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Dynamics of Fine Root Decomposition in Different Vegetation Types: Investigating the Impact of Soil Fungal Communities and Enzyme Activities

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Abstract: Fine root decomposition plays a vital role in driving the carbon cycle in terrestrial ecosystems, as it constitutes a substantial part of annual net primary production and, as transient tissues, returns to the soil within relatively short timescales. Soil fungal communities and enzyme activities strongly influence this process. In this study, we used an in situ soil core decomposition method to compare the fine root decomposition rates of *Liriodendron chinense* (Hemsl.) Sargent, *Cunninghamia lanceolata* (Lamb.) Hook, and *Phyllostachys edulis* (*Carrière*) *J.Houz* forests over a 1-year period (March 2021–March 2022). We quantified the chemical attributes of fine roots and soil enzymatic activities across different forests, detected fungal communities via ITS rRNA gene sequencing, and forecasted fungal functional groups using the FUNGuild database. The results showed that fine root decomposition was fastest in the *Liriodendron chinense* (Hemsl.) Sargent forest (77.2%) and the slowest for *Cunninghamia lanceolata* (Lamb.) Hook (59.2%). Structural equation modeling (SEM) results indicated that the carbon content of fine roots and the functional groups of soil fungi are crucial to fine root decomposition. They not only directly influence fine root decomposition but also promote it through soil enzymatic activities, clearly suggesting that changes in soil enzymatic activities can be employed to explain the ecological effects of the root decomposition process. This study illuminates significant differences in the chemical characteristics of fine roots, soil enzymatic activities, and soil fungal communities among different forest types, all of which significantly affect fine root decomposition.

Keywords: fine root decomposition; soil enzyme activity; ITS; fungal functional groups

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1. Introduction

The decomposition process of plant tissue affects the ecosystem functions and soil nutrient cycles [1]. The turnover of rapidly decomposable plant fine roots (diameter < 2 mm) is faster than aboveground parts of plants [2], so the decay of fine roots is an important source of organic matter substances and nutrients in soil [3]. Globally, it is estimated that fine root turnover accounts for more than one-third of plant net primary productivity [4]. Recent studies using isotopes and root biomarkers have reported that carbon (C) derived from root decomposition remains in the soil for a longer period of time, playing a crucial role in enriching the soil C sink [5]. However, root decomposition is less studied than that of leaf litter due to the difficulty of studying the underground root. Therefore, studying the root decomposition mechanism is essential to understand the biogeochemical processes of soil nutrients [6,7].

The biochemical decomposition of fine roots is a comprehensive process, starting with the loss in less refractory components (e.g., oligosaccharides, organic acids), followed by

the degradation of the remaining highly refractory compounds (e.g., lignin or cellulose) [8]. The factors affecting fine root decomposition mainly include substrate chemical characteristics and soil environmental factors, such as soil temperature, pH, humidity [9,10], and particularly soil microorganisms [11,12]. Fungi are considered to be key players in litter decomposition. This is because they can produce a wide range of extracellular enzymes, which enable them to effectively attack the stubborn lignocellulose substrate that cannot be decomposed by other organisms [13]. These enzymes facilitate the depolymerization of complex plant polymers and the subsequent mineralization of nutrients. Importantly, the activities of these enzymes are closely related to fungal community composition [14].

The changes in soil enzyme activity are a direct expression of metabolic demand and available nutrients by the soil microbial community [15,16]. Therefore, studying the relationship between extracellular enzyme activities, microbial community composition, and microbial community composition in the process of litter decomposition can enhance our understanding of the mechanism of litter decomposition [17]. So far, most studies on litter decomposition have focused on leaf components, and little attention has been paid to understanding the patterns and drivers of large C sources found in roots, partly due to the difficulty of studying invisible underground litter decomposition. Little is known about the community composition of microbial decomposers of dead roots. For example, Kohout et al. [18] studied the composition of the decomposer community involved in dead root decomposition over a 2-year period and found that the community composition and activity were strongly influenced by the root species and soil type; Fisk et al. [19] reported that soil disturbance can have a significant impact on the composition of the fungal community in the rhizosphere of dead roots [20]. Soil microorganisms in native plots and litter environments can better adapt to the decomposition stage of using multiple resources or single resources than in other locations, decomposing plant litter more effectively [21]. The study of fine root decomposition has traditionally employed the litterbag method to evaluate root decomposition [22,23]. However, this method has limitations as the roots and their rhizosphere environment are disrupted during the sampling process, leading to differences between the research results and actual conditions.

Therefore, it is essential to use the in situ soil core decomposition method to explore the effect of soil fungal communities on the decomposition of fine root litter. The in situ soil core decomposition method involves the use of soil cores, which are extracted from the field and then returned to their original position. The decomposition process is allowed to proceed under natural environmental conditions, and samples are periodically collected from the soil cores for the analysis of the decomposition rate, nutrient dynamics, and fungal community composition [24].

This experiment adopts the complete core technology developed by Dornbush [25] and others to avoid the drawbacks of the litterbag method to a great extent and better reveal the changes of fine root decomposition by keeping the normal rhizosphere intact. The purpose of this work is to evaluate the changes in fine root litter decomposition in the most important forest tree species in subtropical China: *Cunninghamia lanceolata* (Lamb.) Hook (Chinese fir), *Phyllostachys edulis* (Carrière) *J. Houz* (Moso bamboo), and *Liriodendron chinense* (Hemsl.) Sargent (Chinese whitewood) [26–28].

In this study, we compared the characteristics of the fine root substrate, soil enzyme activity, and soil fungal community among the three forest types. Our hypotheses were that (1) different aboveground forests lead to different changes in the fine root decomposition rate and fine root residual chemical content; (2) the soil fungal community has a significant effect on the decomposition of fine root litter; and (3) soil enzyme activity has a strong effect on fine root decomposition. This study provides valuable insights into the roles of soil fungal communities and enzyme activities in fine root decomposition, which can contribute to the development of more effective strategies for nutrient management and carbon sequestration in forest ecosystems.

2. Materials and Methods

2.1. Study Site

The research site is located in Xiashu (119°13′20″ E, 32°7′8″ N), Jurong County, Jiangsu Province, China (Figure S1). It covers an area of 3891 ha, with a forest coverage rate of more than 90%, belonging to the north subtropical monsoon climate area. The annual average temperature is 15.5 °C, and the annual average precipitation is 1099.1 mm according to Jurong meteorological station. 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. Refer to Figure S2 for the temperature and precipitation during the study period. The soil in the forest farm is mainly yellow–brown soil and mountain yellow–brown soil and the thickness of the soil layer is generally more than 50 cm. In this study, three main typical artificial pure forests were selected: Chinese fir forest, Moso bamboo forest, and Chinese whitewood forest. The Chinese whitewood forest in the Jiurong Xia Shu Forest Farm in Jiangsu Province was artificially planted in 1994, originating from a cultivated seed source in Fujian Province, China [29]. The Chinese fir forest and Moso bamboo forest were also cultivated and planted in the same year. The three plots are geographically adjacent and ecologically similar. The soil's physical and chemical properties of the three research sites are shown in Table S1.

