework as the mycorrhizal-associated nutrient economy, which was further validated by Rosling et al. (2016) that organic forms of phosphorus were more available in stands dominated by EcM trees than in stands dominated by AM trees, in a deciduous forest. Consequently, it is expected that the

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proportion of AM-associated trees *versus* EcM-associated trees may not only directly mediate the structure and diversity of soil microbial communities through their mycorrhizal types and (root) traits (Eagar et al., 2022; Singavarapu et al., 2022), but also influence soil microbes indirectly through changing soil physicochemical properties (Carrara et al., 2021; Phillips et al., 2013; Schimann et al., 2020). Soil microbes, in turn, are involved in the function of terrestrial ecosystems (Crowther et al., 2019; Wagg et al., 2019) and benefit plants via mycorrhizal (fungus) symbioses (Bücking and Kafle, 2015) and root (bacterium) nodules (Ryu et al., 2020).

Identifying mechanisms of soil microbial community assembly is also critical to revealing the roles of soil microbes (Liu et al., 2021a). Generally, the microbial community assembly is influenced by both deterministic processes and stochastic processes, and their relative importance depends on multiple factors, such as host specificity (Burns et al., 2016), dispersal ability (Chase, 2014; Langenheder and Székely, 2011; Shi et al., 2018), and soil physicochemical properties (Guo et al., 2020; Tripathi et al., 2018). Nevertheless, the relative contribution of these factors to soil fungal and bacterial community assemblies can vary greatly among different forest ecosystems, and can even change with forest conversion, short-term nitrogen supplementation and soil acidification (He et al., 2021; Liu et al., 2018; Yavitt et al., 2021). One question recent studies attempted to answer is how tree species with different mycorrhizal types (e.g., AM and EcM tree species) affect fungal and/or bacterial communities, such as the structural and functional differences of microbial communities between AM and EcM tree-dominated natural forests (Bahram et al., 2020), and the differential effects of AM and EcM tree species on the biomass and metabolic activity of soil microbial communities (Heděc et al., 2020). Despite these studies that have much advanced our understanding of the effects of trees associated with different mycorrhizal types on soil microbial communities, it remains unclear how the assembly of soil fungal and bacterial communities responds to the changing proportion of AM-associated trees *versus* EcM-associated trees in forest ecosystems.

In this study, we collected 1606 soil samples from a 25-ha stem-mapping plot in subtropical China to investigate the influence of trees associated with different mycorrhizal types (i.e., ratio of AM/EcM trees) on the diversities of soil fungi and bacteria and their assemblies. Specifically, we aimed to address the following two questions: (1) How does the AM/EcM tree ratio affect alpha diversities of soil fungal and bacterial communities? (2) Do fungal and bacterial communities share similar assembly processes? If not, how different factors (i.e., AM/EcM tree ratios and soil physicochemical properties) may contribute to regulating the respective communities. Answers to these questions are important to understanding the links between aboveground trees (associating with contrasting mycorrhizal types) and belowground microbes, soil nutrient cycling and diversity maintenance in forests.

## 2. Methods

### 2.1. Study site

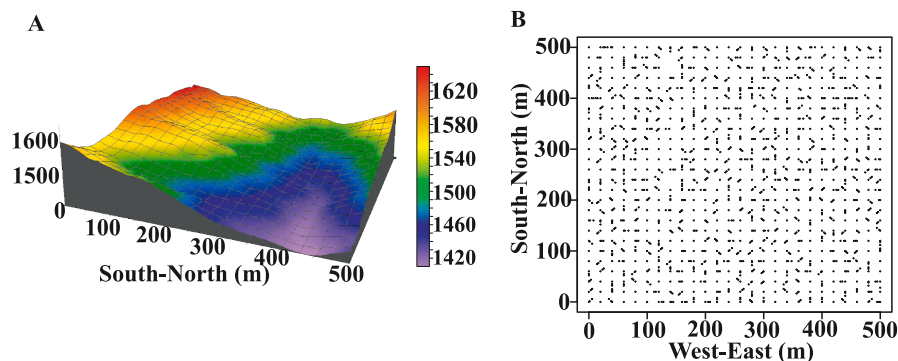
The study site is located in Baishanzu (BSZ) Nature Reserve (27°40'54"-27°50'13" N, 119°3'53"-119°6'44" E) in Zhejiang Province, China. The mean annual temperature of the study area is 12.8 °C and the mean annual precipitation is 2342 mm (Luo et al., 2012).

