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Litter, Root, and Mycorrhiza Input Affected Soil Microbial Community Structure in *Schima superba* Pure Forest in Subtropical China

Liqin Zhu , Rongzhen Huang *, Jinping Wang , Guomin Huang, Hongzhi Guan, Lijing Lin, Mengjia Yang, Yanyan Li and Xianhua Zou

Jiangxi Key Laboratory for Restoration of Degraded Ecosystems & Watershed Ecohydrology, School of Hydraulic & Ecological Engineering, Nanchang Institute of Technology, Nanchang 330099, China
* Correspondence: huangrz@nit.edu.cn

Abstract: During forest vegetation rehabilitation, changes in aboveground litter and underground root inputs affect soil microbial communities. Clarifying the effects of forest ecosystem carbon inputs on soil microbial community structure can provide a theoretical basis for the microbial driving mechanism of soil fertility evolution and ecosystem rehabilitation of vegetation rehabilitation in degraded red soil. Our research focuses on a *Schima superba* pure forest recovered from eroded and degraded red soil in a subtropical region. Five treatments were set as follows: control treatment (CT), mycorrhiza (M), root + mycorrhiza (RM), litter + root + mycorrhiza (LRM), and double litter + root + mycorrhiza (DLRM). We used Illumina HiSeq technology to study the effects of different organic carbon inputs on soil microbial community structure. The results showed that all organic carbon input treatments reduced the total population of soil bacteria by 55–79%; M, RM, and DLRM treatments increased the quantity of operational taxonomic units (OTUs) by 25–37%, ACE index by 25–34%, and Chao1 index by 28–39%. Acidobacteria, Proteobacteria, and Actinobacteria were the dominant bacteriophyta in the *Schima superba* pure forest soil. The relative abundance of Alphaproteobacteria decreased by 55% under LRM treatment, and Thermoleophilia increased by 81% under M treatment. The dominant fungal phyla were Basidiomycota and Ascomycota. RM, LRM, and DLRM treatments reduced the relative abundance of Sordariomycetes by 46–64% and increased the relative abundance of Mortierellomycetes by 251–615%. The order of effects of different organic carbon inputs on the bacterial community composition at the phylum level was LRM > RM > M > DLRM and that on the fungal community composition was DLRM > LRM and RM > M. Alphaproteobacteria, Thermoleophilia, Sordariomycetes, and Mortierellomycetes were the main microbial groups affected by changes in organic carbon inputs. Soil organic carbon and total nitrogen were the key factors affecting the change of Mortierellomycetes. The bacterial community mainly affected the activity of soil acid invertase, while the fungal community affected the activities of various enzymes, with positive or negative effects. We concluded that the organic carbon inputs changed the species and quantity of soil microorganisms in the *Schima superba* forest, and the influence of organic carbon input on the fungal community structure was greater than that of bacteria.

Keywords: bacterial community; fungal community; litter; mycorrhiza; roots; *Schima superba*



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1. Introduction

Soil microorganisms are one of the essential components of soil [1]. Microorganisms regulate the dynamic balance of various biochemical and physiological processes in soil, participate in the process of material transformation and energy flow, and play a crucial role in maintaining soil ecological function and stability [2,3]. Microbial community structure is the main factor driving ecosystem processes, and soil microorganisms can adapt to changes in the soil environment through changes in their community composition [4,5]. Therefore,

microorganisms are crucial to examine better and are indicators of ecosystem productivity and soil quality [6,7].

Self-fertilization—litter, fine root, and mycorrhiza—supplements the organic carbon in forestland soils, which differs from the artificial addition of organic matter that agricultural soils experience. Litter input is the primary way for plants to return soil nutrients and is also considered an essential substrate for soil microbial metabolism in forest ecosystems [8]. Soil microbial communities mediate the decomposition process of litter, which improves the availability of soil carbon and nitrogen nutrients and causes changes in the microbial community structure [9]. Compared with boreal temperate forests, soil microorganisms in tropical and subtropical forests are more sensitive to changes in litter input, which is related to litter residence time [10]. Litter quantity is one of the main factors controlling soil microbial community structure [11], but there is still controversy about the effects of litter addition and removal. Lu et al. [12] showed that the contents of soil bacteria and fungi increased with litter quantity. Li et al. [13] showed that adding litter significantly increased fungi content and reduced Gram-positive bacteria content in the incubation experiment, and removing litter reduced fungal biomass [14]. However, Sayer [15] showed that the addition of litter did not cause a corresponding increase in the abundance of fungi. These results may be affected by factors such as the chemical quality of litter, the length of test period, zonal differences, and having a certain complexity, so more field test data are needed to support or verify these results.

The input of underground roots facilitates the distribution of photosynthates from aboveground to underground. Root input also releases root exudates such as polysaccharides, organic acids, and amino acids into the soil, thus affecting the microbial activity and biomass [16]. Bluhm et al. [8] studied the response of soil microorganisms by cutting off the input of root-derived resources and found that microorganisms not only depended on the decomposition resources of litter but also largely depended on the root-derived resources, indicating that changes in underground root input are also one of the important factors affecting soil microbial community structure. Mycorrhiza is a symbiont of some fungi in soil and plant roots. Mycorrhizal fungi—such as arbuscular mycorrhizal fungi—can interact with soil microbial communities, producing a variety of exudates (e.g., glomalin, soil-related proteins and polysaccharides), affecting the decomposition of organic matter, and changing the composition of bacterial and fungal communities [17,18]. In relatively poor soil with low carbon input of litter, the effect of mycorrhizal fungi on plants is more prominent, and plants can regulate the mycorrhizal fungi community by secreting effective carbon sources from roots [19]. However, the impact of mycorrhiza input on microbial community structure is often rarely considered.

Studies on detritus input and removal treatment (DIRT) mainly focus on the carbon cycle-related indicators such as soil respiration and soil organic carbon, and most of them only focus on the single impact of litter or root input on organic carbon. However, the comprehensive effects of three different input carbon sources of litter, root, and mycorrhiza are still unclear. More specifically, the relationships between the three carbon inputs and soil microbial community structure after vegetation rehabilitation in degraded red soil is rarely examined. In the past, the importance of microorganisms was underestimated because many microbial species were undiscovered or unculturable [20]. In recent years, with the diversification of analysis methods, the research on soil microorganisms has become more accurate. For example, high-throughput sequencing technology can truly reveal the species composition and diversity of microbial communities, but it is relatively less applied in DIRT-related research. In addition, although soil enzyme activities can represent microbial activities to some extent, little is known about which microbial groups affect which soil enzyme activities.

Schima superba is one of the most widely distributed and dominant tree species in subtropical evergreen broad-leaved forests and has universal applicability and a typical role in ecological rehabilitation in the red soil region of China. Therefore, our research object is the *Schima superba* forest rehabilitated from the eroded and degraded red soil

in the subtropical region of China. Illumina HiSeq sequencing technology allows us to study the changes in soil microbial community structure and alpha diversity under different organic carbon input treatments (Control treatment (CT), mycorrhiza (M), root + mycorrhiza (RM), litter + root + mycorrhiza (LRM), and double litter + root + mycorrhiza (DLRM)). We investigated the relationships between microbial community, soil chemical properties, and enzyme activity. The aims of this study were to: (1) reveal the response of soil bacterial and fungal community structure to the changes in organic carbon input; (2) determine the critical soil factors affecting the soil microbial community structure of the artificial rehabilitated forest; and (3) identify the significant microbial communities closely related to soil specific enzyme activities. At the same time, we put forward two hypotheses: (1) organic carbon input (litter, root, and/or mycorrhiza) will increase the population of soil microorganisms compared with the treatment without organic carbon input, and (2) in the low pH environment of red soil, organic carbon input may make acid-resistant fungi more sensitive, so the influence of organic carbon input on the fungal community structure is greater than that of bacteria. This study has important significance for understanding and recognizing soil quality improvement and the maintenance of ecological function in subtropical forests.

