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# Tree species identity surpasses richness in affecting soil microbial richness and community composition in subtropical forests

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ABSTRACT

Plant interactions and feedbacks with soil microorganisms play an important role in sustaining the functions and stability of terrestrial ecosystems, yet the effects of tree species diversity on soil microbial community in forest ecosystems are still not well understood. Here, we examined the effects of tree species richness (1–12 species) and the presence of certain influential tree species (sampling effect) on soil bacterial and fungal communities in Chinese subtropical forests, using high-throughput Illumina sequencing for microbial identification. We observed that beta rather than alpha diversities of tree species and soil microorganisms were strong coupled. Multivariate regression and redundancy analyses revealed that the effects of tree species identity dominated over tree species richness on the diversity and composition of bacterial and fungal communities in both organic and top mineral soil horizons. Soil pH, nutrients and topography were always identified as significant predictors in the best multivariate models. Tree species have stronger effect on fungi than bacteria in organic soil, and on ectomycorrhizal fungi than saprotrophic fungi in mineral topsoil. Concluding, tree species identity, along with abiotic soil and topographical conditions, were more important factors determining the soil microbial communities in subtropical forests than tree diversity *per se*.

## 1. Introduction

Investigating the linkages between above- and below-ground biodiversity has long been a hot topic of ecological studies, because the interplay between the two components drives the functions and stability of terrestrial ecosystems (Hooper et al., 2000; Wardle et al., 2004). As an important colonizer of belowground habitats, soil microorganisms (bacteria and fungi) influence plant diversity and productivity (van der Heijden et al., 2008). Conversely, soil microorganisms are affected by the plant communities as microorganisms depend on the products of plant photosynthesis: litter and rhizodeposits (Wardle, 2006; Blagodatskaya et al., 2009; Prescott and Grayston, 2013). However, less is known about the contribution and underlying mechanisms of plant diversity in driving the diversity and composition of soil microbial communities in the field, particularly in forest ecosystems.

Increasing plant diversity generally increases the soil microbial diversity, with most case studies occurring in temperate grasslands (Pellissier et al., 2014; Chen et al., 2017; Yang et al., 2017) or tropical forests (Peay et al., 2013; Hiiesalu et al., 2017). General explanation is that plant richness diversifies the resource pool, and creates more spatial niches that can accommodate a greater diversity of soil microorganisms (the complementary effect) (Hooper et al., 2000; Waldrop et al., 2006). Meanwhile, it has been also suggested that soil microorganisms depend more on the certain influential plant species - key species, which affect soil microbial communities through specific traits, than on plant richness *per se* (Scheibe et al., 2015; Tedersoo et al., 2016; Gunina et al., 2017). The influence of a particular species is termed as taxonomic sampling effect (Huston, 1997), which is ubiquitous in natural and experimental systems and often masks the effect of biodiversity *per se* (Cardinale et al., 2006; Tedersoo et al., 2014a). Increasing plant richness has a higher chance to contain key plant species or their decreasing relative abundance. Therefore, the observed changes in the soil microbial communities along plant diversity gradient may be caused by plant richness *per se* or by the presence and abundance of

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certain key species. Most biodiversity experiments have employed small model systems with fast-growing primary producers, in particular herbaceous plants. We assume that the plant species effects are stronger in forests compared to the grasslands, as 1) forests harbor the largest and longest lived tree species on land (Bruelheide et al., 2014), 2) spatial scale of the effects of individual trees is much larger than of individual grasses and consequently the overlapping effects are less, and 3) the roots of most trees are associated with ectomycorrhiza, which has much longer hyphae compared to arbuscular mycorrhiza common for grasses. Many of the ecological surveys and experiments failed to separate the hidden sampling effect from diversity effect *per se* (Tedersoo et al., 2014a, 2016). Consequently, it is still poorly understood whether the soil microbial communities in forest ecosystems are influenced to a larger extent by tree species richness *per se* or by tree species identity.

Despite a well-established concept and evidence for strong coupling of plant and soil microbial diversity, these effects remain elusive. Tedersoo et al. (2014b) found only a weak, indirect relationship between soil fungal richness and plant richness over the globe. Similarly, Prober et al. (2015) also found no consistent relationship between plant and soil microbial richness across 25 temperate grassland sites from four continents. The differences in soil types and properties as well as plant communities examined across large scales hide the plant diversity effects. Interactions of plant-soil biota mainly occurred at local or regional scale over short time (Toju et al., 2014; Peay et al., 2016), but the coevolution is ongoing on much larger spatial and temporal scales. Thus, studies over large scales may not be well suited to address subtle links between plant and soil microbial diversity. Moreover, a number of field-based surveys indicated that soil microbial communities are actually poorly predicted by plant diversity, while some abiotic environmental factors such as soil pH and organic matter as well as topography were the more significant ecological drivers (Lauber et al., 2009; Bahram et al., 2012; Ding et al., 2015). This means that potential impacts of plant diversity may also be masked by abiotic environmental factors, which vary across experimental field sites. Because biotic and abiotic factors often covary (Qiu et al., 2018), it is important to disentangle the influences of plant diversity from the effects of abiotic factors.

In this study, we examined soil microbial community composition and diversity along a gradient of tree species richness in typical subtropical forests in southern China. The studied subtropical forests were developed from natural restoration of the destroyed forests since firewood collection was forbidden in the late 1950s, and now consisted of diverse tree species including coniferous *Pinus massoniana*, deciduous broadleaved *Choerospondias axillaris* and evergreen broadleaved species (e.g. *Lithocarpus glaber* and *Cyclobalanopsis glauca*). These secondary forest stands are essential to maintain ecosystem functions in subtropics (Xiang et al., 2013). By using the high-throughput Illumina sequencing, we aimed to disentangle the relative roles of 1) tree species richness, 2) sampling effects as well as 3) edaphic and topographical variables on diversity and community composition of bacteria and fungi in organic and mineral topsoil. We hypothesized that: (1) soil bacterial and fungal diversities are positively related to tree species diversity, whether alpha or beta diversity. Here, microbial alpha diversity is defined as the number of operational taxonomic units (OTUs) of each sample, while beta diversity is defined as microbial community compositional pairwise dissimilarity between quadrats (Yang et al., 2017). (2) The tree species diversity affects on soil microbial richness and composition by taxonomic sampling effect rather than richness *per se*, when accounting for abiotic environmental factors. Here, the sampling effect is taken into account by using model selection, incorporating certain key species as dummy variables (Tedersoo et al., 2016). (3) The effects of tree species are stronger for fungi than bacteria, and for biotrophic fungal guilds (ectomycorrhizal fungi) that directly interact with tree species than saprotrophic fungal guilds that are affected by tree species indirectly. Current methods allow researchers to analysis entire soil fungal communities not just one functional guild (Nguyen et al., 2016a), and thus differences among fungal functional guilds in their response to plant diversity effects might be expected.

## 2. Materials and methods

### 2.1. Study site and experiment design

The study was carried out at Dashanchong Forest Park (28°23′58″-28°24′58″N, 113°17′46″-113°19′08″E), Changsha County, Hunan Province. This area is experiences a humid mid-subtropical monsoon climate, with altitudes ranging from 55 to 260 m above mean sea level, a mean annual air temperature of 17.3 °C and a mean annual precipitation of 1416 mm (Ouyang et al., 2016). The soil is a well-drained clay loam red soil developed on slate and shale rock, classified as Alliti-Udic Ferrosols, corresponding to Acrisol in the World Reference Base for Soil Resource (IUSS Working Group WRB, 2015). Evergreen broadleaved forest is the climax vegetation of this region. Because of historical human disturbances and left for natural regeneration, the Park has no primary forest and possesses a range of secondary forests dominated by different tree species, including (1) *P. massoniana-L. glaber* coniferous and evergreen broadleaved mixed forests (PMF) dominated by the shade-intolerant coniferous species, (2) *C. axillaris* deciduous broadleaved forests (CAF) dominated by shade-intolerant deciduous broadleaf species, and (3) *L. glaber-C. glauca* evergreen broadleaved forests (LGF) dominated by the shade-tolerant evergreen broadleaved species which commonly observed in this Park.