2.2. Sampling

In March 2021, three sample plots of Chinese fir forest, Chinese whitewood forest, and Moso bamboo forest were selected under consistent conditions of altitude, slope, and aspect. In each of these forest types, three sample plots, each measuring 30 m by 30 m, were established. In each plot, 12 sample trees were chosen along the diagonal direction, and using the center tree as the reference, three soil cores with a depth of 30 cm were randomly drilled on the circumference with an inner diameter of 10 cm and a radius of 50 cm. Each forest type had 108 soil cores, with a total of 324 soil cores. The extracted soil cores were placed in nylon mesh bags (mesh size: 0.15 mm), returned to their original positions, and marked for in situ decomposition, with the exception of the initial state soil cores that were measured and brought back to the laboratory. At 120, 240, and 360 days, 27 soil core samples were collected from each forest type and brought back to the laboratory.

The recovered soil cores were placed into a 40 mesh screen and the root system was picked out with tweezers. One part of the selected soil was immediately freeze-dried to extract the total DNA of soil microorganisms for fungal community analysis, and the other part was naturally air-dried, ground, and screened for soil physical and chemical properties and enzyme activity analysis. The fresh fine roots (primary or secondary roots $\leq$ 2 mm) were picked out, washed, dried at 60 °C to constant weight, and weighed, and the decomposition rate of roots was calculated. Then, the dried roots were crushed and sieved, and the contents of total C, N, cellulose, and lignin were measured.

2.3. Fine Root and Soil Physicochemical Properties

After the fine roots were ground into powder, the C and N contents of the fine roots were measured. The contents of C and N in fine roots was estimated using CHNOS elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). The method of Van Soest and Wine (1968) [30] was used to determine the concentration of cellulose and lignin. By calculating the weight remaining after washing fine roots with different reagents, the concentration of cellulose and acid detergent lignin was produced, which was called AUR (acidic nonhydrolyzable residue) [31].

2.4. 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 °C, the soil moisture content (WC, %) was determined with gravimetric method. The soil bulk density (BD) and soil porosity (POR) [32] were

also determined. Soil organic carbon (SOC) was analyzed using oxidation combined with potassium dichromate and measured using visible spectrophotometer (JH-14-08 723, Shanghai Aucy Scientific Instrument Co., Ltd., Shanghai, China). Soil available phosphorus (AP) was determined with hydrochloric acid–sulfuric acid extraction method. Soil available potassium (AK) was extracted using NH_4OAc and measured using atomic absorption spectrometer (AA900T, Perkin Elmer, MA, USA). Soil nitrate nitrogen (NN) and soil ammonium nitrogen (AN) were determined with 2 mol·L^{-1} KCl extraction indophenol blue colorimetry.

2.5. Soil Enzyme Activities

Soil cellulase activity was determined using the 3,5-dinitrosalicylic acid method, phosphatase activity was measured using the p-nitrophenyl phosphate colorimetric method, β-glucosidase activity was measured using the p-nitrophenol colorimetric method, peroxidase activity was determined using the volumetric method, and polyphenol oxidase activity was determined using the volumetric method [33,34].

2.6. Soil Fungal Molecular Analysis

DNA extraction and Illumina sequencing were used to determine the diversity and community composition of soil fungi [35]. The soil microorganism DNA was extracted from the D3142 kit of Gene Denovo Biotechnology Co., Ltd., Guangzhou, China. The concentration of the extracted DNA was measured using a NanoDrop 2000 Spectrophotometer (Thermo Scientific, Wilmington, DE, USA), and its quality and integrity were evaluated with 1% agarose gel electrophoresis [36]. Subsequently, the DNA was amplified using barcode primers, specifically amplifying the ITS2 region of the ITS.

The primer sequences used were ITS3_KYO2: GATGAAGAACGYAGYRAA and ITS4: TCCTCCGCTTATTGATATGC. The PCR reaction was amplified in two rounds, and the amplified products of the second round were purified with AMPure XP Beans (Beckman Coulter Inc., Brea, CA, USA) [37]. Additional details about the PCR reactions can be found in the Supplementary Information. The purified amplified products 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 Inc, Carlsbad, CA, USA), and sequencing was performed according to the PE250 mode of novaseq6000 [38]. FUNGuild v1.0 was used to determine the functional groups of the fungi. FUNGuild v1.0 is a flat database hosted by GitHub (https://github.com/UMNFuN/FUNGuild accessed on 21 September 2023) [39]. To avoid over-interpretation of fungal functional groups, we removed the "probable" confidence level and retained only the "highly probable" and "probable" levels. Communities that could not be identified or identified with multiple complex nutritional methods are collectively "undefined".

2.7. Calculations

(1) Fine root decomposition rate was calculated from dry mass remaining and percent (%) chemical mass remaining is expressed as follows [40]:

$$\text{Mass remaining } (\%) = \frac{X_t}{X_0} \times 100\%$$

$$\text{Chemical mass remaining } (\%) = \frac{C_t X_t}{C_0 X_0} \times 100\%$$

where X_0 is the fine root litter's original weight and X_t is the fine root litter's weight after decomposition during time t; C_0 is the chemical's original concentration, and C_t is the chemical concentration after time t.

(2) Litter decomposition is a dynamic process, and there is a single exponential function relationship between litter residue and decomposition time (Olson 1963). Therefore, Olson proposed an exponential attenuation model:

$$\frac{x}{x_0} = e^{-kt}$$

where:

x_0—initial mass of plant litter, kg;
x—residual mass of litter after t-time decomposition, kg;
k—litter decomposition constant;
t—decomposition time.

2.8. Statistical Analyses

The Duncan test was used when a one-way analysis of variance (SPSS Inc., Chicago, IL, USA) showed that forest type had a significant impact on fine root decomposition rate. The residuals of the model were tested and it was confirmed that the assumptions of normality and homogeneity were met. The main effects and interactions of forest type and decomposition time on soil enzyme activity, fine root decomposition rate, and fine root residual chemical properties were tested with two-way analysis of variance and SPSS 19.0 software (SPSS Inc., Chicago, IL, USA). All histograms and line charts used origin8.5 software (OriginLab Inc, Northampton, MA, USA) fitting. The microbial communities and functional structures were visualized with nonmetric multidimensional scaling (NMDS) based on Bray–Curtis distance. ANOSIM analysis was used to detect differences within and between groups. The linear discriminant analysis (LDA) effect size (lefse) method was used to evaluate the high-dimensional microbial taxa and determine the microbial classification represented by differences between forest types. The significance standard of fungal classification level was LDA > 2, $p < 0.05$.