2. Materials and Methods

2.1. Site Description

Our research was conducted in the Luoxi township (26°44' N, 115°04' E), Taihe County, Jiangxi Province, China. This region has an average altitude of 80 m and a subtropical humid monsoon climate—an 18.6 °C average annual temperature and 1726 mm average annual precipitation [21]. The original evergreen broad-leaved forest was transformed into grassland in the 1960s due to long-term degradation—woodcutting and stump digging—and grows upon red soil developed from quaternary red clay [21]. In 1991, the Jiangxi Agricultural University and Taihe Forestry Bureau selected coniferous and broad-leaved tree species such as *Pinus elliottii*, *Pinus massoniana*, *Liquidambar formosana*, and *Schima superba* for forest rehabilitation. The vegetation recovery area in this region reached 133 ha, forming a typical forest landscape in the hilly region of southern China.

2.2. Experimental Design and Sample Collection

In December 2018, we randomly selected three independent *Schima superba* pure forests planted 27 years ago, and we set a standard plot of 20 m × 20 m in each forest stand. We used a random block method for our experimental design. Five treatments were established in each standard plot (see Table 1, Appendix A Figure A1 for details). (1) CT: trenches of 15 cm wide and 50 cm deep were dug around the treatment plot, and plasterboards were used to isolate the plot from the surrounding soil to prevent roots and hyphae from growing into the plot. After the aboveground litter was removed from the soil surface, a rectangular nylon mesh frame of 1 m × 0.5 m × 0.6 m with a pore diameter of 1 mm (no nylon mesh at the bottom) was placed to avoid external litter entry. (2) M: the ditches around the treatment plot were 50 cm deep, and the roots were isolated by nylon mesh with a pore diameter of 37 µm, allowing hyphae to enter the plot. After the aboveground litter was removed from the soil surface, a rectangular nylon mesh frame of 1 m × 0.5 m × 0.6 m with a pore diameter of 1 mm (no nylon mesh) at the bottom was placed to avoid external litter entry. (3) RM: after the aboveground litter was removed from the soil surface, a rectangular nylon mesh frame of 1 m × 0.5 m × 0.6 m with a pore diameter of 1 mm (no nylon mesh at the bottom) was placed to block the aboveground litter, and the aboveground litter was collected monthly. (4) LRM: undisturbed soil, not treated. (5) DLRM: a rectangular nylon mesh frame of 1 m × 0.5 m × 0.6 m with a pore diameter of 1 mm and no nylon mesh at the top and bottom was placed, and the aboveground litter collected from the nylon mesh frame in RM treatment was placed evenly in this treatment every month. Each treatment was replicated five times, with each treatment area being 0.5 × 1 m². According to our examination, *Schima superba* forests have a stem density

of 2175 stems ha⁻¹, canopy coverage of 94%, mean tree height of 8.31 m, and mean tree diameter at breast height of 11.03 cm.

Table 1. List of abbreviations.

Treatment	Abbreviation	Description
Control treatment	CT	Removing aboveground litter + removing root + removing mycorrhiza
Mycorrhiza	M	Removing aboveground litter + removing root + retaining mycorrhiza
Root + mycorrhiza	RM	Removing aboveground litter + retaining root + retaining mycorrhiza
Litter + root + mycorrhiza	LRM	Retaining aboveground litter + retaining root + retaining mycorrhiza
Double litter+ root + mycorrhiza	DLRM	Doubling aboveground litter + retaining root + retaining mycorrhiza

In August 2020, we used a small soil shovel to collect 0–10 cm topsoil from each treatment in each standard plot. Five samples from the same treatment in the same standard plot were combined to form one composite sample. We took 15 soil samples from 3 standard plots to the laboratory in an incubator on ice. After removing plant residues, gravel, and other sundries, we divided each soil sample into two parts by the quartering method. We put one part through a 2 mm sieve, freeze-dried it, and stored it in a freezer at -20°C to determine the microbial community structure. The other was dried naturally, ground, and screened to determine soil chemical properties and enzyme activities.

2.3. Determination of Soil Chemical Properties and Enzyme Activities

We determined soil pH in the mixed solution with a soil/water ratio of 1:2.5 (*w/v*). We used the dichromate oxidation and Kjeldahl methods to measure soil organic carbon (SOC) and total nitrogen (TN), respectively [22]. The ammonium fluoride–hydrochloric acid extraction method was used to determine available phosphorus (AP), and we used the ammonium acetate extraction method to determine available potassium (AK) [22]. We determined soil sucrase (SC), soil urease (UE), soil acid phosphatase (ACP), soil acid invertase (AI), and soil polyphenol oxidase (PPO) activities using a soil sucrase kit (BC0240), soil urease kit (BC0120), soil acid phosphatase kit (BC0140), soil acid invertase kit (BC3075), and soil polyphenol oxidase kit (BC0110) from Solarbio Science & Technology Co. (Beijing, China), in U/g [23,24].

2.4. Soil DNA Extraction, PCR Amplification, and Sequence Data Analysis

We extracted soil DNA using a metagenomic DNA Extraction Kit (GENErery) and detected DNA integrity by 1% agarose gel electrophoresis. We used a real-time fluorescence quantitative method for PCR amplification of the V3+V4 region of bacteria 16S rRNA and the ITS1 region of fungi. The bacterial primers were 338f (ACTCCTACGGGAGGCAGCAG) and 806r (GGACTACHVGGGTWCTAAT) [25]. The fungal primers were ITS1F (CTTGGT-CATTAGAGGAAGTAA) and ITS2 (GCTGCGTTCATCGATGC) [25]. Illumina HiSeq 2500 sequencing platform and paired-end (PE) sequencing method in Beijing Baimaike Biotechnology Co., Ltd. (Beijing, China) carried out the DNA extraction, PCR amplification, and library construction.

Trimmomatic V0.33 software filtered the raw reads obtained by sequencing. Then, Cutadapt 1.9.1 software identified and removed primer sequences, and we obtained high-quality reads without primer sequences. We acquired clean reads by using Flash V1.2.7 software overlap to splice high-quality reads of samples. We then identified and removed the chimeric sequences using Uchime V4.2 software to obtain effective reads. Usearch software clustered reads at a similarity level of 97%, which obtained operational taxonomic units (OTUs). We used alpha index analysis software QIIME2 to calculate species richness index (ACE and Chao1) and species diversity index (Simpson and Shannon), and we calculated the relative abundance of bacteria and fungi at different classification levels.

