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The Addition of a Small Dose of *Cinnamomum camphora* Biomass Unexpectedly Enhanced Lignocellulose Degradation during the Compost of *Stropharia rugosoannulata* Cultivation Materials

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Abstract: This research explored the effects of the addition of low doses of aromatic plant biomasses (APBs) on the microbial community and carbon source decomposition in compost. APBs were reported to be capable of altering the composition and function of microbial communities in many environments. However, the effects of APB addition on the compost carbon source metabolism, a process highly linked to the microbial community of compost, were still unclarified, especially when added in small doses. In this study, *Cinnamomum camphora* biomass was added to the initial compost of *Stropharia rugosoannulata* cultivation materials, in a mass ratio of 0%, 1%, 2%, and 3%, respectively. The variation in the carbon source contents, the microbial community composition, and the related enzyme activities of the end compost products were measured. The results showed that *Cinnamomum camphora* biomass addition significantly altered the content of cellulose, hemicellulose, lignin, and protein of compost products, but did not affect the starch and soluble sugar content. Meanwhile, the addition significantly reduced lignin peroxidase and cellulase activities, but increased xylanase and laccase activities, and had no effect on magnesium peroxidase and polyphenol oxidase. Both the bacterial and fungal community compositions were significantly altered by the addition, though the alpha diversity indexes were not significantly changed. The relative abundance of *Proteobacteria* and *Sordariomycetes* was significantly increased by the addition, while *Acidobacteria*, *Chloroflexi* and *Eurotiomycetes* significantly decreased. Structural equation modeling found that the variation in the bacterial community composition (0.464 standard total effect) provided a higher contribution to lignocellulose degradation, rather than the fungal community (0.365 standard total effect). A co-occurrence network analysis further revealed that the trade-off between lignin peroxidase and laccase activity, which was induced by the relative abundance variation in *Proteobacteria*, *Actinobacteriota*, and *Firmicute* members, was the main driver in the lignocellulose decomposition variation. This research provides a new insight into the recycling of APB waste, and offers an improvement to mushroom cultivation material compost.

Keywords: lignocellulose; compost; microbial community; *Cinnamomum camphora*; *Stropharia rugosoannulata* cultivation materials

Citation: Zhou, H.; Di, L.; Hua, X.; Deng, T.; Wang, X. The Addition of a Small Dose of *Cinnamomum camphora* Biomass Unexpectedly Enhanced Lignocellulose Degradation during the Compost of *Stropharia rugosoannulata* Cultivation Materials. *Sustainability* **2023**, *15*, 10483. https://doi.org/10.3390/su151310483

Academic Editor: Ali Ayoub

Received: 3 May 2023
Revised: 13 June 2023
Accepted: 30 June 2023
Published: 4 July 2023

1. Introduction

Stropharia rugosoannulata is a famous edible mushroom which is recommended to developing countries by the World Food and Agriculture Organization [1,2]. The yield of *Stropharia rugosoannulata* is closely related to the carbon source composition of the cultivation materials [3,4]. A high content of macromolecular carbohydrate prohibits mycelial growth and hinders the assimilation and utilization of materials, which in turn reduces the

following yield [3,4]. Thus, before production, the cultivation materials generally need to be composted, to break down the macromolecular carbon sources inside, especially aromatic recalcitrant carbons, such as lignin, and transform them into labile carbons that are readily accessible to *Stropharia rugosoannulata* [5]. During the composting process, the microbial community secretes extracellular enzymes (e.g., cellulase) to destroy the covalent bonds that conjunct the monomers into macromolecules, releases oxidative enzymes (e.g., lignin peroxidase) to decompose complex molecular structures, and converts macromolecules into small organic molecules, such as simple sugars [6–8]. Hence, variations in the microbial community composition and function directly influence the lignocellulose contents and the quality of cultivation materials [6–8]. Regulation of the oxygen level [9], the pH [10], and the content of nitrogen [11] and phosphorus [12] had previously been reported as main ways to control the microbial community metabolism activity, and the carbon source composition, of final compost products. However, such regulation is always costly in terms of workers and materials [1,2]. There is a need to find alternative methods to reduce the spend on cultivation material compost, to enhance the quality of composted products, and to increase the income from *Stropharia rugosoannulata* cultivation, so that *Stropharia rugosoannulata* cultivation can be more accepted in developing countries [1,2].