Canoco 5.0 (micropower, Ithaca, NY, USA) was used for redundancy discriminant analysis (RDA) to reveal the relationship between the decomposition rate of fine root litter, fine root chemical properties, and soil enzyme activity and soil fungal community characteristics. Each arrow (usually representing a numeric variable) points to the direction in which the value of the environment variable increases the fastest. The angle between arrows (alpha) indicates the correlation between individual environment variables. When the angle is acute, the approximate correlation is positive, and when the angle is greater than 90 degrees, the approximate correlation is negative. The length of the arrow is an indicator of the suitability of the indicator. AMOS software (IBM Inc, Armonk, NY, USA) was utilized for structural equation modeling (SEM) to examine the relationship between soil enzyme activity, soil fungal community characteristics, and fine root decomposition rate.

3. Results

3.1. Fine Root Mass Loss and k Value of Decomposition Rate

At the end of the study period, the fine root mass loss in different stand types ranged between 49.94% and 66.91% (Figure 1a). The mass residual rates of fine root litters varied significantly among different stands (Table S2). In particular, the decomposition of fine roots varied ($p < 0.001$) with the mass residual rates of the fine root (Table S2), but the cross effect of the stand and time was insignificant with fine root decomposition. The annual decomposition rate of fine root litter was higher ($p < 0.05$) in the Chinese whitewood forest than the Chinese fir forest.

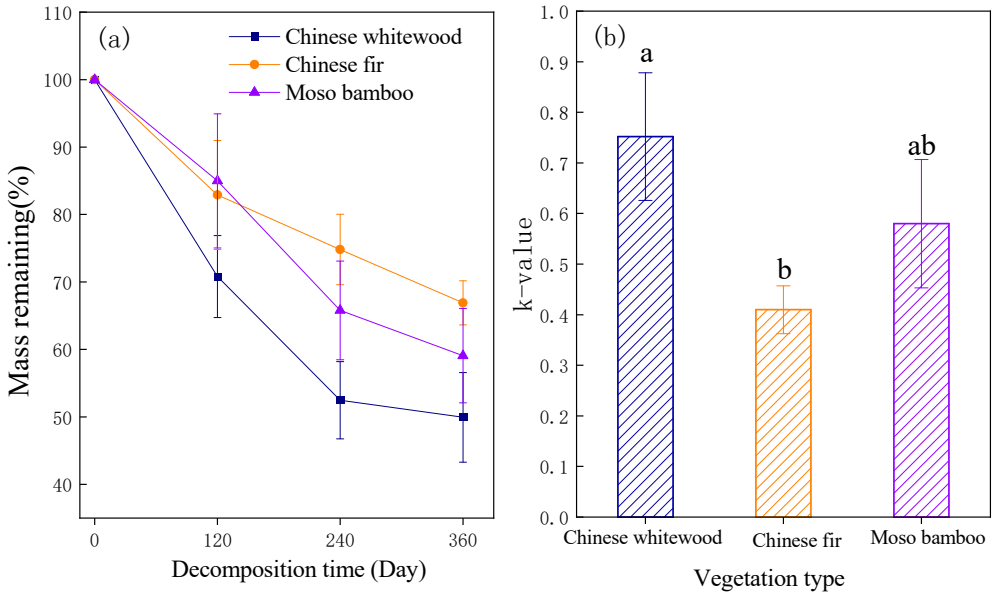

Figure 1. Percentages of mass remaining and annual decomposition rate (k value) from decomposing fine roots in different forest types. (**a**) shows Percentages of mass remaining in different forest types; (**b**) shows k value in different forest types. Note: Different lowercase letters indicate significant differences in k value between different forest types ($p < 0.05$).

3.2. Changes in Chemical Quality of Fine Root Litter during Fine Root Decomposition

The residual loss rates of carbon, nitrogen, cellulose, and lignin ranged from 49.94% to 66.91%, 33.08% to 60.99%, 61.74% to 68.82%, and 52.06% to 70.93%, respectively (Figure 2a,b,d,e), at the end of the study period. However, the fine root C/N ratios exhibited different trends among different forests, with the Moso bamboo forest having the highest C/N ratio and the Chinese whitewood forest having the lowest C/N ratio (Figure 2c). The residual amounts of cellulose and lignin were significantly influenced only by decomposition time, whereas the residual amounts and C/N ratios of C and N in fine roots were significantly influenced by the forest type and decomposition time (Table S2).

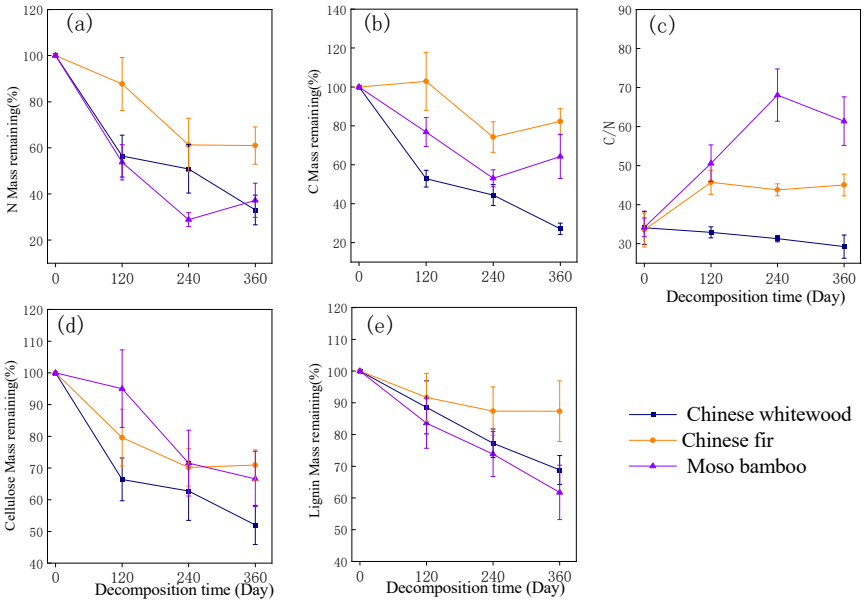

Figure 2. Remaining mass (%) of N (**a**), C (**b**), C/N (**c**), cellulose (**d**), and lignin (**e**) in decomposing fine roots in different forests. Note: values are shown as mean ± S.D. ($n = 27$).

