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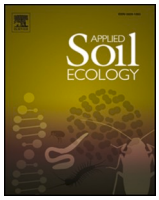

Regenerated woody plants influence soil microbial communities in a subtropical forest

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ABSTRACT

Forests are critical for supporting multiple ecosystem services such as climate change mitigation. Microbial diversity in soil provides important functions to maintain and regenerate forest ecosystems, and yet a critical knowledge gap remains in identifying the linkage between attributes of regenerated woody plant (RWP) communities and the diversity patterns of soil microbial communities in subtropical plantations. Here, we investigated the changes in soil microbial communities and plant traits in a nine hectare Chinese fir (*Cunninghamia lanceolata*; CF) plantation to assess how non-planted RWP communities regulate soil bacterial and fungal diversity, and further explore the potential mechanisms that structure their interaction. Our study revealed that soil bacterial richness was positively associated with RWP richness, whereas soil fungal richness was negatively associated with RWP basal area. Meanwhile, RWP richness was positively correlated with ectomycorrhizal (ECM) fungal richness but negatively correlated with the richness of both pathogenic and saprotrophic fungi, suggesting that the RWP-fungal richness relationship was trophic guild-specific. Soil microbial community beta diversity (i.e., dissimilarity in community composition) was strongly coupled with both RWP beta diversity and the heterogeneity of RWP basal area. Our study highlights the importance of community-level RWP plant attributes for the regulation of microbial biodiversity in plantation systems, which should be considered in forest management programs in the future.

1. Introduction

Soil microbial communities play important roles in driving multiple ecosystem functions such as nutrient cycling, plant primary productivity, and climate regulation (van der Heijden et al., 2008; Fierer et al., 2013). Microbial communities in soil are particularly important to the functioning of forest ecosystems globally, with noted effects on carbon cycling, carbon storage belowground, and tree productivity (Averill et al., 2014; Lladó et al., 2017). The growing global concern over the impacts of deforestation and ecosystem degradation on the maintenance of ecosystem functions has led to multiple initiatives such as the United Nations-Bonn Challenge (UNEP, 2011) and the New York Declaration on Forests (UNCS, 2014), aiming at ameliorating the impacts of anthropogenic climate change and conserving biodiversity. Yet, despite the enthusiasm surrounding forest restoration, how long-term forest restoration affects soil microbial communities in subtropical forests is still largely unknown. Filling this knowledge gap will be critical to guide management decisions that impact the health of forest ecosystems and

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maintain sustainability into the future.

Plant communities are highly sensitive to anthropogenic land-use intensification (Allan et al., 2015), and the shifts in vegetation could have cascading effects on microbial diversity as well as the many functions they support (Le Bagousse-Pinguet et al., 2017). This is especially important in highly diverse ecosystems such as subtropical regions where anthropogenic disturbances (e.g., logging, agriculture) are the major impacts on diversity and function (Felton et al., 2006; Newbold et al., 2014). The native woody plants that regenerated in forest plantations (excluding the planted tree, hereafter "regenerated woody plant", RWP) have the potential to support very rich plant communities, and thus can play an indispensable role in supporting multiple ecosystem functions (Yirdaw, 2001). Indeed, a recent study conducted in mature Mediterranean plantation forests demonstrated that understory biodiversity is fundamental for maintaining plant productivity and soil nutrient cycling (Zhou et al., 2022). Their findings indicate the strong potential role of RWP in regulating soil microbial community structure, as those soil ecological processes are tightly associated with soil microbes and their functioning (Bardgett, 2017). However, how RWP community attributes such as plant diversity, composition, and basal area affect microbial biodiversity in subtropical plantation systems is still largely unknown.

Theoretical and experimental studies have shown that plant community attributes could affect soil microbial diversity in diverse ways. Plant diversity can increase resources through litterfall and rhizodeposition that can be used by soil microbes for energy and metabolic processes, which may further promote niche differentiation and resource partitioning (Wardle et al., 2004; Tedersoo et al., 2016; Cline et al., 2018). Meanwhile, plant basal area, positively related to litterfall and root biomass, is closely associated with soil microbial diversity, because plants with greater basal area are expected to provide more resources (e.g., substrate availability and root exudates), creating more environmental niches that leads to increased microbial growth and diversity (Pietikainen et al., 2007; Hooper et al., 2000). Moreover, specific plant hosts are closely associated with particular microbiota due to host specialisation, and thus changes in plant community composition can also trigger variation in microbial community composition (Prober et al., 2015). Other effects of plant community attributes on soil microbes include changes in habitat conditions (e.g., topography, water regulation) and soil physiochemical conditions (e.g., pH, soil organic matter (SOM), physical structure), which are both recognized as important ecological factors affecting the structure and function of microbial communities (Bellingham and Tanner, 2000; Rousk et al., 2010; Ding et al., 2015; Yang et al., 2021).

Links between plant and soil microbial communities likely depend on taxonomic groups (e.g., bacteria and fungi; Sugiyama et al., 2008). For example, soil fungal communities are linked more tightly to standing plants and trees than soil bacterial communities due to the many symbiotic interactions between fungi and living plants, their saprotrophic activity (Millard and Singh, 2010; Dassen et al., 2017; Chen et al., 2019), as well as the greater sensitivity of fungi to changes in environmental conditions (Lauber et al., 2008). Mycorrhizal and pathogenic fungi tend to be more closely related to plant attributes than saprotrophic fungi. Mycorrhizal host-specific interactions largely facilitate increased acquisition of water and nutrients from the soil (Peay et al., 2010). While saprotrophic fungi have few host-specific adaptations, instead relying on various soil C sources and decomposing organic matter to obtain nutrients (Wardle et al., 2004; Gao et al., 2013). However, previous studies have not systematically explored the responses of soil microbial biodiversity to corresponding plant measures, particularly RWP community-level traits. Identifying these relationships between RWP traits and microbial communities will allow us to better understand microbial diversity responses during forest restoration.

Herein, we used a 31-year subtropical plantation forest experiment (*Cunninghamia lanceolata*; CF) as our model system to explore how RWP community attributes (e.g., basal area, species richness, and composition) influence soil bacterial and fungal diversity (both richness and beta diversity). We also estimated the relative influence of environmental context on soil microbial diversity using measures of soil properties, topographic features, and the potential influence of spatial covariables (Ettema and Wardle, 2002). Specifically, we hypothesized that: (1) RWP community attributes would be more tightly correlated with the richness of soil fungi than with that of bacteria due to the stronger, more tightly linked interactions between plants and soil fungi; (2) the richness of biotrophic fungal guilds, especially mycorrhizal fungi would be more positively related to RWP community attributes than free-living saprotrophic fungi given their symbiotic relationship with plants; and (3) beta diversity of soil microbial communities (i.e., bacteria, fungi, and fungal guilds) will be mainly impacted by the dissimilarity in RWP attributes such as dissimilarity in RWP community composition, because the changes in plant community composition in forest ecosystem are largely contributed by RWP community, particularly in plantation forests characterized by few tree species.