Most aromatic plant biomasses (APBs) are rich in secondary metabolites, such as alkaloids, flavonoids, and terpenoids. The secondary metabolites are capable of shaping the metabolism and reproduction of microorganisms in several environments [13], which leads aromatic plants to have a high value in the pharmaceutical [14], cosmetic [15], and agronomy industries [16]. For instance, the nutrient turnover capacity of the gut microbial community was reported to be significantly enhanced by the additional feed of aromatic plant biomass [17]. The preservation of fish products was also prolonged by the addition of aromatic plant biomass, due to the antibiotic effects [18]. Plant white-rot pathogens were reported to be significantly inhibited by the addition of specific flavonoid compounds [19]. However, it has rarely been reported whether aromatic plants can be used to manipulate the microbial community composition, as well as the microbial carbon metabolism activity, during composting. Aromatic plants are common municipal landscaping vegetation, and generate considerable biomass waste to be treated annually [20,21]. Meanwhile, with the rapid development of the aromatic industry, the production of industrial extraction waste from aromatic plants is also increasing year on year. For instance, over 6.7×10^4 hectares of *Cinnamomum camphora* have been cultivated in China alone since 2019, and more than 98% of *Cinnamomum camphora* biomass has become waste after industrial extraction, which indicates a huge aromatic plant biomass waste production annually [22]. Economic strategies are urgently required to treat the upsurging APB wastes [22]. If APB wastes could be developed to facilitate the degradation of lignocellulose during the composting of mushroom cultivation materials, the cultivation costs could be reduced by consuming aromatic plant waste and, at the same time, the waste treatment cost would also be saved.

The addition of APBs to feeds has been reported to promote lignocellulose degradation by intestinal microorganisms during ruminal fermentation [23,24], which indicates that aromatic plant materials are potentially capable of accelerating microbial carbon metabolism under anaerobic condition, just like compost. However, the *Stropharia rugosoannulata* yield was reported reduced by cultivation materials composted exclusively from aromatic plant biomass [25], which suggests that the excessive secondary metabolite residues in the cultivation materials may also be detrimental to the development of *Stropharia rugosoannulata* [19,26]. The addition of a smaller quantity of APBs can reduce the secondary metabolite accumulation in cultivation materials. However, it is still an open question whether the addition of APBs could reshape the microbial community carbon metabolism in compost, such as promoting lignocellulose degradation, especially when only added in small doses.

To answer this question, 0%, 1%, 2%, and 3% mass ratios of *Cinnamomum camphora* biomass were, respectively, added to a conventional *Stropharia rugosoannulata* cultivation material compost. Then, the lignocellulose content, the microbial community composition, and the enzyme activities related to the carbon resource degradation of the end compost

products were checked. It was hypothesized that, due to the limited secondary metabolite contained, the small dose addition of *Cinnamomum camphora* biomass would be incapable of altering the microbial community composition and function, and would not be able to change the lignocellulose content of compost products.

2. Materials and Methods

2.1. Study Sites and Sampling

The compost was set at the Mandeson Agricultural Development Limited Company (Ji'an City, Jiangxi Province, E 116°07′67.4″ and N 28°34′95.42″) on 10 April 2021; the air temperature ranged between 16 °C and 23 °C. The compost materials were evenly mixed with powders (size less than 0.5 cm) of bamboo litters, hardwood litters, rice straws, wheat brans, and CaO (Table 1). Then, the *Cinnamomum camphora* biomass was crushed and evenly added to the compost in a mass ratio of 0% (C), 1% (A1), 2% (A2), and 3% (A3), respectively. The *Cinnamomum camphora* biomass was collected from the *Cinnamomum camphora* cultivar, from Jiangxi Academy of Forestry. After being thoroughly mixed, the moisture of the compost materials was empirically adjusted to about 60% water content, through watering. The compost pile was approximately 3 m × 2 m × 1.6 m, covered by a plastic membrane. The materials were remixed every 10 days when the temperature reached about 60 °C. The compost products were sampled on the last day (the 30th); ten subsamples (each around 500 g) were randomly selected from each treatment. After passing through 2 mm sieves, 1000 g mixed samples were chosen as one sample. Fifty grams of them were stored at −80 °C in a refrigerator for the following molecular biology test. The others were transported to the lab and stored at 4 °C in a refrigerator, before the measurement of the basic physicochemical properties as soon as possible. The mixed materials were kept at approximately 60% water content, through daily measurement and artificial watering.