2.5. Statistical Analysis

A one-way ANOVA analyzed the effects of different treatments on soil properties, microbial population, and alpha diversity index. We used Duncan's method to detect the differences among treatments, and we set the significance level to $p = 0.05$. We \log_{10} transformed the OTUs of soil bacteria and fungi for normalization. We drew Venn diagrams of soil bacteria and fungi OTUs under different treatments using R 4.0.5 software and Origin 2018 software (OriginLab, Northampton, MA, USA) to draw relative abundance diagrams of dominant bacteria and fungi species at the phylum level. We used Canoco 5 software (Microcomputer Power, Ithaca, NY, USA) to draw the redundancy analysis (RDA) diagram of soil bacterial and fungal communities of bacteria and fungi class levels with a greater than 1% relative abundance. We used Spearman correlation analysis to examine the relationships among soil bacterial and fungal communities, alpha diversity, soil chemical properties, and enzyme activities—all analyses were conducted using SPSS 19.0 (IBM, Armonk, NY, USA).

3. Results

3.1. Effects of Different Treatments on Soil Chemical Properties and Enzyme Activities

Compared with the CT treatment, the DLRM treatment increased the SOC and TN contents by 52% and 30% ($p < 0.05$), respectively. At the same time, there were no significant differences in soil pH value, AP, and AK contents among the different treatments ($p > 0.05$, Table 2). RM, LRM, and DLRM reduced the activities of soil PPO by 34%, 49%, and 62% ($p < 0.05$), respectively, while there were no significant differences in soil SC, UE, and ACP activities among different treatments ($p > 0.05$).

Table 2. Soil chemical properties and enzymatic activity of different treatments.

Index	CT	M	RM	LRM	DLRM
Chemical properties					
pH	4.1 ± 0.1 a	4.2 ± 0.2 a	4.1 ± 0.02 a	4.0 ± 0.1 a	4.2 ± 0.04 a
SOC/(g kg ⁻¹)	29 ± 3 b	30 ± 3 b	30 ± 3 b	33 ± 2 b	45 ± 6 a
TN/(g kg ⁻¹)	2.1 ± 0.2 b	2.2 ± 0.2 ab	2.2 ± 0.2 ab	2.3 ± 0.1 ab	2.8 ± 0.3 a
AP/(mg kg ⁻¹)	0.03 ± 0.003 a	0.03 ± 0.002 a	0.04 ± 0.008 a	0.03 ± 0.003 a	0.04 ± 0.005 a
AK/(mg kg ⁻¹)	96 ± 6 a	116 ± 7 a	77 ± 19 a	96 ± 13 a	105 ± 10 a
Enzymatic activity					
SC/(Ug ⁻¹)	7.1 ± 1.0 a	11 ± 3 a	16 ± 5 a	10 ± 1 a	16 ± 2 a
UE/(Ug ⁻¹)	658 ± 98 a	767 ± 77 a	712 ± 105 a	687 ± 41 a	787 ± 55 a
ACP/(Ug ⁻¹)	48,620 ± 1460 a	45,954 ± 340 a	45,324 ± 1360 a	48,984 ± 3409 a	44,593 ± 3002 a
AI/(Ug ⁻¹)	36 ± 9 ab	38 ± 17 ab	34 ± 2 ab	25 ± 5 a	24 ± 7 b
PPO/(Ug ⁻¹)	49 ± 5 a	49 ± 6 a	32 ± 5 b	19 ± 2 b	105 ± 10 b

The data in the table are mean ± standard error (n = 3), and different lowercase letters indicate significant difference among treatments ($p < 0.05$). pH, soil potential of hydrogen; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorus; AK, available potassium; SC, sucrase; UE, urease; ACP, acid phosphatase; AI, acid invertase; PPO, polyphenol oxidase.

3.2. Effects of Different Treatments on Soil Microbial OTUs and Diversity

The coverage of both bacterial and fungal libraries was above 99.5%, indicating that the sequencing data could represent the actual situation of soil microbial communities under different treatments. However, a small number of microbial species were still undiscovered. We detected 412,446 bacterial gene sequences and 424,230 fungal gene sequences in 15 soil samples from 5 treatments, including 1109 bacterial OTUs and 1004 fungal OTUs. Compared with CT treatment, M, RM, LRM, and DLRM treatments reduced the total population of soil bacteria by 55%, 79%, 67%, and 56% ($p < 0.05$), respectively. At the same time, there was no significant difference in the population of soil fungi among treatments ($p > 0.05$, Table 3). The effect of different treatments on fungal OTUs was greater than that of bacteria OTUs, and the M, RM, and DLRM treatments increased fungal OTUs by 37%, 32%, and 25% ($p < 0.05$), respectively. There were 781 bacteria OTUs and

415 fungi OTUs in common among the 5 treatments (Figure 1). We found 12 unique bacteria OTUs and 18 unique fungi OTUs under the CT treatment, 42 unique bacteria OTUs and 9 unique fungi OTUs under the M treatment, 13 unique bacteria OTUs and 51 unique fungi OTUs under the RM treatment, 5 unique bacteria OTUs and 21 unique fungi OTUs under the LRM treatment, and 16 unique bacteria OTUs and 25 unique fungi OTUs under the DLRM treatment.

Table 3. Soil microbial population, OTUs, and alpha diversity in different treatments.

Type	Treatment	Population/ (10 ⁶ · g ⁻¹ Dry Soil)	OTUs	Richness		Diversity	
				ACE	Chao1	Simpson	Shannon
Bacteria	CT	1982 ± 568 a	852 ± 22 a	920 ± 20 a	946 ± 25 a	0.99 ± 0.001 a	7.9 ± 0.05 a
	M	892 ± 109 b	790 ± 40 a	858 ± 44 a	864 ± 50 a	0.99 ± 0.001 a	7.8 ± 0.11 ab
	RM	413 ± 239 b	799 ± 9 a	880 ± 3 a	898 ± 8 a	0.99 ± 0.001 a	7.6 ± 0.01 ab
	LRM	652 ± 338 b	789 ± 36 a	880 ± 30 a	889 ± 27 a	0.98 ± 0.008 a	7.3 ± 0.38 b
	DLRM	875 ± 171 b	782 ± 29 a	852 ± 34 a	858 ± 37 a	0.99 ± 0.001 a	7.7 ± 0.05 ab
Fungi	CT	39 ± 7 a	501 ± 17 b	590 ± 13 b	580 ± 14 b	0.91 ± 0.023 a	5.2 ± 0.31 b
	M	59 ± 7 a	686 ± 32 a	791 ± 32 a	804 ± 35 a	0.97 ± 0.026 a	6.7 ± 0.39 a
	RM	54 ± 36 a	664 ± 49 a	760 ± 62 a	768 ± 66 a	0.92 ± 0.019 a	6.0 ± 0.26 ab
	LRM	77 ± 57 a	470 ± 24 b	566 ± 14 b	579 ± 24 b	0.91 ± 0.054 a	5.2 ± 0.81 b
	DLRM	111 ± 20 a	624 ± 38 a	738 ± 37 a	743 ± 38 a	0.94 ± 0.010 a	5.9 ± 0.17 ab

The data in the table are mean ± standard error (n = 3), and different lowercase letters indicate significant difference among treatments (*p* < 0.05).