2. Materials and methods

2.1. Study area and sampling design

This study was conducted in a CF plantation in the Yingzuijie Natural Reserve in Huitong County, Hunan Province, China (26°46′ N − 26°59′ N, 109°49′ E−109°58′ E, c. 159 km^2, 270–938 m above sea level (a.s.l.); Fig. 1a-c). The study site has a humid-subtropical monsoon climate. The local mean annual temperature and precipitation are 16.5 °C and 1200 mm, respectively, as described in the World Reference Base for Soil Resources. The soil is classified as Alliti-Udic Ferrosols (Chen et al., 2019). In October 2013, we established a 9-ha permanent plot in this CF plantation according to the forest plot construction standard of Center for Tropical Forest Science (CTFS), and the 9-ha plot was divided into 225 (20 × 20 m) subplots. The CF plantation was planted with an initial planting density of 2 × 2.3 m in late 1988 to early 1989. Thus, this plantation is currently at a mature stage (c. 31 years) and undergoing a natural development process.

2.2. Vegetation survey

Each subplot (20 × 20 m) was divided into sixteen quadrats (5 × 5 m). In 2019, we followed a standard field protocol to survey vegetation; all free-standing trees with at least 1 cm in diameter at breast height (1.3 m above the ground) were mapped, identified to species, and their geographic coordinates were recorded. The total number of living individuals was 34,364, consisting of 133 species (including CF), 75 genera, and 40 families across the 225 subplots in the 9-ha permanent plot in this CF plantation.

2.3. Soil sampling

In May 2019, using regular and random sampling techniques, we sampled 113 non-neighbouring 20 × 20 m subplots with a space distance of 40 m within the 9-ha plot (Fig. 1d), covering a wide range of soil characteristics and plant diversity. Within each subplot, we collected 16 soil cores (2 cm in diameter, 10 cm deep) from evenly spaced spots and pooled to form a composite sample, giving 113 soil samples in total. Stones and litter were removed from the field. Afterwards, a freezer was used to store fresh soil samples during transport to the laboratory. With regard to each sample, one aliquot of fresh soil was air-dried and sieved to 2 mm in order to conduct physiochemical analyses, and additional fresh soil was stored at −80 °C until DNA extraction was conducted.

2.4. Soil physicochemical characteristics

A series of soil characteristics that reflect basic soil environmental conditions were examined: soil organic carbon (SOC), soil total nitrogen

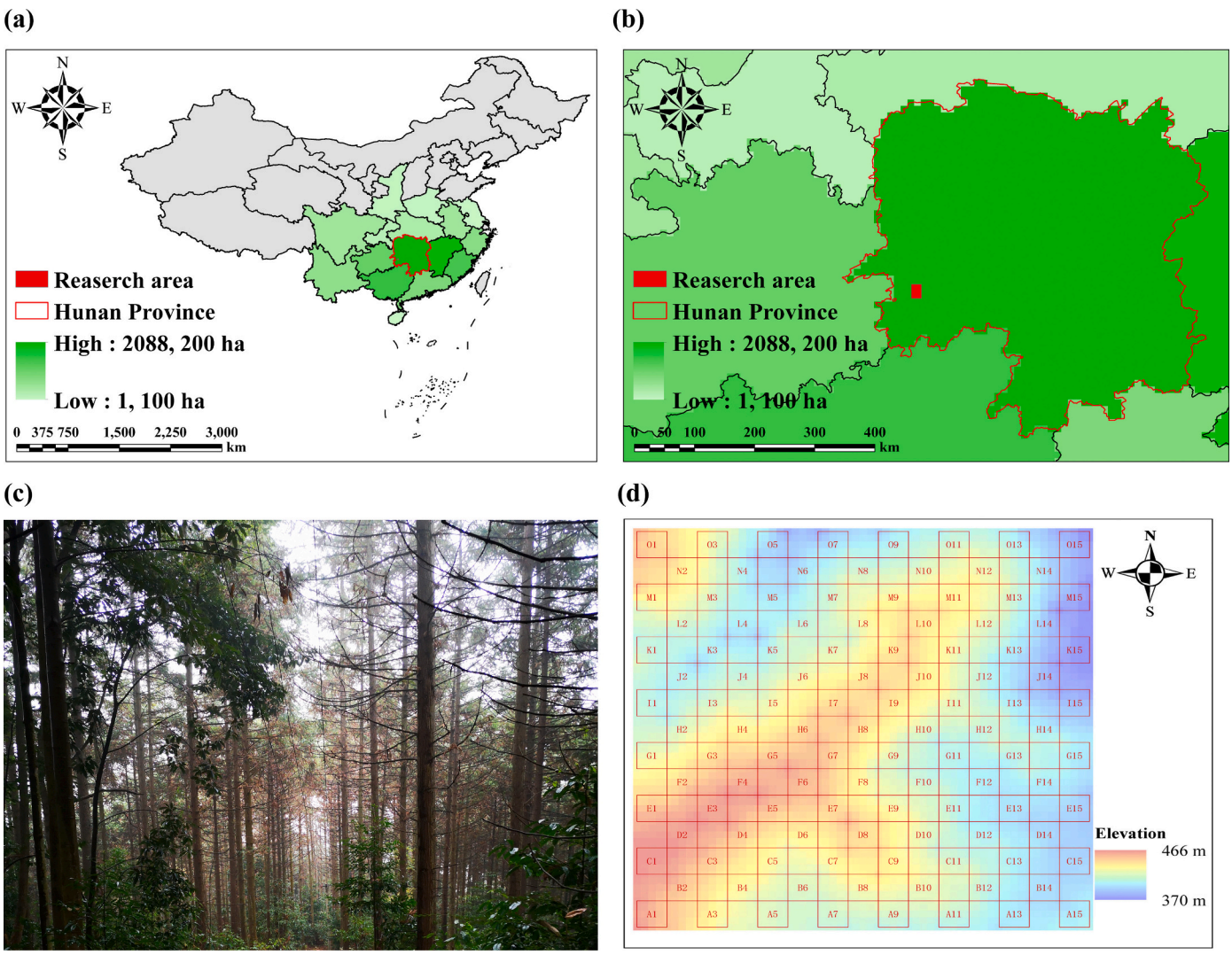

Fig. 1. A local survey of microbial biodiversity to the regenerated woody plant attributes in a subtropical plantation. (a) Map of the plantation area distribution of Chinese fir (*Cunninghamia lanceolata*) across different provinces in China. (b) Location of the study site within Hunan province. (c) Chinese fir stand in the study site. (d) Map of the 113 sampling subplots distributed in the 9-ha Chinese fir plantation plot.