Table 1. The original composition of compost material.

Name	Mass Ratio	Hemicellulose	Cellulose	Lignin
Bamboo litters	40%	23.6%	45.1%	26.3%
Hardwood litters	40%	22.8%	32.6%	35.1%
Rice straw	9%	15.4%	21.9%	20.6%
Wheat brans	10%	30.1%	21.9%	18.6%
CaO	1%			

2.2. Determination of Basic Physicochemical Properties and Enzyme Activities

We used gravimetric methods to test the water content of compost materials. The pH meter (FE20-FiveEasyTM pH, MettlerToledo, Berlin, Germany) was adopted to measure the pH, by testing the compost–water mixture (1:2.5 ratio of mass/volume). An element analyzer (Vario MACRO cube, Elementar Inc., Berlin, Germany) was used to determine the total carbon content and total nitrogen content of the compost materials. The Sommers–Nelson method was adopted to determine the total phosphorus content [27], and the flame-spectrometric method was adopted to determine the total potassium content [28]. The contents of lignin, cellulose, hemicellulose, soluble sugar, starch, and protein, and the activity of xylanase, cellulase, laccase, MnP (magnesium peroxidase), LiP (lignin peroxidase), and polyphenol oxidase were all measured, according to the instructions of the corresponding kit (Comin Biotechnology Co., Ltd., Suzhou, China).

2.3. The DNA Sequencing and Bioinformatic Analysis

According to the protocol of the FastDNA^{TM} SPIN kit (MP Biomedicals, Los Angeles, CA, USA), microbial DNA was extracted. The concentration and quality of the extracted DNA were soon determined using a Nano-100 NanoDrop spectrophotometer. Primers for 16S rRNA gene amplification targeted the V3-V4 hypervariable region, and included 338F 5′-ACTCCTACGGGAGGCAGCAG-3′ and 806R 5′-GGACTACHVGGGTWTCTAAT-3′ [29]. The primers for ITS1 region amplification included 1F 5′-CTTGGTCATTTAGAGGAAGTAA-3′ and 2R 5′-GCTGCGTTCTTCATCGATGC-3′ [30]. After PCR, the amplicons were pooled in equimolar ratios, and sequenced on the Illumina Nova6000 platform (Majorbio Company, Shanghai, China) in paired-end form [31]. After removing the barcodes and primers, the sequences with a minimum overlap length of 20 bp were merged into full-length sequences using FLASH [32,33]. Chimeras were removed using UPARSE, and the sequences with over 97% similarity were treated as one operational taxonomic unit (OTUs) [34]. We adopted the Sliva-138 database and the UNITE-8.0 database to annotate the bacterial OTUs and the fungal OTUs, respectively. A total of 24,561 of bacterial reads, and 38,442 of fungal reads were randomly chosen, to form an evenly resampled OTU table for further analysis.

We used the molecular ecological network analysis pipeline to operate network analysis (MENA, http://ieg4.rccc.ou.edu/MENA/login.cgi, accessed on 10 September 2022) protocols [35]. During the construction of the co-occurrence network, the BOTUs (bacterial OTUs) and FOTUs (fungal OTUs) were combined in one table. The construction parameters were set as majority = 9, missing_fill = fill_paired (0.0100), logarithm = n, similarity = spearman2, and cutoff threshold = 0.87. The richness, the Shannon index, the analysis of similarities among microbial communities (ANOISM), and the principal coordinate analysis (PCoA) based on Bray–Curtis distances at OTU-level were all conducted using the online platform https://cloud.majorbio.com, accessed on 27 January 2023, under the R base [36].

2.4. Statistical Analysis

Amos v18.0 and SPSS v24 were used to construct structure equation modeling (SEM), and the extractions of SEM factors were divided into different groups according to the Pearson correlation metrics for modeling construction [37]. The bacterial and fungal community indicators in the SEM were the bacterial PC1 and fungal PC1 obtained from the PCoA analysis, respectively [31]. The significance of differences among different groups was checked using one-way ANOVA (Tukey's HSD test) on SPSS v24. The pictures were drawn using Origin.v16.0, and the co-occurrence network was visualized using Cytoscape.v3.3.0.