A 25-ha (500 × 500 m) BSZ forest plot, with elevation ranging 1407 to 1646 m, was established in 2016 following the protocol of the ForestGEO network (<https://www.forestgeo.si.edu>; Fig. 1A). Every free-standing woody stem in the plot with a diameter at breast height (DBH) ≥ 1 cm was mapped, tagged and identified to species. Their DBHs were also measured. In total, there were 204,038 stems, belonging to 42 families and 86 genera.

### 2.2. Soil sample data

In October 2018, soils were sampled following the soil sampling protocol of the ForestGEO (John et al., 2007), as described below. We first divided the 25-ha plot into 20 × 20 m grids, leading to 676 grid intersections (including those points on the four edges of the 25-ha plot). These 676 intersections were used as the base points where soil samples were taken (Fig. 1B; Fig. S1). We further randomly selected 70% of the 676 base points (i.e., 473 of them). For each of these 473 selected base points, one of the eight directions (i.e., due east, due west, due south, due north, southeast, southwest, northwest, and northeast) was randomly selected (Fig. S1). Along the selected direction soils at two points of 2, 5, or 8 m distance away from the base point were randomly sampled, yielding 946 soil samples in addition to the 676 base point samples (totaling 1622 soil samples; Fig. 1B). Because a few samples were lost in the field, 1606 soil samples were eventually obtained.

When taking soil sample cores in the field, the litter and humus layers on the surface of a sampling location were removed before sampling, and the topsoil (0–10 cm) was collected using a soil auger of diameter 10 cm. Three or four such soil samples were collected within a radius of 50 cm around each of the 1606 selected sampling points and were then mixed as one composite sample to represent the soil of the sample location. The mixed soil sample was divided into two portions immediately in the field. One portion of fresh soil (ca. 50 g) was used for high-throughput sequencing and was transported to the laboratory in a sterile centrifuge tube on dry ice and stored at –80 °C until DNA extraction. The other portion (ca. 400 g) was packed in a ziplock bag for measuring soil physicochemical properties (after removing small stones and fine roots), including pH, nitrogen (N), phosphorus (P), and organic carbon (C).



**Fig. 1.** Topography of the 25-ha Baishanzu stem-mapping plot (A). Soil sampling scheme (B). 1622 soil samples were taken. Dot points indicate the locations of the 1622 samples. Note: 1606 soil samples were eventually available in this study.

### 2.3. Mycorrhizal information for adult trees

The mycorrhiza-tree symbiosis is known to change with the ontogenetic stage of trees (Chen et al., 2000; Egerton-Warburton and Allen, 2001), and large-diameter trees do not only contribute the greatest biomass (Lutz et al., 2018) but also are more prone to having mycorrhizal associations (Lutz et al., 2018; Mao et al., 2019). Therefore, we only included trees with DBH  $\geq 10$  cm (there were 27,672 trees in total) in this study. Following previous studies (Guo et al., 2008; Soudzilovskaia et al., 2020), only the AM- (e.g. *Aceraceae*) and EcM- (e.g. *Fagaceae*) associated trees were used, including 89 AM and 13 EcM tree species (Table S1). We found no orchid mycorrhizas in the 25-ha plot. Based on the strongest correlation between aboveground tree community composition and soil bacterial or fungal community composition detected at the 20 m neighborhood scale in the BCI 50-ha plot on Barro Colorado Island, Panama (Barberán et al., 2015), we selected a 20 m radius around each soil sampling location to determine the ratio of AM tree abundance versus the EcM tree abundance. Similarly, it was also found that soil bacterial or fungal community composition in our study site had a strongest correlation with aboveground tree community composition at the 20 m neighborhood scale (among 4 scales, including 5, 10, 15, and 20 m; Fig. S2).