Three 1.0-ha permanent plots were previously established for the three typical secondary forest stands in this Park, respectively (Xiang et al., 2013). Each 1.0-ha plot was divided into 100 equally distributed 10 × 10 m subplots for a field census. The locations of individual trees within each subplot were tagged and identified, diameter at breast height (DBH), height (H), and basal area (BA) of all tree species with DBH ≥ 4 cm were measured. We calculated the mean value of the relative elevation (m) at the four corners (using the elevation of original location of X and Y coordinates in each plot as the reference point on the ground) to reflect topography of each subplot. Detail information of stand characteristics of the three 1.0-ha plots refer to our previous studies (Table S1, Zhu et al., 2016). According to the experimental methods described by Leuschner et al. (2009), we then selected non-neighboring subplots within each 1.0-ha plot as much as possible to avoid spatial autocorrelation and edge effects. Finally, a total of 94 quadrats were selected from the three 1.0-ha plots to form a diversity gradient with a range of 1–12 tree species richness (Fig. 1; Table S2).

### 2.2. Sample collection and characterization

In October 2016, samples of organic soil (or O horizon) (*c.* 0.5–3 cm) and mineral topsoil (up to a depth of 10 cm) were collected at five points (one point at the center and four points equidistant from the center toward the corners of the subplots) of each subplot. The five samples from each subplot were pooled to form a composite sample for further analysis. A total of 188 soil samples were obtained from the 94 subplots. Visible stones, roots and other residues were removed in the field. Fresh soil samples were kept in a freezer being transported to the laboratory. For each sample, 500 g of fresh soil were air-dried and sieved to 2 mm for physiochemical analyses, and 200 g of fresh soil were stored under −80 °C for DNA extraction.

Soil water content was measured by oven-drying the fresh soil samples at 105 °C for 24 h. Soil pH were measured with a soil to water ratio of 1:2.5 by an FE20 pH meter (Mettler Toledo, Shanghai, China). Total nitrogen (N) was determined on an element analyzer (Vario EL III, Elementar, Germany). Soil organic carbon (SOC) was measured using a $K_2Cr_2O_7$ oxidation method as described in Walkley (1947). Soil available phosphorus (P) concentrations were determined by the 0.05 mol $L^{-1}$ HCl-0.025 mol $L^{-1}$ (1/2 $H_2SO_4$) method (Mehlich, 1984).

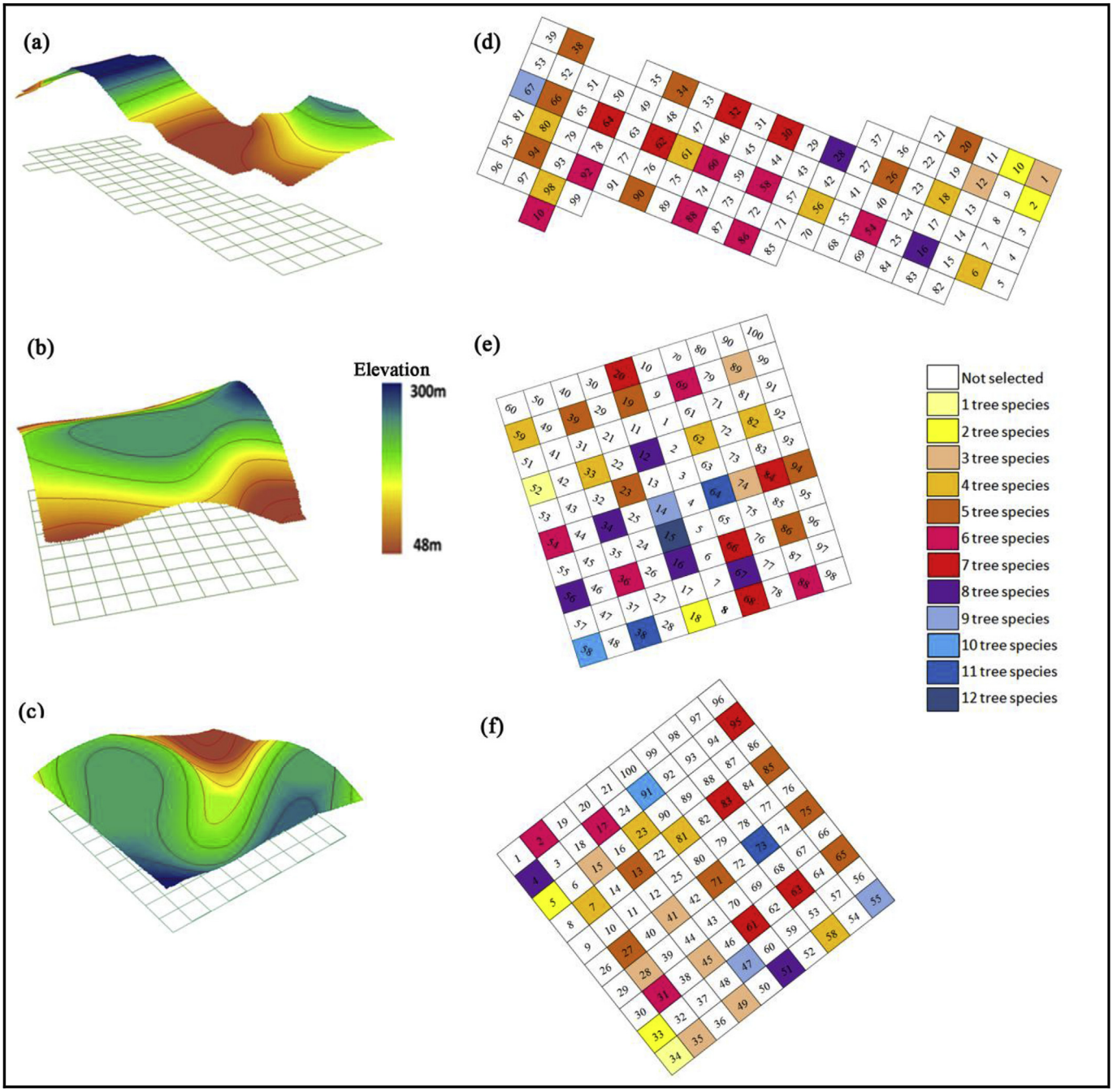


**Fig. 1.** Map of the three 1.0-ha secondary forest plots: (a) *P. massoniana-L. glaber* coniferous and evergreen broadleaved mixed forests, (b) *C. axillaris* deciduous broadleaved forests and (c) *L. glaber-C. glauca* evergreen broadleaved forests. The 94 selected quadrats distributed in the three plots (d, e, f) illustrating different tree species richness levels.

Soil C/N ratio was calculated based on SOC and N concentration. Three parallel measurements were performed for each soil sample to minimize experimental errors. Organic and mineral topsoil physiochemical properties of the 94 subplots are presented in Table S2.

### 2.3. DNA extraction, amplification and sequencing

Soil total genomic DNA was extracted from 0.25 g of fresh organic or mineral topsoil sample using the E.Z.N.A.® soil DNA Isolation Kit (Omega Bio-tek, Norcross, GA, USA) according to the manufacturer's instructions. DNA was extracted three times from each soil sample, and then mixed and homogenized. The quality and concentration of the extracted DNA were quantified using a NanoDropND-2000c UV–Vis Spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA).

The primer set 515R/907F was employed to target the V4 and V5 regions of the bacterial 16S rRNA gene, as described by Xiong et al. (2012). The primer set ITS1F/ITS2 (2043R) was used to amplify the fungal internal transcribed spacer (ITS) region (Gardes and Bruns, 1993; Bokulich and Mills, 2013). The reverse primer contained variable length error-correcting barcodes (10–12 bp) unique to each sample to permit sequencing on the Illumina Miseq platform. PCR amplification was performed for each soil DNA extract in triplicate and combined into a single composite sample. The 25 μl PCR reaction mixtures consisted of 12.5 μl Premix Taq (Takara Biotechnology, Dalian, China), 0.5 μl of each primer (10 μM), 1.5 μl of 10-fold diluted DNA template (1–10 ng), and 10 μl of sterilized dd$H_2O$. The thermal-cycling conditions were

94 °C for 5 min; 35 cycles of 94 °C for 30 s, 55 °C for 30 s, 72 °C for 30 s, followed by 72 °C for 10 min for primers 515R/907F; 94 °C for 3 min; 35 cycles of 94 °C for 45 s, 50 °C for 60 s, 72 °C for 60 s, followed by 72 °C for 10 min for primers ITS1F/ITS2. PCR products were gel-purified using the Wizard SV Gel and PCR Clean-Up System (Promega, San Luis Obispo, USA). The resultant PCR products were combined at equimolar concentrations before being sequenced on an Illumina Miseq sequencer at the Majorbio Bio-Pharm Technology Co., Ltd. (Shanghai, China).