(N), phosphorus (P), potassium (K), pH, sand, silt, and clay (Table S1). The SOC and N contents were determined using an elemental analyser (Model CN, Vario Macro Elementar, GmbH, Germany). The P and K concentrations were determined using inductively coupled plasma mass spectroscopy (ICP-MS) (iCAP-Q, Thermo Scientific, United States) after acid digestion of the soil samples with HNO_3 and HF solutions. Based on a soil-to-water ratio of 1:2.5 (*w/v*), soil pH was determined using a pH digital meter (Mettler Toledo, Shanghai, China). Clay, silt, and sand proportions for each soil sample were estimated by a classical hydrometer-simplified method for soil textual analysis (Gee and Bauder, 1979). A principal component analysis was used to simplify the number of soil variables and reduce multicollinearity. The first four PCA components explained 88 % of the variance of soil variables (Table S2). In further analyses, we used the first four PCA components to represent different important soil variables: SoilPC1 (SOC, N; 37 % of variance), SoilPC2 (silt, sand; 27 %), SoilPC3 (K, P; 14 %), and SoilPC4 (pH, 10 %).

2.5. Topographic features and spatial variables

Topography (elevation, convexity, slope, and aspect) has been measured in 2013. Briefly, the elevations of the edge points of all 20 × 20 m subplots were determined using a total survey station (KTS-442LLCN, KOLIDA, China). Each subplot's elevation was calculated as the average of the elevation values at the four corners. The convexity of each subplot was calculated by subtracting the average elevation of the eight surrounding subplots from the elevation. For the edge subplots, convexity was defined as the elevation of the central point minus the average of the four corners (Legendre et al., 2009). In the landscape, there is a positive convexity value when the focal subplot lies in hillock, and a negative convexity value when in hollow (Gao et al., 2017). The slope is the average angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners. Aspect refers to the direction at which a slope face (ranging from 0 to 1); the higher the value is, the more southward the aspect is.

Spatial variables were represented by both linear trend (XY coordinates) and Moran's eigenvectors with positive eigenvalues (Legendre and Legendre, 2012; López-Angulo et al., 2020). Concretely speaking, Moran's eigenvectors were derived from sampling points' coordinates. For parsimony, we used the forward selection method (Blanchet et al., 2008) based on double-stopping criterion ($\alpha = 0.05$, 9999 permutations) to identify significant dbMEM eigenvectors related to soil bacterial and fungal richness.

2.6. Soil microbial analyses

The soil DNA of each subplot ($n = 113$) was extracted from 0.3 g of

the composite soil sample using the MoBio PowerSoil DNA isolation kit (MoBio Laboratories, Carlsbad, CA, United States). The bacterial 16S rRNA gene and fungal ITS2 region were amplified using the primers 515F/909R for bacteria (Tamaki et al., 2011) and ITS4/gITS7F for fungi (Ihrmark et al., 2012) (details in Methods S1). The sequencing libraries were prepared using TruSeq® DNA PCR-Free Sample Preparation Kits and sequenced on the Illumina MiSeq platform with 2 × 250 bp V2 Kits. The DNA sequence data were processed using the Quantitative Insights Into Microbial Ecology (QIIME) pipeline (Caporaso et al., 2010). Bacterial and fungal sequences were independently clustered into operational taxonomic units (OTUs) at a 97 % identity threshold using UPARSE (Edgar, 2013). The resultant OTU abundance tables were rarefied to an even number of sequences per sample (bacteria: 7108 sequences per sample; fungi: 24325 sequences per sample) (Fig. S1), corresponding to the minimum number of sequences for a single soil sample (details in Methods S1). Considering most soil bacterial lifestyles are not well documented, we only assigned fungal functional guilds according to Põlme et al. (2020). Community richness and Shannon diversity of soil bacteria and fungi were highly correlated (Bacteria: Pearson $r = 0.93$; Fungi: Pearson $r = 0.76$; Fig. S2). We thus used richness as one metric of diversity in further analyses. The DNA sequences of bacteria and fungi from the 113 soil samples have been deposited in the NCBI Sequence Read Archive (BioProject accession no. PRJNA752698;https://www.ncbi.nlm.nih.gov/sra/PRJNA752698).

2.7. Statistical analyses

At the subplot level ($n = 113$), all statistical analyses were conducted independently for each microbial group (bacteria, fungi, and fungal guilds). Pearson correlation analysis was used to show raw trends in the associations of microbial richness (the observed OTU numbers) with the RWP community attributes (basal area, species richness, and composition). Here, the richness of RWP was defined as the number of RWP species in each subplot. RWP composition was ordinated using a nonmetric multidimensional scaling (NMDS) and described by the first two axes (i.e., regenerated woody plant composition.1 and composition.2, Fig. S3; stress, 0.14).

We used a model selection approach based on corrected Akaike's information criterion (AICc, ΔAICc <2) to identify whether RWP attributes still influenced soil microbial richness in our study when accounting for the other environmental factors and spatial covariates. We employed generalized linear models (GLMs) based on the Poisson distribution. Model averaging was performed based on AICc weights when multiple models were selected (Burnham and Anderson, 2002). Based on these selected models, model-averaged parameter estimates were calculated by weighting the estimates of the single model by corresponding Akaike weights. Also, we calculated the 95 % confidence intervals (95 % CIs) for the estimates of model-averaged parameters, and if the 95 % CI did not include zero a parameter was considered to be significant (Burnham and Anderson, 2002). All models were tested for strong multicollinearity with the variance inflation factor (VIF) (Table S3). In all models, we selected suitable variables according to VIF < 5 (James et al., 2013).

We used a partial Mantel test to evaluate the correlations between RWP community beta diversity/basal area and the soil microbial community beta diversity after controlling for the confounding effects of CF basal area, soil properties, topographic features, and spatial distance. In these analyses, the Bray–Curtis distance after Hellinger transformation was used to estimate the beta diversity (compositional dissimilarity between subplots). Similarly, the Euclidean distance was used for the basal area of RWP and CF, the soil properties, topographic features, and spatial covariates. All statistical analyses were performed in R statistical software, v.3.4.4 (R Core Team, 2018) and a detailed information about the packages used is described in Methods S2.