3. Results

The moisture of the initial compost materials was approximately 58.34 ± 1.75%, and the pH of the initial compost materials was approximately 7.02 ± 0.04. The total carbon, total nitrogen, total phosphorus, and total potassium contents (in dry mass) of the initial compost materials were 55.58 ± 0.72%, 6.57 ± 0.06%, 1.91 ± 0.12%, and 2.08 ± 0.47%, respectively. There were no significant differences among the treatments. The main results are shown in the following subsections.

3.1. The Carbon Source and Enzyme Activity Differences

The results show that the addition of *Cinnamomum camphora* biomass significantly reduced the contents of cellulose, hemicellulose, and lignin (Figure 1A–C), and the more *Cinnamomum camphora* biomass was added, the more the lignocellulose was reduced ($p < 0.05$). The cellulose content was 279 ± 21.4 g kg^{-1} in the control, while only being 134 ± 13.7 g kg^{-1} in A3. The hemicellulose content of the control was 200 ± 13.9 g kg^{-1}, nearly twofold that of A3 (102 ± 13.7 g kg^{-1}). The *Cinnamomum camphora* biomass addition exerted the highest acceleration on lignin degradation, the content of which in A3 was 64.6 ± 5.03 g kg^{-1}, only one-fifth of the control (334 ± 18.7 g kg^{-1}). Thus, the proportion of lignin in the structural carbohydrate composition was reduced (from 41.04% of the

control to 21.39% of A3) by the *Cinnamomum camphora* biomass addition, while the cellulose and hemicellulose were proportionally enhanced, instead. In contrast, the effect of the *Cinnamomum camphora* biomass addition on soluble sugars and starch during compost was not significant (Figure 1D,E). Soluble sugars fluctuated between 2.25 ± 0.12 g kg^{-1} (A1) and 2.08 ± 0.03 g kg^{-1} (A3), and starch content fluctuated between 2.70 ± 0.04 g kg^{-1} (A3) and 2.49 ± 0.11 g kg^{-1}(A1), with no significant differences between treatments ($p > 0.05$). The proportion of starch and soluble sugars in compost products was also not changed by the *Cinnamomum camphora* biomass addition, with the starch percentage fluctuating between 55.5% (A3) and 52.5% (A1) (Figure 1M). However, the *Cinnamomum camphora* biomass addition promoted the accumulation of protein during composting, reaching 2.64 ± 0.33 g kg^{-1} in A3, which was nearly 30% higher than the control (2.09 ± 0.08 g kg^{-1}) (Figure 1F).