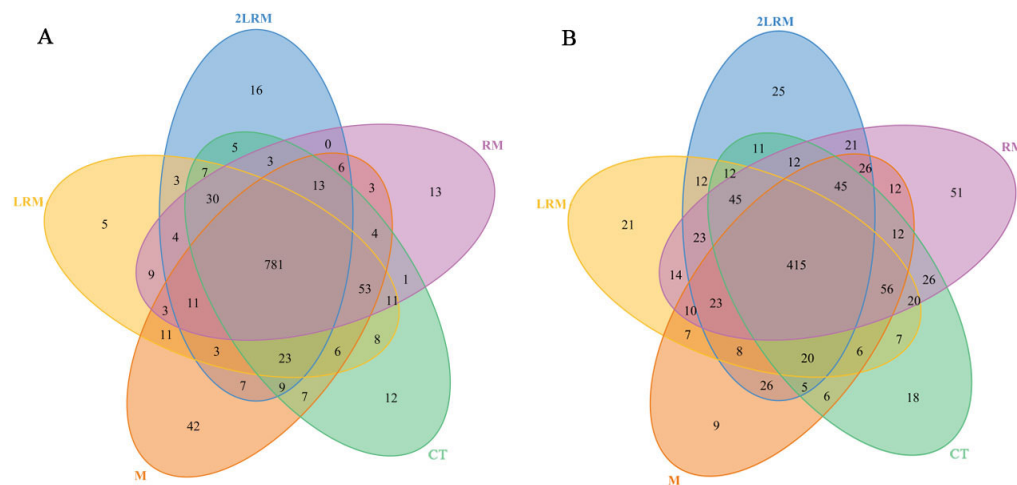


Figure 1. Venn diagram of soil bacteria (A) and fungi (B) in different treatments.

Compared with the CT treatment, the LRM treatment reduced the Shannon diversity index of soil bacteria by 8% (*p* < 0.05), while the richness index (ACE and Chao1) and Simpson index showed no significant difference among all treatments (*p* > 0.05, Table 3). The M, RM, and DLRM treatments significantly increased the soil fungal richness index—the ACE index increased by 34%, 29%, and 25%, and the Chao1 index increased by 39%, 32%, and 28% (*p* < 0.05), respectively. The M treatment increased the Shannon diversity index of soil fungi by 30% (*p* < 0.05), while there were no significant differences in the Simpson index among all treatments (*p* > 0.05). Therefore, the effect of different treatments on the fungal richness index was greater than that of bacteria.

3.3. Effects of Different Treatments on Soil Microbial Community Composition and Structure

We detected 22 bacterial phyla in the soil samples of the 5 treatments. The top ten bacteria phyla in relative abundance were Acidobacteria (35%), Proteobacteria (30%), Actinobacteria (17%), WPS-2 (4.6%), Chloroflexi (3.4%), Verrucomicrobia (3.2%), Planctomycetes

(Planctomycetes, 2.3%), Patescibacteria (1.8%), Bacteroidetes (0.72%), and Gemmatimonadetes (0.54%), as shown in Figure 2A. Among them, the dominant bacteria phyla were Acidobacteria, Proteobacteria, and Actinobacteria, which presented a relative abundance of 82% in total. Compared with the CT treatment, the LRM treatment reduced the relative abundance of Proteobacteria by 43% ($p < 0.05$). The dominant bacteria classes were Acidobacteriia (35%), Alphaproteobacteria (22%), Actinobacteria (6.8%), Gammaproteobacteria (6.7%), and Thermoleophilia (5.9%), accounting for 76% of the total relative abundance (Table 4). The LRM treatment reduced the relative abundance of Alphaproteobacteria by 55% ($p < 0.05$), while the M treatment increased the relative abundance of Thermoleophilia by 81% ($p < 0.05$).

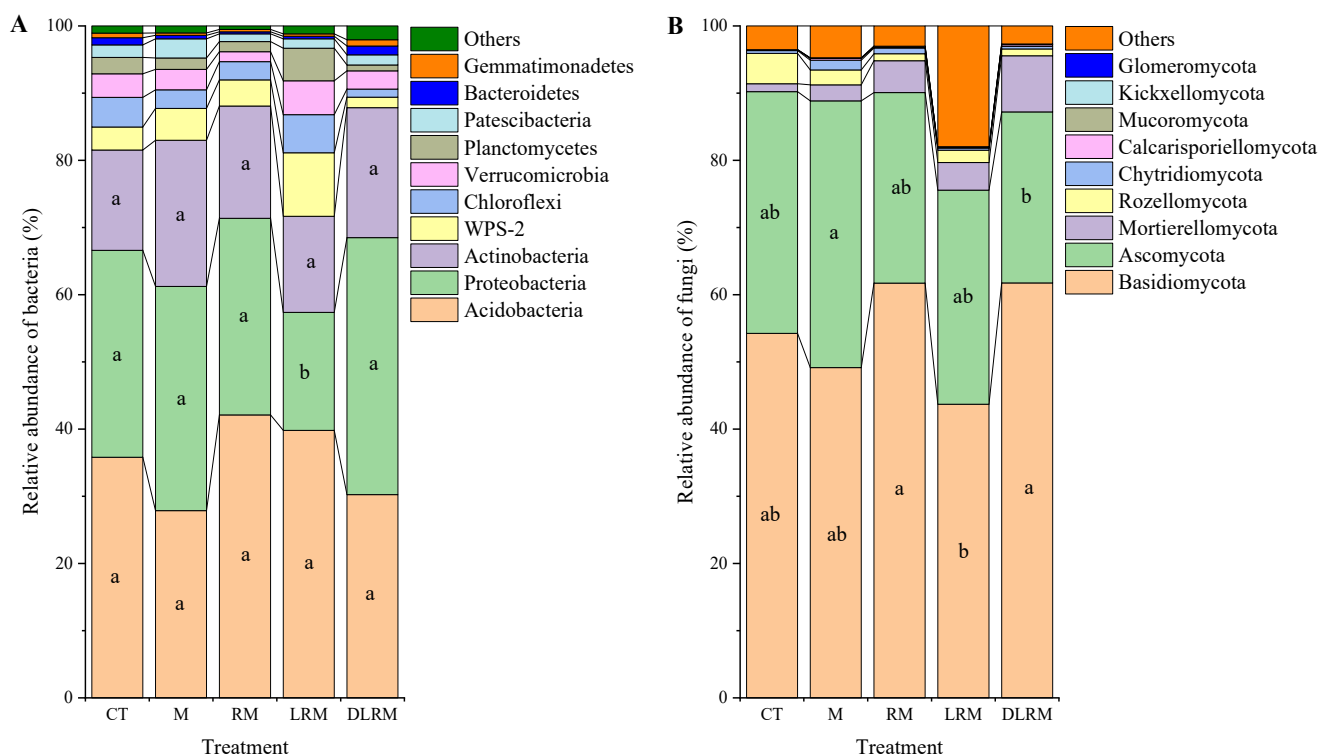


Figure 2. Relative abundance of major soil bacteria (A) and fungi (B) at phylum level in different treatments. Different lowercase letters indicate significant difference among treatments ($p < 0.05$).

For fungi, we detected the nine phyla shown in Figure 2B—Basidiomycota (54%), Ascomycota (32%), Mortierellomycota (4.2%), Rozellomycota (2.1%), Chytridiomycota (0.68%), Calcarisporiellomycota (0.15%), Mucoromycota (0.07%), Kickxellomycota (0.04%), and Glomeromycota (0.01%). Basidiomycota and Ascomycota were the dominant fungi phyla, accounting for 86% of the total relative abundance. Compared with the CT treatment, the relative abundance of Basidiomycota and Ascomycota in other treatments did not change significantly. The dominant fungi classes were Agaricomycetes (47%), Sordariomycetes (10%), and Leotiomyces (9.7%), which presented a relative abundance of 67% in total (Table 4). RM, LRM, and 2LRM treatments decreased the relative abundance of Sordariomycetes (46–64%, $p < 0.05$) but increased the relative abundance of Mortierellomycetes (251–615%, $p < 0.05$).

