Effects of different vegetation restoration types on soil fungal community composition and functional groups

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Abstract

Purpose

This study investigates the structure and functional groups of soil fungal communities in major vegetation types in subtropical China. The main objective is to understand the responses of these communities to different vegetation types, and the influence of soil properties, such as soil organic carbon (SOC), pH, soil ammonium nitrogen (AN), available potassium (AK), and nitrate nitrogen (NN), on the structure and functional groups of the soil fungal communities.

Methods

We explored the impact of different vegetation types on fungal diversity in various plantations, including bare land, *Liriodendron chinense* (Hu) T.C. Chen, *Cunninghamia lanceolata* (Lamb.) Hook, *Phyllostachys pubescens Mazel ex* H.de Lehaie (moso bamboo), and mixed fores. We also analyzed variations in soil properties across different soil depths.

Results

The results showed that the soil available potassium (AK) and soil nitrate nitrogen (NN) in mixed forests were significantly lower than those in bare land by 47% and 57%, respectively. The Soil organic carbon (SOC), NN, and pH decreased significantly by 49%, 45%, and 8%, respectively with increasing the soil depth. The diversity of soil fungal communities in mixed forest and mandarin forest was 20% higher than that in bare land. The relative abundance of Ectomycorrhizal fungi was highest in bamboo forests, while the relative abundance of Arbuscular Mycorrhizal fungi and plant pathogens increased with increasing soil depth, by 12% and 7%, respectively.

Conclusions

Our findings indicate that vegetation types and soil properties significantly impact the structure and diversity of soil fungal communities in subtropical plantations. These changes in the fungal community may stimulate the soil nutrient cycle, contributing to the ecosystem sustainability.

1. Introduction

Soil microbial communities play a crucial role in ecosystem functioning and sustainability, with soil fungi being a key component of these communities. Vegetation restoration is an important strategy to mitigate soil degradation, enhance soil fertility, and maintain ecosystem stability (Bright et al. 2014). It is increasingly recognized that planted forests can reduce the cutting pressure on natural forests (Jia et al. 2005), thus contributing to the restoration of degraded land. In recent years, China has undertaken

extensive afforestation efforts to mitigate environmental degradation and support ecological restoration (Hai 2021). Several studies in subtropical China have shown that soil bacterial communities vary among different vegetation restoration types and bare land, with certain bacterial groups being more abundant in specific plantations (Hou et al. 2019, Liu et al. 2019). In contrast, the responses of soil fungal communities to various restoration strategies have received less attention.

Fungal diversity is positively correlated with the versatility of terrestrial ecosystem (Bachelot et al. 2016, Albright and Martiny 2018). Soil fungal communities contribute to the decomposition of organic matter, nutrient cycling, and plant health. In particular, studies have shown that the loss of fungal diversity is considered to affect nutrient cycling and reduce the climate regulation function of forest ecosystems(Yan et al. 2017). For example, broadleaf forests promote the growth of ectomycorrhizal fungi and arbuscular mycorrhizal fungi due to their associations with specific plant species (Vörösmarty et al. 2010), while coniferous forests favor acid-tolerant fungi due to lower soil Ph (Li et al. 2019). Moreover, soil fungal communities are sensitive and rapidly responsive to environmental changes, making them reliable indicators of environmental health (Chai et al. 2019), especially mycorrhizal fungi associated with specific plant types or basidiomycetes involved in the decomposition of lignified plant debris (Lauber et al. 2008).Therefore, investigating the distribution patterns and key ecological drivers of soil fungal communities is crucial for enhancing our understanding of ecosystem responses to widespread environmental changes. Fungi are more sensitive to changes in vegetation types than soil bacteria, Therefore, there is a need for further investigation of soil fungal community to explore the adaptive strategies and functional transformation of soil fungi in different vegetation types.

There is increasing evidence that many fungi have more complex niches and form different functional guilds, playing different roles in nutrient cycling and carbon storage (Bahram et al. 2018, Chen et al. 2020). For instance, ectomycorrhizal (ECM) fungi that form symbiotic relationships with many trees are particularly important because they promote the acquisition of host nutrients (Lin et al. 2011) and protect them from soil pathogens (Castaño et al. 2019). Plant community composition greatly affects soil properties, which can be considered as the main driving force to shape the structure of soil fungal community (Frąc et al. 2018, Nakayama et al. 2019). Mounting evidence suggests that soil fungi act as the primary consumers of belowground plant inputs (Ballhausen and de Boer 2016b, Thakur et al. 2020) and the main decomposers of recalcitrant organic matter, such as cellulose and lignin (Treseder et al. 2015). Consequently, plant variation may significantly influence soil fungal communities by providing diverse sources of plant litter, thereby creating more heterogeneous niches for fungi. The change of soil microbial community is affected by soil physical and chemical factors, such as pH, soil organic carbon (SOC) and nutrient availability, and vegetation type(Smith et al. 2015, Lladó et al. 2018, Ahmed et al. 2019), due to the differences in litter types and decomposition between plant species(Nakayama et al. 2019). The impact of different soil factors on the biogeographic pattern of soil microbial community varies with the vegetation restoration type, however it is not clear which of these factors has a dominant role.

Therefore, we investigate the effects of different vegetation restoration types on soil fungal communities and their functional groups in subtropical China. We collected soil samples from different profiles to assess the influence of soil layers on fungal communities. Using Illumina sequencing, we analyzed the diversity and composition of soil fungi across different locations. We tested the hypotheses: (1) the composition and functional groups of soil fungal communities differ among vegetation restoration types; (2) the observed differences in soil microbial community characteristics are related to soil properties.

2. Materials and methods

2.1. Study site and soil sampling

The research site is located in Xiashu (119° 13'20 "E, 32° 7'8" N), Jurong County, Jiangsu Province, China. It covers an area of 3891ha, with a forest coverage rate of more than 90%, belonging to the north subtropical monsoon climate area. According to the observation data of Jurong meteorological station and forest farm for many years, the annual average temperature is 15.5 ℃, and the annual average precipitation is 1099.1 mm. The precipitation is the most in summer, followed by spring and autumn. The annual average air relative humidity is 79%, and the average frost-free period is 233 d. The soil of the forest farm was mainly yellow-brown soil and mountain yellow-brown soil and the thickness of the soil layer was generally more than 50 cm.

In May 2021, this study randomly selected areas with similar altitude of bare land and four different types of vegetation restorations (*Liriodendron chinense (Hu) T.C. Chen, Cunninghamia lanceolata (Lamb.) Hook, Phyllostachys pubescens Mazel ex H.de Lehaie (moso bamboo*) and mixed *Liriodendron chinense (Hu) T.C. Chen* and moso bamboo forest). The L. chinense forest in Jurong Xiashu forest farm of Jiangsu Province is L. chinense provenance from Fujian Province of China in 1994(Yang et al. 2014). *C. lanceolata* and *P. eduli* forests are also cultivated and planted in the same year. These vegetation restoration plots were geographically adjacent and ecologically similar. We selected 3 stands respectively in these plots, with a total of 15 sampling stands. In each sampled stand, a sample plot of 20 20m^2 plot was randomly established to represent the stand, at least 500 meters away from the forest edge. When sampling, take a point along the diagonal intersection of each sample plot and excavate the soil profile. Samples were collected from 0–10 cm, 10–20 cm and 20–30 cm soil layers respectively, while below 30 cm contained more gravel, and each layer was 20 mm high 61.8 mm Ø. All soil samples were triplicated for each layer resulting in a total of 135 soil samples. Sample 1 was sealed with plastic film to determine the physical properties of undisturbed soil, placed in a sealed box, sent to the laboratory immediately. Sample 2 was immediately stored in a − 80 ° refrigerator for extracting the total DNA of soil microorganisms for fungal community analysis. Sample 3 was air dried and sieved to < 0.147mm to determine the chemical properties of the soil.