### 2.4. Bioinformatic analyses

The obtained raw 16S rRNA and ITS sequence data were processed using the Quantitative Insights Into Microbial Ecology (QIIME) pipeline (Caporaso et al., 2010). Briefly, paired-end reads with at least a 10-bp overlap and < 0.2 mismatches were combined using FLASH (Magoc and Salzberg, 2011), and a threshold of average quality scores > 50 over 20-bp window size was used to trim the unqualified sequences using BTRIM (Kong, 2011). A joined sequence with ambiguous bases and lengths < 200-bp were discarded. The obtained sequences were normalized to the minimum number of reads across all samples for the downstream analysis. Bacterial and fungal sequences were than independently clustered into operational taxonomic units (OTUs) at a 97% identity threshold using UPARSE (Edgar, 2013) with the chimeras and all singletons being discarded meanwhile. Taxonomy of bacteria and fungi was assigned to each sequence through BLASTing against the RDP (Cole et al., 2009) and UNITE database (Abarenkov et al., 2010), respectively. Fungal functional guilds (funguilds) were assigned according to Tedersoo et al. (2014b) and Nguyen et al. (2016a). The bacterial and fungal DNA sequences of the 188 soil samples have been deposited in the SRA of the NCBI database under the Accession no. SRP128847 (SRR6460891-SRR6461078) and SRP130039 (SRR6479064-SRR6479251), respectively.

### 2.5. Statistical analyses

All the analyses were performed at the subplot level (n = 94). One-way analysis of variance (ANOVA) followed by *t*-test was performed to assess the differences in the relative abundance of the major microbial taxa between the two soil horizons at $p < 0.05$ level. The observed microbial OTU numbers and tree species richness were selected to represent microbial and tree species alpha diversity, respectively. Community tables describing the relative abundance of microbial OTUs and tree species composition were used as primary data to calculate Bray-Curtis site distance tables for microorganisms and trees, respectively. Bray-Curtis dissimilarity between each soil samples pair was used as a representation of microbial and plant beta diversities as calculated using the "ECODIST" (version 2.0-1) and "VEGAN" (version 2.3–3) packages in R (Chen et al., 2017; R Development Core Team, 2015). To test our first hypothesis, Pearson correlation analyses and Mantel tests were used to examine the correlation of alpha and beta diversities between microorganisms and plants, respectively.

In addition to tree species richness, the relative BA ($R_{BA}$) of the dominant tree species (i.e. *P. massoniana*, *C. axillaris*, *L. glaber* and *C. glauca*) was selected as explanatory variables to estimate taxonomic sampling effect (Tedersoo et al., 2016). As potential abiotic variables we selected the soil physiochemical properties (i.e. water content, pH, SOC, TN, AP and C/N ratio) and topographical factors (i.e. topography and convexity). To disentangle the effects of these biotic and abiotic variables on OTU richness of soil microorganisms, individual variables were subjected to the best ordinary least squares (OLS) multiple regression model selection. All variables and OTU numbers were standardized (average = 0 and SD = 1) using the "scale" function before the OLS multiple regression analysis. Akaike's information criterion (AIC) was used to identify the best OLS model, as implemented in the R package "MASS" (version 7.3–45). The variance inflation factor (VIF) was calculated for OLS multiple regression models using the R package "CAR" (version 2.1-2). We used the criterion VIF < 3 to select suitable variables in the best multiple regression models to remove strongly multicollinear variables (Yang et al., 2017).

To test whether these biotic and abiotic variables influence community composition of soil microorganisms, distance-based redundancy analysis (db-RDA) was performed with forward selection of the explanatory variables using the CANOCO 5.0 software (Microcomputer Power, Ithaca, NY, USA). Community distance was calculated with the Bray-Curtis measure, and explanatory variables were included into the model if $P_{adj}$ was < 0.05. The relative effects of tree species richness, taxonomic sampling effect, and edaphic and topographical variables on microbial community composition were calculated based on the best multivariate model.

## 3. Results

### 3.1. An overview of the Illumina sequencing results for the soil microbial communities

Quality filtering recovered a total of 5,987,197 bacterial sequences (on average, 31,847 per sample) from the 188 soil samples, and normalized to 18,870 sequences per sample. The classified bacterial sequences were binned into 5737 OTUs and 5523 OTUs at 97% sequence identity in organic and mineral topsoil, respectively. The most dominant bacterial phyla across organic soil was *Proteobacteria* (43.0% of the total sequences, harbored 2008 OTUs), while *Acidobacteria* (43.6%, 331 OTUs) was dominated in mineral topsoil (Fig. 2a). In addition, *Actinobacteria* was higher ($p < 0.01$) in organic soil and *Chloroflexi* was higher ($p < 0.01$) in mineral topsoil (Fig. 2a).

In total, 6,980,917 fungal sequences that survived quality trimming and chimera removal (on average 37,132 and normalized to 29,739 sequences per sample) were clustered into 6351 OTUs. Organic and mineral topsoil harbored 5410 and 4165 OTUs respectively, and were dominated by *Ascomycota* and *Basidiomycota*, which accounted for >

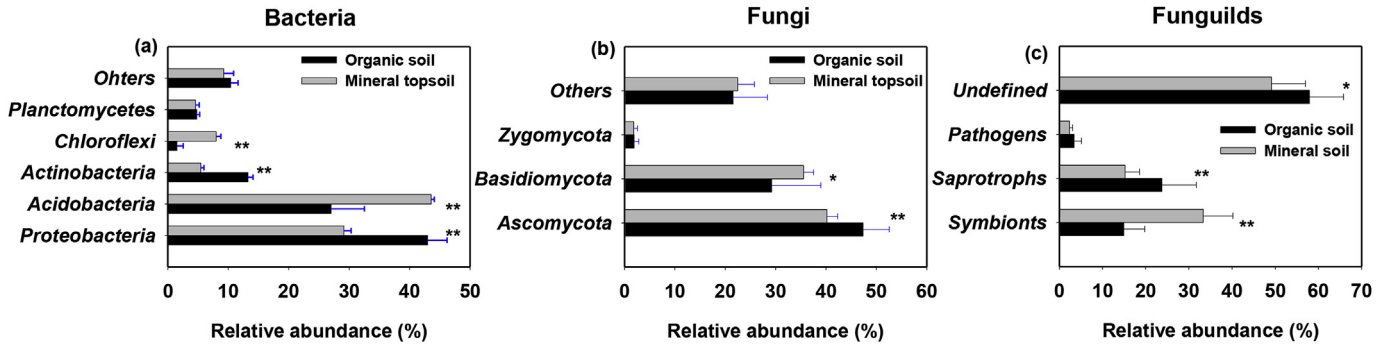


**Fig. 2.** Comparison of taxonomic distribution of total sequences of bacteria (a), fungi (b) and funguilds (c) in the organic and mineral topsoil horizons. The asterisk (*) denotes significance at the $p < 0.05$ level, and asterisk (**) denotes significance at the $p < 0.01$ level.