### 2.4. Molecular analyses of microbial communities

DNA was extracted using a MagPure Soil DNA KF kit (Magigene Biotechnology Co., Ltd. Guangzhou, China) according to the manufacturer's instructions. The concentration and purity were measured using NanoDrop One (Thermo Fisher Scientific, MA, USA) based on the ratios of 260/280 nm and 260/230 nm absorbance (Yuan et al., 2018).

The polymerase chain reaction (PCR) primers were synthesized by Invitrogen (Invitrogen, Carlsbad, CA, USA). In the case of fungi, a nested PCR approach was used to target the internal transcribed spacer (ITS) region of fungal rDNA. We sequenced the second ITS (ITS2) regions of the rRNA operon using primer pairs, namely ITS3 (5'-GCATCGATGAA-GAACGCAGC-3') and ITS4 (5'-TCCTCCGCTTA TTGATATGC-3') primer pairs. For bacteria, the V4–V5 hypervariable regions of 16S rRNA genes were sequenced using the primers 515F (5'-GTGCCAGCMGCCGCGG-TAA-3') and 907R (5'-CCGTCGAATTCMTTTRAGTTT-3') (Li et al., 2020). Each PCR included 25  $\mu$ L of 2x Premix Taq (Takara Biotechnology, Dalian Co. Ltd., Dalian, China), 1  $\mu$ L of each primer (10 mM stocks), 20  $\mu$ L of nuclease-free water, and 3  $\mu$ L of DNA template (at a concentration of 20 ng/ $\mu$ L) in 50  $\mu$ L volumes. The PCR process included an initial denaturation cycle at 94 °C for 5 min, 30 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, extension at 72 °C for 30 s, and final elongation at 72 °C for 10 min. The PCR was done on a Bio-Rad S1000 (Bio-Rad Laboratory, CA, USA). The length and concentration of PCR products were detected by 1% agarose gel electrophoresis. The triplicate PCR reactions were pooled and the PCR products were mixed in equidensity ratio. The PCR products were purified using the EZNA Gel Extraction Kit (Omega Bio-tek, GA, USA). The sequencing library was sequenced on an Illumina HiSeq 2500 platform, and 250-bp paired-end reads were generated (Magigene Biotechnology Co. Ltd., Guangzhou, China).

### 2.5. Processing sequencing data of microbial communities

Filtering and subsequent analyses of raw reads were conducted using QIIME v1.9.0 (<http://qiime.org/>) (Caporaso et al., 2010), and barcodes and primers were removed to obtain effective clean tags using Mothur v1.35.1 (<https://mothur.org/>). Sequence analyses were performed using Usearch v10 (<https://www.drive5.com/usearch/>), and the sequences were clustered into operational taxonomic units (OTUs) with 97% sequence similarity. For each representative sequence, the UNITE database for fungi (<http://unite.ut.ee/index.php>) and SILVA database for 16S (<https://www.arb-silva.de/>) were selected to annotate

taxonomic information (setting the confidence threshold  $\geq 0.5$  by default) (Veach et al., 2018).

The Basic Local Alignment Search Tool (BLAST) was used for ITS sequences, and the Ribosomal Database Project classification method was used for 16S sequences (Liu et al., 2019). For fungi, sequences of each soil sample ranged from 28,843 to 367,435, and sequences of bacteria ranged from 22,247 to 107,325 per soil sample. Normalized OTU tables were obtained based on the samples with the fewest sequences (28,843 sequences for fungi and 22,247 for bacteria) (Zotti et al., 2020), which were used for subsequent analyses (unless otherwise noted). (Note raw sequence data for the ITS genes and 16S rRNA amplicons used in this study will be deposited in the NCBI database following the publication of this study.)