3.3. Dynamic Changes in Soil Enzyme Activities during the Decomposition of Fine Root Litter

Among different enzyme activities, acid phosphatase showed the highest range (793.3–1528.1 μmol·g^{-1}·h^{-1}) during the decomposition of fine roots, followed by β-GC (355–992.9 μmol·g^{-1}·h^{-1}), whereas cellulose was the lowest (0.37–0.88 μmol·g^{-1}·h^{-1}) (Figure 3b–d). The forest type and decomposition time influenced the enzyme activities differently during the decomposition of fine root litters (Figure 3). In particular, the perox enzyme activity of the Moso bamboo forest was the highest, particularly at the beginning of the decomposition time, while it was the lowest in the Chinese whitewood forest (Figure 3e). The β-GC enzyme activity was the highest in the Chinese whitewood forest and the lowest in the Chinese fir forest.

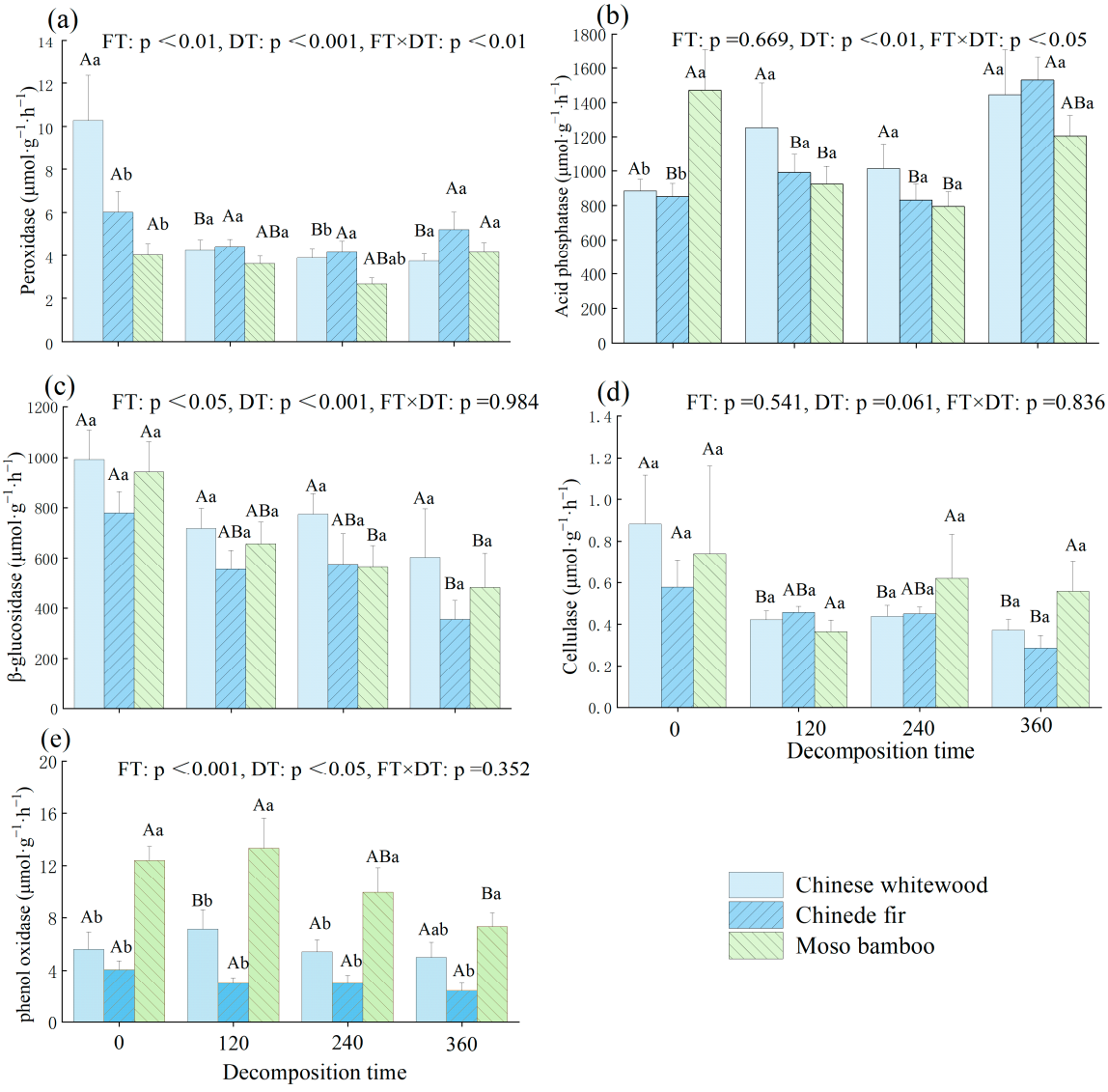

Figure 3. Enzyme activities in the different forests at different periods. Values are shown as mean ± S.D. (n = 27). (**a**) shows Peroxidase activities in the different forests, (**b**) shows Acid phosphatase activities in the different forests, (**c**) shows β-Glucosidase activities in the different forests, (**d**) shows Cellulase activities in the different forests and (**e**) shows Polyphenol oxidase activities in the different forests. Note: different capital letters indicate significant differences among different decomposition periods within each forest type ($p < 0.05$), and different lowercase letters indicate significant differences forest-wise in the same decomposition period ($p < 0.05$). Note: Perox—Peroxidase; ACP—Acid phosphatase; β-GC—β-Glucosidase; CL—Cellulase; PPO—Polyphenol oxidase. FT—Forest type; DT—Decomposition time.

3.4. Soil Fungal Community Diversity during the Decomposition of Fine Root Litters

Ascomycota, Basidiomycota, Mortierellomycota, and Rozellomycota were the dominant phyla present (Figure 4). The relative abundance of Mortierellomycota, Mucoromycota, and Rozellomycota increased significantly during decomposition, while the relative abundance of Ascomycota decreased (Figure 4b–d). Overall, the composition of the fungal community varied with the decomposition time and forest type.