Table 4. Relative abundance of major soil bacteria and fungi at class level in different treatments (%).

Type	Class	CT	M	RM	LRM	DLRM
Bacteria	Acidobacteriia	36 a	28 a	42 a	39 a	30 a
	Alphaproteobacteria	24 a	25 a	22 a	11 b	28 a
	Actinobacteria	6.2 a	6.7 a	7.3 a	7.4 a	6.3 a
	Gammaproteobacteria	5.9 a	7.4 a	5.7 a	6.1 a	8.3 a
	Thermoleophilia	5.4 bc	9.8 a	4.6 bc	2.3 c	7.3 ab
	Acidimicrobiia	3.4 a	5.3 a	4.8 a	4.6 a	5.7 a
	uncultured_bacterium_p_WPS-2	3.4 a	4.7 a	3.9 a	9.5 a	1.6 a
	Verrucomicrobiae	3.5 a	3.1 a	1.5 a	5.0 a	2.7 a
	Planctomycetacia	2.1 a	1.3 a	1.4 a	4.5 a	0.7 a
	Ktedonobacteria	3.0 a	1.3 ab	1.2 ab	2.5 ab	0.47 b
	Saccharimonadia	1.8 ab	2.8 a	1.1 b	1.3 b	1.3 b
	Deltaproteobacteria	1.1 b	1.1 b	1.1 b	0.83 b	1.8 a
	AD3	0.78 a	0.81 a	0.79 a	2.0 a	0.38 a
	Bacteroidia	1.0 a	0.42 b	0.22 b	0.37 b	1.0 a
	Gemmatimonadetes	0.70 ab	0.35 b	0.40 b	0.33 b	0.94 a
	JG30-KF-CM66	0.39 a	0.32 a	0.40 a	0.63 a	0.22 a
	Thermoplasmata	0.33 b	0.18 b	0.04 b	0.16 b	1.1 a
	Fimbriimonadia	0.17 b	0.32 a	0.14 b	0.11 b	0.42 a
	Phycisphaerae	0.27 a	0.32 a	0.10 a	0.32 a	0.13 a
	Subgroup_6	0.18 a	0.16 a	0.12 a	0.50 a	0.11 a
Fungi	Agaricomycetes	45 a	41 a	58 a	36 a	56 a
	Sordariomycetes	15 a	16 a	7.8 b	7.8 b	5.3 b
	Leotiomycetes	13 a	12 a	9.7 a	7.1 a	3.7 a
	Mortierellomycetes	1.2 d	2.4 cd	4.7 b	4.1 bc	8.4 a
	Eurotiomycetes	3.2 a	4.1 a	3.7 a	3.7 a	3.2 a
	Dothideomycetes	1.4 ab	1.3 ab	1.8 a	0.65 b	1.5 ab
	Rozellomycotina_cls_Incertae_sedis	3.6 a	0.55 a	0.24 a	1.2 a	0.46 a
	Chytridiomycetes	0.22 b	1.0 a	0.20 b	0.20 b	0.13 b
	Archaeorhizomycetes	0.16 a	0.52 a	0.27 a	0.15 a	0.44 a
	GS13	0.05 b	0.18 b	0.51 a	0.04 b	0.11 b
	Calcarisporiellomycetes	0.09 b	0.26 a	0.10 b	0.06 b	0.25 a
	Umbelopsidomycetes	0.05 a	0.05 a	0.06 a	0.11 a	0.07 a
	Tremellomycetes	0.04 a	0.05 a	0.02 bc	0.02 c	0.04 ab
	Pezizomycetes	0.004 c	0.07 a	0.03 bc	0.002 c	0.04 b
	Orbiliomycetes	0.03 a	0.03 a	0.02 a	0.01 a	0.03 a
	Rhizophydiomycetes	0.01 a	0.01 a	0.04 a	0.01 a	0.03 a
	Microbotryomycetes	0.01 b	0.01 b	0.02 ab	0.01 b	0.04 a
	Cystobasidiomycetes	0.005 a	0.01 a	0.02 a	0.01 a	0.01 a
	Saccharomycetes	0.01 a	0.01 a	0.004 a	0.01 a	0.01 a

The data in the table are mean values (n = 3), and different lowercase letters indicate significant difference among treatments ($p < 0.05$).

3.4. Effects of Soil Properties on Microbial Community Composition

RDA analysis based on microbial OTUs at the class level and soil chemical properties showed that soil chemical properties had a specific impact on microbial community structure. For bacterial communities, the first and second axes explained 50% and 12% of variation, respectively, and the two axes jointly explained 62% of variation (Figure 3A). Uncultured_bacterium_p_wps-2 and Planctomycetacia were positively correlated with soil AI, while Alphaproteobacteria, Thermoleophilia, and Deltaproteobacteria were negatively correlated with soil AI (Table 5). The first and second axes explained 31% and 19% of the variation for soil fungal communities, respectively. The two axes jointly explained 50% of the variation (Figure 3B). Sordariomycetes and Leotiomycetes were positively correlated with soil PPO. Mortierellomycetes were positively correlated with soil SOC, TN, and SC but negatively correlated with soil PPO. Dothideomycetes were negatively correlated with soil AI. Rozellomycotina_cls_Incertae_sedis was negatively correlated with soil UE (Table 5). In addition, among bacteria classes, Ktedonobacteria was positively correlated

with the species richness index, while Alphaproteobacteria, Actinobacteria, Acidimicrobiia, and Saccharimonadia were positively correlated with the species diversity index. Among fungi classes, Sordariomycetes, Eurotiomycetes, and Dothideomycetes were also positively correlated with the species diversity index (Table 5).