### 2.6. Statistical analyses

Soil fungal and bacterial alpha diversities were measured by Shannon index and were regressed with the ratio of AM/EcM trees. To explore whether the changes of fungal and bacterial communities were dominated by deterministic or stochastic processes, we calculated Bray-Curtis index for fungal and bacterial communities using their OTU abundance data, respectively, and compared the observed Bray-Curtis index with that of a null community model (Ning et al., 2019). The null model was generated by randomizing the observed community for 999 times (by randomly shifting the observed abundances across all the OTUs of the site  $\times$  OTU table; this randomization does not preserve row sum or column sum). The null model was calculated based on the algorithm PF (proportional taxa occurrence frequency, fixed richness;  $P_{ij}$ ), in which “proportional ( $P$ )” means that the occurrence probability of a taxon is proportional to its observed occurrence frequency and “fixed ( $F$ )” means the occurrence frequency of a taxon is fixed as observed (Ning et al., 2019).

$$P_{ij} = \frac{f_i}{F} \quad (1)$$

where  $P_{ij}$  is the probability of OTU  $i$  occurring in soil sample  $j$  in the null model,  $f_i$  is the observed occurrence frequency of OTU  $i$ , and  $F$  is the total number of occurrences.

The ratio of the expected similarity of the null model to the observed similarity was represented as the stochasticity ratio ( $ST$ ), which was used to quantify the relative importance of stochastic processes (Jiao et al., 2021; Ning et al., 2019). Following Ning et al. (2019), we further used the normalized stochasticity ratio ( $NST$ ) to quantify the relative importance of deterministic and stochastic processes.  $NST$  is calculated as following. Denote  $C_{ij}$  as the observed similarity of the two sites  $i$  and  $j$ , and dissimilarity  $D_{ij} = 1 - C_{ij}$ .  $E_{ij}$  is the null expected similarity between sites  $i$  and  $j$ .  $\bar{E}_{ij}$  is the average of 999 times. If microbial communities across sites are affected by deterministic processes, the average selection strength of communities ( $SS$ ) is:

$$SS = \frac{C_{ij} - \bar{E}_{ij}}{C_{ij}} \quad (2)$$

The stochasticity ratio is then defined as  $ST = 1 - SS$ , and the normalized selection strength ( $NSS$ ) is:

$$NSS = \frac{SS - SS^T}{SS^D - SS^T} \quad (3)$$

where  $SS^D$  is the theoretical maximum value of  $SS$  under completely deterministic assembly and  $SS^T$  is the theoretical minimum value of  $SS$  under completely stochastic processes, respectively. The  $NST$  is,  $NST = 1 - NSS$  (Ning et al., 2019).  $NST < 50\%$  indicates a community is dominated by deterministic processes, while  $NST > 50\%$  suggests stochastic processes at work (Ning et al., 2019). In this study, we also used  $ST$  because it could measure the strength of stochasticity based on the value of 0–100%. Both  $ST$  and  $NST$  were calculated using R package “NST”

(Ning et al., 2019). To further reveal the contributions of deterministic processes and stochastic processes to the microbial community assembly, we also calculated the niche breadth values of fungal and bacterial communities using Levins' niche breadth ( $B$ ) index (Levins, 1968). The community-level  $B$  value ( $B_{com}$ ) was the average of the  $B$  values of all taxa in a community (i.e., the average of all OTUs niche breadth values for fungal or bacterial community) using R package "spaa" (Jiao et al., 2021; Wu et al., 2018).

To explore possible relationships between the soil microbial communities and aboveground tree communities, we estimated the contribution of the AM/EcM tree ratio to microbial community stochastic processes (as measured by  $ST$ ). Specifically, the composition of AM and EcM trees in the 1606 locations where soil samples were taken were divided into 13 groups according to the values of AM/EcM tree ratio, i.e., locations that had similar ratios of AM/EcM trees were considered as a group, so that to make the within-group ratios as similar as possible while between-group ratios as different as possible (Jiao and Lu, 2020a), resulting in 13 groups. We then calculated the pairwise  $ST$  values between soil sample pairs in each group and the average values of  $ST$  in that group using the "tNST ()" function in the NST package. Boxplots were used to show the variation in pairwise  $ST$  values across the 13 groups for fungi and bacteria, respectively. Moreover, a linear regression was performed to test the effect of the AM/EcM tree ratios on the average  $ST$  values of each group.

The Mantel test was conducted to explore the correlations between  $ST$  (measuring the relative importance of stochastic assembly processes) and the ratio of AM/EcM trees and soil properties (16 soil properties as a whole), respectively. Euclidean distance matrices were calculated to represent the distance matrices of the variables (Jiao and Lu, 2020b). We also performed Spearman's correlations between each individual variable and the  $ST$  value of microbial communities. Soil properties were standardized using Z-scores. All data visualizations were conducted using the "ggplot2" package in R (Ginestet, 2011). All statistical analyses were carried out with R (v 4.1.1; <https://www.r-project.org/>).

