forests

MDPI

Article

Variance in Woody Debris Components Is Largely Determined by the Belowground Microbial Phylum-Level Composition

Yongxue Yan [1,2,†], Zhen Bai [1,†], Shaokui Yan [1], Jiabing Wu [1,*] and Hai-Sheng Yuan [1,*]

[1] Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
[2] University of Chinese Academy of Sciences, Beijing 100049, China
* Correspondence: wujb@iae.ac.cn (J.W.); hsyuan@iae.ac.cn (H.-S.Y.)
† These authors contributed equally to this work.

Abstract: Although the bioconversion of lignocellulosic residues is essential for nutrient storage in forest floors, little is known about the mechanisms behind wood decay and its interactions with site-specific belowground microbial community composition and chemical properties. This study examined the components of white-rot vs. brown-rot woody debris, closely contacted soil chemical properties and microbial community composition using high-throughput Illumina MiSeq sequencing in coniferous and deciduous temperate forests. The lignin concentrations were higher in the brown-rot than in the white-rot woody debris of the coniferous forest. However, lower cellulose concentrations were observed in the brown-rot sets than in the white-rot sets of both coniferous and deciduous forest stands. Furthermore, the woody debris had higher concentrations of nonstructural compounds and ash in the brown-rot than in the white-rot sets of the coniferous and deciduous forests, respectively. Surprisingly, nearly 90% of the variation in the woody debris components was explained by the belowground fungal and bacterial phylum-level compositions. Of these major phyla, Basidiomycota was closely related to the lignin concentration and accounted for 26.62% of the variation in woody debris components, while Ascomycota was related to the hemicellulose concentration and accounted for 17.7% of the variance in the woody debris components. Furthermore, soil total carbon, available phosphorus, and available potassium were 131%, 138%, and 91% higher in the brown-rot than white-rot sets of the coniferous (but not deciduous) forest stand. In addition, Basidiomycota fungi presented an oligotrophic life strategy and were significantly negatively correlated with the soil total carbon, total nitrogen, alkali-hydrolysable nitrogen, and available phosphorus contents. In contrast, Ascomycota fungi were characterized by a copiotrophic strategy and were positively correlated with the contents of soil total carbon, total nitrogen, and total phosphorus. These findings indicate that wood decay processes are strongly determined by site-specific microbial community structure and nutrient status in temperate forests.

Keywords: wood decay; fungi; bacteria; white rot; brown rot; soil nutrient; temperate forests

check for updates

Citation: Yan, Y.; Bai, Z.; Yan, S.; Wu, J.; Yuan, H.-S. Variance in Woody Debris Components Is Largely Determined by the Belowground Microbial Phylum-Level Composition. *Forests* **2022**, *13*, 1446. https://doi.org/10.3390/f13091446

Academic Editor: Simon Curling

Received: 27 July 2022
Accepted: 7 September 2022
Published: 9 September 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Globally, deadwood residuals play an indispensable role in soil nutrient immobilization of forest ecosystems, accounting for up to 54% of organic matter, 8% of total carbon (C), 5% of total nitrogen (N), and 10% of total phosphorus (P) [1–3]. Such wood decay impacts are usually dependent upon decomposer community structure and belowground physicochemical properties [4–6]. However, the underlying mechanisms about deadwood decomposition have rarely been revealed, especially in the context of the rot type distinction and its interaction with site-specific microbial-mediated nutrient cycling in forest floors.

The wood structural framework is mainly composed of lignin, cellulose and hemicellulose, which account for over 90% of the wood stuff [7]. Such polymeric constituents can be mainly utilized by fungi and slightly modified by bacteria [8–10]. Different strategies are deployed by decomposer communities, which result in rot type distinctions such as

white-rot vs. brown-rot sets [11]. White-rot fungi can efficiently degrade lignin, whereas brown-rot fungi have enzymatic systems to degrade carbohydrates (cellulose and hemicellulose), leaving modified lignin in a brown and cubic form [12,13]. As a result, there are significantly different chemical components of woody debris between white-rot and brown-rot sets [1]. Additionally, wood decomposition caused by white-rot and brown-rot fungi may also differ between wood types such as coniferous vs. deciduous tree species [14]. It is believed that brown-rot fungi prefer to utilize coniferous substrates, while white-rot fungi predominantly degrade deciduous wood [15]. Moreover, brown-rot woody debris contains high concentrations of soluble aromatic, phenolic compounds and metals which enter the soil through leaching and benefit the formation and protection of soil organic matter, whereas white-rot woody debris continuously releases soluble sugars and other rapidly metabolized components which promote the nearby fast-growing microbiomes in the co-metabolism of available nutrients [4]. In addition to lignocellulosic materials, wood stuff contains nonstructural substances (e.g., soluble sugars) and ashes, which may have significant effects on wood-decay fungi and enzyme activities [7].

Soil contact is essential for wood decomposition [16], as the soil microbiome and nutrient status are usually regarded as the dominant factors explaining the variability in decomposition [7,17]. A previous study showed that fallen woods directly contacting the forest floor decomposed 1.4 times faster than those separate from the forest floor [18]. Once contacting fallen woods, soil microorganisms colonize wood through mycelial growth (such as fungi and actinomycetes) to acquire nutrients of polymeric constituents and thus accelerate wood decomposition processes [19]. It is believed that taxonomic richness, evenness, and species associations (i.e., co-occurrence patterns) of fungal decomposers account for over 50% of the variation in wood decomposition rates [20]. The soil-borne decomposers, moreover, are closely determined by site-specific soil chemical properties, such as the C:N ratio [21], pH value [22], available phosphorus [23] and alkali-hydrolysable nitrogen contents [24]. In general, Ascomycota fungi are copiotrophic and are positively influenced by nutrient availability, whereas Basidiomycota fungi are oligotrophic and are reduced with enriched nutrient status [25,26]. Furthermore, soil physicochemical properties usually vary among different forest stands [27]. For example, birch forests may have higher soil pH and base saturation, thinner humus layers, and less C and N stored in the soil than do pine and spruce forests [28]. Consequently, wood decomposition (e.g., red maple wood (*Acer rubrum* L.)) is largely dependent upon belowground abiotic conditions, including soil pH, total nitrogen, moisture and temperature [20].

Although site-specific biotic and abiotic factors strongly influence wood lignocellulose decomposition [1,29], their roles in wood decay and the consequences for woody debris components have rarely been unraveled. By investigating white-rot vs. brown-rot wood components, belowground microbial communities and chemical properties, this study aimed to delineate the mechanisms behind in situ wood decay in different forest ecosystems. We hypothesized that (1) the white-rot and brown-rot type distinctions would vary significantly between coniferous and deciduous forest stands; (2) the components of woody debris would be determined by closely contacted belowground microbiomes; and (3) the wood-decay-related microbial community would be dependent upon site-specific edaphic chemical properties.

2. Materials and Methods

2.1. Study Sites

The study area is located in Changbai Mountain in Jilin Province, China. The mean annual precipitation is 700 mm. The mean annual air temperature is 2.8 °C. The maximum and minimum air temperatures are 27.9 °C (July) and −32.0 °C (January), respectively. The study area consists of coniferous and deciduous forest stands. The evergreen coniferous forest (42°12′00.44″ N, 128°10′10.40″ E, altitude 1107 m) is dominated by the tree species *Picea jezoensis* Carr. *var. microsperma* (Lindl.) Cheng et L.K.Fu and *Abies nephrolepis* (Trautv.) Maxim. The deciduous forest (42°23′05.13″ N, 128°05′31.36″ E, altitude 800 m) is dom-

inated by the tree species *Tilia amurensis* Rupr., *Quercus mongolica* Fisch. ex Ledeb. and *Pinus koraiensis* Sieb. et Zucc. The soil is affiliated with an Andosol that developed from volcanic ash [4].