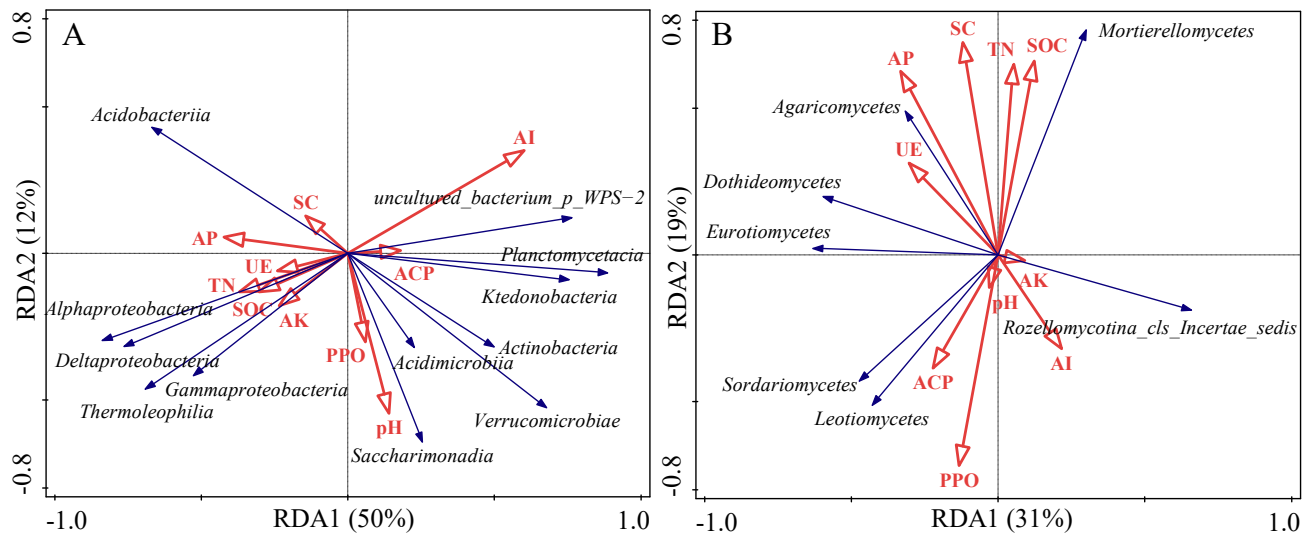


Figure 3. Redundancy analysis (RDA) of soil bacteria (A) and fungi (B) at class level and soil chemical properties and enzymatic activity. pH, soil potential of hydrogen potential of hydrogen; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorus; AK, available potassium; SC, sucrose; UE, urease; ACP, acid phosphatase; AI, acid invertase; PPO, polyphenol oxidase.

Table 5. Relationships between microbial community at class level and alpha diversity, soil chemical properties, and enzymatic activity.

Class	Alpha Diversity				Soil Chemical Properties and Enzymatic Activity									
	ACE	Chao1	Simpson	Shannon	pH	SOC	TN	AP	AK	SC	UE	ACP	AI	PPO
Bacteria														
Acidobacteriia	0.047	0.098	−0.372	−0.337	−0.439	−0.004	0.085	0.285	0.077	0.044	0.063	0.015	−0.209	0.054
Alphaproteobacteria	0.033	0.052	0.519 *	0.483	0.025	0.085	0.160	0.240	0.056	0.154	0.115	−0.011	− 0.572 *	0.279
Actinobacteria	0.078	0.045	0.633 *	0.536 *	0.419	−0.178	−0.188	−0.184	−0.402	0.140	−0.133	0.065	0.104	0.044
Gammaproteobacteria	−0.038	−0.095	0.279	0.246	0.048	0.213	0.349	0.263	0.300	−0.140	0.007	0.012	−0.504	0.053
Thermoleophilia	−0.300	−0.311	0.501	0.442	0.169	0.168	0.231	0.213	0.351	−0.070	0.291	−0.218	− 0.519 *	0.235
Acidimicrobiia	−0.261	−0.296	0.564 *	0.421	0.418	0.156	0.104	−0.008	−0.179	0.256	0.149	−0.226	−0.037	−0.206
uncultured_bacterium_p_WPS-2	0.071	0.057	0.027	0.027	0.070	−0.42	−0.414	−0.397	−0.215	−0.082	−0.175	0.100	0.556 *	0.184
Verrucomicrobiae	0.356	0.295	0.13	0.250	0.262	0.018	−0.069	−0.242	0.096	−0.261	−0.165	0.212	0.212	0.105
Planctomycetacia	0.313	0.292	0.019	0.085	0.130	−0.344	−0.396	−0.422	−0.261	−0.152	−0.301	0.304	0.525 *	0.154
Ktedonobacteria	0.589 *	0.591 *	0.143	0.300	0.004	−0.446	−0.465	−0.391	−0.235	−0.297	−0.310	0.284	0.455	0.452
Saccharimonadia	0.061	0.007	0.672 **	0.676 **	0.319	−0.219	−0.174	−0.263	0.124	−0.250	−0.014	0.073	0.039	0.510
Deltaproteobacteria	−0.074	−0.064	0.257	0.214	0.069	0.402	0.416	0.339	0.113	0.238	0.038	−0.138	− 0.703 **	−0.067
Fungi														
Agaricomycetes	0.262	0.238	0.147	0.173	0.151	0.139	0.118	0.299	−0.085	0.277	0.116	−0.324	−0.453	−0.300
Sordariomycetes	0.040	−0.007	0.613 *	0.561 *	−0.185	−0.465	−0.335	−0.202	0.209	−0.425	−0.187	0.227	−0.150	0.762 **
Leotiomycetes	0.144	0.115	0.193	0.298	−0.152	−0.423	−0.304	−0.071	−0.031	−0.138	0.036	0.287	0.217	0.578 *
Mortierellomycetes	0.363	0.371	0.389	0.383	−0.119	0.632 *	0.578 *	0.422	0.013	0.576 *	0.203	−0.338	−0.255	− 0.662 **
Eurotiomycetes	0.133	0.105	0.611 *	0.666 **	−0.138	−0.190	0.025	0.143	−0.026	−0.028	−0.008	0.360	−0.160	0.252
Dothideomycetes	0.441	0.397	0.563 *	0.589 *	0.004	−0.033	−0.033	0.052	−0.299	0.114	−0.267	−0.056	− 0.600 *	0.294
Rozellomycotina_cls_Incertae_sedis	−0.294	−0.273	−0.112	−0.254	−0.127	−0.172	−0.153	−0.323	−0.049	−0.288	− 0.549 *	−0.084	−0.088	0.331

Bold indicates a significant correlation; * $p < 0.05$; ** $p < 0.01$. pH, soil potential of hydrogen potential of hydrogen; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorus; AK, available potassium; SC, sucrase; UE, urease; ACP, acid phosphatase; AI, acid invertase; PPO, polyphenol oxidase.

4. Discussion

In our study, the comparison of RM, LRM, and DLRM treatments showed that the population of soil bacteria and fungi increased with litter input but did not reach a statistically significant level (Table 3). Nadelhoffer et al. [26] also observed no change in bacterial or fungal biomass in the soil of a deciduous site after the addition of aboveground litter. However, Lu et al. [12] found that litter addition increased soil bacterial and fungal contents, and litter could significantly change the soil microbial community through incubation experiments. Notably, unlike the study by Lu et al. [12], which added Chinese fir litter after crushing, the decomposition of *Schima superba* litter may be slower under natural conditions. Our study also found that compared with the CT treatment, each organic carbon input treatment greatly reduced the soil bacteria population but increased the soil fungi population, although the increase was not statistically significant, which was inconsistent with our first hypothesis. Bacteria have long been thought to benefit from labile carbon input. However, recent studies have shown that fungi also benefit from labile carbon inputs and may utilize them more quickly than bacteria [27,28]. Conversely, removing litter, roots, and mycorrhiza means a lack of labile organic carbon input and leads to carbon limitation. Carbon constraint increases physiological stress on microbial communities, with bacteria and fungi competing for similar resources [14]. Elser [29] believed that microbes change their substances and community structure to cope with environmental changes when there is an insufficient carbon source supply. Trenching causes bacteria to experience extraordinary stress [8], so bacteria strengthen the use of alternative resources by increasing their population. Another reason may be related to the soil water content since the addition of litter impedes the infiltration of rainwater. Roots also increase the absorption of water, resulting in a decline in soil moisture, which in turn affects microbial activity [16,30]. Of course, this needs to be verified because of the lack of soil moisture monitoring. Brant et al. [14] showed that rootless plots usually contain larger quantities of actinomycete biomarkers and lower amounts of fungal biomarkers. In our study, the isolation of roots also reduced the population of soil fungi. However, it did not reach a statistically significant level, which may be related to the duration of the treatments. We waited less than 2 years from the establishment of treatments to sampling. The treatments had existed for 5 years in the study by Brant et al. [14], and the change in soil microbial community was relatively noticeable.