3. Results

3.1. Basic data survey for soil microbial and plant communities

All examined samples contained 14,260 bacterial and 5811 fungal OTUs. In each sample, the bacterial and fungal richness ranged from 1599 to 2462 OTUs (2182 ± 18; mean ± SE) and 1286 to 1989 OTUs (1598 ± 13), respectively. At the phylum level, Acidobacteria (39 % of the sequences, Fig. S4a), Proteobacteria (38 %), and Actinobacteria (11 %) were the dominant bacterial phyla. The fungal community was dominated by Ascomycota (51 % of the fungal ITS2 sequences, Fig. S4b), with Basidiomycota being the second most abundant fungal phylum (23 %). Furthermore, three major fungal functional groups were observed, with symbionts (i.e., ectomycorrhizal (ECM) fungi), pathogens, and saprotrophs accounting for 6 %, 2 %, and 22 %, respectively (Fig. S4c).

For the plant community, there were 122 plant species and 38 families across the 113 subplots in the 9-ha permanent plot established in a CF plantation forest (Table S4). The RWP species (including trees and shrubs) mainly constituted the aboveground plant composition. The RWP species more frequently encountered in our selected subplots were *Camellia oleifera*, *Machilus pauhoi*, *Diospyros kaki* var. *silvestris*, *Clethra faberi*, and *Vaccinium carlesii* (Table S4). The basal area of RWP was 8.73 ± 0.69 (m^2 ha^{-1}) on average (mean ± SE; Fig. S5), accounting for approximately 24 % of the total basal area in our selected subplots. While the basal area of CF was 29.11 ± 0.93 (m^2 ha^{-1}) on average, accounting for approximately 76 % of the total basal area.

3.2. Soil microbial community richness

The richness of soil microbial community was significantly affected by aboveground plants, and the effect was mainly mediated by RWP. Pearson correlation analysis showed that soil bacterial richness was positively related to basal area ($r = 0.25$, Fig. 2a), richness ($r = 0.39$, Fig. 2b), and composition ($r = 0.33$, Fig. 2c) of the RWP. Whereas soil fungal richness was negatively regulated by these RWP attributes (basal area: $r = -0.21$, Fig. 2e; richness: $r = -0.23$, Fig. 2f; composition: $r = -0.19$, Fig. 2g). Specially, the richness of ECM fungi significantly increased with RWP basal area (r = 0.39, Fig. 3a) and RWP richness ($r = 0.51$, Fig. 3b), but significantly decreased the richness of both pathogenic fungi (basal area: r = −0.21, Fig. 3e; richness: $r = -0.36$, Fig. 3f) and saprotrophic fungi (basal area: $r = -0.27$, Fig. 3i; richness: $r = -0.38$, Fig. 3j). Further model selection analysis confirmed the influence of RWP attributes (richness and/or basal area; Tables 1 and 2) on the richness of soil bacteria, fungi, and fungal guilds, when simultaneously considering confounding factors that were potentially associated with soil microbes.

Soil microbial richness was also influenced by soil properties, topographic features, and spatial variables in our study site. SoilPC1 (SOC, N) significantly increased soil bacterial richness, whereas decreased fungal richness (Tables 1 and 2). Topographic features (i.e., elevation, convexity, slope, and aspect) played certain roles in explaining the richness patterns of soil bacteria, ECM, pathogenic, and saprotrophic fungi (Tables 1 and 2). Besides these, the spatial structure represented by dbMEM also exerted significant effects on the richness of each microbial group at broad (dbMEM4, dbMEM5) and fine (dbMEM12, dbMEM13, dbMEM20, dbMEM29, dbMEM34, dbMEM43, dbMEM47) spatial scales (Tables 1 and 2).

3.3. Soil microbial community beta diversity

Beta diversity of RWP was significantly correlated with that of soil bacteria (Mantel $r = 0.26$, Fig. 4a; Table S5), fungi (Mantel $r = 0.23$, Fig. 4c; Table S5) and fungal guilds (ECM fungi: $P = 0.023$; pathogenic fungi: $P = 0.001$; saprotrophic fungi: $P = 0.036$; Table 3) after controlling for the CF basal area, soil, topographic, and spatial factors. Similarly, the dissimilarity in basal area of RWP between samples did so

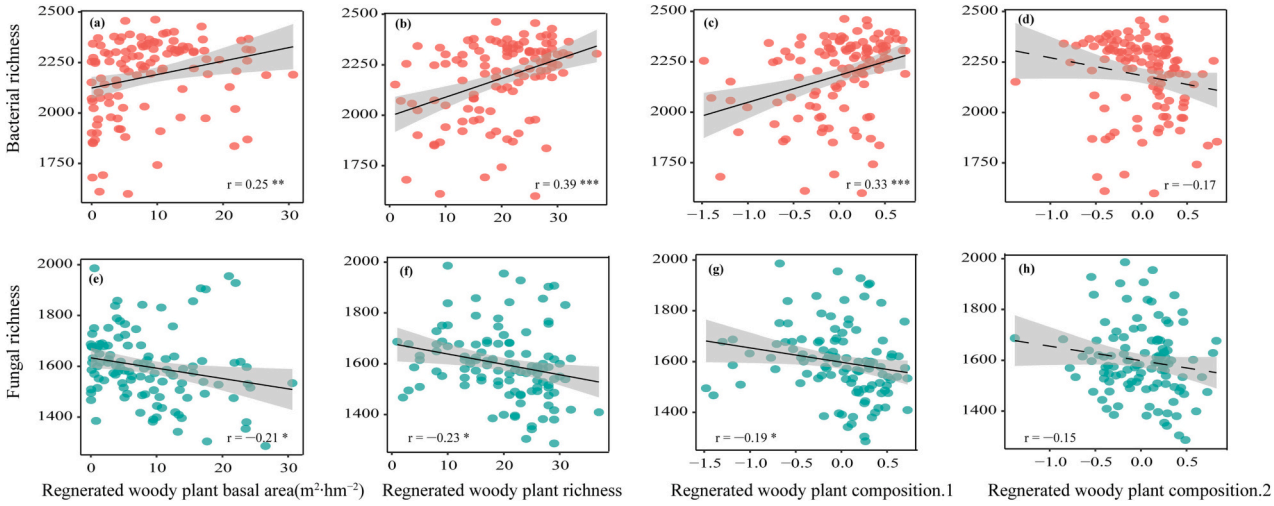

Fig. 2. Correlations of soil bacterial (a–d) and fungal (e–h) richness with the regenerated woody plant community attributes. The solid and dashed regression lines indicate significant and nonsignificant effects, respectively. Significance level: *p < 0.05, **p < 0.001, ***p < 0.001.