2.2. Log Identification and Sample Collection

In July 2015, decayed logs (ca. 20 cm in diameter) dominated by white-rot and brown-rot fungi were identified according to Mäkinen et al. [30] and Bai et al. [4]. A total of 5 decayed logs (5 replicates) with each rot type were collected in coniferous and deciduous forests, respectively. Thus, a total of 4 wood decay (rot) sets (2 forest stands × 2 rot types) were formed.

In each rot set, sawdust samples were taken from each decayed log using an electric drill (bit diameter 6 mm). At least 5 drilled holes were sampled in each decayed log to form a composite woody debris sample. The drill bit was sterilized between samples with 75% ethanol. Soil samples at the 0–5 cm depth were collected right beneath each decayed log, where we marked five evenly spaced sampling points, and then samples were mixed and pooled together to form a composite soil sample. At the same time, we collected soils located 1 m horizontally from the decaying logs as controls. Each composite sample was divided into two parts: one part was air-dried to analyze the soil chemical properties or woody debris components, and the other part was stored at −80 °C for DNA extraction.

2.3. Chemical Analyses

The hemicellulose, cellulose, and lignin contents were determined by the Van Soest method [31,32]. In short, sawdust stuff was separated by stepwise chemical digestion into neutral detergent fiber (NDF), acid detergent fiber (ADF), strong acid detergent fiber (SADF) and ash. Ash in wood is mainly composed of inorganic materials, such as silicates, sulfates, carbonates and metals [33,34], and was determined with the residues from SADF being combusted at 550 °C in a muffle furnace for 3 h. The nonstructural compounds (NS) are primarily composed of soluble carbohydrates, soluble proteins and lipids [35], and were determined by the difference between the starting weight and NDF. The contents of the remaining three polymeric constituents were separately calculated as "NDF minus ADF" for hemicellulose, "ADF minus SADF" for cellulose, and "SADF minus ash" for lignin. Soil total carbon (TC) and total nitrogen (TN) concentrations were determined using an elemental analyzer (Vario Macro cube, Elementar, Germany). The C:N ratios were presented as mass ratios. Alkali-hydrolysable N (AN, alkali solution diffusion method), readily available potassium (AK, extracted using 1 mol/L ammonium acetate acid) and available phosphorus (AP, extracted with 0.5 mol/L of $NaHCO_3$ (pH 8.5)) were measured according to [36]. Soil pH was determined using a glass electrode (soil:water = 1:2.5).

2.4. Bacterial and Fungal Community Taxonomic Profiling

We analyzed the soil microbial community composition using high-throughput sequencing from 0.5 g subsamples. The DNA was extracted using a PowerSoil DNA Isolation Kit (MoBio, Carlsbad, CA, USA). Bacterial and fungal DNA were amplified using the 16S rRNA gene (primers were 5′-GTGCCAGCMGCCGCGGTAA-3′ (515F) and 5′-CCGTCAATTCCTTTGAGTTT-3′ (907R)) and the internal transcribed spacer (ITS) region (primers were 5′-GCATCGATGAAGAACGCAGC-3′ (ITS3-2024F) and 5′-TCCTCCGCTTATTGATATGC-3′ (ITS4-2409R)) [37], respectively. The 25 μL reaction mixture contained 5–10 ng of total DNA, 1 unit of Ex Taq (TaKaRa, Dalian, China), 1 × Ex Taq buffer, 0.2 mmol of each dNTP and 0.4 μmol of each primer. The polymerase chain reaction (PCR) was performed as follows: initial denaturation at 94 °C for 2 min, followed by thirty-five cycles (95 °C for 45 s, 56 °C for 45 s, and 72 °C for 50 s), and a final extension at 72 °C for 5 min. The PCR product was then checked on 1% agarose gel electrophoresis. PCR product was purified and sequenced using the Ion Plus Fragment Library Kit 48 rxns (Thermo Fisher Scientific Inc., Waltham, MA, USA). Illumina sequencing reads were analyzed and demultiplexed using QIIME. Sequences with ≥97% similarity were clustered into operational

taxonomic units (OTUs). The relative abundance of an individual taxon was defined as its percentage (%) in the total number of OTUs.

2.5. Statistical Analysis

All statistical analyses were performed using R (version 3.6.3). The Shapiro–Wilk test and Levene's test were used to check the normality and homogeneity of variances prior to statistical analysis. Analysis of variance (ANOVA) was used to assess the differences between the mean values of the measured indexes. Eight representative key microbial phyla closely related to dead wood residues were selected through the forward selection method (Table 1). We used redundancy analysis (RDA) to elucidate the relationships between the soil properties and soil microbial compositions and rotten-wood components. To calculate the relative influence of each microbial phylum, we also employed the hierarchical partitioning method to distinguish a single variable's contribution via the "rdacca.hp" package in R [38]. Pearson correlation coefficients were also used to analyze relationships between the key microbial phyla and soil properties.

Table 1. Composition of rotten wood, soil properties and relative abundances of soil microbial key phylum.

		Indexes	DB	DW	CB	CW
Rotten-wood composition %		Lignin	61.62 ± 1.84 a	29.96 ± 1.72 b	30.39 ± 4.92 b	36.95 ± 2.09 b
		Cellulose	9.61 ± 0.79 b	31.10 ± 4.50 a	13.15 ± 1.18 b	31.06 ± 1.99 a
		Hemicellulose	4.61 ± 1.42 a	7.33 ± 1.15 a	7.63 ± 1.76 a	4.48 ± 1.16 a
		NS	16.16 ± 2.46 b	30.82 ± 6.45 ab	47.09 ± 6.57 a	25.87 ± 3.96 b
		Ash	7.99 ± 0 a	0.793 ± 0.19 c	1.75 ± 0.35 b	1.64 ± 0.28 bc
Soil physical–chemical proprieties		TC %	14.85 ± 1.56 ab	12.94 ± 4.76 ab	8.17 ± 2.59 b	18.86 ± 1.06 a
		TN %	0.88 ± 0.04 a	0.87 ± 0.25 a	0.45 ± 0.12 a	0.84± 0.15 a
		C/N	16.88 ± 1.00 ab	14.20 ± 1.27 b	17.69 ± 0.80 ab	21.77 ± 4.28 a
		AN mg/kg	829.7 ± 95.71 a	849.8 ± 228.11 a	461.5 ± 103.19 a	802.6 ± 219.86 a
		AP mg/kg	27.24 ± 10.46 ab	26.40 ± 7.67 ab	15.85 ± 4.10 b	37.77 ± 4.78 a
		AK mg/kg	320.50 ± 1.00 ab	304.83 ± 74.04 ab	188.17 ± 13.57 b	358.83 ± 43.86 a
		pH	5.30 ± 0.26 a	4.95 ± 0.20 a	4.81 ± 0.13 a	4.70 ± 0.37 a
Major phyla %	Fungi	Basidiomycota	46.44 ± 7.36 c	68.71 ± 5.59 ab	82.74 ± 4.23 a	60.10 ± 4.97 bc
		Ascomycota	12.47 ± 0.72 ab	13.00 ± 4.49 ab	5.09 ± 0.74 b	15.72 ± 0.95 a
		Rozellomycota	1.12 ± 0.55 a	0.97 ± 0.34 a	0.50 ± 0.47 a	1.08 ± 0.81 a
		Glomeromycota	1.07 ± 0.17 a	0.82 ± 0.33 ab	0.24 ± 0.05 b	0.47 ± 0.17 ab
	Bacteria	Acidobacteria	35.19 ± 13.04 a	26.48 ± 9.16 a	34.16 ± 13.26 a	31.71 ± 6.55 a
		Actinobacteria	3.77 ± 1.19 ab	7.18 ± 1.99 a	1.39 ± 0.60 b	3.96 ± 0.46 ab
		Nitrospirae	1.01± 0.12 a	0.75 ± 0.18 ab	0.39 ± 0.16 b	0.32 ± 0.15 b
		Armatimonadetes	0.28 ± 0.04 a	0.17 ± 0.06 a	0.31 ± 0.05 a	0.18 ± 0.03 a