2.2. Soil physicochemical properties

The soil pH was measured in a suspension with a ratio of soil to water of 1:2.5 using a pH meter (sartorius PB-10, Gottingen, Germany). After the fresh soil samples were dried to constant weight at 105 ℃, the soil moisture content (WC, %) was determined by gravimetric method. The soil bulk density (BD) and soil porosity (POR), soil capillary porosity (CP); soil non-capillary porosity (NCP) was measured using a soil ring knife ring (100 cm^3) (Liu et al. 2021). Soil organic carbon (SOC) was analyzed by oxidation combined with potassium dichromate and measured by visible spectrophotometer (jh-14-08 723, China). Soil available phosphorus (AP) was determined by hydrochloric acid sulfuric acid extraction method. Soil available potassium (AK) was extracted by NH_4OAc and measured by atomic absorption spectrometer (AA900T, Perkin Elmer, MA, USA). Soil nitrate nitrogen (NN) and soil ammonium nitrogen (AN) were determined by 2mol / L^{-1}KCl extraction indophenol blue colorimetry.

2.3. DNA extraction, PCR amplification, and Illumina sequencing

The soil microbial DNA was extracted with d3142 kit of Guangzhou Meiji Biotechnology Co., Ltd., and the extracted DNA products were detected with nanodrop microspectrophotometer and agarose gel electrophoresis instrument. The ITS2 region of ITS was amplified with specific primers with barcode. Primer sequence: ITS3_ KYO2: GATGAAGAACGYAGYRAA; ITS4:TCCTCCGCTTATTGATATGC. The PCR reaction was amplified in two rounds, and the amplified products of the second round were purified by AMPure XP Beans. The purified amplified products (i.e., amplicons) were connected to the sequencing connector to construct the sequencing library, and Illumina was used for computer sequencing. Quantification was performed with ABI StepOnePlus Real Time PCR System (Life Technologies, USA), and sequencing was performed according to the PE250 mode of Novaseq6000.

2.4. Sequencing Data Processing

The original sequences were filtered to eliminate low-quality sequences using the method described by Caporaso et al(Caporaso et al. 2010). The ITS2 region was then extracted by the same method used by Bengtsson Palme et al(Bengtsson-Palme et al. 2013). The OTU clustering program follows the vsearch process (https://github.com/torognes/vsearch/wiki/VSEARCH-pipeline), and the similarity of OTU is 97% (Edgar 2013). We used FUNGuild to analyze the functional groups of fungi. FUNGuild v1. 0 is a flat database hosted by GitHub (https://github.com/UMNFuN/FUNGuild)(Nguyen et al. 2016). In order to avoid over interpretation of fungal functional groups, we deleted the confidence level of "possible" and retained only the two levels of "highly probable" and "probable". Communities that cannot be identified or identified as multiple complex nutritional methods are unified as "undefined"(Jiang et al. 2021).

2.5. Statistical analyses

When performing one-way ANOVA (SPSS, Chicago, Illinois, USA), using Duncan test, we checked the model residuals and confirmed that the assumptions of normality and homogeneity were met. Two factor analysis of variance (ANOVA) was used to test the effects of land use, soil layer and their interaction on different indicators (SPSS 23.0). All histograms use origin8.5 software fitting. Microbial communities and

functional structures were visualized by non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance. ANOSIM analysis was used to detect differences within and between groups. Linear discriminant analysis (LDA) effect size (lefse) method(http://huttenhower.sph.harvard.edu/lefse/) was used to evaluate high-dimensional microbial groups and determine the microbial classification represented by differences between different vegetation types. The significance standard of fungal classification level was LDA > 3, $p < 0.05$.

Redundant discriminant analysis (RDA) used R (version 4.0.0) to analyze the effects of soil properties on soil fungal community structure and functional groups. Each arrow (usually representing a numerical variable) points in the direction of the most dramatic increase in the environment variable, and the angle between the arrows (alpha) represents the correlation between individual arrows and the environment variable. When the angle was acute, the approximate correlation was positive, and when the angle was greater than 90 degrees, it was negative. The length of the arrow represents the measure of applicability. The size of the red dot in Figs. 7 (a, c) represents abundance. A positive correlation is indicated when the line connecting the red dot to the origin in the figure is less than 90 ° with the solid arrow in the figure, and a negative correlation is indicated when the angle is greater than 90 °.

3. Results

3.1. Physical and chemical properties of soil in different vegetation types

The AK, SOC, AN, NN, and pH were significantly affected by vegetation types (Fig. 1). Among them, the AK and NN levels in MF were significantly lower than those in BL, by 47% and 57% respectively. The pH of CFF was significantly lower than that of BL by 10%. The SOC content in LCF was significantly lower than that in BL by 47%. At the same time, soil depth also had a significant impact on SOC, AN, NN, and pH. Specifically, SOC, NN, and pH decreased gradually with increasing soil depth, with reductions of 49%, 45%, and 8% respectively. For AP, except for CFF, the highest content for the other forest stands was found in the 10–20 cm soil layer.

The WC, CP, and NCP were significantly influenced by vegetation types (Fig. 2, a, d, e). The CP content in CFF was significantly higher than that in BL by 24%. In contrast, the lowest NCP content is found in MF, which is 61% lower than in BL.

3.2. Diversity of soil fungi in different vegetation types

The Ace index of the BBF was found to be markedly lower than that of the BL by 18%, while the Chao1 index of the CFF was significantly lower than the BL by 20% (Table 1). These observations indicate reduced soil fungal community richness at the BBF and CFF. Furthermore, the Simpson and Shannon indices for the 0–10 cm soil depth at the BBF and CFF were significantly lower than those at the BL, with reductions of 19% and 16%, respectively (Table 1). In contrast, the Shannon index for the LCF and MF

was 20% higher than that of the BL. Collectively, these findings reveal that the soil fungal community diversity was higher at the LCF and MF.