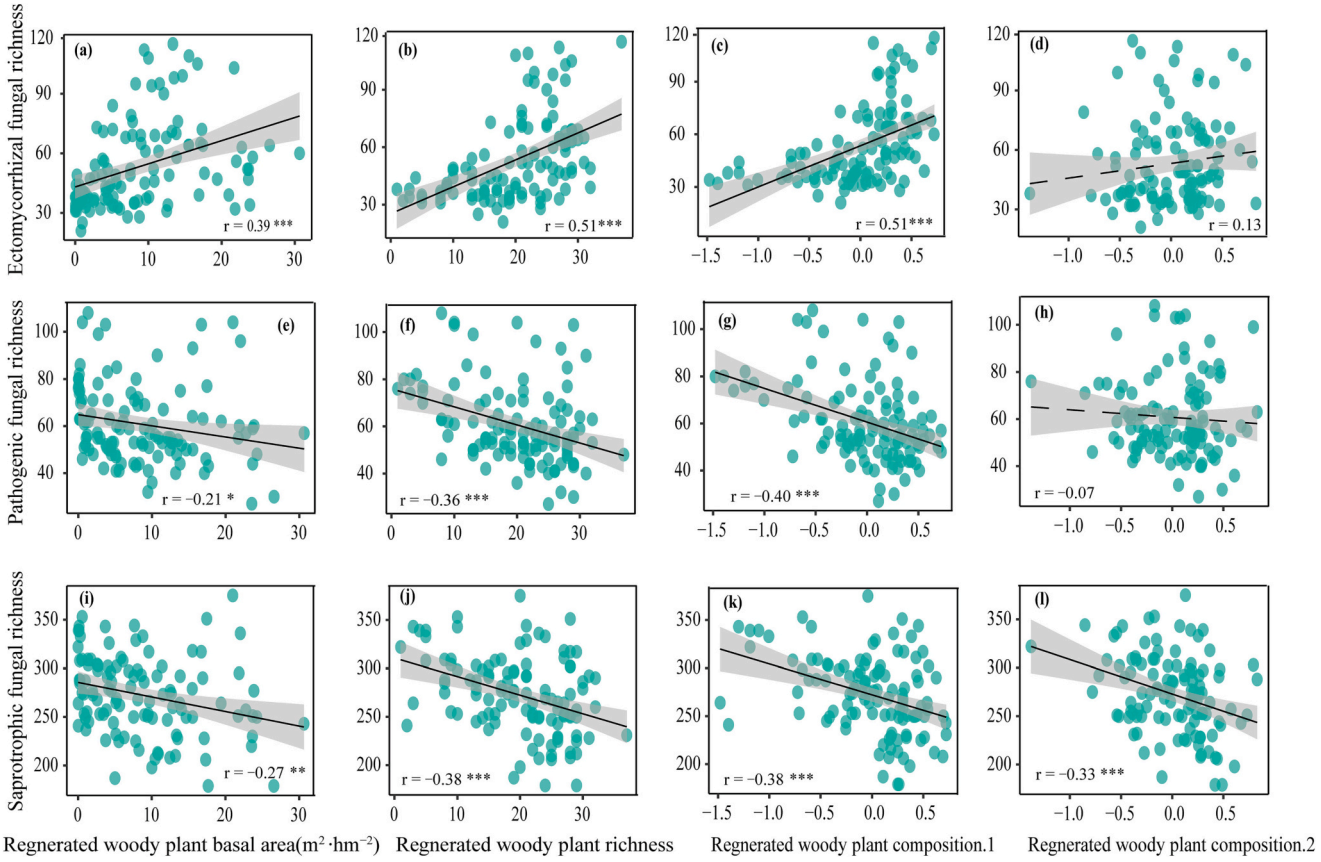

Fig. 3. Correlations of ectomycorrhizal (a–d), pathogenic (e–h), and saprotrophic (i–l) fungal richness to the regenerated woody plant community attributes. The solid and dashed regression lines indicate significant and nonsignificant effects, respectively. Significance level: *p < 0.05, **p < 0.001, ***p < 0.001.

on the beta diversity of soil bacteria (Mantel $r = 0.24$, Fig. 4b; Table S5), fungi (Mantel $r = 0.30$, Fig. 4d; Table S5), and fungal guilds (ECM fungi: $P = 0.008$; pathogenic fungi: $P = 0.003$; saprotrophic fungi: $P = 0.001$; Table 3).

The dissimilarity in soil properties between samples were significantly correlated with the beta diversity of soil bacteria ($P = 0.001$, Table S5), fungi ($P = 0.001$, Table S5), pathogenic ($P = 0.011$, Table 3), and saprotrophic fungi ($P = 0.001$, Table 3), except for the ECM fungi. Variations in topographic features between samples were also correlated with the beta diversity of soil bacteria ($P = 0.001$, Table S5), fungi ($P = 0.001$, Table S5), pathogenic ($P = 0.012$, Table 3), and saprotrophic fungi ($P = 0.001$, Table 3), except for the ECM fungi. In addition, after controlling for RWP attributes, CF basal area, soil properties, and topographic features, spatial distance between samples was only significantly correlated with the beta diversity of bacteria ($P = 0.001$, Table S5), but not that of fungi and fungal guilds (Table 3; Table S5).

Table 1
Model selection based on Poisson GLMs showing the response of bacterial and fungal richness.

	Estimate	2.5 % CI	97.5 % CI	VIF
Bacteria				
(Intercept)	7.6864	7.6825	7.6904	
S_RWP	0.0205	0.0156	0.0253	3.6486
NMDS2_RWP	−0.0115	−0.0162	−0.0069	2.0943
SoilPC1 (SOC, N)	0.0211	0.0164	0.0259	2.2283
SoilPC2 (silt, sand)	0.0255	0.0210	0.0300	1.3567
Convexity	0.0138	0.0096	0.0180	1.2404
dbMEM4	−0.0175	−0.0216	−0.0135	1.3244
dbMEM29	0.0161	0.0121	0.0201	1.0806
dbMEM34	−0.0116	−0.0156	−0.0075	1.1415
Fungi				
(Intercept)	7.3751	7.3704	7.3798	
B_RWP	−0.0147	−0.0196	−0.0098	3.5357
SoilPC1 (SOC, N)	−0.0157	−0.0209	−0.0104	2.3544
SoilPC3 (K, P)	0.0141	0.0092	0.0190	2.6364
SoilPC4 (pH)	−0.0179	−0.0231	−0.0127	1.3218
dbMEM4	0.0128	0.0080	0.0177	1.3435
dbMEM5	−0.0251	−0.0319	−0.0184	1.2828
dbMEM12	−0.0223	−0.0272	−0.0174	1.3169
dbMEM20	0.0160	0.0106	0.0213	1.1335
dbMEM43	0.0195	0.0147	0.0242	1.1077
dbMEM47	−0.0177	−0.0227	−0.0128	1.1262

Only variables with 95 % CI excluding zero are shown. CI: confidence interval (2.5 % and 97.5 %); VIF: variance inflation factor; B_RWP: regenerated woody plant basal area; S_RWP: regenerated woody plant richness; NMDS2_RWP: the axis 2 of a nonmetric multidimensional scaling representing regenerated woody plant composition (Fig. S3); SoilPC: PCA components representing variation in soil physicochemical variables; SOC: soil organic carbon (g kg^{-1} soil); N: soil total nitrogen (g kg^{-1} soil); P: soil total phosphorus (g kg^{-1} soil); K: soil total potassium (g kg^{-1} soil); dbMEM: distance-based Moran's eigenvectors.