All results are reported as mean ± standard error and different letters behind indicate significant differences between different treatments ($p < 0.05$). DB: Brown-rotten wood in the deciduous forest; DW: White-rot wood in the deciduous forest; CB: Brown-rotten wood in the coniferous forest; CW: White-rot wood in the coniferous forest. NS: non-structural compounds; TC: total carbon; TN: total nitrogen; AN: alkali-hydrolysable nitrogen; AP: available phosphorus; AK: available potassium.

3. Results and Discussion

3.1. Site-Specific Woody Debris Composition

The cellulose concentrations of woody debris were much higher in white-rot than in brown-rot sets, which increased by 223.62% and 136.20% in the deciduous and coniferous forest stands, respectively ($p < 0.05$, Table 1). In contrast, the lignin concentration was 105.67% higher in the brown-rot sets than in the white-rot sets of the deciduous forest stand ($p < 0.05$, Table 1). Such rot type effects occurred because white-rot fungi can competently mineralize lignin but gradually degrade cellulose and, thus, result in the accumulation of cellulosic materials [12,13]. However, brown-rot fungi can efficiently hydrolyze cellulose and hemicellulose but merely modify lignin compounds and, therefore, enrich lignin materials [11,39]. Consistent with lignin, the ash content was 908% higher in the brown-rot than in the white-rot sets of the deciduous forest stand ($p < 0.05$, Table 1). Ash is concentrated in woody debris probably because soluble substances (e.g., silicates,

sulfates, carbonates and metals) continuously infiltrate from closely contacted belowground minerals [33,34]. In particular, lignin-rich residues are abundant in aromatic products and can efficiently immobilize metals (e.g., calcium, iron, manganese, and magnesium) [40,41].

Interestingly, the abovementioned white-rot vs. brown-rot type distinction varied to greater extents in the deciduous than in the coniferous forest stand (Table 1). These observations suggest lower resistance of deciduous substrates against wood inhabitors compared to coniferous ones. Such an effect is probably related to lower contents of extractives (e.g., wax, resin) in the deciduous wood, indicating their hydrophilic properties and hence higher susceptibility to water absorption. This, in turn, could potentially facilitate access of mycelium hyphae to the deeper layers of plant materials and facilitate deciduous biodegradation [42]. Additionally, deciduous stems have higher contents of living parenchymas and lignocellulosic materials per unit volume and can accumulate higher concentrations of minerals than coniferous ones [6]. Such initial composition distinction may cause greater rot type difference in deciduous than in coniferous woody debris [40].

Contrary to the above site-specific rot type distinction, in the coniferous (but not deciduous) forest stand, the nonstructural (NS) content of the brown-rot sets concentrated as high as 47% and was over 80% greater than that of the white-rot sets (Table 1). The NS compounds in woody debris are soluble substances, including soluble carbohydrates, starch, nonprotein N, soluble proteins, and lipids; in particular, pine wood NS enriches alkyl C compounds and resin acids, which could be very resistant to decomposition [35]. Note that coniferous wood decomposition might be more closely related to belowground decomposers and nutrient cycling than deciduous wood decomposition [35]. Accordingly, we found that soil nutrient status was significantly influenced by rot type in the coniferous forest stand but not in the deciduous forest stand, as the contents of TC, AP and AK were significantly lower in the brown-rot than in the white-rot sets of the coniferous forest stand (Table 1). Probably because coniferous NS is highly resistant and coniferous wood decomposition is closely relevant to belowground nutrient availability [15,35,43], filamentous brown-rot fungi might be better adapted to utilizing soil nutrients (e.g., TC, AP, and AK) beneath decomposing wood, and brown-rot woody NS accumulated to a greater extent in the coniferous forest stand than in the deciduous forest stand. Together, these findings supported our first hypothesis that the white-rot and brown-rot type distinctions varied significantly between coniferous and deciduous forest stands.

3.2. Belowground Microbial Potential for Wood Decomposition

As previously reported [44], decaying wood can recruit specific decomposers and may result in a more diversified (i.e., Shannon and Simpson) and independent soil fungal community compared to the control (3 m away from decaying wood). In turn, wood decay processes may be profoundly influenced by these newly introduced decomposers. However, our results showed that there was no significant difference in the relative abundances of microbial phyla between wood rot sets (underneath the deadwood) and controls (1 m away from the deadwood) (except for Glomeromycota under CB, Table S1). To our surprise, nearly 90% of the variance in decomposed wood components was explained by the closely contacted belowground fungal and bacterial community structures based on the abundances of the eight major phyla ($p < 0.001$, Figure 1a,b). Such a great explanation potential of soil microbial communities underneath the woody debris is reasonable, as soil microbial communities can be crucial drivers of wood decomposition [44–46].

The soil fungal community structure at the phylum level alone explained nearly 60% of the variance in the woody debris components (Figure 1c), as Basidiomycota, Ascomycota and Glomeromycota contributed 26.62%, 17.74% and 12.25%, respectively (Figure 1b). Basidiomycota was negatively correlated with the rest of the fungal phyla (Figure 1a). In particular, Basidiomycota and Glomeromycota pointed to the exact opposite directions. Along the Basidiomycota vs. Glomeromycota negative correlation axis, the coniferous white-rot and brown-rot sets were separated from each other (but not for deciduous ones).