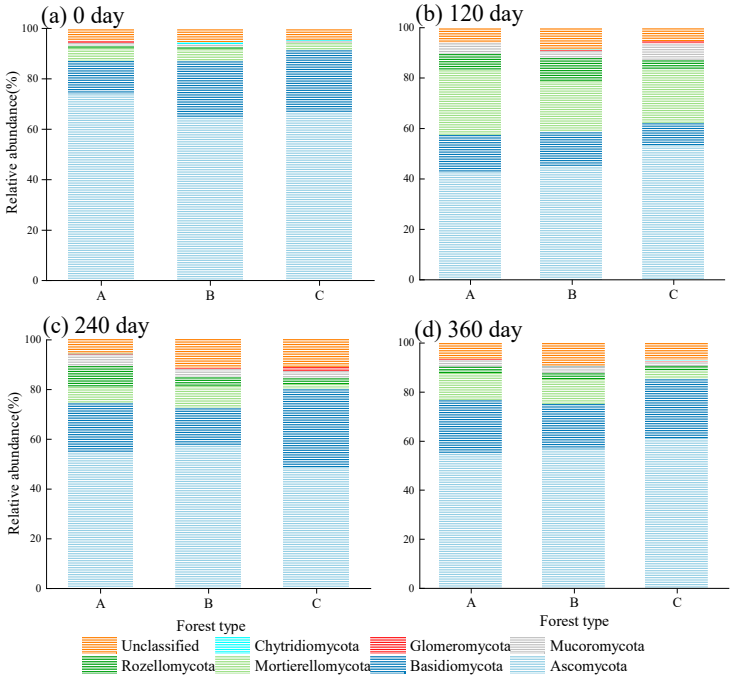

Figure 4. Relative abundance of phylum at the level of fungi during the decomposition of fine root litter in different forest types (n = 27). A represents Chinese whitewood forest, B represents Chinese fir forest, and C represents Moso bamboo forest.

The results of α diversity variance analysis indicate that during the decomposition of fine root litter, the Chao1 index of the three forest types significantly decreased ($p < 0.001$) at 360 days (Left panel of Figure 5a).

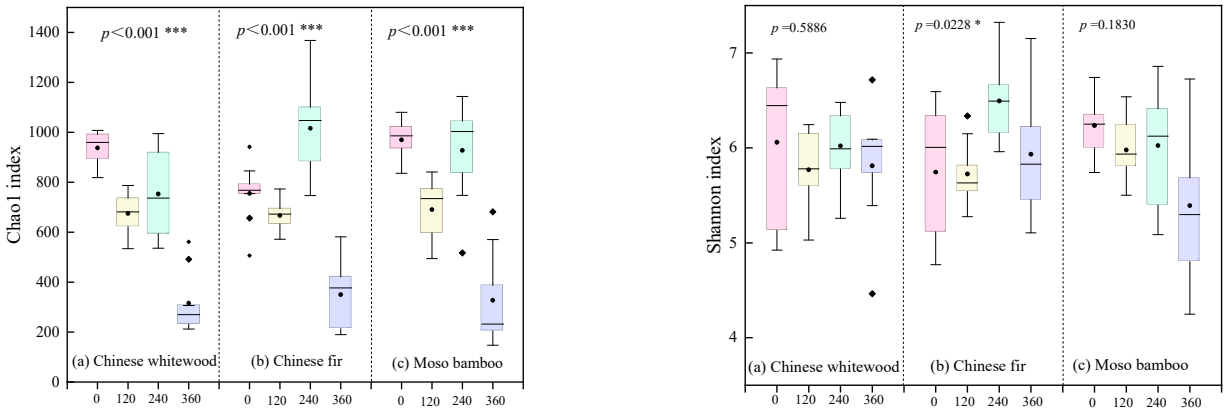

Figure 5. Changes in alpha diversity of fungi during the decomposition of fine root litter in different forest types. (**Left**) shows the index of Chao1 in different forest types; (**Right**) shows the index of Shannon in different forest types. (a) represents Chinese whitewood forest, (b) represents Chinese fir forest, and (c) represents Moso bamboo forest. *** Significant correlation at the 0.001 level (bilateral). * Significant correlation at 0.05 level (bilateral).

3.5. Soil Fungal Community Structure during the Decomposition of Fine Root Litters

The fungal community in the decomposition process of fine root litter can be divided into four areas according to the decomposition stage (stress = 0.175) (Figure 6). The decomposition of fine roots in three stands had a significant ($p < 0.01$) effect on the soil fungal community structure. However, in different stages of fine root decomposition, there were significant ($p < 0.05$) differences in soil fungal communities in different stands only at 240 days (Table 1).

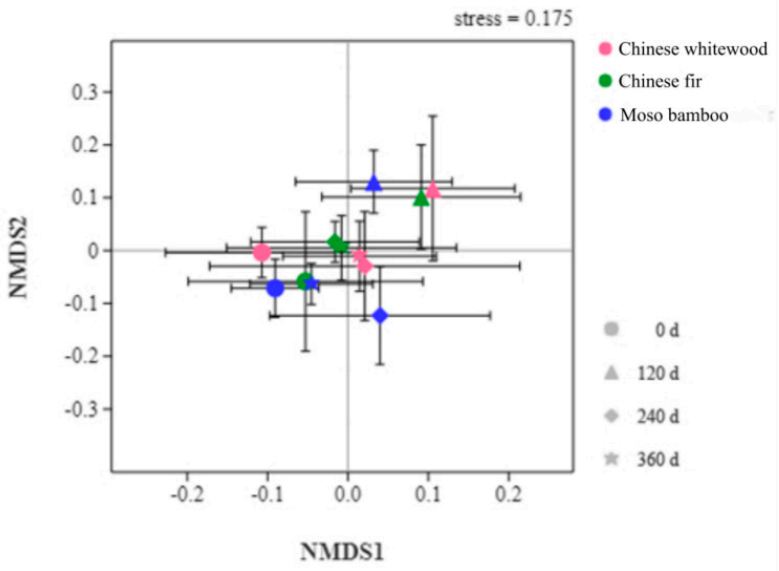

Figure 6. Non-metric multidimensional scale (NMDS) based on Bray–Curtis difference of fine root decomposition of soil fungal communities in different stands. The figures of different shapes represent different stages of fine root decomposition: circle, triangle, diamond, and pentagram represent 0 days, 120 days, 240 days, and 360 days of fine root decomposition, respectively. Different colors represent forest types: red represents Chinese whitewood forest, green represents Chinese fir forest, and blue represents Moso bamboo forest.

Table 1. Difference test of similarity analysis of soil fungal community structure.

Differences		R-Value	*p*-Value	Significance
Decomposition time	Chinese whitewood	0.2118	0.001	**
	Chinese fir	0.1265	0.012	**
	Moso bamboo	0.3687	0.001	**
Forest type	0 day	0.071	0.063	NS
	120 days	0.0357	0.201	NS
	240 days	0.1744	0.018	*
	360 days	0.0617	0.125	NS

** Significant correlation at 0.01 level (bilateral). * Significant correlation at 0.05 level (bilateral). NS: no significant correlation.