Table 2
Model selection based on Poisson GLMs showing the response of fungal guilds richness.

	Estimate	2.5 % CI	97.5 % CI	VIF
Ectomycorrhizal fungi				
(Intercept)	3.9385	3.9120	3.9650	
B_CF	−0.0903	−0.1278	−0.0529	3.7494
S_RWP	0.0933	0.0515	0.1351	3.1417
SoilPC2 (silt, sand)	0.0463	0.0174	0.0752	1.4976
Elevation	0.0815	0.0446	0.1184	2.9022
Aspect	−0.0621	−0.0892	−0.0350	1.5160
dbMEM5	0.1189	0.0918	0.1460	1.2601
dbMEM13	−0.0554	−0.0899	−0.0209	1.8345
Pathogenic fungi				
(Intercept)	4.0900	4.0657	4.1144	
S_RWP	−0.0640	−0.1098	−0.0182	3.4086
SoilPC2 (silt, sand)	−0.0681	−0.0955	−0.0406	1.4063
SoilPC3 (K, P)	0.0599	0.0151	0.1047	2.2168
Elevation	0.0191	0.0267	0.0952	2.7738
Slope	−0.0360	−0.0780	−0.0247	1.8885
Aspect	−0.0660	−0.0927	−0.0394	1.4941
dbMEM5	−0.0862	−0.1122	−0.0601	1.2711
dbMEM20	0.0617	0.0368	0.0865	1.1318
dbMEM43	0.0563	0.0320	0.0807	1.1011
Saprotrophic fungi				
(intercept)	5.6033	5.5919	5.6146	
S_RWP	−0.0495	−0.0632	−0.0357	3.7855
NMDS2_RWP	−0.0292	−0.0440	−0.0145	2.1852
SoilPC3 (K, P)	0.0179	0.0026	0.0333	2.2810
SoilPC4 (pH)	−0.0257	−0.0378	−0.0136	1.2346
dbMEM5	−0.0300	−0.0421	−0.0178	1.2687
dbMEM20	0.0310	0.0191	0.0430	1.1090
dbMEM43	0.0270	0.0152	0.0386	1.1013

Only variables with 95 % CI excluding zero are shown. B_CF: Chinese fir basal area; others see Table 1.

4. Discussion

4.1. Response of soil bacterial and fungal richness to regenerated woody plant attributes

Our study provides strong evidence that RWP richness had a significant and positive influence on soil bacterial richness (Fig. 2b; Table 1). Similar to our findings, Li et al. (2018) also reported that soil bacterial richness increased with increasing plant diversity in a semi-arid grassland. Niche differentiation (or complementarity effect) may explain the strong RWP-bacterial richness relationship. A more species-rich RWP assemblage is likely to support a wider range of root types (Bezemer et al., 2006) and exudates, thus facilitating higher soil bacterial taxonomic richness by creating a greater range of resources and microhabitats (Lamb et al., 2011). It is also expected that a more diverse RWP community will produce more various litter of differing qualities (e.g., C:N ratio; Berg and McClaugherty, 2008) and thereby supporting more bacterial taxa via substrate availability (Osanai et al., 2013).

In contrast with soil bacterial richness, we found that the richness of soil fungi significantly decreased with increasing RWP basal area in the plantation forest (Fig. 2e; Table 1). This result contradicts multiple earlier experiments reporting the positive response of soil fungal richness to plant diversity or biomass in terrestrial ecosystems (Peay et al., 2013; Cline et al., 2018). However, our finding does parallel a study covering two experimental systems at a regional scale, in which soil fungal richness was negatively impacted by plant cover (Delgado-Baquerizo et al., 2018). The inconsistent findings among these studies indicate that the relevance of plant traits for the organization of soil fungal diversity is complicated and typically system-dependent (Tedersoo et al., 2016). The observed negative correlation of RWP basal area with soil fungi rather than with bacteria in our study could be explained by a few important unexplored factors. First, plants are known to produce compounds (e.g., terpenes and phenolic compounds) that can inhibit fungal growth (Xiao et al., 2014), thereby reducing fungal richness. It could be important to consider the capacity of certain plant species to produce these fungi-inhibiting compounds in forest restoration management if the goal is to increase fungal taxonomic richness. Second, the positive influence of plant species on microbial diversity can occur when both taxa respond similarly to the same environmental driving factors (Hooper et al., 2000). In our study, both RWP attributes (e.g., richness and basal area) and bacterial richness were positively associated with soil C and N (Table 1; Table S6), but fungal richness exhibited the opposite trend (Table 1). We speculate that the different responses of fungi and RWP to these soil properties, may have influenced the observed negative correlation. Furthermore, it is important to consider the potential influence of fungal trophic guild responses, which contribute to the diversity relationship of plants with overall fungi.

4.2. Response of the richness of soil fungal guilds to regenerated woody plant attributes

We show that the direction of the RWP-fungal richness relationship was fungal trophic guild-specific. Specifically, we observed that ECM fungal richness positively responded to RWP richness (Fig. 3b; Table 2), which is consistent with a previous study conducted in subtropical forest (Gao et al., 2013). Other studies have also found a positive correlation between plant and ECM fungal community diversity (Dickie, 2007; Yang et al., 2022). The positive diversity relationship between RWP and ECM fungi may result from the fact that more ECM fungi, acting as symbiotic mycorrhizal fungi, can typically build more associations belowground as plant richness increases (de Deyn et al., 2010).