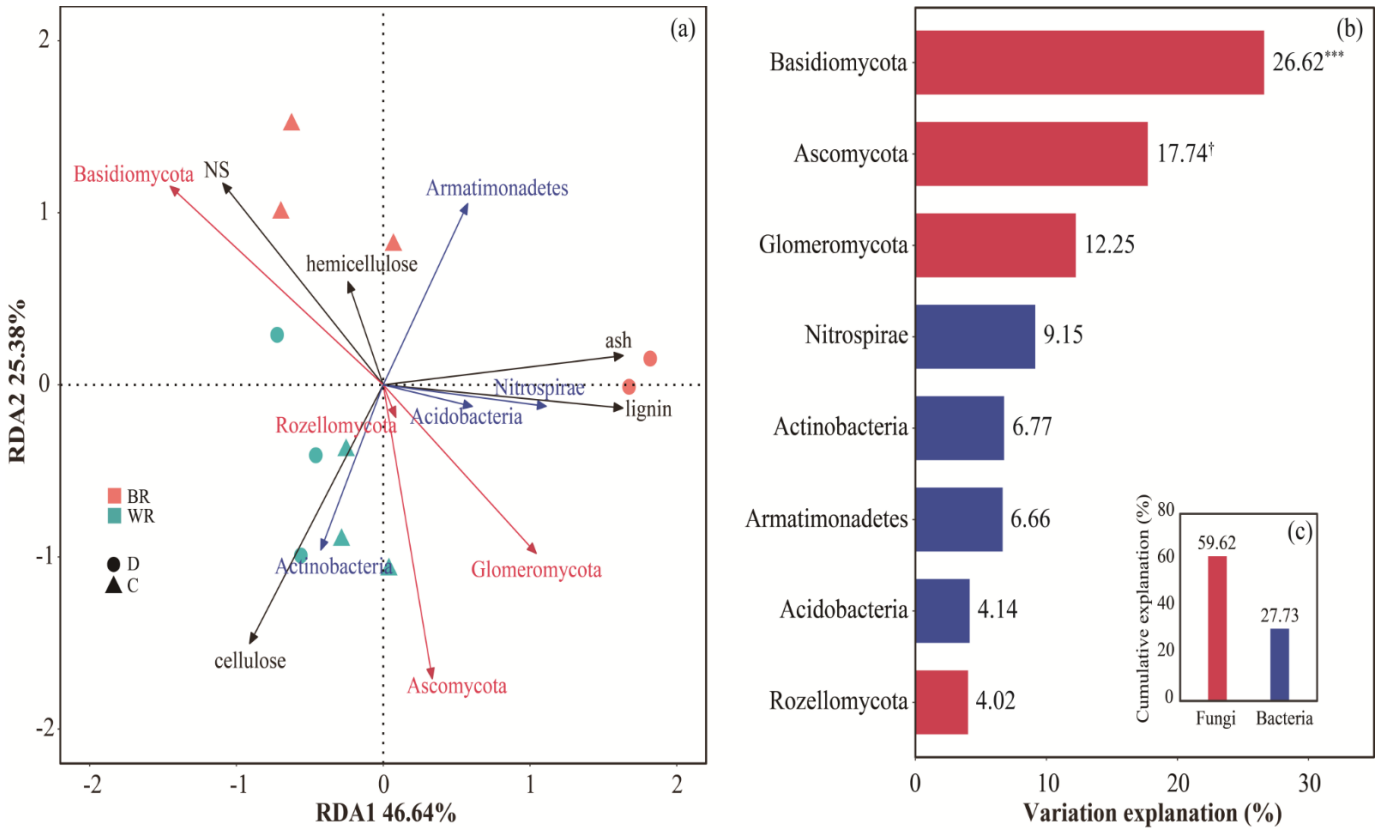


Figure 1. Rotten-wood components explained by key microbial phyla. (**a**) Redundancy analysis of rotten-wood components and belowground key microbial phyla; (**b**) The proportion of the total variation in rotten-wood components explained by key microbial phyla; and (**c**) The explanatory percentages assigned to each microbial function type. BR: brown-rot wood, WR: white-rot wood, D: deciduous, C: coniferous. †: $0.05 < p < 0.1$, ***: $p < 0.001$.

All of the abovementioned fungal phyla ubiquitously exist in soil and are highly related to the decomposition of lignocellulosic substances [44,47–49]. In general, basidiomycetous wood-decaying fungi (especially for white-rot decay) owe more powerful abilities in decomposing aromatic lignin polymers compared to ascomycetous fungi [47,48,50]. Under oxic condition, for instance, Basidiomycota isolates may prefer to degrade lignin via ligninolytic enzymes, whereas Ascomycota members are more likely to produce cellulose-degrading extracellular enzymes [51]. Although Ascomycota fungi may lack ligninolytic peroxidases in lignin degradation, they can rapidly consume easy-to-access substrates such as hemicellulose [52,53]. Accordingly, we found that Ascomycota was negatively relevant to hemicellulose, whereas Basidiomycota showed a negative relationship with lignin (Figure 1a). In addition, basidiomycetous wood-decaying fungi usually secrete versatile secondary metabolites such as lignin-derived phenolic and aromatic compounds, organic acids and smaller peptides [33,47]. Therefore, we observed a close and positive correlation between Basidiomycota fungal abundance and NS concentration (Figure 1a).

Glomeromycota fungi may have low cellulolytic and ligninolytic potentials due to a lack of genes encoding for cellulolytic glycoside hydrolase families and ligninolytic auxiliary activity enzymes. However, they can exhibit a large number of genes encoding for Kyoto Encyclopedia of Genes and Genomes (KEGG) metabolic and regulatory pathways, including amino acid metabolism, carbohydrate metabolism and lipid metabolism [48]. Their existence may not cause much consumption of lignin and cellulose but definitely reduce certain NS components (e.g., lipids and amino acids). Therefore, we observed a negative relationship between NS and Glomeromycota fungi; however, no correlation was observed between Glomeromycota fungi and cellulose (Figure 1a). In addition, Glom-

eromycota (arbuscular mycorrhizal (AM)) fungi are ubiquitous microorganisms living in symbiosis with vascular plants, and their symbiotic mycorrhizae help plants obtain inorganic micronutrients (e.g., phosphate ions) from the soil [48]. Their existence may cause high ash accumulation in wood; thus, a positive relationship occurred between the Glomeromycota fungi and the ash content (Figure 1a). Furthermore, Glomeromycota (AM) fungal colonization is strongly related to enriched lignin and organic acids [49]; thus, we found that Glomeromycota was more positively related to lignin than were the rest of the fungal phyla (Figure 1a).

Bacterial phylum composition alone explained nearly 28% of the variance in the woody debris components; their potential for wood decomposition variance ranked as follows: Nitrospirae (9.15%), Actinobacteria (6.77%), Armatimonadetes (6.66%) and Acidobaceria (4.14%) (Figure 1b). Interestingly, across the Basidiomycota vs. Glomeromycota negative correlation axis, we observed another negative correlation along the Actinobacteria vs. Armatimonadetes axis (Figure 1a), which was either highly positively or negatively related to the cellulose content. The remaining bacterial phyla, i.e., Nitrospirae and Acidobacteria, were both highly related to the lignin and ash contents (Figure 1a). In particular, the deciduous brown-rot and white-rot sets varied with the Nitrospirae and Acidobacteria abundances (Figure 1a).

Actinobacteria, Armatimonadetes and Acidobacteria are common deadwood-inhabiting prokaryotes [21,54–57]. Similar to our study, a previous study found that Acidobacteria in decaying wood were highly positively related to lignin content, whereas Actinobacteria were negatively related to wood ash content based on a redundancy analysis [58]. Actinobacteria and Acidobacteria possess diverse gene sets for the efficient decomposition of plant and fungal cell wall biopolymers and open reading frames encoding enzymes in the pretreatment and hydrolysis of complex carbohydrates, including cellulose, hemicelluloses, chitin and pectin [59–62]. In particular, Actinobacteria have great potential in the early colonization and decomposition of dead wood logs, and their relative abundances always significantly decline during the wood decay process. Their early predominant detection in wood decay is most likely due to the fast germination of dormant spores [63]. In addition, Actinobacteria members may degrade a large proportion of hemicellulose (which is more easily mineralizable C compared to lignin and cellulose) [64]. Furthermore, the early degradation of easily mineralizable C (xylose) was dominated by Actinobacteria at day 7 of the ^{13}C-xylose treatment; xylose consumption occurred before cellulose consumption [65]. These previous studies support a negative relationship between Actinobacteria abundance and hemicellulose concentration (Figure 1a). Moreover, Armatimonadetes encode cellulase genes and are potential decomposers of cellulose [66]; they are significantly enriched under polyethylene plastics, indicating their ability to use a very stable C-C or C-heteroatom backbone [67]. Together, these findings supported our second hypothesis that the woody debris components were strongly determined by the underlying soil microbial communities.