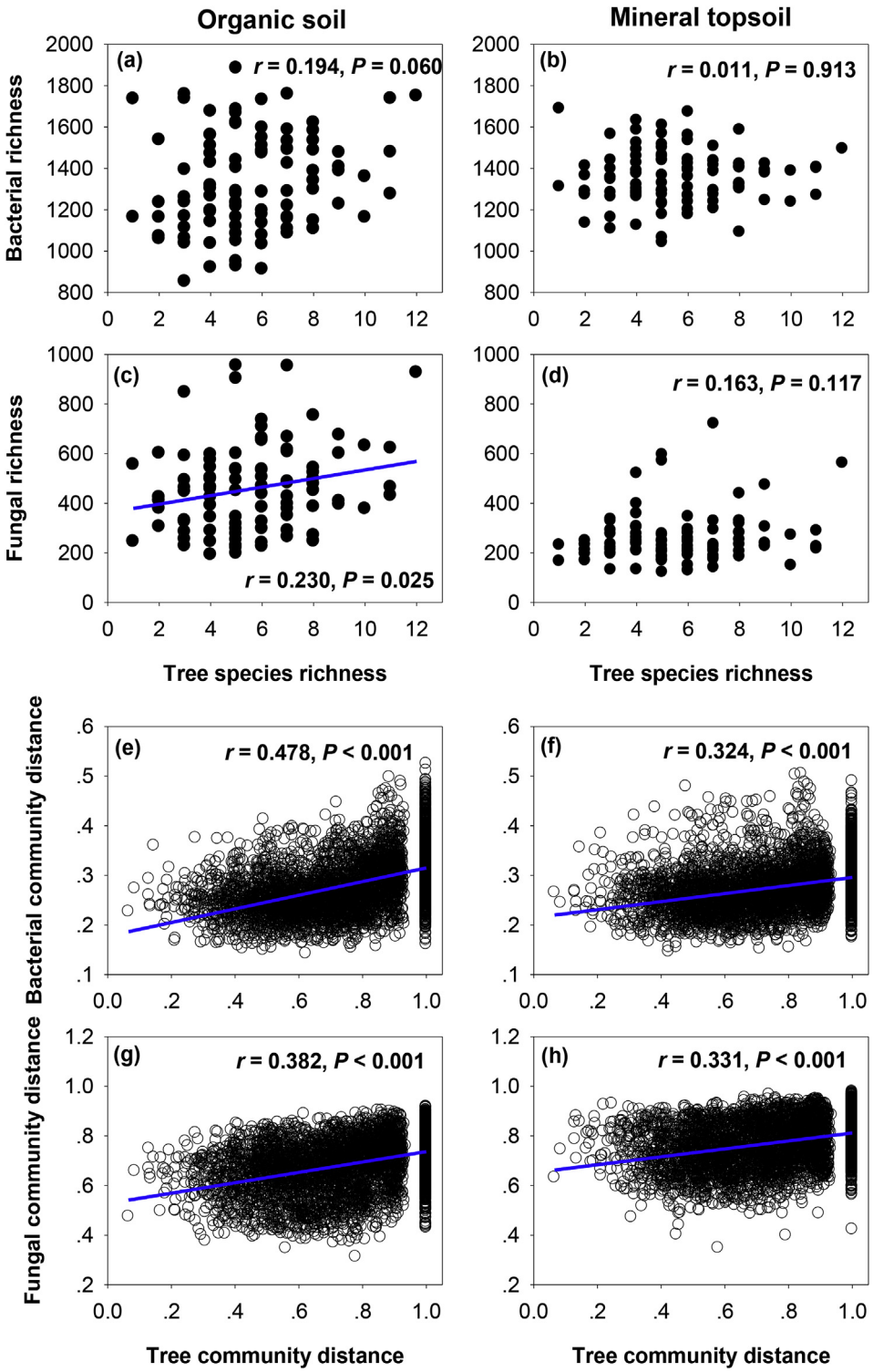


**Fig. 3.** Correlations of soil bacterial and fungal diversities with tree diversity across the studied subtropical forest. Alpha diversity (a-d, solid circle) shows linear regression of soil microbial richness against tree species richness (n = 94), and beta diversity (e-h, hollow circle) shows linear regression of the pairwise Bray-Curtis distance for microbial and tree communities (a total of 4371 points and each point represents the dissimilarity in taxonomic composition between a pair of plots).

75% of the total sequences. However, *Ascomycota* was higher ($p < 0.01$) in organic soil and *Basidiomycota* was higher ($p < 0.05$) in mineral topsoil (Fig. 2b). When the observed fungal taxa were divided into three major functional groups (symbionts, saprotrophs and pathogens), the proportions of saprotrophs was higher ($p < 0.01$) in organic soil while symbionts was higher ($p < 0.01$) in mineral topsoil (Fig. 2c). Notably, almost all of symbionts are ectomycorrhizal (ECM) fungi rather than arbuscular mycorrhizal (AM) fungi.

### 3.2. Correlations of soil microbial diversity with tree diversity

Pearson correlation analysis revealed that a significant and positive relationship was only found between tree species richness and fungal richness in the organic soil ($p < 0.05$, Fig. 3c). Correlation between

**Table 1**
Summary of the best ordinary least squares (OLS) multiple linear regression models for the effects of biotic and abiotic factors on richness of microorganisms in the organic soil.

| Variable | Estimate | SE | t-value | *P*-value | VIF |
|---|---|---|---|---|---|
| **Bacterial richness: df = 85; $R^2_{adj}$ = 0.767; $SE_{resid}$ = 0.482; F = 39.35; AIC = -126.7** | | | | | |
| Soil pH | 0.265 | 0.067 | 3.959 | < 0.001 | 1.681 |
| Topography | −0.328 | 0.073 | −4.473 | < 0.001 | 2.025 |
| *P. massoniana* $R_{BA}$ | −0.212 | 0.072 | −2.960 | 0.004 | 1.926 |
| *C. glauca* $R_{BA}$ | −0.170 | 0.061 | −2.804 | 0.006 | 1.386 |
| Soil C/N ratio | −0.187 | 0.067 | −2.782 | 0.007 | 1.699 |
| *L. glaber* $R_{BA}$ | −0.131 | 0.062 | −2.119 | 0.037 | 1.439 |
| **Fungal richness: df = 89; $R^2_{adj}$ = 0.451; $SE_{resid}$ = 0.741; F = 20.1; AIC = -55.2** | | | | | |
| *C. glauca* $R_{BA}$ | −0.279 | 0.088 | −3.182 | 0.002 | 1.308 |
| *P. massoniana* $R_{BA}$ | −0.286 | 0.092 | −3.096 | 0.003 | 1.444 |
| *L. glaber* $R_{BA}$ | −0.271 | 0.089 | −3.029 | 0.003 | 1.355 |
| Topography | −0.285 | 0.105 | −2.718 | 0.008 | 1.856 |
| **ECM fungal richness: df = 88; $R^2_{adj}$ = 0.480; $SE_{resid}$ = 0.721; F = 18.14; AIC = -55.59** | | | | | |
| *C. glauca* $R_{BA}$ | 0.302 | 0.084 | 3.616 | < 0.001 | 1.245 |
| Soil C/N ratio | 0.305 | 0.095 | 3.221 | 0.002 | 1.605 |
| *L. glaber* $R_{BA}$ | 0.195 | 0.084 | 2.316 | 0.023 | 1.271 |
| *C. axillaris* $R_{BA}$ | −0.205 | 0.094 | −2.176 | 0.032 | 1.588 |
| *P. massoniana* $R_{BA}$ | 0.185 | 0.104 | 1.784 | 0.048 | 1.913 |
| **SAP fungal richness: df = 90; $R^2_{adj}$ = 0.348; $SE_{resid}$ = 0.813; F = 16.86; AIC = -37.43** | | | | | |
| Topography | −0.432 | 0.100 | −4.307 | < 0.001 | 1.414 |
| *L. glaber* $R_{BA}$ | −0.215 | 0.098 | −2.199 | 0.030 | 1.373 |

(AIC, Akaike's information criterion; VIF, variance inflation factor).