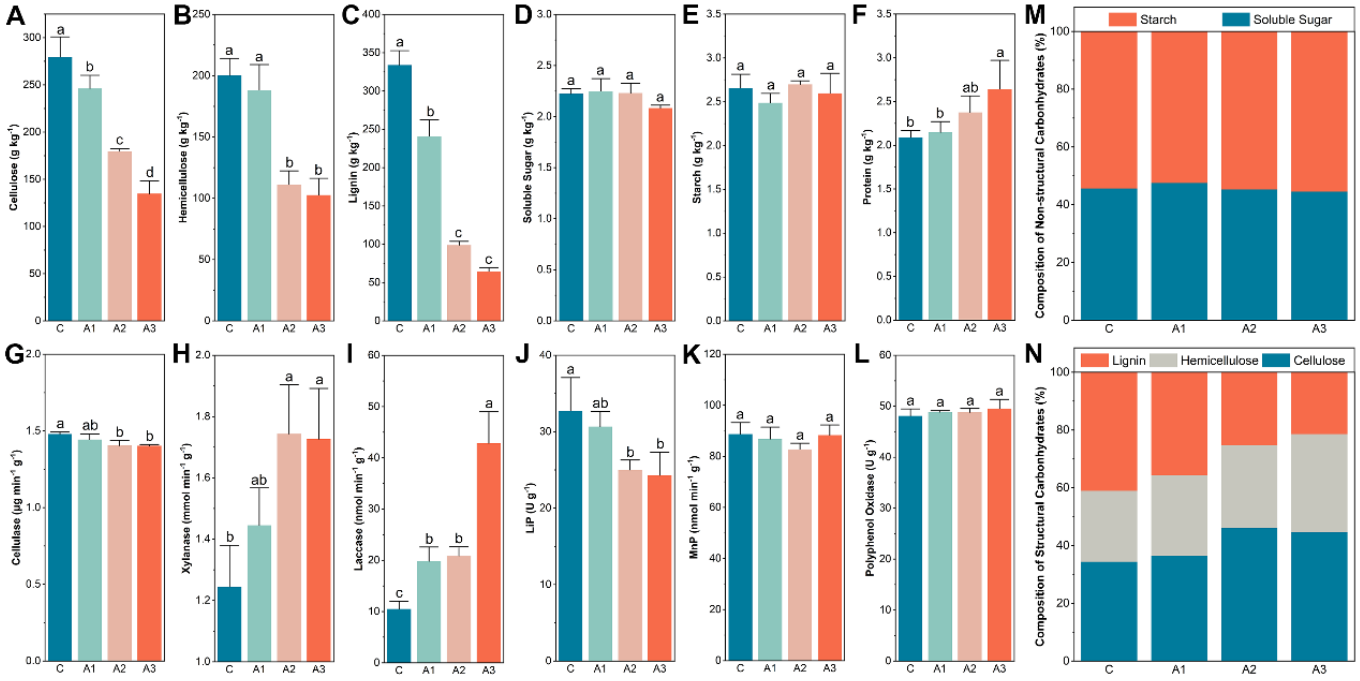

Figure 1. The carbon sources and enzyme activities of the different treatments. C in x-axis indicates the control, while A1, A2, and A3 indicate 1%, 2%, and 3% *Cinnamomum-camphora*-biomass-added treatment, respectively. The a, b, c, and d above the bars indicate the significance of differences among treatments, using one-way ANOVA Turkey's HSD ($p < 0.05$). LiP and MnP are abbreviations for lignin peroxidase and magnesium peroxidase, respectively. The subfigure (**A**–**F**) depict the variation on cellulose, hemicellulose, lignin, soluble sugar, starch, and protein, respectively. The subfigure (**G**–**L**) depict the variation on cellulase, xylanase, laccase, LiP, MnP and polyphenol oxidase, respectively. The subfigure (**M**) depict the relative ratio of starch and soluble sugar, subfigure (**N**) depict the relative ratio of lignin, cellulose, and hemicellulose.

The results show that the *Cinnamomum camphora* biomass addition significantly altered the activities of some enzymes related to carbon source metabolism in composting, including cellulase, xylanase, laccase, and lignin peroxidase (Figure 1G–J). The activity of cellulase was slightly but significantly lowered by the *Cinnamomum camphora* biomass addition, from 1479 ± 13.4 μg min^{-1} g^{-1} (C) to 1403 ± 8.74 μg min^{-1} g^{-1} (A3). Lignin peroxidase also decreased with the *Cinnamomum camphora* biomass addition, from 32.73 ± 4.36 μg min^{-1} g^{-1} (C) to 24.30 ± 3.04 μg min^{-1} g^{-1} (A3). However, the addition of *Cinnamomum camphora* biomass caused significant increments in both xylanase and laccase activities; the former increased from 1.24 ± 0.14 nmol min^{-1} g^{-1} (C) to 1.73 ± 0.16 nmol min^{-1} g^{-1} (A3), and the latter upsurged nearly threefold, from 10.49 ± 1.54 nmol min^{-1} g^{-1} (C) to 42.83 ± 6.17 nmol min^{-1} g^{-1} (A3). The MnP and polyphenol oxidase activities were

not significantly affected by the *Cinnamomum camphora* biomass addition. The minimum value of the MnP was 82.73 ± 2.43 nmol min^{-1} g^{-1} (A2), and the maximum value was 88.70 ± 4.55 nmol min^{-1} g^{-1} (C). The polyphenol oxidase ranged from 48.10 ± 1.38 U g^{-1} (C) to 49.55 ± 1.80 U g^{-1} (A3). No significant differences were found between treatments ($p > 0.05$).