3.6. Fungal Guilds during the Decomposition of Fine Root Litter

The abundance of functional groups of soil fungi varied during the decomposition of fine root litters in different stands (Figure 7). In particular, the abundance of saprotroph fungi was more than that of Endophytes and pathogens by 81.3 and 60.4%, respectively. Wood Saprotroph fungi were the most abundant, except for Undefined Saprotroph fungi, accounting for 20% of all sequences. With the decomposition of fine roots, the number of wood saprotrophs decreased at 120 days and then increased. The abundance of Ectomycorrhizal fungi and Arbuscular Mycorrhizal fungi in the Moso bamboo forest is higher than that in the Chinese whitewood forest and Chinese fir forest. The abundance of plant–

pathogen fungi increased first and then decreased with the decomposition time in the three forests, and the abundance was the highest in the Chinese fir forest.

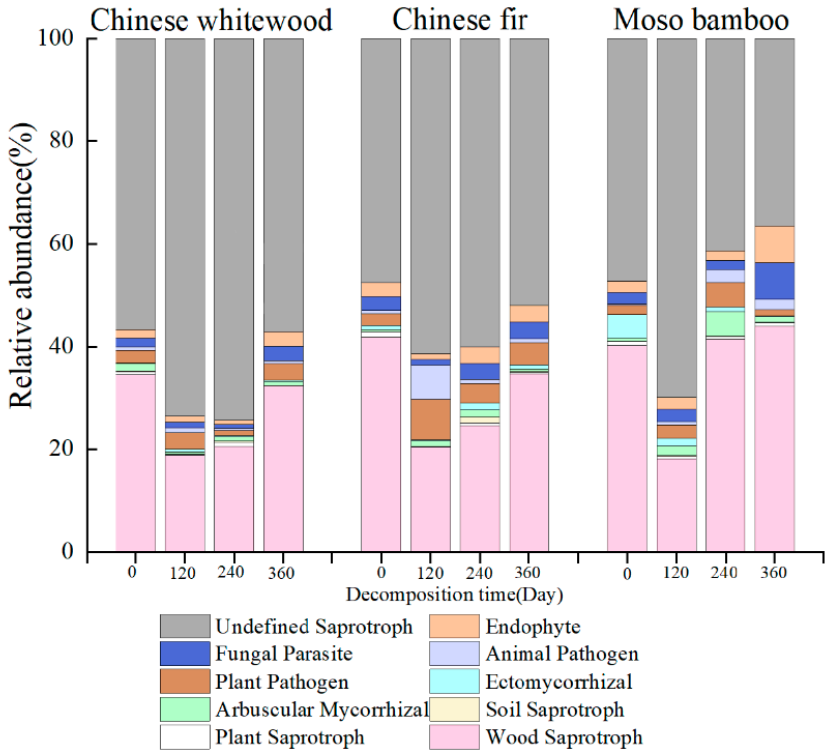

Figure 7. Relative abundance of soil fungal functional guild assignment with fine root decomposition using FUNGuild.

3.7. The Relationship between Fine Root Decomposition and Root Chemistry, Soil Fungal Community, and Soil Enzyme Activity

The results of the RDA analysis showed that AMF and EF were the main functional factors of the fungal community, affecting the fine root decomposition rate, and Perox, GC, and PPO were the main soil enzyme activity factors, affecting fine root decomposition (Figure 8).

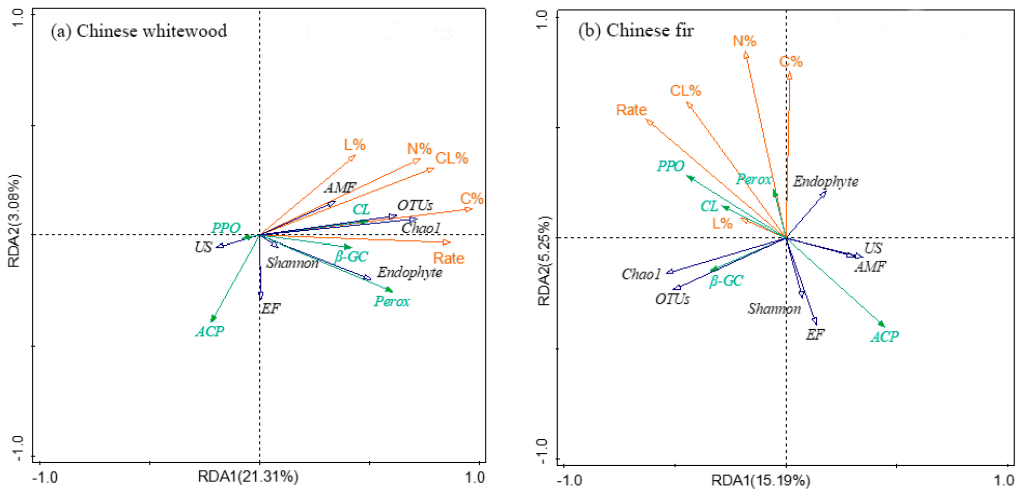

Figure 8. *Cont.*

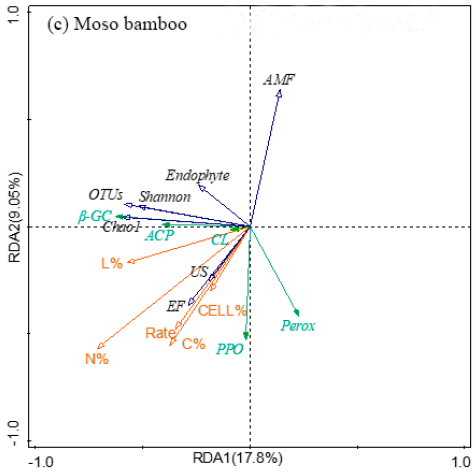

Figure 8. Redundancy analysis (RDA) of fine root decomposition, soil enzyme activity, fine root chemical properties, and fungal community characteristics in different stands. The angle and length of the arrow indicate the direction and intensity, respectively, of the decomposition rate of fine root litter and root chemistry, soil fungal community characteristics, and soil enzyme activity. (**a**) represents Chinese whitewood forest, (**b**) represents Chinese fir forest, and (**c**) represents Moso bamboo forest. Note: Rate—Decomposition rate of fine root litter; C%—C content in fine roots; N%—N content in fine roots; CELL%—Cellulose content in fine roots; L%—Lignin content in fine roots; AMF—Arbuscular Mycorrhizal fungi; EF—Ectomycorrhizal; US—Undefined Saprotroph; Perox—Peroxidase; ACP—Acid phosphatase; GC—β-glucosidase; CL—Cellulase; PPO—Polyphenol oxidase.