3.3. Wood Inbabitors Mediated by Soil Nutrient Status

Of the abovementioned putatively wood decomposition phyla, Basidiomycota, Ascomycota and Acidobacteria presented site-specific rot type distinctions (Table 1). For instance, the relative abundances of Basidiomycota ranged from 46.44% to 82.74% and declined by 48% from the white-rot sets to the brown-rot sets in the deciduous stand but presented an opposite trend in the coniferous forest stand (38% higher in the brown-rot sets than in the white-rot sets) ($p < 0.05$, Table 1). However, the relative abundances of Ascomycota (5.09%–15.72%) under the white-rot sets was 209% higher than those under the brown-rot sets in coniferous forest stand ($p < 0.05$, Table 1) but had no rot type distinction in deciduous forest stand ($p > 0.05$, Table 1). Such a rot type distinction on Ascomycota is probably because coniferous extracts of brown-rot sets are generally more active in inhibiting Ascomycota fungi than deciduous extracts are [68]. In addition, the relative abundance of Glomeromycota (0.24%–1.07%) was consistently higher in the deciduous forest than in the coniferous forest, especially for the white-rot sets (350% higher, $p < 0.05$, Table 1).

Similarly, the bacterial phylum Nitrospirae (0.32%–1.01%) was more abundant in the deciduous forest than in the coniferous forest, and the white-rot sets showed a significant forest type distinction (160% higher, $p < 0.05$, Table 1). Moreover, the relative abundances of Actinobacteria (1.39%–7.18%) were consistently slightly higher in the white-rot sets than in the brown-rot sets, separately declining by 90% and 185% in the deciduous and coniferous forest stands, respectively (Table 1). However, the opposite trends were observed with Acidobacteria (26.48%–35.19%), whose relative abundances were by 33% and 8% higher in brown- than white-rot sets in the deciduous and coniferous forest stands, respectively (Table 1).

Site-specific trends also occurred with soil chemical properties. For instance, in the coniferous (but not deciduous) forest stands, the contents of TC, AP and AK were 131%, 138%, and 91% higher in the white-rot sets than in the brown-rot sets, respectively ($p < 0.05$, Table 1). Soil properties (e.g., pH and AN) strongly influence microbial communities dominating wood decomposition [55,69]. In this study, all measured soil physical–chemical properties influenced the fungal phyla to a greater extent than the soil bacterial phyla, as soil properties were significantly related to the relative abundances of major fungal phyla but not to bacterial phyla (Table 1). Such fungi vs. bacteria distinction might be due to the fact that the fungi often form a complex mycelium network which can penetrate both wood tissues and belowground matrix and result in the relocation of available nutrients in between [70–72]. These findings suggest that fungi, but not bacteria, are a hot hub for nutrient mobilization and transportation during the process of wood decomposition in temperate forests.

The major fungal phyla showed opposite correlations with soil nutrient status: the relative abundance of Basidiomycota was negatively related to the soil nutrient contents (e.g., TC, TN, AN and AP); conversely, significantly positive relationships were observed between nutrient status (e.g., TC, TN, AP, AK or pH) and Ascomycota (or Glomeromycota) ($p < 0.05$, Table 2). Similar reverse trends among Basidiomycota, Ascomycota and Glomeromycota were also observed previously. For instance, Basidiomycota abundances were significantly positively related to TP but negatively related to pH, whereas the opposite relationships emerged for Ascomycota and Glomeromycota [44]; moreover, Basidiomycota and Ascomycota exhibited positive or negative correlations with edaphic properties [73]. Such opposite trends might be due to their distinct lifestyle strategies, as Basidiomycota fungi are oligotrophs and prefer nutrient-poor environments, but Ascomycota and Glomeromycota are characterized by copiotrophic features and prefer nutrient-rich environments [25,26]. Particularly, an increased availability of soil nutrients (e.g., AP, NH_4^+-N, TN, and/or SOC) promotes the growth of Glomeromycota (Arbuscular mycorrhizal) fungi [25,74]; additionally, Ascomycota was previously reported to be significantly positively related to soil C and N contents [75]. On the contrary, Basidiomycota fungi are always negatively related to soil nutrient availability (e.g., TC, TN, AN, and AP) [26]. In addition, soil saprophytes that colonize and decompose decayed wood may greatly improve the soil nutrients underneath decaying wood [76,77]. Conversely, increased nutrient (e.g., N) availability has an inhibitory effect on the lignin degradation potential of Basidiomycetes by substantially reducing their phenol oxidase activity [78].

The above oligotrophy vs. copiotrophy distinctions and their reverse relationships with soil available nutrients can clearly explain the correlations between the fungal phyla and woody debris composition (Figure 1a). For instance, as oligotrophic Basidiomycota fungi were less dependent upon or even inhibited by available nutrients, they might be less restrained by the concentration of easily available woody NS. This means that NS could be accumulated in woody debris under the predominant Basidiomycota communities. Therefore, a strongly positive relationship occurred between Basidiomycota and NS (Figure 1a). In contrast, the copiotrophic fungal phyla (Ascomycota and Glomeromycota) were both strongly dependent upon soil nutrient availability (Table 1); thus, their dominance in woody debris must consume a great amount of easily available NS (e.g., a negative relationship between Glomeromycota and NS, Figure 1a). In particular,

Glomeromycota (AM) fungi may promote wood residue decomposition under situations of high available N belowground [25,79–81]. Glomeromycota was accompanied by lower NS contents in woody debris (Figure 1a) and higher TN and AN content belowground (Table 1), suggesting that Glomeromycota decomposers are strongly constrained by soil nutrient availability (e.g., NH_4^+-N) underneath woody debris. Soil microbial phylum relative abundances (especially for fungi) were closely related to soil traits (Table 2), supporting our third hypothesis.

Table 2. Pearson coefficients between microbial phyla and soil properties.

	Taxa	TC	TN	C/N	AN	AP	AK	pH
Fungi	Basidiomycota	−0.67 *	−0.72 *	−0.02	−0.70 *	−0.70 *	−0.57	−0.43
	Ascomycota	0.62 *	0.55	0.26	0.46	0.72 *	0.77 **	0.17
	Rozellomycota	0.40	0.52	−0.18	0.53	0.34	0	0.49
	Glomeromycota	0.43	0.74 **	−0.41	0.72 *	0.39	0.49	0.74 **
Bacteria	Acidobacteria	−0.06	−0.05	−0.09	0.01	0.10	−0.18	0.11
	Actinobacteria	0.41	0.55	−0.08	0.47	0.24	0.46	−0.01
	Nitrospirae	−0.03	0.20	−0.37	0.16	0.10	0.05	0.54
	Armatimonadetes	−0.14	−0.08	−0.14	0	−0.15	−0.18	0.19

*: $p < 0.05$. **: $p < 0.01$. TC: total carbon; TN: total nitrogen; AN: alkali-hydrolysable nitrogen; AP: available phosphorus; AK: available potassium.

4. Conclusions

To the best of our knowledge, this study is the first to experimentally disentangle the mechanisms behind site-specific wood decomposition in the context of rot type distinction. Importantly, our results revealed that in situ wood decomposition differed in white-rot vs. brown-rot sets and in coniferous vs. deciduous forest stands via differences in soil microbial communities and chemical properties underneath the decaying woods. More importantly, the potential wood inhabitors such as Ascomycota and Basidiomycota are distinct in life strategy and substrate utilization and are strongly dependent upon site-specific soil physical–chemical properties. Our findings suggest that the accurate prediction of wood decay in forest ecosystems is needed to fully unravel the contributions of belowground microbial communities and nutrient status distinctions.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13091446/s1, Table S1: T-test results of relative abundance of soil microbial phyla in deadwood and control soils.