In contrast with ECM fungi, saprotrophic fungal richness was negatively associated with RWP richness (Fig. 3j; Table 2). The finding concurs with a study by Gilbert et al. (2002), who found a negative

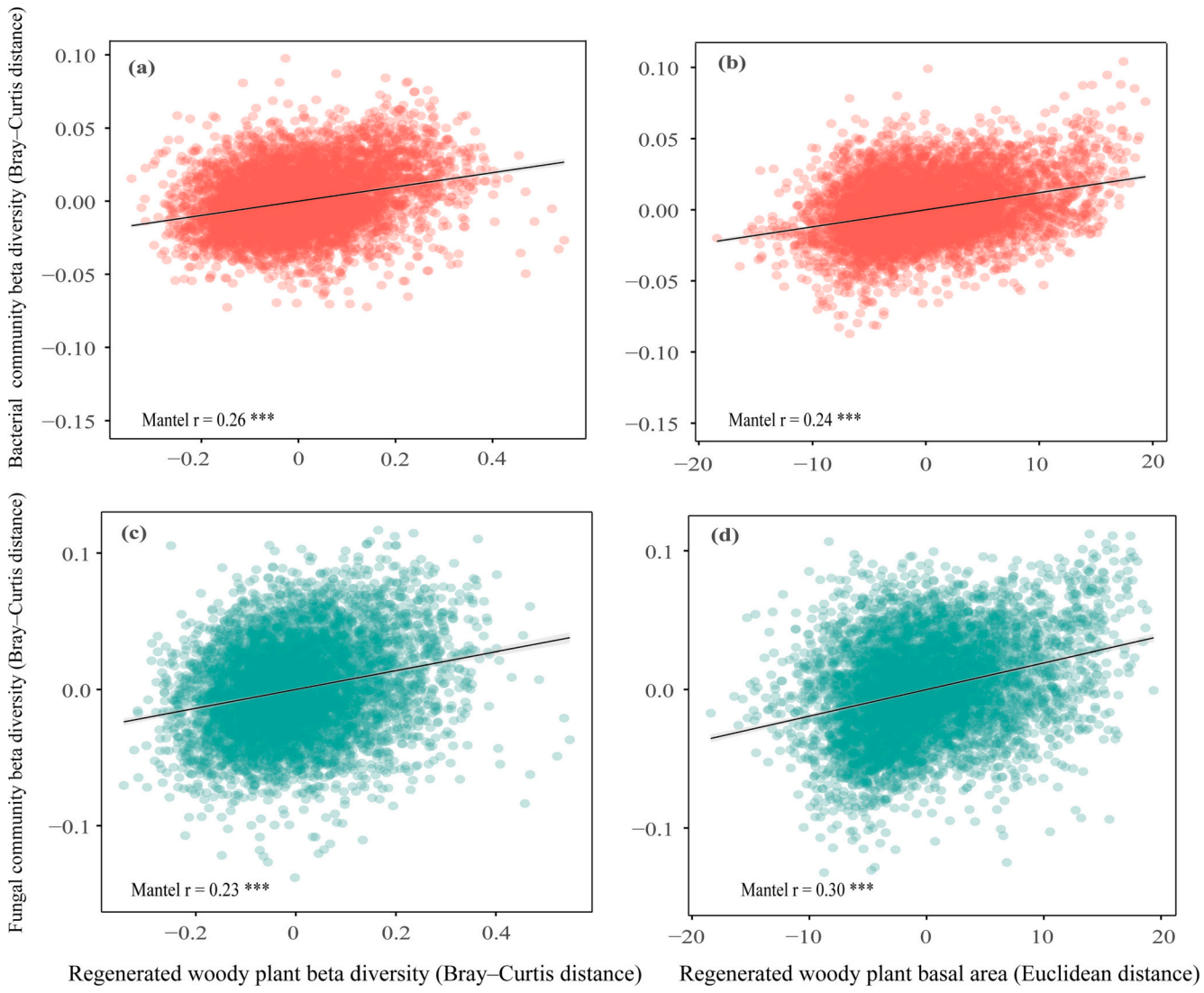

Fig. 4. Relationships between the community beta diversity (based on Bray–Curtis distance) of soil bacteria (a–b) and fungi (c–d) and the community beta diversity of regenerated woody plants and the basal area (based on Euclidean distance) of regenerated woody plants. The effects of the plant attributes (Chinese fir basal area, regenerated woody plant community beta diversity and basal area), soil physicochemical characteristics, topographic features, and spatial covariates (based on Euclidean distance) were statistically controlled with the partial Mantel analyses. The solid and dashed lines indicate significant and nonsignificant relationships, respectively. Significance level: *p < 0.05, **p < 0.001, ***p < 0.001.

Table 3
Partial Mantel tests showing the correlations between the community beta diversity of fungal guilds and the RWP community beta diversity and basal area, soil properties, topographic features, and spatial covariates, as determined by partial Mantel tests. CF is the common controlling factor for these responsible variables. Significant values (<0.05) are shown in bold. RWP: regenerated woody plant, CF: Chinese fir.

Explanatory	Ectomycorrhizal fungi		Pathogenic fungi		Saprotrophic fungi	
	Mantel r	P	Mantel r	P	Mantel r	P
RWP beta diversity	−0.12	**0.023**	0.19	**0.001**	0.11	**0.036**
RWP basal area	0.12	**0.008**	0.12	**0.003**	0.20	**0.001**
Soil properties	0.08	0.086	0.13	**0.011**	0.29	**0.001**
Topographic features	0.04	0.340	0.10	**0.012**	0.24	**0.001**
Spatial covariates	0.06	0.107	−0.01	0.684	0.01	0.706

relationship between tree species diversity and saprotrophic fungal richness in a moist tropical forest. Saprotrophic fungi belong to a free-living, opportunistic fungal guild (Baldrian et al., 2011), and mainly rely on the nutrients released from soil organic matter decomposition to maintain their growth and activity (Berg and McClaugherty, 2008; van der Wal et al., 2013). Thus, it seems plausible that the nutrient competition (i.e., nutrient availability) might be an important aspect in shaping the negative relationship between RWP richness and saprotrophic fungal richness in our studied plantation ecosystem. First, plants may act as a direct competitor to saprotrophic fungal taxa, as both plants and microorganisms require nearly the same nutrients for their maintenance and growth (Kuzyakov and Xu, 2013). Therefore, we speculate that with the increase in the growth and richness of RWP, more nutrients (such as N and P) were removed from the soil, leading to a reduction in saprotrophic species richness. Secondly, plants could also indirectly influence saprotrophic fungi through their ECM partners through the "Gadgil effect" (Fernandez and Kennedy, 2016), which indicates that more host-specific ECM fungi can exert a significant suppression effect on growth of saprotrophic fungi via competing for soil N (Yang et al., 2022), reflecting competitive exclusion of saprotrophic fungi by ECM

fungi.