Soil microbial community structure is vital in maintaining forest ecosystem structure and function. Many studies have documented that the aboveground and underground carbon input changes can affect the composition of soil microbial communities [31,32]. In our study, the proportion of OTUs shared by bacteria and fungi in different treatments was 70% and 41%, respectively (Figure 1). A considerable proportion of unique microbial OTUs (especially fungi) indicated that carbon input changed the species and quantity of soil microorganisms in *Schima superba* pure forest, and different input modes had different effects. Wan et al. [33] studied the soil microbial communities of two subtropical plantations (*Cunninghamia lanceolata* and *Mytilaria laosensis*), and the results showed that the change of carbon input from aboveground litter had a greater impact on soil microbial communities than that from underground roots. Brant et al. [14] and Wang et al. [32] found that root-derived carbon had a greater impact on soil microbial community composition in temperate and subtropical coniferous forests through DIRT experiments. Unfortunately, we did not consider the treatment with root input only in the design. Instead, we considered the combined effect of mycorrhizal input, both root and mycorrhizal input, and simultaneous input with litter. We found that the order of effects of different organic carbon inputs on the bacterial community structure at the phylum level was LRM > RM > M > DLRM, and that the order of effects for the fungal community structure was DLRM > LRM and RM > M (Figure 2; Appendix A Table A1). Among the main microbial communities at the phylum and class levels studied, different organic carbon inputs significantly affected two bacterial phyla, seven bacterial classes, five fungal phyla, and eight fungal classes (Figure 2; Table 4). Meanwhile, the inputs of mycorrhiza, root + mycorrhiza, and double

litter + root + mycorrhiza significantly increased the soil fungi's richness index (Chao1 and ACE) and OTUs. In contrast, the richness index and OTUs of soil bacteria were not statistically significant among treatments (Table 3). These results indicated that different organic carbon inputs had a greater impact on the fungal community than the bacterial community. Thus, this supports our second hypothesis. The reason may be that most bacteria are more suitable for growth in neutral or alkaline environments, and the acidic conditions of red soil restrict the growth and development of soil bacteria. At the same time, acid-resistant fungi that can grow normally in acidic soil can replace bacteria to decompose organic matter. As a result, fungi are more sensitive to organic carbon inputs. Liu et al. [34] also showed that soil pH was the main factor affecting the composition and diversity of the microbial community. For example, pH influences the form of soil compounds, thus affecting the absorption of nutrients by microorganisms. The different responses of bacteria and fungi to different inputs of organic carbon indicate that they occupy different ecological niches. Bacteria are mainly affected by soil nutrients and root exudates (such as organic acids, amino acids, and polysaccharides), while fungi obtain nutrients mainly through decomposition of aboveground and underground litter such as fallen branches, leaves, and root cortex tissues [35].

In addition, litter significantly affects the microbial community structure through the availability of nutrients produced by its different chemical components and the unique soil microenvironment the litter creates [36,37]. The relative abundance of microbial communities may be altered by changes in resource quality due to differences in aboveground and belowground litter quality, with potentially important effects on the metabolic functions of microbial communities. Meanwhile, the production of aboveground litter and the growth of underground roots have strong seasonality. However, this study only discussed the changes in microbial communities in a single sampling after adding and removing litter, roots, and mycorrhiza in *Schima superba* forests. Moreover, this study used plasterboards to isolate roots and mycorrhiza, potentially blocking the lateral migration process of soil water and nutrients. The limitations of this method might have an impact on the soil microbial community. Therefore, one μm nylon mesh should be considered in a follow-up study, which can prevent the growth of roots and hyphae and ensure the migration of water and air. At the same time, considering the effects of different organic carbon input treatments on soil temperature, moisture, soil respiration, and carbon storage, the dynamics of soil microorganisms in different vegetation rehabilitation types of forestlands can be carried out to explore further the evolution of soil fertility and ecological function in eroded and degraded forestland.

The dominant bacterial phyla in the soil of the *Schima superba* forest were Acidobacteria, Proteobacteria, and Actinobacteria, among which the relative abundance of Acidobacteria was the highest (Figure 2A), which was consistent with the results of Sang et al. [38] in subtropical forests. Acidobacteria are acidophilic and oligotrophic, can be distributed in various habitats, and are comparable in quantity to Proteobacteria. The bacteria in this phylum can degrade plant residue polymers, participate in the iron cycle, have photosynthetic capacity, and participate in the metabolism of single-carbon compounds [39–43]. Low pH environments can promote the abundance of Acidobacteria [35]. Sun et al. [44] found that the top three dominant bacterial groups in the relative abundance of boreal forest soil were also the bacterial phyla mentioned above. However, the relative abundance of Proteobacteria was higher than that of Acidobacteria, which was related to the high soil nutrient content. Proteobacteria are the most abundant phylum among bacteria, most of which are facultative or obligate anaerobic microorganisms, and many groups of this phylum can fix nitrogen in soil [25]. Previous studies have shown that the relative abundance of Proteobacteria increases with the increase of organic matter and is higher in nutrient-rich soils [45,46]. However, in our study, the LRM treatment reduced the relative abundance of soil Alphaproteobacteria (the main class of Proteobacteria), mainly because organic carbon input was more conducive to the growth and utilization of fungi. Different treatments increased the relative abundance of related fungal phyla (Figure 2; Table A1). In the bacterial

classes with high relative abundance, the M treatment significantly increased the relative abundance of Thermoleophilia (Table 4). Thermoleophilia belongs to Actinomycetes and copiotrophic microbiological groups, which are more inclined to use labile carbon [47,48]. Mycelium in mycorrhiza can produce a variety of exudates [17], providing more labile carbon sources, which are beneficial to the growth of microorganisms.

The dominant fungi phyla of *Schima superba* were Basidiomycota and Ascomycota (Figure 2B), which was similar to the results of Tedersoo et al. [49] on soil fungi in terrestrial ecosystems. Basidiomycota are the most common type of fungi, which are widely distributed, diverse and abundant, and are positively correlated with highly stable organic components such as cellulose and lignin [50]. *Schima superba* is an arbuscular mycorrhizal species whose mycorrhiza cannot decompose organic matter. *Schima superba* can only stimulate the decomposition of saprophytic fungi by providing photosynthate to saprophytic fungi [51]. Ascomycetes are mostly saprophytic fungi, which can decompose refractory organic matter [52]. The RM, LRM, and 2LRM treatments significantly reduced the relative abundance of Sordariomycetes and increased the relative abundance of Mortierellomycetes (Table 4), which benefited from the increase of carbon input and supported the growth of many microorganisms. The leaching and decomposition of fresh litter releases a large amount of labile carbon, providing many carbon sources for microorganisms [51]. Since Mortierellomycota has high utilization efficiency for simple carbohydrates and is positively correlated with the content of active carbon components in soil [53], the relative abundance of Mortierellomycetes is improved.