Table 1
α diversity of soil fungi in different vegetation types

Forest types	Soil layer	Shannon index	Simpson index	Chao1 index	Ace index
BL	0-10cm	5.44 ± 0.27ABb	0.97 ± 0.01Aa	999.54 ± 33.49Aa	994.60 ± 19.89Aa
	10-20cm	6.24 ± 0.05Aa	0.95 ± 0.01Aa	1014.90 ± 77.91ABa	1051.53 ± 76.95Aa
	20-30cm	5.97 ± 0.15Aab	0.95 ± 0.01Aa	1007.95 ± 43.38Aa	998.13 ± 36.68Aa
LCF	0-10cm	6.52 ± 0.24Aa	0.92 ± 0.02ABb	1038.83 ± 9.89Aa	1010.11 ± 38.55Aa
	10-20cm	5.96 ± 0.58Aa	0.96 ± 0.00Aa	1041.17 ± 15.45Aa	1004.12 ± 64.79Aa
	20-30cm	5.42 ± 0.46Aa	0.95 ± 0.01Aab	1009.22 ± 39.45Aa	1017.29 ± 46.06Aa
CFF	0-10cm	4.59 ± 0.83Ba	0.96 ± 0.01Aa	839.72 ± 59.23Ba	1040.53 ± 6.94Aa
	10-20cm	6.24 ± 0.08Aa	0.92 ± 0.05Aa	850.39 ± 22.86Ba	1050.06 ± 17.92Aa
	20-30cm	5.51 ± 0.49Aa	0.92 ± 0.03Aa	735.37 ± 31.37Ba	1024.91 ± 32.76Aa
BBF	0-10cm	6.24 ± 0.20Aa	0.79 ± 0.10Ba	1020.35 ± 23.59Aa	863.37 ± 53.99Ba
	10-20cm	5.98 ± 0.25Aa	0.96 ± 0.00Aa	1033.31 ± 52ABa	873.24 ± 32.85Aa
	20-30cm	6.18 ± 0.05Aa	0.94 ± 0.02Aa	982.05 ± 19.88Aa	746.99 ± 41.12Ba
MF	0-10cm	6.47 ± 0.2Aa	0.96 ± 0.00Aa	993.03 ± 25.48Aa	1008.32 ± 23.25Aa
	10-20cm	6.14 ± 0.41Aa	0.95 ± 0.01Aa	1048.35 ± 77.44Aa	1020.35 ± 59.11Aa
	20-30cm	5.65 ± 0.43Aa	0.97 ± 0.00Aa	963.64 ± 53.48Aa	978.57 ± 17.98Aa

Note: values are shown as mean ± S.D. (n = 3). The lower case letters indicate a significant difference among different soil layers of the same land use types ($p < 0.05$), the upper-case letter indicates a significant difference between different vegetation types of the same soil layer ($p < 0.05$). BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

The vegetation types-induced differences were greater than those induced by the soil layer. Specifically, the Chao1 and Ace indices were significantly influenced by vegetation types, with a difference of 13.047 and 12.188, respectively ($p < 0.001$) (Table 2.). The interaction between vegetation types and soil layer is significant for all four indices, with the greatest difference observed in the Choa1 index ($p < 0.05$). Soil layer also exhibited a significant effect on the Shannon and Simpson indices, but to a lesser extent than vegetation types and their interaction with soil layer

Table 2
Effect of vegetation types, soil layer and their interactions on α diversity index based on repeated measure-ANOVA

Diffs	Shannon index	Simpson index	Chao1 index	Ace index
Vegetation types	1.585	2.259	13.047***	12.188***
Soil layer	1.242	1.261	2.243	1.560
Vegetation types × Soil layer	2.064	2.422	0.337*	0.530

*** was significantly correlated at the0.001 level (bilateral). ** Significant correlation at 0.01 level (bilateral). * Significant correlation at 0.05 level (bilateral).

Similarly, different vegetation types can cause changes in fungal community structure, with a stress index of 0.127. (Fig. 3). ANOSIM test (Bray - Curtis distance) showed that the community structure of soil fungi in each soil layer was significantly affected by different vegetation types ($p < 0.01$). For vegetation types, there was a significant difference in fungal community structure between different vegetation types in the 0-10cm and 10-20cm soil layer ($p < 0.01$, Table 3).

Table 3
Difference test of similarity analysis of soil fungal community structure

diffs		R-value	*p*-value	significant
Vegetation types	0-10cm	0.637	0.001	**
	10-20cm	0.8593	0.001	**
	20-30cm	0.6207	0.001	0.6207
Soil layer	BL	0.177	0.212	NS
	LCF	-0.0288	0.552	NS
	CFF	0.2016	0.135	NS
	BBF	0.1029	0.208	NS
	MF	0.1605	0.233	NS

BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest. ** Significant correlation at 0.01 level (bilateral).

3.3. Composition of soil fungal communities in different vegetation types

Among all soil samples, 3950360 effective fungal sequences were obtained by high-throughput sequencing, and a total of 3714 OTUs were classified. Five domain, 19 phyla, 57 class, 160 orders, 306 families 529 genus and 490 species groups were identified in tags of all soil samples.

The phylum Glomeromycota had significantly higher relative abundance in mixed forest compared to other vegetation types, while the phylum Basidiomycota had significantly higher relative abundance in bamboo forest. Furthermore, we found that the relative abundance of Glomeromycota was significantly higher in the 0–10 cm soil layer compared to deeper layers (10–20 cm and 20–30 cm) (Fig. 4). In terms of the interaction between vegetation type and soil layer, we found that the relative abundance of Ascomycota and Mortierellomycota were significantly higher in mixed forest in the 0–10 cm soil layer compared to other vegetation types and soil layers ($p < 0.01$, Table 4). The relative abundance of Basidiomycota, on the other hand, was significantly higher in bamboo forest in the 10–20 cm soil layer compared to other vegetation types and soil layers ($p < 0.05$, Table 4).

Table 4
Effect of vegetation types, soil layer and their interactions on composition of soil fungal relative abundance based on repeated measure-ANOVA

Diffs	Vegetation types	Soil layer	Vegetation types × Soil layer
Ascomycota	0.888	7.883**	0.923
Basidiomycota	3.077*	2.245	0.718
Mortierellomycota	0.869	8.334**	0.649
Mucoromycota	3.161*	3.014	1.147
Rozellomycota	3.896*	2.622	1.005
Glomeromycota	6.428**	2.137	1.49
Chytridiomycota	1.251	1.868	0.702
Other	1.948	1.274	0.506

Note: *p<0.05;**p<0.01 ***p<0.001. Numbers are F-values.

Some fungal groups were significantly enriched at the phylum, class and genus levels in different vegetation types (Fig. 5). At 0–10 cm soil layer, most fungi were mainly enriched on MF and LCF. At 10-20cm, most fungi were mainly enriched on CFF and LCF. At 20-30cm, most fungi were mainly enriched on BL and LCF, and there was no group with LDA > 3 in MF.

3.4. Functional groups of soil fungi communities in different vegetation types

Fungi was annotated using the fungal database and provided three nutritional models: symbiotic fungal, saprophytic fungal and pathogens. FUNGuild obtained more detailed nutrient pattern information from selected soils (Fig. 5). The relative abundance of undefined saprophytic fungal was the highest in different vegetation types. The relative abundance of Ectomycorrhiza in BBF was the highest. Moreover, at deeper soil layers, the relative abundance of Arbuscular Mycorrhizal fungi and plant pathogen increased, and the relative abundance of endophyte and wood saprotroph decreased.

The relative abundance of Ectomycorrhizal fungi was highest in BBF. At deeper soil layers, the relative abundance of Arbuscular Mycorrhizal fungi and Plant Pathogen increased, while the relative abundance of endophyte and wood saprotroph decreased. Soil depth had a significant effect on Ectomycorrhizal fungi ($p < 0.05$). Undefined saprotroph and Arbuscular mycorrhizal were affected by the interaction of vegetation type and soil depth ($p < 0.05$) (Table 5.).