### 3. Results

There were 15,444 OTUs (with no less than 20 sequences across 1606 samples) for fungi (643–2047 OTUs for each sample; Fig. S3), of which Basidiomycota was the most abundant phylum (45.6%), followed by Ascomycota (30.8%; Fig. S4A). In the case of bacteria, there were 16,045 OTUs (with no less than 20 sequences across 1606 samples; Fig. S4B) with 1811–3524 OTUs for each sample (Fig. S3). Acidobacteria (35.5%) and Proteobacteria (33.9%) were the two most abundant phyla of bacteria.

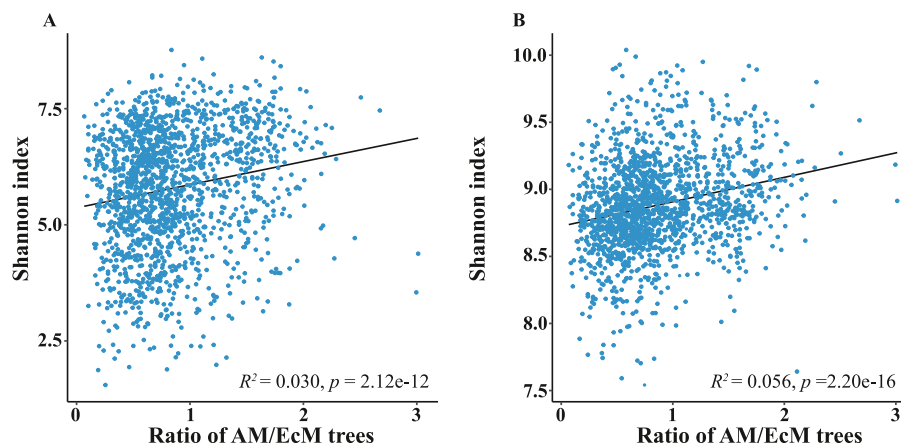


Fig. 2. Relationships between the ratio of AM/EcM trees and Shannon index of soil fungi (A) and soil bacteria (B). The solid lines are the linear regression models.

#### 3.1. Correlation between microbial diversities and the ratio of AM/EcM trees

The alpha diversities (Shannon index) of both soil fungal and bacterial communities were significantly positively correlated with the AM/EcM tree ratio ( $R^2 = 0.030$ ,  $p = 2.12e-12$ ;  $R^2 = 0.056$ ,  $p = 2.20e-16$ , respectively; Fig. 2) despite small  $R^2$  values.

#### 3.2. AM/EcM tree ratio contributes to microbial community assembly

The results showed that the mean  $B_{com}$  value of fungi was significantly smaller than that of bacteria ( $p < 0.001$ ), indicating bacteria had a wider niche width (Fig. 3A). Similarly, bacteria had a much larger  $NST$  value ( $>50\%$ ) than that of fungi ( $NST < 50\%$ ; Fig. 3B).

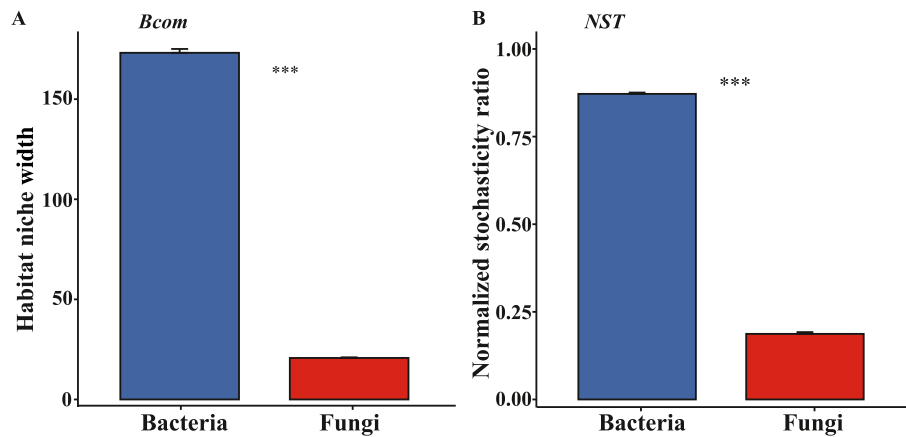
Compared with the fungal communities (Fig. 4A), the  $ST$ s of the bacterial communities were greater than 0.8 (Fig. 4B), which further indicates that the bacteria were more affected by stochastic processes. The results from the linear regression analysis between the AM/EcM tree ratio and  $ST$ s for the 13 AM/EcM ratio groups showed that the  $ST$ s of the fungal communities were significantly negatively correlated with the AM/EcM tree ratio ( $R^2 = 0.576$ ,  $p = 0.003$ ; Fig. 4A). Conversely, the  $ST$ s of the bacterial communities tended to increase with an increase in the ratio of AM/EcM trees (with a marginally significant relationship;  $R^2 = 0.304$ ,  $p = 0.051$ ; Fig. 4B).