Author Contributions: Conceptualization and methodology, Z.B.; writing—original draft preparation, Y.Y.; writing—review and editing, Z.B. and S.Y.; project administration and funding acquisition, J.W. and H.-S.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This research was financially supported by the National Natural Science Foundation of China (31870625), Natural Science Foundation of Hunan Province (2022JJ50322) and Science & Technology Projects of Hunan Province (2022KJH39).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; et al. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **1986**, *15*, 133–302. [CrossRef]
2. Laiho, R.; Prescott, C.E. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. *Can. J. For. Res.* **2004**, *34*, 763–777. [CrossRef]

3. Martin, A.R.; Domke, G.M.; Doraisami, M.; Thomas, S.C. Carbon fractions in the world's dead wood. *Nat. Commun.* **2021**, *12*, 889. [CrossRef] [PubMed]
4. Bai, Z.; Ma, Q.; Dai, Y.; Yuan, H.; Ye, J.; Yu, W. Spatial heterogeneity of SOM concentrations associated with white-rot versus brown-rot wood decay. *Sci. Rep.* **2017**, *7*, 13758. [CrossRef] [PubMed]
5. Stutz, K.P.; Dann, D.; Wambsganss, J.; Scherer-Lorenzen, M.; Lang, F. Phenolic matter from deadwood can impact forest soil properties. *Geoderma* **2017**, *288*, 204–212. [CrossRef]
6. Khan, K.; Tuyen, T.T.; Chen, L.; Duan, W.; Hussain, A.; Jamil, M.A.; Li, C.; Guo, Q.; Qu, M.; Wang, Y.; et al. Nutrient dynamics assessment of coarse wood debris subjected to successional decay levels of three forests types in northeast, China. *Forests* **2021**, *12*, 401. [CrossRef]
7. Prewitt, L.; Kang, Y.; Kakumanu, M.L.; Williams, M. Fungal and bacterial community succession differs for three wood types during decay in a forest soil. *Microb. Ecol.* **2014**, *68*, 212–221. [CrossRef]
8. Bugg, T.D.; Ahmad, M.; Hardiman, E.M.; Singh, R. The emerging role for bacteria in lignin degradation and bio-product formation. *Curr. Opin. Biotechnol.* **2011**, *22*, 394–400. [CrossRef]
9. Iimura, Y.; Abe, H.; Otsuka, Y.; Sato, Y.; Habe, H. Bacterial community coexisting with white-rot fungi in decayed wood in nature. *Curr. Microbiol.* **2021**, *78*, 3212–3217. [CrossRef]
10. Riley, R.; Salamov, A.A.; Brown, D.W.; Nagy, L.G.; Floudas, D.; Held, B.W.; Levasseur, A.; Lombard, V.; Morin, E.; Otillar, R.; et al. Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 9923–9928. [CrossRef]
11. Floudas, D.; Held, B.W.; Riley, R.; Nagy, L.G.; Koehler, G.; Ransdell, A.S.; Younus, H.; Chow, J.; Chiniquy, J.; Lipzen, A.; et al. Evolution of novel wood decay mechanisms in Agaricales revealed by the genome sequences of *Fistulina hepatica* and *Cylindrobasidium torrendii*. *Fungal Genet. Biol.* **2015**, *76*, 78–92. [CrossRef] [PubMed]
12. Atiwesh, G.; Parrish, C.C.; Banoub, J.; Le, T.T. Lignin degradation by microorganisms: A review. *Biotechnol. Prog.* **2022**, *38*, e3226. [CrossRef] [PubMed]
13. Fukasawa, Y.; Matsukura, K. Decay stages of wood and associated fungal communities characterise diversity–decomposition relationships. *Sci. Rep.* **2021**, *11*, 8972. [CrossRef] [PubMed]
14. Aleinikovas, M.; Varnagirytė-Kabašinskienė, I.; Povilaitienė, A.; Šilinskas, B.; Škėma, M.; Beniušienė, L. Resistance of Wood Treated with Iron Compounds against Wood-Destroying Decay and Mould Fungi. *Forests* **2021**, *12*, 645. [CrossRef]
15. Tuor, U.; Winterhalter, K.; Fiechter, A. Enzymes of white-rot fungi involved in lignin degradation and ecological determinants for wood decay. *J. Biotechnol.* **1995**, *41*, 1–17. [CrossRef]
16. Gora, E.M.; Lucas, J.M.; Yanoviak, S.P. Microbial composition and wood decomposition rates vary with microclimate from the ground to the canopy in a tropical forest. *Ecosystems* **2019**, *22*, 1206–1219. [CrossRef]
17. Fravolini, G.; Egli, M.; Derungs, C.; Cherubini, P.; Ascher-Jenull, J.; Gómez-Brandón, M.; Bardelli, T.; Tognetti, R.; Lombardi, F.; Marchetti, M. Soil attributes and microclimate are important drivers of initial deadwood decay in sub-alpine Norway spruce forests. *Sci. Total Environ.* **2016**, *569–570*, 1064–1076. [CrossRef]
18. Wu, C.; Ulyshen, M.D.; Shu, C.; Zhang, Z.; Zhang, Y.; Liu, Y.; Wang, G.G. Stronger effects of termites than microbes on wood decomposition in a subtropical forest. *For. Ecol. Manag.* **2021**, *493*, 119263. [CrossRef]
19. Fukasawa, Y. Ecological impacts of fungal wood decay types: A review of current knowledge and future research directions. *Ecol. Res.* **2021**, *36*, 910–931. [CrossRef]
20. Maynard, D.S.; Covey, K.R.; Crowther, T.W.; Sokol, N.W.; Morrison, E.W.; Frey, S.D.; van Diepen, L.T.A.; Bradford, M.A. Species associations overwhelm abiotic conditions to dictate the structure and function of wood-decay fungal communities. *Ecology* **2018**, *99*, 801–811. [CrossRef]
21. Kielak, A.M.; Scheublin, T.R.; Mendes, L.W.; Van Veen, J.A.; Kuramae, E.E. Bacterial community succession in pine-wood decomposition. *Front. Microbiol.* **2016**, *7*, 231. [CrossRef] [PubMed]
22. Goldmann, K.; Schöning, I.; Buscot, F.; Wubet, T. Forest management type influences diversity and community composition of soil fungi across temperate forest ecosystems. *Front. Microbiol.* **2015**, *6*, 1300. [CrossRef] [PubMed]
23. Ding, J.; Jiang, X.; Ma, M.; Zhou, B.; Guan, D.; Zhao, B.; Zhou, J.; Cao, F.; Li, L.; Li, J. Effect of 35 years inorganic fertilizer and manure amendment on structure of bacterial and archaeal communities in black soil of northeast China. *Appl. Soil Ecol.* **2016**, *105*, 187–195. [CrossRef]
24. Gai, X.; Zhong, Z.; Zhang, X.; Bian, F.; Yang, C. Effects of chicken farming on soil organic carbon fractions and fungal com-munities in a Lei bamboo (*Phyllostachys praecox*) forest in subtropical China. *Forest Ecol. Manag.* **2021**, *479*, 118603. [CrossRef]
25. Guo, J.; Feng, H.; Roberge, G.; Feng, L.; Pan, C.; McNie, P.; Yu, Y. The negative effect of Chinese fir (*Cunninghamia lanceolata*) monoculture plantations on soil physicochemical properties, microbial biomass, fungal communities, and enzymatic activities. *For. Ecol. Manag.* **2022**, *519*, 120297. [CrossRef]
26. Yao, F.; Yang, S.; Wang, Z.; Wang, X.; Ye, J.; Wang, X.; DeBruyn, J.M.; Feng, X.; Jiang, Y.; Li, H. Microbial taxa distribution is associated with ecological trophic cascades along an elevation gradient. *Front. Microbiol.* **2017**, *8*, 2071. [CrossRef] [PubMed]
27. Yuan, S.; Tang, T.; Wang, M.; Chen, H.; Zhang, A.; Yu, J. Regional scale determinants of nutrient content of soil in a cold-temperate forest. *Forests* **2018**, *9*, 177. [CrossRef]
28. Hansson, K.; Olsson, B.A.; Olsson, M.; Johansson, U.; Kleja, D.B. Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden. *For. Ecol. Manag.* **2011**, *262*, 522–530. [CrossRef]