3.8. SEM Results

The C content of fine roots had a significant direct positive effect on the decomposition rate of fine roots, with impact coefficients of 0.945, 0.620, and 0.863 for the Chinese whitewood, Chinese fir, and Moso bamboo forests, respectively (Table 2). In addition to the Chinese whitewood forest, the C content affected the fine root decomposition rate by affecting soil enzyme activity and soil fungal characteristics. In different forest types, the characteristics of the soil fungal community indirectly affect the fine root decomposition rate by affecting soil enzyme activity. In addition, the soil fungal characteristics of the Chinese whitewood forest and Moso bamboo forest have a direct positive impact on the fine root decomposition rate, but AMF and US of the Chinese fir forest have a direct negative impact on the fine root decomposition rate (Figure 9).

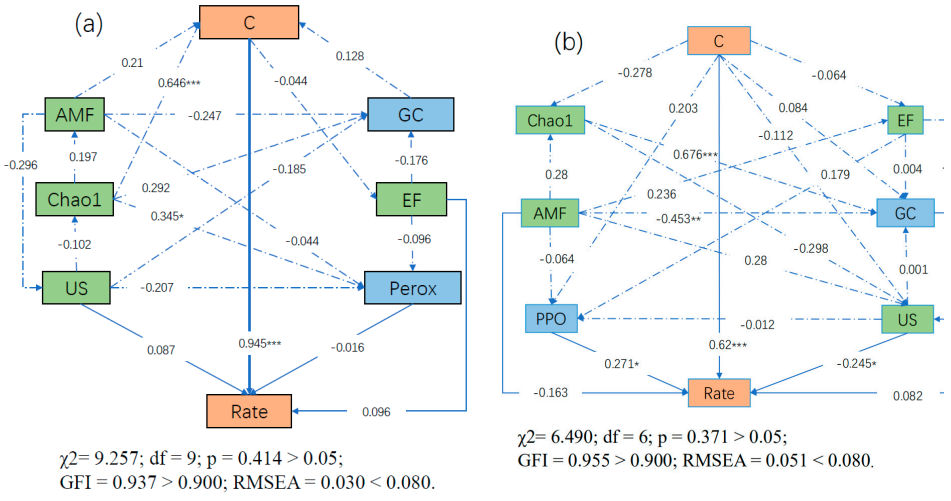

Figure 9. *Cont.*

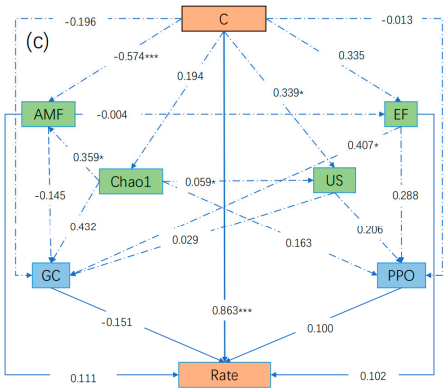

Figure 9. Structural equation model of effects of root characteristics, soil fungal community, and soil enzyme activity on the decomposition rate of fine root litter. The numbers on the arrows are normalized path coefficients. (**a**) represents Chinese whitewood forest, (**b**) represents Chinese fir forest, and (**c**) represents Moso bamboo forest. The solid line shows the direct effect of each parameter on the decomposition rate, while the dotted line shows the indirect effect of root characteristics, soil fungal community, and soil enzyme activity on the decomposition rate of fine roots. *** Significant correlation at the 0.001 level (bilateral). ** Significant correlation at 0.01 level (bilateral). * Significant correlation at 0.05 level (bilateral). Note: Rate—Decomposition rate of fine root litter; C%—C content in fine roots; AMF—Arbuscular Mycorrhizal fungi; EF—Ectomycorrhizal; US—Undefined Saprotroph; Perox—Peroxidase; GC—β-glucosidase; PPO—Polyphenol oxidase.

Table 2. Direct, indirect, and total effects of root characteristics, soil fungal community, and soil enzyme activity on the decomposition rate of fine root litter in different stands based on the structural equation model.

		C%	AMF	Chao1	EF	US	PPO	Perox	GC
Rate (Chinese Whitewood)	Direct Effects	0.945	0.000	0.000	0.096	0.087	-	−0.016	0.000
	Indirect Effects	−0.003	0.169	0.671	−0.020	−0.087	-	0.000	0.120
	Total Effects	0.942	0.169	0.671	0.076	−0.001	-	−0.016	0.120
Rate (Chinese fir)	Direct Effects	0.620	−0.163	0.000	0.000	−0.245	0.271	-	0.082
	Indirect Effects	0.048	−0.068	0.130	0.084	0.000	−0.003	-	0.000
	Total Effects	0.668	−0.231	0.130	0.084	−0.249	0.267	-	0.082
Rate (Moso bamboo)	Direct Effects	0.863	0.111	0.000	0.102	0.000	0.100	-	−0.151
	Indirect Effects	−0.019	0.022	0.280	−0.033	0.016	0.000	-	0.000
	Total Effects	0.844	0.132	0.280	0.069	0.016	0.100	-	−0.151

Note: Rate—Decomposition rate of fine root litter; C%—C content in fine roots; AMF—Arbuscular Mycorrhizal fungi; EF—Ectomycorrhizal; US—Undefined Saprotroph; Perox—Peroxidase; GC—β-glucosidase.

4. Discussion

The decomposition of fine root litter is a complex process that involves the interaction of multiple factors, including the litter chemistry, microbial community composition, and physical structure [41]. There were significant differences in the loss of fine root litter and the rate constant (k value) of fine root decomposition among different forest types during the 360-day decomposition process (Figures 1 and 2). The fine roots of the Chinese whitewood decomposed the fastest, while those of the Chinese fir decomposed the slowest. This may be attributed to that the fine roots in the Chinese fir had the highest content of cellulose and lignin, while broadleaf tree fine roots had higher nutrient content and lower acid-insoluble matter. Previous studies have shown that lignin itself is difficult to degrade and can delay the litter decomposition process [42]. Several studies have shown that

the microbial abundance and diversity in broadleaf forest soils are generally higher [43], which may lead to faster decomposition rates of fine roots. At the same time, the rapid decomposition of fine roots in the Chinese whitewood forest also results in a decreasing trend of the dynamic curves of the C element and C/N ratio in fine roots (Figure 2b,c). This further confirms that the characteristics of the litter chemical content are one of the main factors regulating the decomposition process [44]. In many studies, C and lignin accumulated relatively over time during fine root decomposition because C is mainly present in structures such as keratin, cork, or lipids, which are similar to lignin in that they are stubborn and require specific enzymes to break down [45]. When root decomposition occurs rapidly, it can significantly impact the C/N ratio in the soil, as it affects the relative amounts of available C and N in the system. C from roots is released into the soil as CO_2, while N is converted into various forms such as ammonium and nitrate, which are available for use by microbes and plants [46]. Therefore, when rapid root decomposition leads to a decrease in the C/N ratio, microbial activity may increase.