Soil microbial community composition is directly and indirectly affected by soil properties. RDA analysis results in this study showed that soil pH, SOC, TN, AP, and AK contents and enzyme activities explained 62% and 50% of the variation in soil bacterial and fungal communities, respectively (Figure 3). Our results indicate that in addition to the above soil properties, the variation in soil microbial community composition was also affected by other environmental factors, e.g., temperature, soil pores, texture, aggregates, protozoa [54–56]. Liu et al. [57] found that Actinobacteria and Deltaproteobacteria were significantly correlated with SOC. However, similar results were not observed in this study, which is consistent with the results of Zhong et al. [58] and Zeng et al. [59]. We also found that other soil chemical properties had no significant effect on soil bacterial classes (Table 5), indicating that bacteria in this area were less sensitive to these soil chemical properties. Different from bacterial classes, Mortierellomycetes were significantly positively correlated with SOC and TN, indicating that SOC and TN were the key soil factors affecting the change in Mortierellomycetes.

Soil enzymes, mainly produced by microorganisms, plant roots, and animals, participate in the synthesis or decomposition of soil organic matter and other nutrients. Enzymes directly or indirectly affect soil biochemical reactions with soil bacteria and fungi. In this study, RM, LRM, and DLRM treatments all reduced the activity of soil polyphenol oxidase, mainly because the inputs of litter, roots, and mycorrhiza increased available carbon sources. Microorganisms did not need to secrete more polyphenol oxidase to promote the release of nutrient elements from lignin, phenols, and other refractory components of organic matter. Here we also illuminated which microbial groups affect soil enzyme activity: uncultured_bacterium_p_WPS-2 and Planctomycetacia, Alphaproteobacteria, Thermoleophilia, and Deltaproteobacteria affected soil acid sucrose activity in positive or negative directions. Mortierellomycetes affected the activities of soil sucrose and polyphenol oxidase. Mortierellomycetes was positively correlated with soil sucrose activity, indicating that the existence of Mortierellomycetes, a fungus group, promoted the hydrolysis of sucrose into monosaccharides and increased soil carbon availability, thus contributing to the direct uptake and utilization of organisms. In contrast, the presence of Rozellomycotina_cls_Incertae_sedis inhibited soil urease activity and reduced soil nitrogen availability. In addition, the correlation between soil microorganisms and alpha diversity showed that there were more microbial species in some classes of bacteria and fungi (such as Actinobac-

teria, Ktedonobacteria, and Sordariomycetes) which caused a significant increase in species richness or diversity indices.

5. Conclusions

The main bacterial groups affected by changes of organic carbon inputs were Alphaproteobacteria and Thermoleophilia, while the main fungal groups affected were Sordariomycetes and Mortierellomycetes, and the fungal community was more sensitive to carbon input than the bacterial community. Organic carbon input significantly reduced the population of soil bacteria. The inputs of mycorrhiza, root + mycorrhiza, and double litter + root + mycorrhiza significantly increased soil fungi's OTUs and richness index. Nevertheless, the bacteria population was much larger than the fungi population under different treatments, indicating that organic carbon input did not change the dominance of bacteria in this region. The order of effects of different organic carbon inputs on the bacterial community composition at the phylum level was LRM > RM > M > DLRM, and that on the fungal community composition was DLRM > LRM and RM > M. Whether the effects of carbon inputs on soil microbial community composition change with the increase of treatment time needs to be further demonstrated by long-term experimental field data. Soil organic carbon and total nitrogen were the key soil factors affecting the change of Mortierellomycetes, indicating that organic carbon input could affect microbial communities by changing soil chemical properties. The bacterial community mainly affected the activity of soil acid invertase, while the fungal community affected the activities of various enzymes. Here, we identified the significant microbial groups closely related to soil specific enzyme activities. These findings will help to further understand the important role of microorganisms in soil quality improvement and ecosystem rehabilitation.

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Appendix A

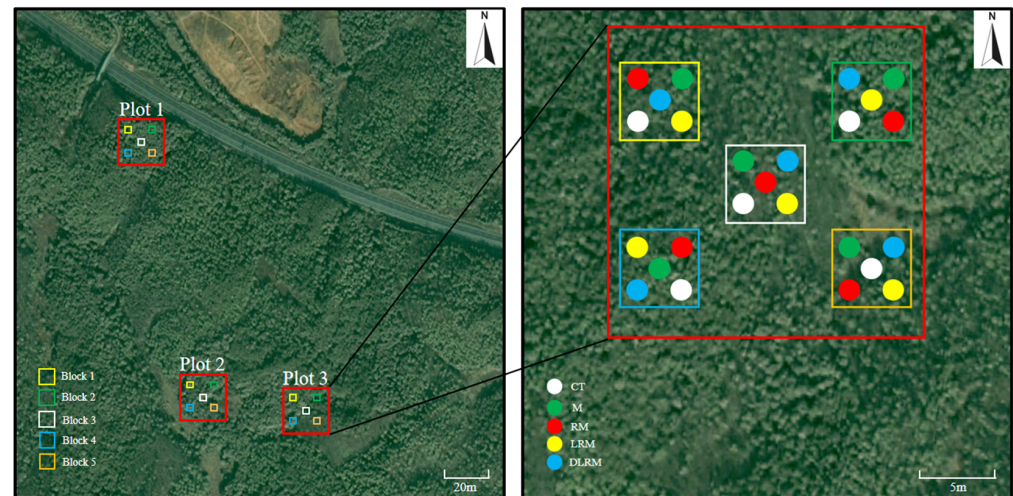


Figure A1. Locations of the plots and treatments of *Schima superba* forests. CT, control treatment; M, mycorrhiza; RM, root + mycorrhiza; LRM, litter + root + mycorrhiza; DLRM, double litter + root + mycorrhiza.

Table A1. Relative abundance of major soil bacteria and fungi at class level in different treatments (%).

Type	Phylum	CT	M	RM	LRM	DLRM
Bacteria	Acidobacteria	36 a	28 a	42 a	40 a	30 a
	Proteobacteria	31 a	33 a	29 a	17.5 b	38 a
	Actinobacteria	15 a	22 a	17 a	14 a	19 a
	WPS-2	3.4 a	4.7 a	3.9 a	9.5 a	1.6 a
	Chloroflexi	4.4 a	2.8 a	2.7 a	5.7 a	1.2 a
	Verrucomicrobia	3.5 a	3.1 a	1.5 a	5.0 a	2.7 a
	Planctomycetes	2.4 a	1.7 a	1.5 a	4.9 a	0.88 a
	Patescibacteria	1.9 ab	2.8 a	1.2 b	1.4 b	1.5 b
	Bacteroidetes	1.1 a	0.55 b	0.28 b	0.41 b	1.3 a
	Gemmatimonadetes	0.70 ab	0.35 b	0.40 b	0.33 b	0.94 a
Fungi	Basidiomycota	54 ab	49 ab	62 a	44 b	62 a
	Ascomycota	36 ab	40 a	28 ab	32 ab	25 b
	Mortierellomycota	1.2 d	2.4 cd	4.7 b	4.1 bc	8.4 a
	Rozellomycota	4.5 a	2.2 a	1.0 a	1.8 a	1.0 a
	Chytridiomycota	0.40 c	1.4 a	0.87 b	0.35 c	0.36 c
	Calcarisporiellomycota	0.09 b	0.26 a	0.10 b	0.06 b	0.25 a
	Mucoromycota	0.05 a	0.05 a	0.06 a	0.11 a	0.07 a
	Kickxellomycota	0.01 b	0.03 ab	0.08 a	0.01 b	0.05 ab
Glomeromycota	0.004 b	0.03 a	0.005 b	0.004 b	0.002 b	

The data in the table are mean values ($n = 3$), and different lowercase letters indicate significant difference among treatments ($p < 0.05$).

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