Similar to saprotrophic fungi, our results revealed that pathogenic fungal richness negatively responded to RWP richness (Fig. 3f; Table 2). Generally, the richness and abundance of soil pathogenic fungi are thought to be host density-dependent (Keesing et al., 2010). With the increase of the richness of aboveground plants, the distance between conspecifics tends to be enlarged, which can potentially reduce the transmission rates of pathogenic fungi, thus causing a negative plants-soil pathogenic fungal richness relationship (Keesing et al., 2010). Indeed, one study conducted in natural forest ecosystems in California has found that the risk of oak infection by *Phytophthora ramorum* is negatively associated with plant species richness (Haas et al., 2016). Therefore, the increased RWP species in the studied plantation ecosystem would be expected to decrease disease incidence at the community level by decreasing the density of the pathogens' hosts.

4.3. Response of soil bacterial and fungal beta diversity to regenerated woody plant attributes

In this study, we found significant correlations between RWP attributes (e.g., basal area and beta diversity) and the beta diversity of soil microbial (bacteria, fungi, and fungal guilds) communities (Fig. 4; Table 3), suggesting that a more heterogeneous RWP community could contribute to more distinct soil microbial composition responses. These findings provided support for our third hypothesis and are in line with two recent studies that demonstrated the importance of understory vegetation for soil microbial community composition in both birch and spruce stands (Danielsen et al., 2021; Mundra et al., 2022). The observed strong coupling of dissimilarity in RWP and soil microbial community composition are likely due to the effects of two important mechanisms that control plant-microbial interactions; growth-limiting nutrient competition and litter input diversity. From the perspective of nutrient uptake, plants can interact with soil microbes via competition, facilitation, and mutualism to obtain nutrients (Vellend, 2010), which largely forms the basis of regulation and control of soil microbial interaction. RWP species are at a fast-growing life stage, requiring considerable nutrient supply. Therefore, the high nutrient requirements of RWP likely led to more competitive plant-microbial interactions, and resulted in the significant influence on soil microbial community composition in the current study. Indeed, we found high spatial variability in RWP basal area (CV: 0.83, Fig. S5), which could contribute to the observed changes in the composition of soil microbial communities. Similar results were also reported in one study, where soil microbial beta-diversity is linked with the variation in plant biomass in a semi-arid grassland ecosystem (Li et al., 2018).

From the perspective of resource input, plants can produce litter (leaf litter and root deposition) with different qualities delivered to the soil, which in turn are key energy sources for soil microbes (Hooper et al., 2000). Qualitative differences in plant compounds, such as C:N ratio, lignin concentrations, can evoke differential microbial responses (Prescott and Grayston, 2013). In our study, variation in litter quality of RWP species was also likely important in shaping soil microbial responses. Litterfall of RWP was mostly affiliated to the broadleaf species (excluding *Pinus massoniana*), and is easily decomposed by soil microorganisms due to their high leaf litter quality with low content of lignin and low C:N ratio (Zhang et al., 2016). Consequently, the increased energy flows derived from distinct RWP taxa in the studied CF plantation ecosystem may easily trigger the shifts in soil microbial communities (Nilsson and Wardle, 2005). Taken together, our results clearly showed that the changes in plant community composition due to the presence of RWP could induce a strong driving effect on soil microbial community composition in the subtropical plantation ecosystem.

4.4. Abiotic factors influencing soil microbial community

Abiotic factors exhibited a significant correlation with the richness and beta diversity of soil microbial communities. Soil properties displayed an important impact on the bacterial and fungal richness and beta diversity (Table 1; Table S5), which is in line with previous studies (Rousk et al., 2010; Ding et al., 2015). Specifically, soil bacterial richness increased with the increasing content of SOC and N, but soil fungal richness displayed the opposite trend (Table 1). The differential responses of bacteria and fungi to SOC and N might be due to their differing growth strategies. Having high growth and turnover rate, bacteria can rapidly flourish in nutrient-rich habitats (Fierer et al., 2007). By contrast, fungi are more adapted to stressful environments with slower growth and turnover rate (Fierer et al., 2007; Zhou et al., 2017).

Our results further showed that topography significantly impacted the diversity patterns of soil microbial communities in our studied plantation ecosystem (Tables 1–3; Table S5). It is possible that the microclimate (moisture and temperature) differed across the 113 subplots due to different topographic features (elevation, convexity, slope, and aspect) in the subtropical montane forest ecosystem, which may affect the soil microbial communities. As an example, soil bacterial richness decreased with the decreasing convexity value (Table 1). Generally, soil moisture is high at the sampling subplots with a low convexity value (Gao et al., 2017), and precipitation is very abundant (>1200 mm yr^{-1}) at our study site. The extremely high soil moisture at the sampling subplots with low convexity value may easily inhibit certain bacteria taxa by limiting the oxygen supply in the soils (Meng et al., 2013), subsequently reducing bacterial richness. Additionally, although the elevational gradient is small in the current study (ranging from 370 to 466 m, Fig. 1d), we still observed that the richness of fungal guilds (e.g., ECM and pathogenic fungi) increased with increasing elevation (Table 2). Similar results were found in cool-temperate montane forests (856.9–1831.8 m asl; Shigyo and Hirao, 2021) and neotropical forests (0–3000 m asl; Geml et al., 2022).

Here, we also found that the more distinct bacterial community was more strongly related to spatial distance between samples than that of fungi (Table S5). This result could be explained by the difference in soil bacterial and fungal dispersal abilities. Soil bacterial motility directly depends on soil texture, including soil pore network characteristics and forces of attraction exerted by the soil surfaces that bacterial cells are exposed to (MacDonald and Duniway, 1978). We thus reasoned that the bacteria may be confined to their microhabitats in soil due to the larger proportion of silt content at our study site (51.1 % on average, Table S1). However, the spreading hyphae of soil fungi can extend to larger areas in comparison to bacteria, facilitating dispersal within the same site (Morrison-Whittle and Goddard, 2015; Bahram et al., 2016), and therefore the distribution dispersion of soil fungi may not be significant in our study site.

5. Conclusions

Forest restoration has been a global priority for addressing climate change and protecting biodiversity (Poorter et al., 2021; Zhou et al., 2022). Our study provides new insights that soil microbial diversity patterns are related to easily measurable RWP community-level traits in a subtropical plantation during restoration. We found that RWP factors had contrasting influence on bacterial (positive) and fungal (negative) community richness. Meanwhile, the patterns observed for RWP-fungal richness relationship are fungal trophic guild-specific, where ECM fungal richness is positively related to RWP richness, and both saprotrophic and pathogenic fungal richness are negatively related to RWP richness. In addition, RWP community metrics also significantly influence beta diversity of soil microbial communities suggesting that more distinct RWP community assemblages are likely to produce more distinct soil microbial communities. Our study suggests that the maintenance of RWP and RWP diversity may be a crucial strategy to regulate soil microbial community structure, which has the potential to increase valuable ecosystem services and promote healthy forest development.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2023.104890.

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