**Table 2**
Summary of the best ordinary least squares (OLS) multiple linear regression models for the effects of biotic and abiotic factors on richness of microorganisms in the mineral topsoil.

| Variable | Estimate | SE | t-value | *P*-value | VIF |
|---|---|---|---|---|---|
| **Bacterial richness: df = 88; $R^2_{adj}$ = 0.425; $SE_{resid}$ = 0.758; F = 14.76; AIC = -44.26** | | | | | |
| *P. massoniana* $R_{BA}$ | −0.569 | 0.085 | −6.683 | < 0.001 | 1.171 |
| *C. glauca* $R_{BA}$ | −0.398 | 0.086 | −4.632 | < 0.001 | 1.197 |
| *L. glaber* $R_{BA}$ | −0.317 | 0.083 | −3.819 | < 0.001 | 1.116 |
| Tree richness | −0.247 | 0.086 | −2.616 | 0.010 | 1.193 |
| Soil water content | −0.167 | 0.083 | −2.017 | 0.046 | 1.109 |
| **Fungal richness: df = 88; $R^2_{adj}$ = 0.240; $SE_{resid}$ = 0.872; F = 6.86; AIC = -19.95** | | | | | |
| Soil AP | −0.378 | 0.102 | −3.696 | < 0.001 | 1.281 |
| Topography | −0.320 | 0.105 | −3.056 | 0.003 | 1.334 |
| Soil pH | −0.271 | 0.092 | −2.934 | 0.004 | 1.045 |
| *C. glauca* $R_{BA}$ | −0.200 | 0.095 | −2.100 | 0.038 | 1.113 |
| **ECM fungal richness: df = 87; $R^2_{adj}$ = 0.494; $SE_{resid}$ = 0.711; F = 16.15; AIC = -57.36** | | | | | |
| *P. massoniana* $R_{BA}$ | 0.460 | 0.083 | 5.552 | < 0.001 | 1.262 |
| *C. glauca* $R_{BA}$ | 0.342 | 0.077 | 4.445 | < 0.001 | 1.085 |
| *L. glaber* $R_{BA}$ | 0.276 | 0.080 | 3.443 | < 0.001 | 1.183 |
| Soil AP | −0.188 | 0.085 | −2.222 | 0.029 | 1.321 |
| **SAP fungal richness: df = 88; $R^2_{adj}$ = 0.231; $SE_{resid}$ = 0.877; F = 6.598; AIC = -18.93** | | | | | |
| Topography | −0.408 | 0.106 | −3.864 | < 0.001 | 1.348 |
| Soil AP | −0.320 | 0.105 | −3.055 | 0.003 | 1.326 |
| Soil pH | −0.251 | 0.093 | −2.698 | 0.013 | 1.049 |
| *P. massoniana* $R_{BA}$ | 0.268 | 0.104 | 2.572 | 0.049 | 1.313 |

(AIC, Akaike's information criterion; VIF, variance inflation factor).

tree species richness and bacterial richness in both two soil horizons or fungal richness in the mineral topsoil were absent (Fig. 3a, b and d). However, microbial beta diversities in the two soil horizons were all significantly and positively correlated with tree beta diversity. With increasing tree beta diversity, there was a corresponding increase in bacterial and fungal diversities, respectively (Fig. 3e–h).

### 3.3. Effects of biotic and abiotic factors on soil microbial richness

The best OLS multiple regression model (the highest $R^2_{adj}$ and lowest AIC) indicated that tree species identity and soil variables were usually the best predictors of soil microbial richness (Tables 1 and 2). Bacterial richness responded significantly to soil pH, topography, *P. massoniana* $R_{BA}$, *C. glauca* $R_{BA}$, soil C/N ratio and *L. glaber* $R_{BA}$, which collectively explained 76.7% of the variation in the organic soil. In contrast, the strong predictors (*P. massoniana* $R_{BA}$, *C. glauca* $R_{BA}$, *L. glaber* $R_{BA}$, tree richness and soil water content) explained 42.5% of variation of bacterial richness in the mineral topsoil.

Fungal richness in the organic soil was best explained by *C. glauca* $R_{BA}$, *P. massoniana* $R_{BA}$, *L. glaber* $R_{BA}$ and topography, which totally explained 48.7% of the variation. Soil AP, topography and *C. glauca* $R_{BA}$ were the best predictors of fungal richness in mineral topsoil, altogether explaining 24.0% of variation. For ECM fungal richness, *C. glauca* $R_{BA}$, soil C/N ratio, *L. glaber* $R_{BA}$, *C. axillaris* $R_{BA}$ and *P. massoniana* $R_{BA}$ accumulatively explained 48.0% of the variation in the organic soil, while *P. massoniana* $R_{BA}$, *C. glauca* BA, *L. glaber* $R_{BA}$ and soil AP explained 49.4% of the variation in the mineral topsoil. For SAP fungal richness, topography and *L. glaber* $R_{BA}$ explained 36.9% of the variation in the organic soil, whereas topography, soil AP, soil pH and *P. massoniana* BA explained 23.1% of the variation in the mineral topsoil.

### 3.4. Driving factors of soil microbial community composition

The microbial community compositions were influenced by biotic and abiotic variables as revealed by the db-RDA (Fig. 4, Tables S3 and S4). For bacterial community composition in the organic soil, 8 significant predictors taken together explained 39.6% of the variation, in which tree species identity (*C. axillaris* $R_{BA}$, *C. glauca* $R_{BA}$, *P. massoniana* $R_{BA}$ and *L. glaber* $R_{BA}$), edaphic (soil pH, C/N ratio and AP) and topographical factors explained 8.1%, 13.7% and 17.8%, respectively. For bacterial community composition in the mineral topsoil, tree species identity (*P. massoniana* $R_{BA}$, *C. glauca* $R_{BA}$ and *L. glaber* $R_{BA}$), tree species richness, edaphic (soil pH, AP, C/N ratio and water content) and topographical factors explained 15%, 1.3%, 14% and 5.7% of the variation, respectively.

The fungal community composition in the organic soil was explained by tree species identity (*P. massoniana* $R_{BA}$, *C. glauca* $R_{BA}$ and *L. glaber* $R_{BA}$), edaphic (soil C/N ratio and AP) and topographical factors with 18.6%, 4.1% and 7.0%, respectively, whereas by tree species identity (*P. massoniana* $R_{BA}$, *C. glauca* $R_{BA}$ and *L. glaber* $R_{BA}$, 9.7%), edaphic (soil AP and pH, 3.5%) and topographical (6.8%) factors in the mineral topsoil. For ECM fungal community, tree species identity (*C. glauca* $R_{BA}$, *P. massoniana* $R_{BA}$ and *L. glaber* $R_{BA}$) and topographical factors accumulatively explained 11.5% and 13.3% of the variation in the organic soil; and tree species identity (*L. glaber* $R_{BA}$, *C. glauca* $R_{BA}$ and *P. massoniana* $R_{BA}$) and topography explained 17.2% and 28.4% of the variation in the mineral topsoil. For SAP fungal community structure in the organic soil, tree species identity (*P. massoniana* $R_{BA}$, *C. glauca* $R_{BA}$ and *L. glaber* $R_{BA}$), edaphic (soil C/N ratio and AP) and topographical factors explained 10.3%, 3.8% and 13.9% of the variation. By contrast, SAP fungal communities in mineral topsoil was mainly explained by topography (7.6%), followed by tree species identity (*P. massoniana* $R_{BA}$ and *C. glauca* $R_{BA}$, 5.8%) and edaphic variables (soil AP and pH, 3.8%).

## 4. Discussion

### 4.1. Tree species richness versus species identity

In this study, we just found significant correlation between tree species and fungal alpha diversity in the organic soil (Fig. 3c), providing little support for our first hypothesis that the alpha diversity of soil microorganisms and tree species are positively associated. This indicates that more diverse tree forest would not necessarily promote microbial richness. In contrast to the lack of relationship for alpha diversity, our first hypothesis predicting positive correlation between soil