Soil microorganisms and fine root decomposition are considered to be part of the same continuum [47], but different groups in soil fungal communities contribute differently to fine root decomposition [48]. The Chao1 changed significantly during fine root decomposition. The response of the horizontal phylum of fungi was different in the process of fine root decomposition, and Mortierellomycota, Basidiomycota, and Ascomycota were relatively sensitive compared with other groups. The Basidiomycota and Ascomycota were dominant in different stages of decomposition. This may be attributed to their ability to utilize different substrates or the presence of specific enzymes required for decomposition. For example, it is known that the phylum Ascomycota is involved in the decomposition of cellulose and hemicellulose, while the phylum Basidiomycota is involved in the decomposition of lignin and other complex organic compounds. At 120 days, Mortierellomycota was more common, and Basidiomycota was much less than at 0 days; this suggests that such fungal groups may respond more quickly during the early stages of fine root decay [4]. Mortierellomycota is another highly abundant taxon at 120 days, which is the common root rot fungus. Previous studies have found that Basidiomycota plays a major role in the decomposition of intractable organic matter [49]. Many Mortierellomycota lack the ability to metabolize structural carbon [50], and most Ascomycota also lack this ability [51]. Over time, this may limit their competitiveness in decaying communities. The increase in abundance of basidiomycetes at 360 days of decomposition may be attributed to their importance as key decomposers of wood and litter, as many species within Basidiomycota are known to effectively degrade recalcitrant materials [51,52]. As previous studies have shown, as the main factor affecting fine root decomposition, the soil fungal community plays a multifaceted role in fine root decomposition [53]. Among them, enzyme measurement can directly track the functional response of the microbial community to litter quality and other environmental factors, so enzyme activity can provide a closer link between nutrients, availability, and waste decomposition [54].

The results showed that the forest type and fine root decomposition time significantly affected the activities of Perox, β-GC, and PPO enzymes associated with the C cycle. The enzyme activity of ACP associated with the P cycle was significantly affected by fine root decomposition and was also influenced by the interaction between the forest type and fine root decomposition (Figure 3), which is consistent with the results of previous studies [6]. The main reason is that the decomposition enzyme is an important driving force in the process of fine root decomposition. Previous studies have shown that in the early leaching stage of decomposition, cellulolytic enzyme activity related to soluble sugars plays a dominant role and tends to reach a peak with the decomposition process. Polysaccharide substances such as cellulose are preferred for decomposition, and the concentration of extractable substances in fine roots decreases rapidly and gradually leaches out [55]. However, the concentration of acid-insoluble substances and other compounds that are difficult to decompose gradually accumulates, and the activity of lignin decomposition enzymes related to these compounds gradually increases during the decomposition process, which

becomes the leading factor of the decomposition speed [56]. Studies have shown that only a few microorganisms can produce the enzymes needed to decompose the substances in the later stage, and only when no other more easily decomposed substrates are available [57]. PPO is an important lignin-degrading enzyme, which is produced by white-rot fungi and other special microorganisms in Basidiomycota and Ascomycota [58]. In contrast, cellulase and ligninase can be produced by a large number of bacterial and microfungal species [59].

Changes in forest types may have a feedback effect on fine root decomposition through soil microorganisms [60]. The RDA redundancy analysis showed that fine root decomposition and fine root characteristics have a significant correlation with soil enzyme activity and soil fungal community characteristics (Figure 8). The SEM showed that the fitting results of fine root litter decomposition were varied among different forest types. The forest type was the main exogenous factor controlling fine root decomposition and an important driving force for the difference in fine root litter characteristics. We consistently found that C in fine roots is essential for decomposition, and that most water-soluble compounds such as glucose and fructose are easily used as a C source for microbial decomposition [61]. On the contrary, lignin has a negative impact on fine root decomposition by limiting microbial degradation [62]. Our research indicates that fungal community diversity indirectly affects the fine root decomposition rate by affecting fungal functional groups and soil enzyme activities. Fungal functional groups play different roles in regulating fine root decomposition in SEM. Consistent with previous research, different fungal functional groups may play different roles in the process of fine root decomposition. For example, the decomposer fungi group is generally considered to be able to decompose plant materials rich in lignin, such as the lignin part of fine roots. In contrast, the nutrient fungi group may mainly decompose other compounds in fine roots, such as proteins and carbohydrates. Fungal functional groups play a role in the decomposition of fine roots from various pathways, and sometimes even exhibit opposite effects. For example, rhizobia may compete with other fungi for nutrients and reduce the rate of fine root decomposition in the soil [63]. However, these factors ultimately promote fine root decomposition through soil enzyme activity, which clearly indicates that the change in soil enzyme activity can be used to explain the ecological effect of the root decomposition process [64]. Studies have shown that the complete degradation of litter is the result of the comprehensive influence of soil enzymes [65], and the decline in enzyme activity is the result of a series of ecosystem responses affecting microbial community composition and underground carbon distribution [66]. Our study investigates the relationship between forest types and the decomposition of fine root litter, shedding light on the specific characteristics of this process. Furthermore, our results demonstrate the close coupling between changes in soil fungal communities and soil enzyme activity during the decomposition of fine roots [67]. However, its mechanism still needs further research. Future in-depth research should mainly focus on how functional microorganisms affect fine root decomposition.

5. Conclusions

Soil fungal diversity and enzyme activity play crucial roles in the process of fine root decomposition and were influenced by the forest type. The C content of fine roots was a key factor affecting decomposition, with higher C content having a positive effect. From a microbial perspective, mycorrhizal fungal functional groups had a greater impact than other fungal functional groups, with AMF and EF being the main functional factors affecting the rate of fine root decomposition. At the level of enzyme activity, microorganisms directly affected root decomposition through the production of enzymes, with Perox, β-GC, and PPO being the main soil enzyme activity factors affecting fine root decomposition. These findings emphasize the importance of understanding the potential mechanisms underlying fine root decomposition for predicting soil carbon and nutrient cycling, as well as developing effective soil management strategies.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f14071321/s1, Figure S1: Location of study site; Figure S2: Meteorological data for the study area: (a) Air Temperature; (b) Rainfall; Table S1: Comparison of the soil characteristics between the different vegetation during fine root decomposition; Table S2: Significant of the effect of forest type, decomposition time and their interactions on mass loss and loss of each component based on repeated measure-ANOVA.

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