#### 3.3. Contributions of the AM/EcM tree ratio and soil properties to microbial community assembly

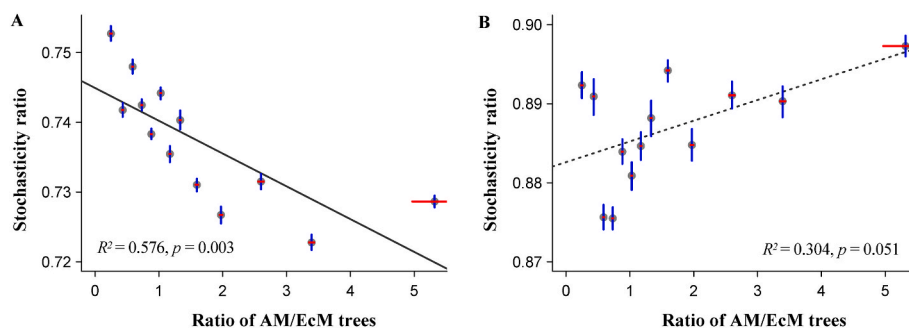
The results of the Mantel test show that there were significant positive correlations between the  $ST$ s of soil fungal community and the AM/EcM tree ratio (Spearman  $r = 0.437$ ,  $p = 0.005$ ; Table 1) and soil properties ( $r = 0.411$ ,  $p = 0.006$ ). In the case of bacteria, neither of the two sets of variables had a significant correlation with the  $ST$  ( $p > 0.106$ ; Table 1). Spearman's rank correlations test in Table 2 also showed that the ratio of AM/EcM trees ( $p < 0.001$ ) was strongly associated with the  $ST$  of the fungal community, while it was not related to the  $ST$  of the bacterial community. However, soil pH was detected to strongly correlate with the  $ST$  of the bacterial community ( $p = 0.040$ ; Table 2).

### 4. Discussion

Although it has been widely recognized that both AM- and EcM-associated trees could regulate belowground microbial communities (Hedèc et al., 2020; Singavarapu et al., 2022), it is far from clear how the proportion of AM- and EcM-associated trees contributes to the assembly of the microbial communities. This study demonstrates that the relative abundance of trees associated with different mycorrhizal types



**Fig. 3.** Community-level *B* values (*Bcom*) for bacteria and fungi (A), and normalized stochasticity ratios (*NST*) between bacterial and fungal communities (B) in the study forest. “\*\*\*” indicates the significant difference between bacteria and fungi ( $p < 0.001$ ).



**Fig. 4.** Relationships between the AM/EcM tree ratio and soil microbial stochasticity ratio of fungi (A) and bacteria (B) for the 13 AM/EcM ratio groups. The solid line represents the fitted linear regression model with a significant relationship in (A), and the dashed line is the fitted linear regression model with a marginal significant relationship in (B). Points denote means; the horizontal segment and the vertical segment for each point indicate the 95% confidence intervals for each group of the ratio of AM/EcM trees and for each group of stochasticity ratio, respectively.

**Table 1**

Results of Mantel test for correlations between the stochastic ratio (*ST*) of microbial communities and two sets of predictors (i.e., AM/EcM trees ratio and soil properties). Significant differences were tested based on 999 permutations. Bold values indicate significant correlations ( $p < 0.05$ ).