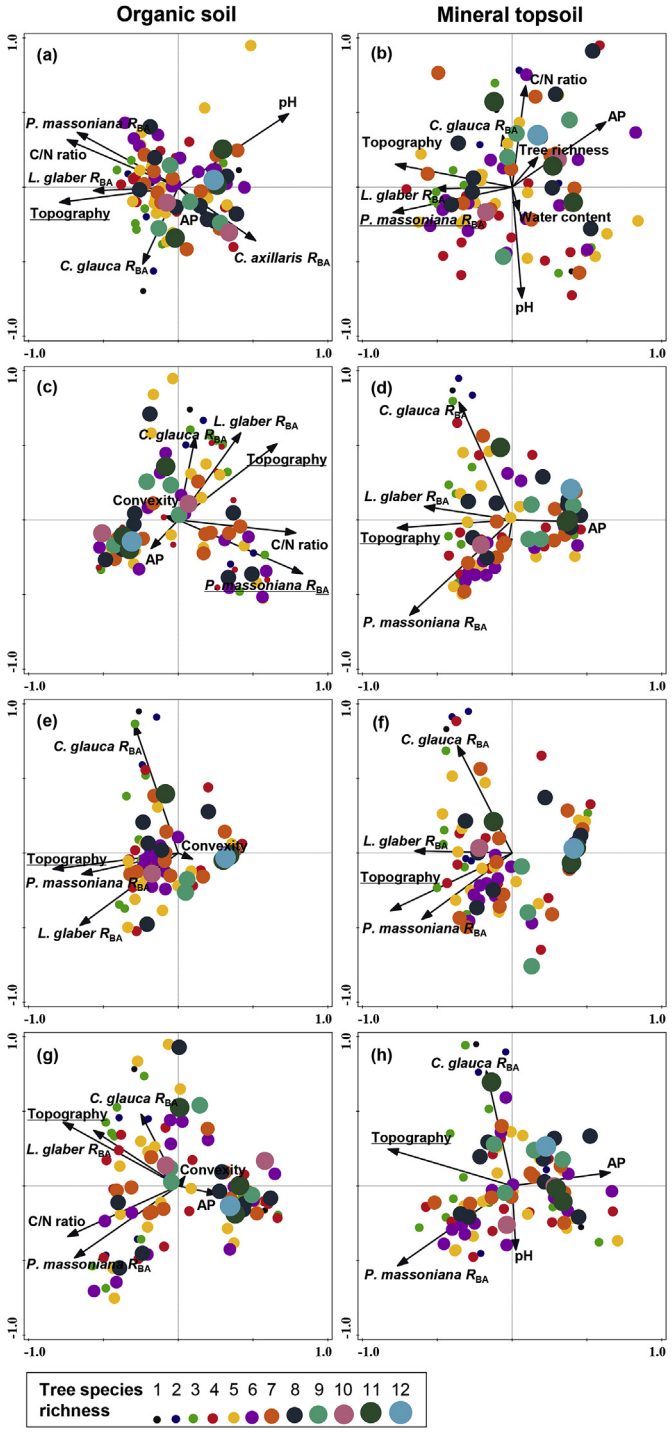


**Fig. 4.** Distance-based redundancy analyses (db-RDA) plot showing the relationship of biotic and abiotic factors to community composition of bacteria (a, b), fungi (c, d), ECM fungi (e, f) and SAP fungi (g, h) in the organic and mineral topsoil horizons, respectively. The ordination is based on Bray-Curtis distance with forward selection, and factors were chosen that significantly ($P_{adj} < 0.05$) contributed to the model. The strongest predictors in the best community models are underlined.

microorganisms and tree species was supported for beta diversity; i.e. quadrats that were more distinct in the composition of their tree communities also harbored more distinct soil microbial communities (Fig. 3e–h). The OLS multiple regression models, db-RDA and variation partitioning analyses further indicated that tree species richness itself is rarely as a strong predictor of soil microbial richness and community composition after accounting for confounding soil and topographical factors. This result contrasts from previous studies, in which tree species richness was an important driver of soil microbial communities (Gao et al., 2013; Hiiesalu et al., 2017). However, our results are consistent with Nguyen et al. (2016b) who found that no significant effect of tree species richness on either ectomycorrhizal or saprotrophic fungal species richness in a field experiment. The discrepancy among aforementioned studies may resulted from the use of field-based tree diversity gradients which contain some factors that covary with plant diversity or other factors that unrelated to plants but influence soil microorganisms (Waldrop et al., 2006). Therefore, it is necessary to incorporating higher tree species gradients (> 20 species) to clearly observe the cumulative nature of this relationship in the future studies. Soil microbial communities are largely structured by the supply of growth limiting substrates, which enter soil via plant detritus and/or root exudation (Prescott and Grayston, 2013; Uroz et al., 2016). The lack of relationship between tree species richness and soil microbial communities should be arose from the fact that resource availability (i.e. litter and root production from different tree species and functional groups) did not change consistently with tree species richness.

Supporting our second hypothesis, tree species identity usually significantly influences the soil microbial richness and community composition, reinforcing the strong sampling effects on ecosystem services (Cardinale et al., 2006; Tedersoo et al., 2014a). Tree species with various traits return organic matter of differing qualities to the soil, which in turn affects the soil microbial richness and composition. Our previous study showed that litter quality differs among the dominant tree species in these forests, with the highest N contents in *C. axillaris*, the lowest N and P contents in *P. massoniana* and relatively high N/P ratio in *L. glaber* (Zeng et al., 2017). Principal coordinate analyses of bacterial and fungal community compositions further revealed that soil under the forest dominated by the same tree species typically clustered together (Fig. S1), which clearly supports tree species identity effects on the microbial community structure. It has been frequently reported that specific soil microbial communities exist under specific tree species. Urbanová et al. (2015) showed that among the seven dominant tree species, some tree species such as *Alnus* and *Pinus* presented distinguishable soil bacterial and fungal communities. Pfeiffer et al. (2013) also observed differentiation of bacterial communities according to tree species. These findings provided obvious evidence that tree species differ in the belowground communities.

Our results showed that the directionality and magnitude of individual tree species effects are different (Fig. S2; Tables 1 and 2). For example, the increasing proportion of *P. massoniana* strongly suppressed bacterial richness but increased ECM fungal richness in mineral topsoil. Moreover, *C. glauca* $R_{BA}$, *L. glaber* $R_{BA}$ and *P. massoniana* $R_{BA}$ increased ECM fungal richness in organic soil, whereas the contrary effects were observed for the effect of *C. axillaris*. The negative effects are probably related to i) low palatability, ii) poor compatibility with mutualistic partners or iii) strong defense mechanisms. The positive effects may be ascribed to abundance of a particularly suitable substrate or facilitation (Tedersoo et al., 2016).

### 4.2. Non-negligible of abiotic factors in determining soil microbial community

Abiotic factors strongly determined soil microbial richness and community composition (Tables 1 and 2; Fig. 4). Soil pH had important effect on the bacterial but less for fungal richness and community composition, which is consistent with the crucial pH effect on bacteria (Lauber et al., 2009; Rousk et al., 2010). Moreover, both bacterial and fungal communities were influenced by soil C/N ratio or AP content, which is consistent with other studies (Coince et al., 2013; Ding et al., 2015). It appears that soil microbial communities inhabiting the most nutritive soil were less diverse compared to poor soil, as richness of bacteria and fungi responded negatively to increasing soil C/N ratio and

soil AP, respectively (Fig. S2, Tables 1 and 2). Species diversity and community composition of fungi functional guilds is also influenced by soil nutrients, which are in accordance with other studies (Kernaghan et al., 2003; Twieg et al., 2007; Lauber et al., 2008). Although variation in edaphic factors directly explained most of the variability in the richness and composition of soil microorganisms, these factors were themselves largely influenced by the tree species and their specific traits. Mantel test indicated that tree communities are tightly related with soil properties (Table S5). These results supported the concept that soil geochemical parameters served as a bridge to link the aboveground plant community with the belowground microbial community (Rasche et al., 2010). Our results further demonstrated that topography was another important driving factor for microbial communities in the subtropical forest soil (Fig. 4). Bacterial, fungal, and especially SAP fungal species richness were declines linearly with increasing topography (Fig. S2). These results was corroborated with Gao et al. (2017) who found that ridge and valley habitats (with different topography) harboring distinct fungal communities in subtropical montane forest.

### 4.3. Differential responses of soil bacteria and fungi to biotic and abiotic factors

As bacteria and fungi differ in their abilities to metabolize and compete for different C sources (Uroz et al., 2016), it is reasonable to assume that bacterial and fungal communities respond differently to the biotic and abiotic factors. Our results showed that fungal richness correlated better with tree species richness than bacteria in the organic horizon (Fig. 3). Moreover, the tree species identity affected fungal composition larger than bacterial composition in both the organic and mineral topsoil, which supports our third hypothesis. This is because fungi are more directly dependent on tree litter and biotrophic interactions with trees as many fungi are obligate root symbionts and pathogens (Wardle, 2006; Gao et al., 2013). In contrast, bacteria inhabit soil niches on a very small scale that often have no direct connection to tree roots (Vos et al., 2013). Thus, the tree effects on bacteria were mainly indirect and thus less pronounced. For funguilds, tree host specificity is an important driver of symbiotic fungi (Buée et al., 2009) as well as saprotrophic fungi (Lang et al., 2011). We can intuitively expect a more important impact of tree host specificity on ectomycorrhizal communities due to the biotrophic link established between the tree species and ECM fungi. For example, *P. massoniana*, *C. glauca* and *L. glaber* had been identified as ECM plants by observing the root morphology under dissecting microscope (Wang and Qiu, 2006; Gao et al., 2015). These ECM fungal host specialists had significant positive effects on ECM fungal richness (Fig. S2, Tables 1 and 2). Moreover, our results revealed the tree species identity effects explained more variation of ECM fungal community composition than SAP fungal community composition, particularly in the mineral topsoil (Fig. 4, Tables S3 and S4). This was parallel to the results of Peay et al. (2013), who found that symbiotic fungal community richness responded more strongly to plant community changes than that of SAP fungi.