Table 5
Significant of the effect of vegetation types, soil layer and their interactions on composition of soil fungal functional groups based on repeated measure-ANOVA

Diffs	Vegetation types	Soil layer	Vegetation types × Soil layer
Undefined Saprotroph	1.903	1.747	2.423*
Wood Saprotroph	3.425*	0.453	0.163
Plant Pathogen	6.428*	2.137	1.49
Ectomycorrhizal	1.278**	5.124*	0.46
Arbuscular Mycorrhizal	1.343**	1.659	2.42*
Animal Pathogen	0.686	1.456	0.83
Endophyte	2.716*	1.295	1.836
Fungal Parasite	1.295	0.469	1.002
Plant Saprotroph	0.815	2.536	1.565
Soil Saprotroph	1.605	1.106	0.207
Epiphyte	1.764	0.634	1.607
Dung Saprotroph	1.141	1.206	0.958
Note: *p<0.05;**p<0.01 ***p<0.001. Numbers are F-values.			

3.5. Soil factors affecting microbial community structure and function

The RDA explained 68.23% of the relationship between soil fungi and soil factors at fungal phylum level (Fig. 7. a, b). At the same time, the RDA explained 59.14% of the relationship between fungal functional groups and soil factors (Fig. 7. c, d). In particular, the SOC ($p < 0.001$), AN ($p < 0.05$) and pH ($p < 0.05$) were

important soil factors affecting fungal community structure and functional groups. In addition, WC ($p < 0.001$), CP ($p < 0.001$) and NCP ($p < 0.01$) were also significantly correlated with the changes of fungal functional groups, and AK ($p < 0.01$) and NN ($p < 0.01$) were significantly correlated with the changes of fungal community structure.

4. Discussion

4.1. Taxa-specific changes in soil fungal communities in different vegetation type

Changes in aboveground vegetation types induced changes in soil properties such as soil organic carbon, soil pH and ammonium, which affect soil fungal diversity(Blackwell 2011, Yarwood and Högberg 2017). Our study revealed that Ascomycetes, Basidiomycetes, and Mortierella were the most abundant fungi in the soil community. These findings align with the dominant position of Ascomycetes reported by Chen[22] and the identification of Ascomycetes as the dominant fungi in grass soil communities by Hugoni[23].Among them, Ascomycetes are considered to be the key players in the decomposition of soil organic matter[24]. The NMDS analysis based on β diversity showed that vegetation type was closely associated with observed differences in fungal community structure (Fig. 3), suggesting that vegetation types may be the driving factor for the construction of microbial communities, which was consistent with previous research results(Rousk et al. 2010). In addition, pine species such as *P. abies* and *L. gmelinii* are reported to promote soil acidification, which is consistent with our results(Verstraeten et al. 2018). As shown in Fig. 1, the pH value of CFF is the lowest among all vegetation types. This may be attributed to the effects of plant litter and root exudates, which contain organic acids that contribute to soil acidification. This is consistent with the results of several previous studies. For example, a study by Fierer et al. (Wang et al. 2017)found that soil pH was negatively correlated with the relative abundance of conifers. Likewise, a study by Noh et al. (2017) found that the acidity of coniferous forest soils was attributed to the decomposition of coniferous litter and the release of organic acids from coniferous roots. Overall, these findings suggest that vegetation type can have a significant impact on soil properties, including pH, which in turn can influence the composition and abundance of soil fungal communities.

LEfSe analysis provides new insights into the response of soil fungi to changed soil niche. LEfSe analysis showed that the indicator group of fungi was enriched in the 0–10 cm soil layer of MF and LCF, the 10-20cm soil layer of the CFF and LCF, and the 20-30cm soil layer of BL and LCF (Fig. 5). Ascomycetes and basidiomycetes are abundant. It is well-documented that in a long-term stable community (i.e. a community with little interference), some highly competitive species will reproduce in large numbers, making a few species dominant in the community(Doležal et al. 2013). In conclusion, the niche of microbial species in different forest ecological environments may determine the structure of soil microbial community.

4.2. Functional changes in soil fungal communities in different vegetation type

Studies have shown that Glomeromycota can form arbuscular mycorrhizal with plants and can directly absorb nutrients (Cai et al. 2011), demonstrating the important role of fungi in the rhizosphere niche (Ballhausen and de Boer 2016a). Our study showed that saprotroph account for more than half of the sequence of soil and litter communities, while other functional associations showed greater variability. The saprophytic rhizosphere term defines the area affected by saprophytic mycelium. The contribution of the saprophytic rhizosphere to the food web is underestimated, especially from the perspective of saprophytic fungi(Bahnmann et al. 2018). Therefore, this underestimates the status of fungi in the ecological cycle. In this study, as shown by the results of our RDA (Fig. 7C), AN had a significant positive correlation with Ectomycorrhizal. Previous studies have shown that larger Ectomycorrhizal fungal networks can directly degrade and obtain organic forms of nitrogen and are expected to dominate "slow" nitrogen cycling ecosystem with low levels of inorganic nutrients(Phillips et al. 2013, Crowther et al. 2019). In our study, bamboo forest had the highest Ectomycorrhizal content, and with the increase of soil depth, the Ectomycorrhizal content of BL, CFF and BBF increased first and then decreased. The relative content of AMF was abundant in LCF and MF, but scarce in CFF. The relative content of AMF increased with the increase of soil depth. The observed increase in ECM content with soil depth in BL, CFF, and BBF may be due to that ECM fungi are more adapted to the nutrient-poor and acidic conditions found in deeper soil layers. This is supported by previous research, such as a study by Tedersoo et al.(Zeglin et al. 2016), which found that the abundance of ECM fungi increased with soil depth in boreal forests. The lower relative content of AM fungi in CFF may be due to the acidic conditions created by the decomposition of coniferous litter and the release of organic acids from coniferous roots, which are not conducive to the growth of AM fungi. This is consistent with the findings of previous studies, such as a study by Noh et al. (McGuire et al. 2012) mentioned earlier, which found that the acidity of coniferous forest soils was attributed to the release of organic acids from coniferous roots, which negatively impacted the growth of AM fungi. Changes in Ectomycorrhizal fungi may indicate changes in the nitrogen cycle(Averill et al. 2014). With the increase of Ectomycorrhizal fungi, the relative abundance of wood saprophytic fungi and plant pathogenic fungi decreased, which may be attributed to the interaction between mycorrhizal fungi and free microorganisms(Strickland et al. 2017). According to the nutrient competition hypothesis, mycorrhizal fungi and free microorganisms need nutrients to supply their own growth and reproduction(Zeglin et al. 2016). In conclusion, we conclude that the changes of fungal functional groups may affect the nutrient cycle of different vegetation types.

4.3. Factors shaping soil fungal communities in different vegetation type

Previous studies have shown that there is a significant correlation between abiotic factors and soil microbial community diversity and abundance(Kõljalg et al. 2013). In our study, the pH, SOC and AN were significantly correlated with fungal community structure and fungal functional groups. In particular,

fungal community structure was significantly correlated with soil nutrient indexes (NN, AK), while fungal functional groups were significantly correlated with soil physical properties (WC, CP, NCP). The soil pH and SOC have a significant impact on microbial community structure, and the artificial increase of biochar can affect the properties of soil(Yao et al. 2017) The interaction between pH and base cation availability, and the change of pH may affect the ability of soil fungi to obtain soil resources(Tedersoo et al. 2016). Fungi form a strong combination with plants, supporting more effective use of available carbon in plants(Dini-Andreote et al. 2016). Due to the establishment of a biological nutritional relationship between trees and fungi, previous studies have predicted that the impact of tree host specificity on mycorrhizal communities is more important(Orwin et al. 2011, Uroz et al. 2016). This can explain the sensitivity of fungi to vegetation changes in different habitats.