Selected variables	Fungi		Bacteria	
	r	p	r	p
Ratio of AM/EcM trees	0.437	<b>0.005</b>	0.221	0.143
Soil properties	0.341	<b>0.030</b>	0.162	0.163

**Table 2**

Spearman’s rank correlation of the stochastic ratio (*ST*) of microbial communities with the ratio of AM/EcM trees and soil properties [i.e., pH,  $\text{NH}_4^+$ -N,  $\text{NO}_3^-$ -N, total N (TN), total P (TP), available P (AP) and organic C (OC)]. Bold values indicate significant correlations ( $p < 0.05$ ).

Potential variables	Fungi		Bacteria	
	R	p	R	p
Ratio of AM/EcM trees	-0.885	<b>&lt;0.001</b>	0.407	0.170
pH	-0.511	0.078	0.582	<b>0.040</b>
$\text{NH}_4^+$ -N (mg/kg)	-0.082	0.793	-0.445	0.130
$\text{NO}_3^-$ -N (mg/kg)	-0.242	0.426	-0.143	0.643
TN (%)	0.253	0.404	-0.500	0.085
TP (g/kg)	-0.214	0.482	-0.060	0.849
AP (mg/kg)	-0.346	0.247	-0.176	0.566
OC (%)	0.473	0.106	-0.527	0.067

(the ratio of AM/EcM trees) not only plays critical roles in structuring the diversity of soil microbes in a subtropical forest, but also is significantly negatively correlated with the fungal community assembly (based on the value of *ST*). These findings emphasize the importance to

incorporate the ratio of AM/EcM trees into studying the relationship between aboveground tree diversity and underground microbe diversity and revealing mechanisms underlying the soil microbial community assembly in forest ecosystems (Hed nec et al., 2020; Singavarapu et al., 2022).

With the increase in the ratio of AM/EcM trees, alpha diversities of both soil fungi and bacteria increased, which answered our first question. This finding is consistent with Bahram et al. (2020) who showed that there were more bacteria and fungi in the topsoil of sites dominated by AM trees in a temperate forest. This could be ascribed to the contrasting nutrient-acquisition strategies of AM versus EcM tree species (Averill et al., 2019; Bahram et al., 2020). Briefly, EcM tree species can make use of EcM fungi to absorb nutrients directly from organic matter, whereas AM tree species benefit from rapid litter decomposition to get more inorganic nutrients (Ayuso-Fern ndez et al., 2018; Tedersoo and Bahram, 2019). In forests dominated by EcM tree species, high abundance of EcM fungi can strongly inhibit other soil fungi as well as bacteria (B deker et al., 2016). A high proportion of AM trees thereby leads to a high alpha diversity of both fungi and bacteria.

Based on the *Bcom* value, this study found that the habitat niche width of the fungal community was narrower than that of the bacterial community. This finding is in line with one recent study showing that soil bacteria had the largest niche widths while soil fungi displayed the smallest niche widths among four soil communities, including bacteria, archaea, fungi and protist (Malard et al., 2022). It might be expected that dispersal limitation has a much stronger effect on the fungal community than on the bacterial community (Chen et al., 2020). As species with a wide habitat niche are generally more resilient to environmental change than species with a narrow habitat niche, microbes with a wider habitat niche may use a wider range of soil resources and are metabolically more plastic (Pandit et al., 2009), thereby less affected by deterministic processes than those with narrower habitat niches (Chen et al.,

2021; Pandit et al., 2009).

Indeed, the *NST* values in our study confirmed that soil fungal communities were mainly driven by deterministic processes, whereas soil bacterial communities were mainly driven by stochastic processes. This finding is consistent with previous studies that bacteria are more influenced by stochastic processes while fungi are relatively more regulated by deterministic processes (Luan et al., 2020). Such distinction could be ascribed to the differences in body size between fungi and bacteria (Powell et al., 2015), such as 1.5–380  $\mu\text{m}$  for fungi versus 0.1–5  $\mu\text{m}$  for bacteria (Luan et al., 2020; Malard et al., 2022). Given fungi being relatively larger than bacteria, their dispersal ability could be more limited, leaving them more strongly filtered by the environmental sieve (Luan et al., 2020).