The changes of bacterial and fungal (apart from ECM fungi) communities in organic soil were better predicted by the explanatory factors than in the mineral topsoil (Tables 1 and 2, Tables S3 and S4). The finding that the extent of biotic and abiotic factors influence on microbial communities differs between organic and mineral topsoil is not surprising as different microbial communities distributing in the two horizons (Prescott and Grayston, 2013; Voříšková et al., 2014). For example, *Proteobacteria*, *Actinobacteria*, and *Bacterioidetes* were more abundant in organic soil, while *Acidobacteria* and *Chloroflexi* were significantly enriched in the mineral topsoil (Fig. 2), which is consistent with Uroz et al. (2013). The difference in microbial communities depends on environmental conditions between the two horizons, with organic soil is formed mainly by the tree litter. This finding suggest that the distinctness in environmental conditions between the two soil horizons has profound influences on microbial niche differentiation, and further imply that horizon specific variables should be used to predict their soil microbial communities.

## 5. Conclusions

We examined how richness and species identity of trees and abiotic factors affect soil microbial richness and community composition in subtropical forest ecosystems. Our results revealed that soil microbial richness and community composition are influenced stronger by particular tree species as well as abiotic soil and topographical factors, than by changes in tree richness *per se*. This suggests relatively stronger sampling effects of dominant tree species compared to complementary effects among all tree species on the soil microbial communities. Our results also demonstrated that the relative contribution of these selected environmental predictors differed between bacteria and fungi, ectomycorrhizal and saprotrophic fungi, as well as between the organic and mineral topsoil. This illustrates the importance of considering microbial taxonomic groups and their specific to soil horizons when predicting microbial responses to environmental changes in forest ecosystems. We conclude that species identity at least in forests – with long-term effects of the specific trees on edaphic conditions – is more important than just general tree biodiversity on biodiversity of bacterial and fungal communities in soil.

## Conflicts of interest

The authors have no conflicts of interest to declare.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2018.12.008.

## References

Abarenkov, K., Nilsson, R.H., Larsson, K.H., Alexander, I.J., Eberhardt, U., Erland, S., Hoiland, K., Kjoller, R., Larsson, E., Pennanen, T., et al., 2010. The UNITE database for molecular identification of fungi–recent updates and future perspectives. New Phytologist 186, 281–285.

Bahram, M., Põlme, S., Kõljalg, U., Zarre, S., Tedersoo, L., 2012. Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forest of northern Iran. New Phytologist 193, 465–473.

Blagodatskaya, E.V., Blagodatsky, S.A., Anderson, T.H., Kuzyakov, Y., 2009. Contrasting effects of glucose, living roots and maize straw on microbial growth kinetics and substrate availability in soil. European Journal of Soil Science 60, 186–197.

Bokulich, N.A., Mills, D.A., 2013. Improved selection of internal transcribed spacer-specific primers enables quantitative, ultra-high-throughput profiling of fungal communities. Applied and Environmental Microbiology 79, 2519–2526.

Bruelheide, H., Nadrowski, K., Assmann, T., Bauhus, J., Both, S., Buscot, F., Chen, X.Y., Ding, B.Y., Durka, W., Erfmeier, A., et al., 2014. Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. Methods in Ecology and Evolution 5, 74–89.

Buée, M., Reich, M., Murat, C., Morin, E., Nilsson, R.H., Uroz, S., Martin, F., 2009. 454 pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. New Phytologist 184, 449–456.

Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Pena, A.G., Goodrich, J.K., Gordon, J.I., et al., 2010. QIIME allows analysis of high-throughput community sequencing data. Nature Methods 7, 335–336.