29. Jaroszewicz, B.; Cholewińska, O.; Chećko, E.; Wrzosek, M. Predictors of diversity of deadwood-dwelling macrofungi in a European natural forest. *Forest Ecol. Manag.* **2021**, *490*, 119123. [CrossRef]
30. Mäkinen, H.; Hynynen, J.; Siitonen, J.; Sievänen, R. Predicting the decomposition of Scots Pine, Norway Spruce, and Birch Stems in Finland. *Ecol. Appl.* **2006**, *16*, 1865–1879. [CrossRef]
31. Van Soest, P.J. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *J. Assoc. Off. Anal. Chem.* **1963**, *46*, 829–835.
32. Van Soest, P.J.; Wine, R.H. Use of detergents in the analysis of fibrous feeds. Iv. Determination of plant cell-wall constituents. *J. Assoc. Off. Anal. Chem.* **1967**, *50*, 50–55.
33. Shukla, A.N.; Singh, I.D. Biodegradation ofShorea robusta Gaertn. leaf litter and the cycling of minerals in a tropical sal forest. *Plant Soil* **1984**, *81*, 403–409. [CrossRef]
34. Gelbrich, J.; Mai, C.; Militz, H. Chemical changes in wood degraded by bacteria. *Int. Biodeterior. Biodegrad.* **2008**, *61*, 24–32. [CrossRef]
35. Strukelj, M.; Brais, S.; Quideau, S.A.; Angers, V.A.; Kebli, H.; Drapeau, P.; Oh, S.-W. Chemical transformations in downed logs and snags of mixed boreal species during decomposition. *Can. J. For. Res.* **2013**, *43*, 785–798. [CrossRef]
36. Lu, R. *Soil and Agro-Chemical Analytical Methods*; China Agricultural Science and Technology Press: Beijing, China, 2000. (In Chinese)
37. Bai, Z.; Ye, J.; Wei, Y.-L.; Yan, S.-K.; Yuan, H.-S. Soil depth-dependent C/N stoichiometry and fungal and bacterial communities along a temperate forest succession gradient. *Catena* **2021**, *207*, 105613. [CrossRef]
38. Lai, J.; Zou, Y.; Zhang, J.; Peres-Neto, P.R. Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca.hp R package. *Methods Ecol. Evol.* **2022**, *13*, 782–788. [CrossRef]
39. Blanchette, R.A. Degradation of the lignocellulose complex in wood. *Can. J. Bot.* **1995**, *73*, 999–1010. [CrossRef]
40. Filley, T.R.; Cody, G.D.; Goodell, B.; Jellison, J.; Noser, C.; Ostrofsky, A. Lignin demethylation and polysaccharide decomposition in spruce sapwood degraded by brown rot fungi. *Org. Geochem.* **2002**, *33*, 111–124. [CrossRef]
41. Ostrofsky, A.; Jellison, J.; Smith, K.T.; Shortle, W.C. Changes in cation concentrations in red spruce wood decayed by brown rot and white rot fungi. *Can. J. Forest Res.* **1997**, *27*, 567–571. [CrossRef]
42. Barton-Pudlik, J.; Czaja, K.; Grzymek, M.; Lipok, J. Evaluation of wood-polyethylene composites biodegradability caused by filamentous fungi. *Int. Biodeterior. Biodegrad.* **2017**, *118*, 10–18. [CrossRef]
43. Worrall, J.J.; Anagnost, S.E.; Zabel, R.A. Comparison of wood decay among diverse lignicolous fungi. *Mycologia* **1997**, *89*, 199–219. [CrossRef]
44. Wang, Q.; Peñuelas, J.; Tan, B.; Wang, Z.; Li, H.; Cao, R.; Chang, C.; Jiang, Y.; Yang, W. The role of decaying logs in nursing soil fungal diversity varies with decay classes in the forest ecosystem. *Eur. J. Soil Sci.* **2022**, *73*, e13243. [CrossRef]
45. Bradford, M.A.; Maynard, D.S.; Crowther, T.W.; Frankson, P.T.; Mohan, J.E.; Steinrueck, C.; Veen, G.F.; King, J.R.; Warren, R.J. Belowground community turnover accelerates the decomposition of standing dead wood. *Ecology* **2021**, *102*, e03484. [CrossRef]
46. Buresova, A.; Kopecky, J.; Hrdinkova, V.; Kamenik, Z.; Omelka, M.; Sagova-Mareckova, M. Succession of microbial decom-posers is determined by litter type, but site conditions drive decomposition rates. *Appl. Environ. Microbiol.* **2019**, *85*, e01760-19. [CrossRef]
47. Lundell, T.K.; Makela, M.R.; Hilden, K. Lignin-modifying enzymes in filamentous basidiomycetes–ecological, functional and phylogenetic review. *J. Basic Microbiol.* **2010**, *50*, 5–20. [CrossRef]
48. Kameshwar, A.K.S.; Qin, W. Systematic review of publicly available non-Dikarya fungal proteomes for understanding their plant biomass-degrading and bioremediation potentials. *Bioresour. Bioprocess.* **2019**, *6*, 30. [CrossRef]
49. Fukasawa, Y. Effects of wood decomposer fungi on tree seedling establishment on coarse woody debris. *For. Ecol. Manag.* **2012**, *266*, 232–238. [CrossRef]
50. Lundell, T.K.; Mäkelä, M.R.; de Vries, R.P.; Hildén, K.S. Genomics, lifestyles and future prospects of wood-decay and litter-decomposing Basidiomycota. *Adv. Bot. Res.* **2014**, *70*, 329–370. [CrossRef]
51. Perkins, A.K.; Rose, A.L.; Grossart, H.-P.; Rojas-Jimenez, K.; Prescott, S.K.B.; Oakes, J.M. Oxic and anoxic organic polymer degradation potential of endophytic fungi from the marine macroalga, *Ecklonia radiata*. *Front. Microbiol.* **2021**, *12*, 726138. [CrossRef]
52. Arnstadt, T.; Hoppe, B.; Kellner, H.; Kruger, D.; Bauhus, J.; Hofrichter, M. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. *For. Ecol. Manag.* **2016**, *382*, 129–142. [CrossRef]
53. Ferrari, R.; Gautier, V.; Silar, P. Lignin degradation by ascomycetes. *Adv. Bot. Res.* **2021**, *99*, 77–113. [CrossRef]
54. Kwaśna, H.; Szewczyk, W.; Baranowska, M.; Behnke-Borowczyk, J. Bacteria associated with vascular wilt of poplar. *Arch. Microbiol.* **2021**, *203*, 4829–4838. [CrossRef] [PubMed]
55. Moll, J.; Kellner, H.; Leonhardt, S.; Stengel, E.; Dahl, A.; Bässler, C.; Buscot, F.; Hofrichter, M.; Hoppe, B. Bacteria inhabiting deadwood of 13 tree species are heterogeneously distributed between sapwood and heartwood. *Environ. Microbiol.* **2018**, *20*, 3744–3756. [CrossRef]
56. Probst, M.; Ascher-Jenull, J.; Insam, H.; Gómez-Brandón, M. The molecular information about deadwood bacteriomes partly depends on the targeted environmental DNA. *Front. Microbiol.* **2021**, *12*, 640386. [CrossRef]
57. Sun, H.; Terhonen, E.; Kasanen, R.; Asiegbu, F.O. Diversity and community structure of primary wood-inhabiting bacteria in boreal forest. *Geomicrobiol. J.* **2014**, *31*, 315–324. [CrossRef]