On the basis of previous studies uncovering the effects of tree species with different mycorrhizal types and soil properties on soil microbe community (Canini et al., 2019; Schappe et al., 2017; Tripathi et al., 2018), this study further detected that the stochastic ratio (*ST*) of soil fungal communities decreased with the increased ratio of AM/EcM trees. This change could also be ascribed to contrasting differences in fungal diversity under between AM and EcM tree species (Bahram et al., 2020; Eagar et al., 2022). One possible reason is that fungi are influenced to a greater extent by habitats and host plants than bacteria (Liu et al., 2021b; Peay et al., 2013), which makes fungi more closely associate with plants (Bonfante and Anca, 2009; Neuenkamp et al., 2018; Nguyen et al., 2016). Specifically, fungi can co-evolve with their host plants to form intimate relationships, such as obligate root symbionts and specific pathogens (Averill et al., 2019; Gao et al., 2013), while bacteria usually have no direct connection with trees but only inhabiting specific soil niches (Vos et al., 2013). Another possible reason is that plants have more persistent effects on soil fungi than on bacteria (Hannula et al., 2021), which in turn induces strong plant-soil feedback on plant community (Heinen et al., 2020). But to our knowledge, no previous studies have yet investigated the difference in microbial community assemblages between AM and EcM forests.

It has been increasingly acknowledged that tree mycorrhizal types can influence the cycling patterns of soil C, N and P. For example, by quantifying soil C and N under AM and EcM tree species in three temperate forests, Craig et al. (2018) verified that tree mycorrhizal types could predict the variation in soil organic matter storage and distribution, base don location. In this study, we also detected significant correlations between the ratio of AM/EcM trees and soil C and N (Table S3), but neither soil C nor soil N had a significant correlation with the soil community assembly (Table 2). Nevertheless, given the dominance of AM trees in the BSZ forest plot (Table S1), together with a potential increase of the dominance under the ongoing N deposition (Jo et al., 2019), it is expected that the increasing ratio of AM/EcM trees may further structure the soil microbial community. It should be noted that there was a significant positive correlation between pH and bacterial community *ST* in this study, which is in line with previous findings that soil pH mediated the balance between stochastic processes and deterministic processes of bacterial community (Tripathi et al., 2018). In our study site, the soil pH was overall acidic ( $4.251 \pm 0.009$ , Table S2). Under such acidic conditions, stochastic processes underlying bacterial community assembly are likely weakened, while stochastic processes will take the major role when pH conditions are neutral (Tripathi et al., 2018). This might explain why there was a significant positive correlation between pH and the bacterial community stochastic ratio, i.e., the stochastic ratio of the bacterial community increased with soil pH (changing from acidic to neutral).

## 5. Conclusions

By quantifying the relative importance of deterministic and stochastic processes in fungal and bacterial community assembly in a 25-ha subtropical forest plot, this study reveals a previously unrecognized importance of trees associated with different mycorrhizal types in

structuring soil microbial communities in forests. We found a significantly negative correlation between the AM/EcM tree ratio and the fungal community *ST*, whereas a marginally significant reverse pattern was observed for bacterial communities. This result shows that the AM/EcM tree ratio contributes to regulating the fungal and bacterial communities differently, suggesting the importance to incorporate AM/EcM tree ratios into studying the underlying assembly processes of soil microbial communities in forests, which in turn influence soil nutrient cycling and belowground biodiversity in forest ecosystems.

## Authors' contributions

Y.L. and H.X. conceived the study. H.X., X.W., M.Z., S.D., and Y. L. collected data. H.X., S.J., and Y.L. analyzed the data and interpreted the results. H.X., Y.L., and F.H. wrote the manuscript. All authors reviewed the manuscript.

## Data accessibility

The raw sequence dataset that supports the findings of this study will be deposited in the NCBI database following the publication of this study.

## Declaration of competing interest

The authors declare no competing interests for *Proportion of mycorrhiza-associated trees mediates community assembly of soil fungi but not of bacteria*.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.funeco.2023.101251>.

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