The changes of fungal functional groups were also related to water content, bulk density and soil non capillary porosity (Fig. 7c, d). The root development and absorption of different tree species determine the soil porosity and water content, which may be confirmed by the significant changes in the community structure of ectomycorrhizal fungi. Previous studies have found tree host specificity of ectomycorrhiza, and host specificity has been proved to be an important driver of symbiotic fungi (Hartmann et al. 2014). Therefore, compared with the changes of soil nutrients, the changes of tree species in different habitats may be the main reason for the changes of fungi in our study. Plant communities play important roles in soil microbial community structure through litter chemical properties and root exudates (McGuire et al. 2012). Tree species diversity may have a positive impact on the structure of soil microbial community through root exudates and nutrient and water absorption (Talbot et al. 2015). Therefore, diverse soil fungal groups can coexist in forest ecosystem (Gao et al. 2015, Martino et al. 2018). In general, we can predict the succession process of microorganisms by comparing the changes of soil microorganisms in different habitats, which is very helpful to study the changes of microorganisms in the succession process.

In conclusion, this study provided information on Rhizosphere fungal communities and diversity of different vegetation types. Mastering these relationships can help us to artificially adjust the diversity of fungal communities, so as to predict the future forest development and adapt to the changing environmental conditions after artificial vegetation restoration.

5. Conclusions

Soil properties and fungal communities varied among different vegetation types, soil depths, and forest types. The mixed forests exhibited higher soil capillary porosity (CP) and fungal diversity compared to other forest types. The study also identified SOC, pH, and AN as significant factors affecting soil fungal community structure and functional groups. Overall, the results emphasized the importance of maintaining diverse forest ecosystems to promote soil health and ecosystem functioning. This study provides critical information for forest management practices, which can be utilized to develop effective strategies for sustainable forest management. Future research should focus on understanding the

underlying mechanisms behind these relationships and identifying best management practices for enhancing soil health and biodiversity in forest ecosystems.

Declarations

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Conflicts of Interest: The authors declare that they have no competing interests.

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Figures

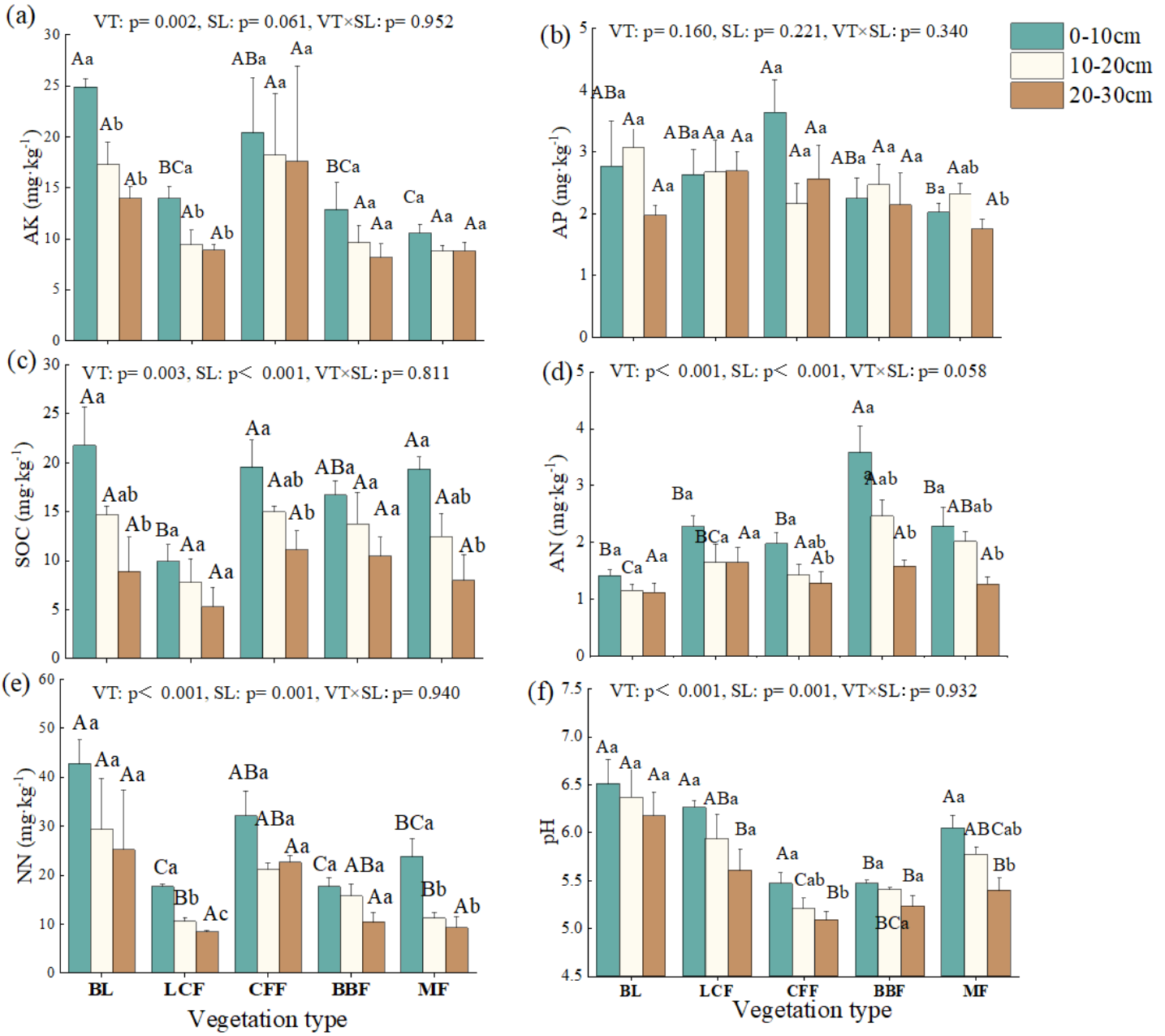

Figure 1

Soil chemical properties of different vegetation types(mean ± SE, n = 3). SE is the variance of the index. The error line indicates standard error; lower case letters indicate a significant difference among different soil layers of the same land use types ($p < 0.05$); the upper-case letter indicates a significant difference between different vegetation types of the same soil layer ($p < 0.05$). AK-Soil available potassium; AP-Soil available phosphorus; SOC-Soil organic carbon; AN-Soil ammonium nitrogen; NN-Soil nitrate nitrogen; pH-Soil pH. BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