58. Peng, M.; Jing, Y.; Wang, Q.; Yan, S. Different decaying wood effects on bacterial diversity: Insights from molecular methods. *Phyton-Int. J. Exp. Bot.* **2021**, *90*, 207–222. [CrossRef]
59. Eichorst, S.A.; Kuske, C.R.; Schmidt, T.M. Influence of plant polymers on the distribution and cultivation of bacteria in the phylum *Acidobacteria*. *Appl. Environ. Microbiol.* **2011**, *77*, 586–596. [CrossRef]
60. Tláskal, V.; Baldrian, P. Deadwood-inhabiting bacteria show adaptations to changing carbon and nitrogen availability during decomposition. *Front. Microbiol.* **2021**, *12*, 685303. [CrossRef]
61. Štursová, M.; Žifčáková, L.; Leigh, M.B.; Burgess, R.; Baldrian, P. Cellulose utilization in forest litter and soil: Identification of bacterial and fungal decomposers. *FEMS Microbiol. Ecol.* **2012**, *80*, 735–746. [CrossRef]
62. Le, T.T.; Nguyen, T.B.; Nguyen, H.D.; Nguyen, H.D.; Le, N.G.; Dao, T.K.; Nguyen, T.Q.; Do, T.H.; Truong, N.H. De novo metagenomic analysis of microbial community contributing in lignocellulose degradation in humus samples harvested from Cuc Phuong tropical forest in Vietnam. *Diversity* **2022**, *14*, 220. [CrossRef]
63. Hoppe, B.; Krüger, D.; Kahl, T.; Arnstadt, T.; Buscot, F.; Bauhus, J.; Wubet, T. A pyrosequencing insight into sprawling bacterial diversity and community dynamics in decaying deadwood logs of *Fagus sylvatica* and *Picea abies*. *Sci. Rep.* **2015**, *5*, 9456. [CrossRef] [PubMed]
64. Oh, H.N.; Lee, T.K.; Park, J.W.; No, J.H.; Kim, D.; Sul, W.J. Metagenomic SMRT Sequencing-Based exploration of novel lignocellulose-degrading capability in wood detritus from Torreya nucifera in Bija forest on Jeju Island. *J. Microbiol. Biotechnol.* **2017**, *27*, 1670–1680. [CrossRef] [PubMed]
65. Pepe-Ranney, C.; Campbell, A.N.; Koechli, C.N.; Berthrong, S.; Buckley, D.H. Unearthing the ecology of soil microorganisms using a high resolution DNA-SIP approach to explore cellulose and xylose metabolism in soil. *Front. Microbiol.* **2016**, *7*, 703. [CrossRef] [PubMed]
66. Liu, L.; Huang, W.-C.; Liu, Y.; Li, M. Diversity of cellulolytic microorganisms and microbial cellulases. *Int. Biodeterior. Biodegrad.* **2021**, *163*, 105277. [CrossRef]
67. Wang, J.; Huang, M.; Wang, Q.; Sun, Y.; Zhao, Y.; Huang, Y. LDPE microplastics significantly alter the temporal turnover of soil microbial communities. *Sci. Total Environ.* **2020**, *726*, 138682. [CrossRef]
68. Alfredsen, G.; Solheim, H.; Slimestad, R. Antifungal effect of bark extracts from some European tree species. *Eur. J. Forest Res.* **2008**, *127*, 387–393. [CrossRef]
69. Sellan, G.; Thompson, J.; Majalap, N.; Robert, R.; Brearley, F.Q. Impact of soil nitrogen availability and pH on tropical heath forest organic matter decomposition and decomposer activity. *Pedobiol. J. Soil Ecol.* **2020**, *80*, 150645. [CrossRef]
70. Baldrian, P. Wood-inhabiting ligninolytic basidiomycetes in soils: Ecology and constraints for applicability in bioremediation. *Fungal Ecol.* **2008**, *1*, 4–12. [CrossRef]
71. Boddy, L. Saprotrophic cord-forming fungi: Warfare strategies and other ecological aspects. *Mycol. Res.* **1993**, *97*, 641–655. [CrossRef]
72. Boddy, L.; Hynes, J.; Bebber, D.P.; Fricker, M.D. Saprotrophic cord systems: Dispersal mechanisms in space and time. *Mycoscience* **2009**, *50*, 9–19. [CrossRef]
73. Zeng, Q.; Jia, P.; Wang, Y.; Wang, H.; Li, C.; An, S. The local environment regulates biogeographic patterns of soil fungal communities on the Loess Plateau. *CATENA* **2019**, *183*, 104220. [CrossRef]
74. Li, W.-Q.; Huang, Y.-X.; Chen, F.-S.; Liu, Y.-Q.; Lin, X.-F.; Zong, Y.-Y.; Wu, G.-Y.; Yu, Z.-R.; Fang, X.-M. Mixing with broad-leaved trees shapes the rhizosphere soil fungal communities of coniferous tree species in subtropical forests. *For. Ecol. Manag.* **2021**, *480*, 118664. [CrossRef]
75. Carron, A.I.; Garibaldi, L.A.; Marquez, S.; Fontenla, S. The soil fungal community of native woodland in Andean Patagonian forest: A case study considering experimental forest management and seasonal effects. *For. Ecol. Manag.* **2020**, *461*, 117955. [CrossRef]
76. Moghimian, N.; Jalali, S.G.; Kooch, Y.; Rey, A. Downed logs improve soil properties in old-growth temperate forests of northern Iran. *Pedosphere* **2020**, *30*, 378–389. [CrossRef]
77. Mäkipää, R.; Rajala, T.; Schigel, D.; Rinne, K.T.; Pennanen, T.; Abrego, N.; Ovaskainen, O. Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. *ISME J.* **2017**, *11*, 1964–1974. [CrossRef] [PubMed]
78. Saiya-Cork, K.R.; Sinsabaugh, R.L.; Zak, D.R. The effects of long term nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. *Soil Biol. Biochem.* **2002**, *34*, 1309–1315. [CrossRef]
79. Boldt-Burisch, K.; Schillem, S.; Schneider, B.U.; Hüttl, R.F. The effect of nitrogen-modified lignite granules on mycorrhization and root and shoot growth of *Secale cereale* (winter rye) in a nutrient-deficient, sandy soil. *Arch. Agron. Soil Sci.* **2022**, *68*, 1117–1130. [CrossRef]
80. Tedersoo, L.; Kõljalg, U.; Hallenberg, N.; Larsson, K.-H. Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. *N. Phytol.* **2003**, *159*, 153–165. [CrossRef]
81. Tu, C.; Booker, F.L.; Watson, D.M.; Chen, X.I.N.; Rufty, T.W.; Shi, W.E.; Hu, S. Mycorrhizal mediation of plant N acquisition and residue decomposition: Impact of mineral N inputs. *Glob. Chang. Biol.* **2006**, *12*, 793–803. [CrossRef]