Cardinale, B.J., Srivastave, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992.
Chen, Y.L., Xu, T.L., Veresoglou, S.D., Hu, H.W., Hao, Z.P., Hu, Y.J., Liu, L., Deng, Y., Rillig, M.C., Chen, B.D., 2017. Plant diversity represents the prevalent determinant of soil fungal community structure across temperate grasslands in northern China. Soil Biology and Biochemistry 110, 12–21.
Coince, A., Cael, O., Bach, C., Lengellé, J., Cruaud, C., Gavory, F., Morin, E., Murat, C., Marcais, B., Buée, M., 2013. Below-ground fine-scale distribution and soil versus fine root detection of fungal and soil oomycete communities in a French beech forest. Fungal Ecology 6, 223–235.
Cole, J.R., Wang, Q., Cardenas, E., Fish, J., Chai, B., Farris, R.J., Kulam-Syed-Mohideen, A.S., McGarrell, D.M., Marsh, T., Garrity, G.M., Tiedje, J.M., 2009. The ribosomal database project: improved alignments and new tools for rRNA analysis. Nucleic Acids Research 37, D141–D145.
Ding, J.J., Zhang, Y.G., Wang, M.M., Sun, X., Cong, J., Deng, Y., Lu, H., Yuan, T., Van Nostrand, J.D., Li, D.Q., Zhou, J.Z., Yang, Y.F., 2015. Soil organic matter quantity and quality shape microbial community compositions of subtropical broadleaved forests. Molecular Ecology 24, 5175–5185.
Edgar, R.C., 2013. UPARSE: highly accurate OUT sequences from microbial amplicon reads. Nature Methods 10, 996–998.
Gao, C., Shi, N.N., Liu, Y.X., Peay, K.G., Zheng, Y., Ding, Q., Mi, X.C., Ma, K.P., Wubet, T., Buscot, F., Guo, L.D., 2013. Host plant genus-level diversity is the best predictor of ectomycorrhizal fungal diversity in a Chinese subtropical forest. Molecular Ecology 22, 3403–3414.
Gao, C., Zhang, Y., Shi, N.N., Zheng, Y., Chen, L., Wubet, T., Bruelheide, H., Both, S., Buscot, F., Ding, Q., Erfmeier, A., Kuhn, P., Nadrowski, K., Scholten, T., Guo, L.D., 2015. Community assembly of ectomycorrhizal fungi along a subtropical secondary forest succession. New Phytologist 205, 771–785.
Gao, C., Shi, N.N., Chen, L., Ji, N.N., Wu, B.W., Wang, Y.L., Xu, Y., Zheng, Y., Mi, X.C., Ma, K.P., Guo, L.D., 2017. Relationships between soil fungal and woody plant assemblages differ between ridge and valley habitats in a subtropical mountain forest. New Phytologist 213, 1874–1885.
Gardes, M., Bruns, D., 1993. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Molecular Ecology 2, 113–118.
Gunina, A., Smith, A.R., Godbold, D., Jones, D.L., Kuzyakov, Y., 2017. Response of soil microbial community to afforestation with pure and mixed species. Plant and Soil 412, 357–368.
Hiiesalu, I., Bahram, M., Tedersoo, L., 2017. Plant species richness and productivity determine the diversity of soil fungal guilds in temperate coniferous forest and bog habitats. Molecular Ecology 26, 4846–4858.
Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Van Der Putten, P.L.W.H., De Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M., Wolters, V., 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. BioScience 12, 1049–1061.
Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110, 449–460.
IUSS Working Group WRB, 2015. World Reference Base for Soil Resources 2014, Update 2015. International Soil Classification System for Naming Soils and Creating Legends for Soil Maps. World Soil Resources Reports No. 106. FAO, Rome.
Kernaghan, G., Widden, P., Bergeron, Y., Légaré, S., Paré, D., 2003. Biotic and abiotic factors affecting ectomycorrhizal diversity in boreal mixed-woods. Oikos 102, 497–504.
Kong, Y., 2011. Btrim: a fast, lightweight adapter and quality trimming program for next-generation sequencing technologies. Genomics 98, 152–153.
Lang, C., Seven, J., Polle, A., 2011. Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed Central European forest. Mycorrhiza 21, 297–308.
Lauber, C.L., Strickland, M.S., Bradford, M.A., Fierer, N., 2008. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. Soil Biology and Biochemistry 40, 2407–2415.
Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Applied and Environmental Microbiology 75, 5111–5120.
Leuschner, C., Jungkunst, H.F., Fleck, S., 2009. Functional role of forest diversity: pros and cons of synthetic stands and across site comparison in established forests. Basic and Applied Ecology 10, 1–9.
Magoc, T., Salzberg, S.L., 2011. FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics 27, 2957–2963.
Mehlich, A., 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis 15, 1409–1416.
Nguyen, N.H., Song, Z.W., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016a. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20, 241–248.
Nguyen, N.H., Williams, L.J., Vincent, J.B., Stefanski, A., Cavender-Bares, J., Messier, C., Paquette, A., Gravel, D., Reich, P.B., Kennedy, P.C., 2016b. Ectomycorrhizal fungal diversity and saprotrophic fungal diversity are linked to different tree community attributes in a field-based tree experiment. Molecular Ecology 25, 4032–4046.
Ouyang, S., Xiang, W.H., Wang, X.P., Zeng, Y.L., Lei, P.F., Deng, X.W., Peng, C.H., 2016. Significant effects of biodiversity on forest biomass during the succession of subtropical forest in south China. Forest Ecology and Management 372, 291–302.
Peay, K.G., Baraloto, C., Fine, P.V.A., 2013. Strong coupling of plant and fungal community structure across western Amazonian rainforests. The ISME Journal 7, 1852–1861.
Peay, K.G., Kennedy, P.G., Talbot, J.M., 2016. Dimensions of biodiversity in the Earth mycobiome. Nature Reviews Microbiology 14, 434–447.
Pellissier, L., Niculita-Hirzel, H., Dubuis, A., Pagni, M., Guex, N., Ndiribe, C., Salamin, N., Xenarios, I., Goudet, J., Sanders, I.R., Guisan, A., 2014. Soil fungal communities in grasslands are environmentally structured at a regional scale in the Alps. Molecular Ecology 23, 4274–4290.
Pfeiffer, B., Fender, A.C., Lasota, S., Hertel, D., Jungkunst, H.F., Daniel, R., 2013. Leaf litter is the main driver for changes in bacterial community structures in the rhizosphere of ash and beech. Applied Soil Ecology 21, 5110–5123.
Prescott, C.E., Grayston, S.J., 2013. Tree species influence on microbial communities in litter and soil: current knowledge and research needs. Forest Ecology and Management 309, 19–27.
Prober, S.M., Leff, J.W., Bates, S.T., Borer, E.T., Firn, J., Harpole, W.S., Lind, E.M., Seabloom, E.M., Adler, P.B., Bakker, J.D., et al., 2015. Plant diversity predicts beta but not alpha diversity of soil microorganisms across grasslands worldwide. Ecology Letters 18, 85–95.
Qiu, H., Ge, T., Liu, J., Chen, X., Hu, Y., Wu, J., Su, Y., Kuzyakov, Y., 2018. Biotic and abiotic factors of soil organic matter mineralization: experiment and structural modeling analysis. European Journal of Soil Biology 84, 27–34.
R Development Core Team., 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria. Available from: http://www.R-project.org/.
Rasche, F., Knapp, D., Kaiser, C., Koranda, M., Kitzler, B., Zechmeister-Boltenstern, S., Richter, A., Sessitsch, A., 2010. Seasonality and resource availability control bacterial and archaeal communities in soils of a temperate beech forest. The ISME Journal 19, 1918–1927.
Rousk, J., Baath, E., Brokes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. The ISME Journal 4, 1340–1351.
Scheibe, A., Steffens, C., Seven, J., Jacob, A., Hertel, D., Leuschner, C., Gleixner, G., 2015. Effects of tree identity dominate over tree diversity on the soil microbial community structure. Soil Biology and Biochemistry 81, 219–227.
Tedersoo, L., Bahram, M., Dickie, I.A., 2014a. Does host plant richness explain diversity of ectomycorrhizal fungi? Re-evaluation of Gao et al. (2013) data sets reveals sampling effects. Molecular Ecology 23, 992–995.
Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., et al., 2014b. Global diversity and geography of soil fungi. Science 346, 1256688.
Tedersoo, L., Bahram, M., Cajthaml, T., Põlme, S., Hiiesalu, I., Anslan, S., Harend, H., Buegger, F., Pritsch, K., Koricheva, J., 2016. Tree diversity and species identity effects on soil fungi, protists and animals are context dependent. The ISME Journal 10, 346–362.
Toju, H., Guimaraes, P.R., Olesen, J.M., Thompson, J.N., 2014. Assembly of complex plant-fungus networks. Nature Communications 5, 5273.
Twieg, B.D., Durall, D.M., Simard, S.W., 2007. Ectomycorrhizal fungal succession in mixed temperate forests. New Phytologist 176, 437–447.
Urbanová, M., Šnajdr, J., Baldrian, P., 2015. Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominate trees. Soil Biology and Biochemistry 84, 53–64.
Uroz, S., Ioannidis, P., Lengelle, J., Cebron, A., Morin, E., Buée, M., Martin, F., 2013. Functional assays and metagenomic analyses reveals differences between the microbial communities inhabiting the soil horizons of a Norway spruce plantation. PLoS One 8, e55929.
Uroz, S., Buée, M., Deveau, A., Mieszkin, S., Martin, F., 2016. Ecology of the forest microbiome: highlights of temperate and boreal ecosystems. Soil Biology and Biochemistry 103, 471–488.
van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microorganisms as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11, 296–310.
Voříšková, J., Brabcová, V., Cajthaml, T., Baldrian, P., 2014. Seasonal dynamics of fungal communities in a temperate oak forest soil. New Phytologist 201, 269–278.
Vos, M., Wolf, A.B., Jennings, S.J., Kowalchuk, G.A., 2013. Micro-scale determinants of bacterial diversity in soil. FEMS Microbiology Reviews 37, 936–954.
Waldrop, M.P., Zak, D.R., Blackwood, C.B., Curtis, C.D., Tilman, D., 2006. Resource availability controls fungal diversity across a plant diversity gradient. Ecology Letters 9, 1127–1135.
Walkley, A., 1947. A critical examination of a rapid method for determining organic carbon in soils-effect of variations in digestion conditions and of inorganic soil constituents. Soil Science 63, 251–264.
Wang, B., Qiu, Y.L., 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16, 299–363.
Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9, 870–886.
Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633.
Xiang, W.H., Liu, S.H., Lei, X.D., Frank, S.C., Tian, D.L., Wang, G.J., Deng, X.W., 2013. Secondary forest floristic composition, structure, and spatial pattern in subtropical China. Journal of Forest Research 18, 111–120.
Xiong, J.B., Liu, Y.Q., Lin, X.G., Zhang, H.Y., Zeng, J., Hou, J.Z., Yang, Y.P., Yao, T.D., Knight, R., Chu, H.Y., 2012. Geographic distance and pH drive bacterial distribution in alkaline lake sediments across Tibetan Plateau. Environmental Microbiology 14, 2457–2466.
Yang, T., Adams, J.M., Shi, Y., He, J.S., Jing, X., Chen, L.T., Tedersoo, L., Chu, H.Y., 2017. Soil fungal diversity in natural grasslands of the Tibetan Plateau: associations with plant diversity and productivity. New Phytologist 215, 756–765.
Zeng, Y.L., Fang, X., Xiang, W.H., Deng, X.W., Peng, C.H., 2017. Stoichiometric and nutrient resorption characteristics of dominant tree species in subtropical Chinese forests. Ecology and Evolution 7, 1–11.
Zhu, W.J., Xiang, W.H., Pan, Q., Zeng, Y.L., Ouyang, S., Lei, P.F., Deng, X.W., Fang, X., Peng, C.H., 2016. Spatial and seasonal variations of leaf area index (LAI) in subtropical secondary forests related to floristic composition and stand characters. Biogeosciences 13, 3819–3831.