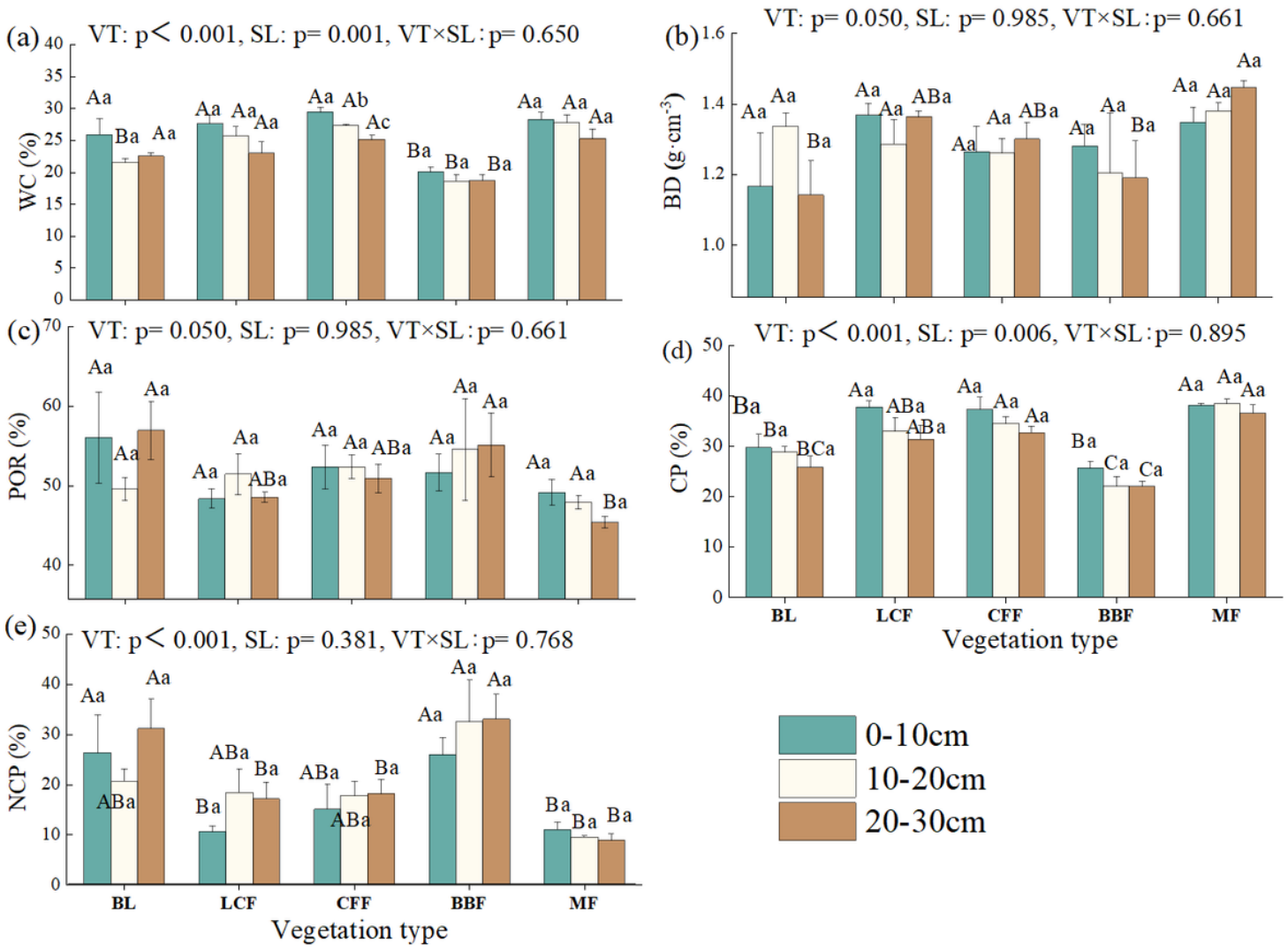

Figure 2

Soil physical properties of different vegetation types (mean ± SE, n = 3). SE is the variance of the index. The error line indicates standard error; lower case letters indicate a significant difference among different soil layers of the same land use types ($p < 0.05$); the upper-case letter indicates a significant difference between different vegetation types of the same soil layer ($p < 0.05$). WC-Soil water content; BD-Soil bulk density; POR-Soil total porosity; CP-Soil capillary porosity; NCP-Soil non-capillary porosity. BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

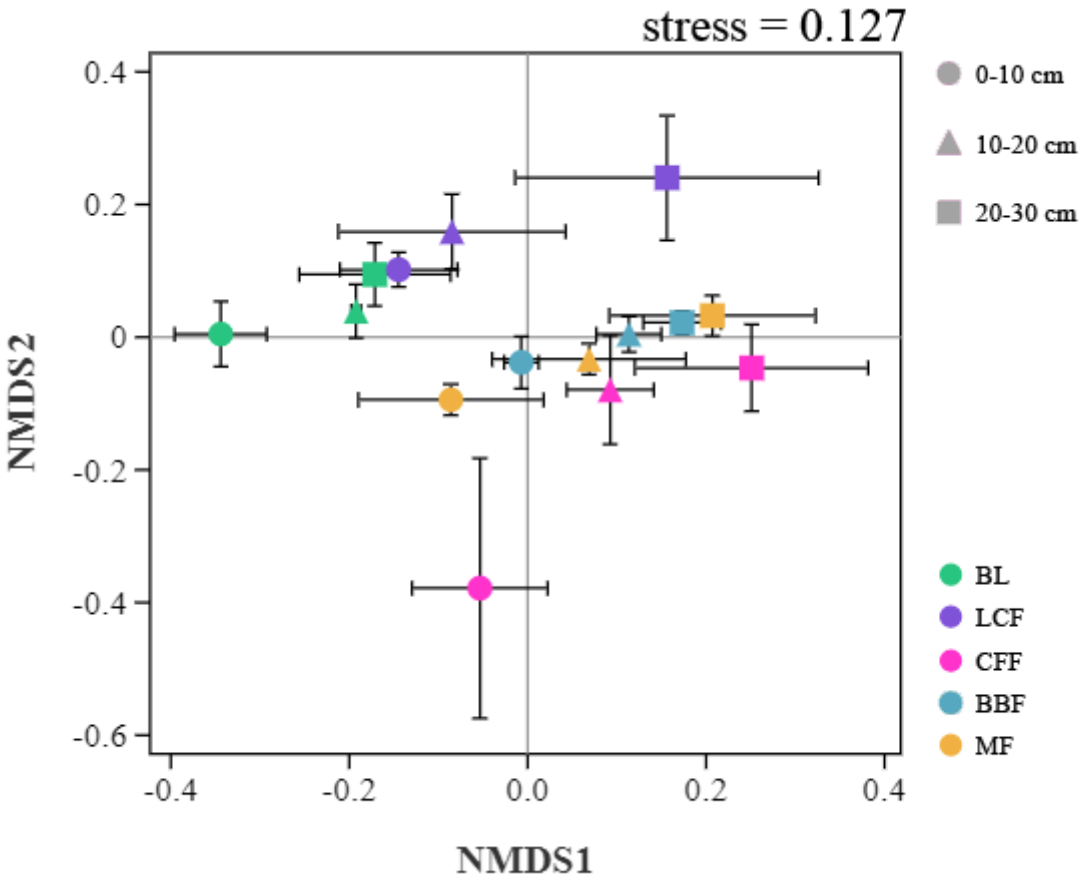

Figure 3

Non-metric multidimensional scale (NMDS) of soil fungal communities in different layers of different vegetation based on Bray-Curtis differences.

BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

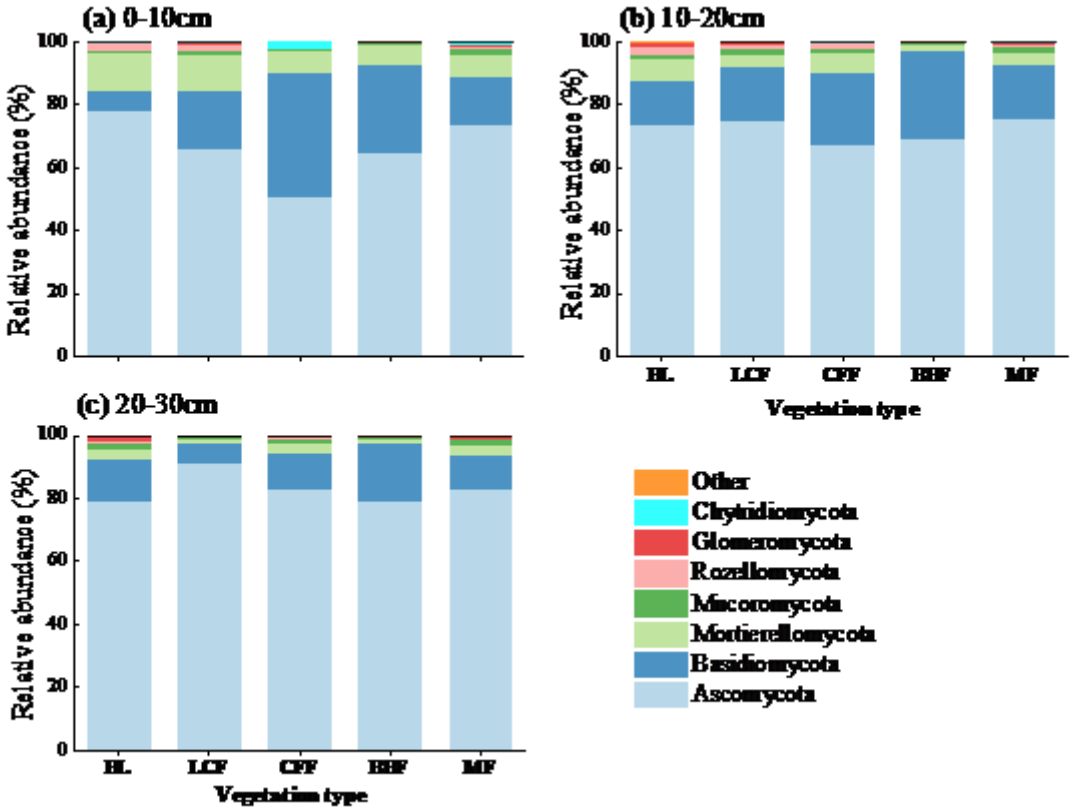

Figure 4

The average of relative abundance (%) of fungal taxa at the phylum level.

BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

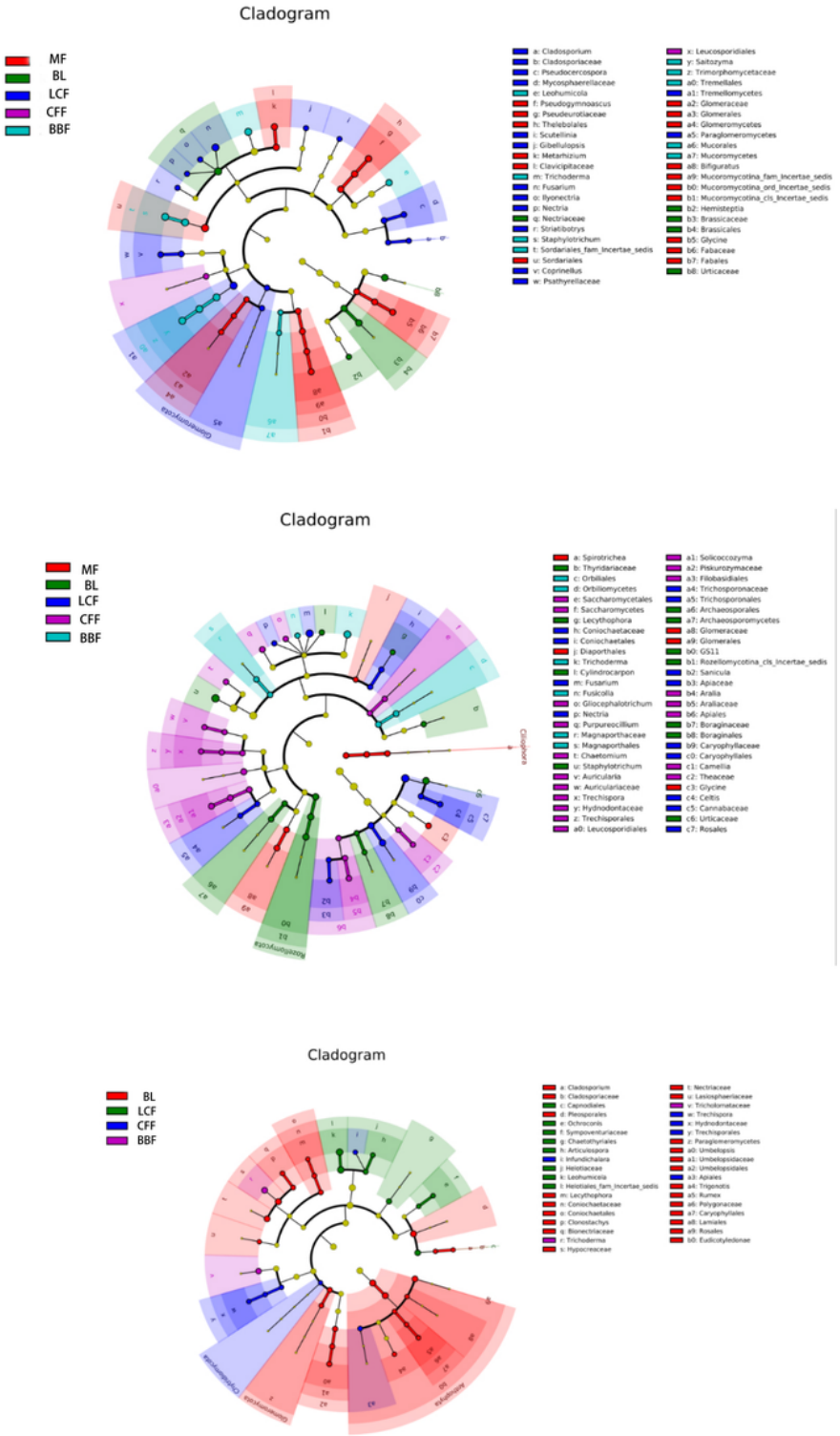

Figure 5

Cladogram shows significant differences between fungal enrichment groups. Taxa with significant differences in abundance between different vegetation types are represented by colored dots, and Cladogram circles represent phylogenetic taxa from domain to genus. Only the LDA score >3 for fungi were shown. BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

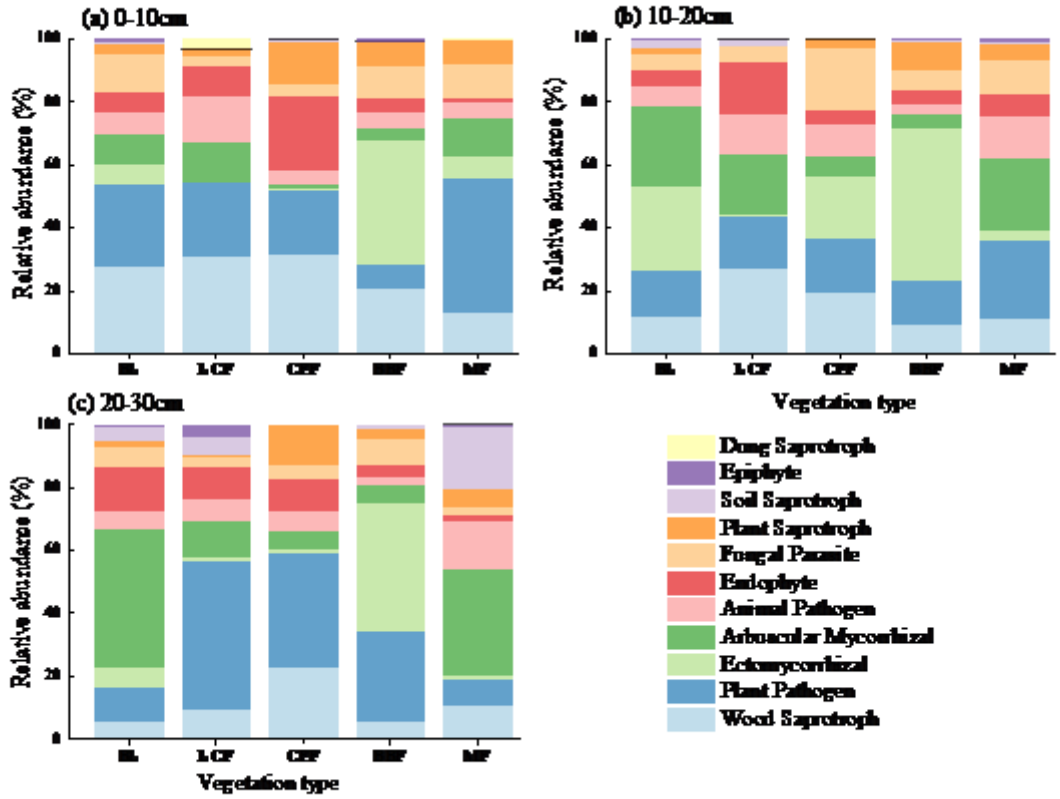

Figure 6

Relative abundance of soil fungal functional guild assignment with different vegetation types using FUNGuild. BL-Bare land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest.

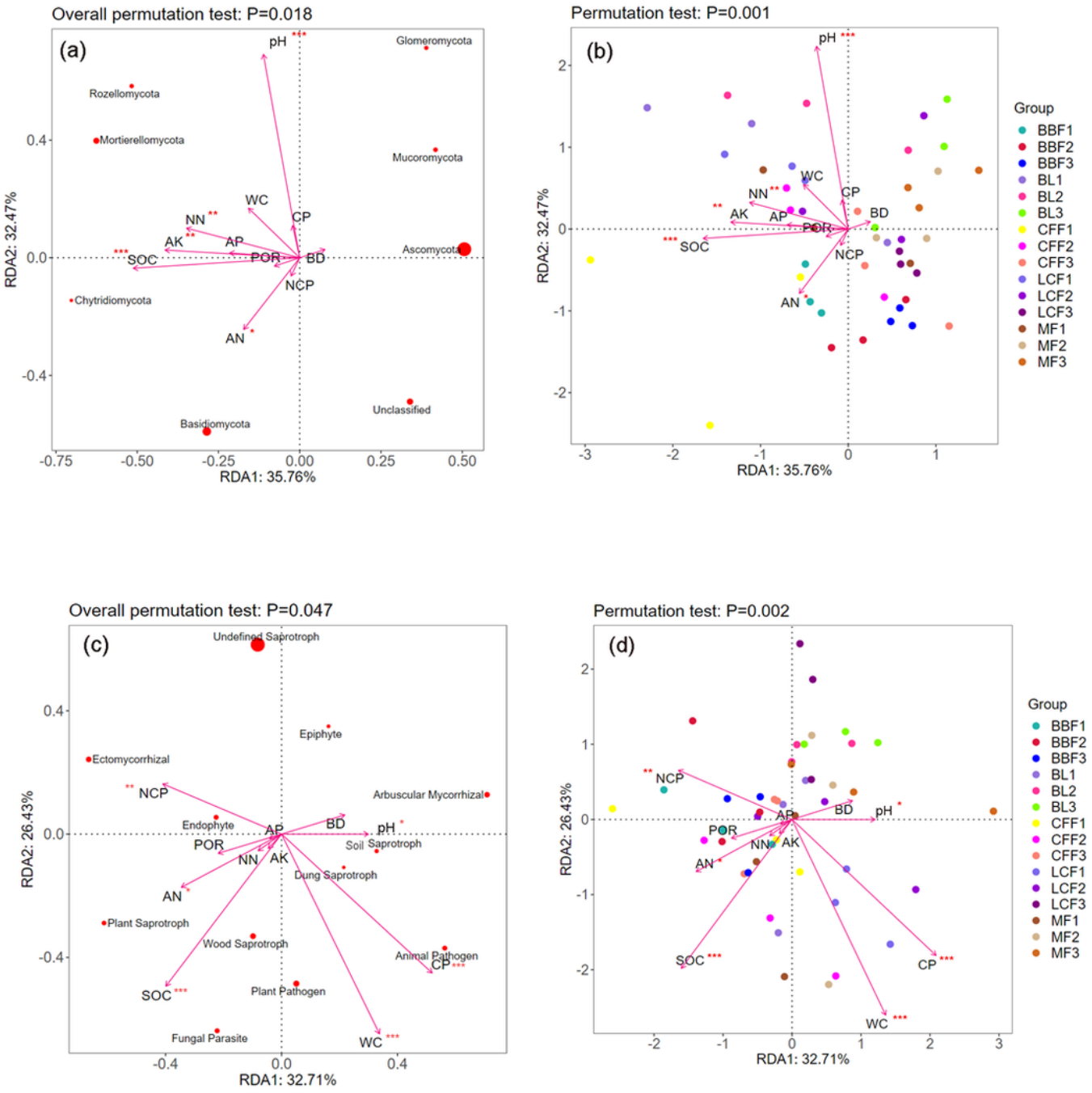

Figure 7

Redundancy analysis (RDA) showed the correlation between the community and soil physicochemical parameters in different vegetation types.

Fungal phylum-level taxonomy (a, b), function category for fungal function (c, d). The size of the red dots in (a) and (b) represents the level of abundance, and P represents the significance of the model. BL-Bare

land; LCF-Liriodendron Chinese forest; CFF-Chinese fir forest; BBF-Bamboo forest; MF-Mixed forest. In the legend of figure6 (c) (d): 1, 2 and 3 respectively represent the soil layers of 0-10cm, 10-20cm and 20-30cm. AK-Soil available potassium; AP-Soil available phosphorus; SOC-Soil organic carbon; AN-Soil ammonium nitrogen; NN-Soil nitrate nitrogen; pH-Soil pH; WC-Soil water content; BD-Soil bulk density; POR-Soil total porosity; CP-Soil capillary porosity; NCP-Soil non-capillary porosity.