3.2. The Microbial Commuinty Composition Differences

The results show that the alpha diversity of both the bacteria and fungi communities was not significantly changed by the *Cinnamomum camphora* biomass addition, but the community structure of bacteria and fungi was significantly altered ($p < 0.05$). The bacterial Chao index ranged between 1036 ± 19.0 (A2) and 947 ± 11.5 (A3), and the bacterial Shannon index ranged between 5.53 ± 0.17 (A1) and 5.24 ± 0.33 (C), and no significant differences were found among the groups ($p > 0.05$) (Figure 2A,B). The minimum value of fungal Chao index occurred at A2 (92.9 ± 12.9), and the maximum value at C (111 ± 10.8), while the minimum and maximum values of fungal Shannon index were 1.44 ± 0.32 (A2) and 2.07 ± 0.30 (A3), respectively, with no significant differences among groups ($p > 0.05$) (Figure 2E,F). However, the PCoA analysis revealed that both the bacterial and fungal community structure varied significantly due to the *Cinnamomum camphora* biomass addition, as the corresponding *p* values were 0.002 and 0.003, respectively (Figure 2C,G). The most significant change in the RA of bacterial taxa was in *Proteobacteria*, which reached 53.88% in A3, and was nearly 60% higher than the control (32.08%). *Bacteroidota* also showed an increasing trend with the *Cinnamomum camphora* biomass addition, but only from 5.66% (C) to 8.26% (A3). On the contrary, *Cloroflexi*, *Acidobacteria*, and others showed a decreasing trend with the addition. The RA of *Acidobacteria* decreased most prominently; the RA of A3 (1.72%) was only one-eighth of the control (8.67%). *Cloroflexi* decreased from 15.2% (C) to 6.61% (A3). *Firmicutes* in A2 possessed the highest RA (17.3%), which was nearly three times higher than in A3 (6.48%), while *Actinobacteriota* had the lowest RA in A2 (15.06%), and the highest in the control (21.97%) (Figure 2D). The fungal community variations were mainly characterized by the change in *Eurotiomycetes*, the RA of which decreased from 81.01% (C) to 54.44% (A3). In contrast, *Sordariomycetes* increased from 6.06% (C) to 26.4% (A3), showing a near-fourfold increment. Rare taxa such as those included in "others" also increased from 2.01% (C) to 7.29% (A3). However, *Mortierellomycetes* were not sensitive to the *Cinnamomum camphora* biomass addition; their RA ranged between 8.59% (A1) and 11.8% (A3). *Pezizomycetes* were found in both A1 and A2, but not in the control or A3 (Figure 2H).

3.3. The Structure Modelling Equation

The SEM shows an R^2 of 0.95 for the explanation power of the substrate variation, which was composed of lignin, cellulose, and hemicellulose. The *p*-value was higher than 0.05, the RMSEA was less than 0.05, and both CFI and GFI were higher than 0.95, which indicates a parsimonious fitness. The results show that the variation in the bacterial composition offered a slightly higher standard total effect (0.464) to substrates, when compared to its fungal counterpart (0.365). The enzyme1 (comprising LiP, xylanase, laccase, and cellulase) was the main contributor to the substrate degradation, as it offered a standard total effect as high as 0.973, while enzyme2 (comprising MnP and polyphenol oxidase) offered only −0.011 (Figure 3).

3.4. The Co-Ocuurance Network Analysis

The co-occurrence network analysis showed that lignin, cellulose, hemicellulose, LiP, laccase, and protein appeared in a central large module, with twenty-one OTUs directly related to them; twenty OTUs were BOTUs, but only one was FOTU. Eight BOTUs belonged to *Proteobacteria*, eight BOTUs were *Firmicutes*, two BOTUs were *Actinobacteria*, one BOTU was *Myxococcota*, one BOTU was *Acidobacterota*, and one FOTU was *Ascomycota*. Further analysis found that BOTU1339, BOTU2370, and BOTU2354 were module hubs, as

they contained Zi of over 2.5, and Pi of less than 0.62, while BOTU1613 was a connector, as the Zi-value was less than 2.5, and the Pi-value was over 0.62 (Table 2). Only LiP and laccase appeared in the co-occurrence network, highlighting that they were the potential contributors to the lignocellulose degradation differences caused by the *Cinnamomum camphora* biomass addition. In the module hubs, BOTU1339 was directly connected to LiP, BOTU2370 was directly connected to protein and LiP, BOTU2354 was directly connected to protein, and the connector BOTU1613 was directly related to lignin. In total, nine OTUs were directly connected to the protein, followed by LiP (seven OTUs), lignin (six OTUs), cellulose (four OTUs), hemicellulose (four OTUs), and laccase (three OTUs) (Figure 4).

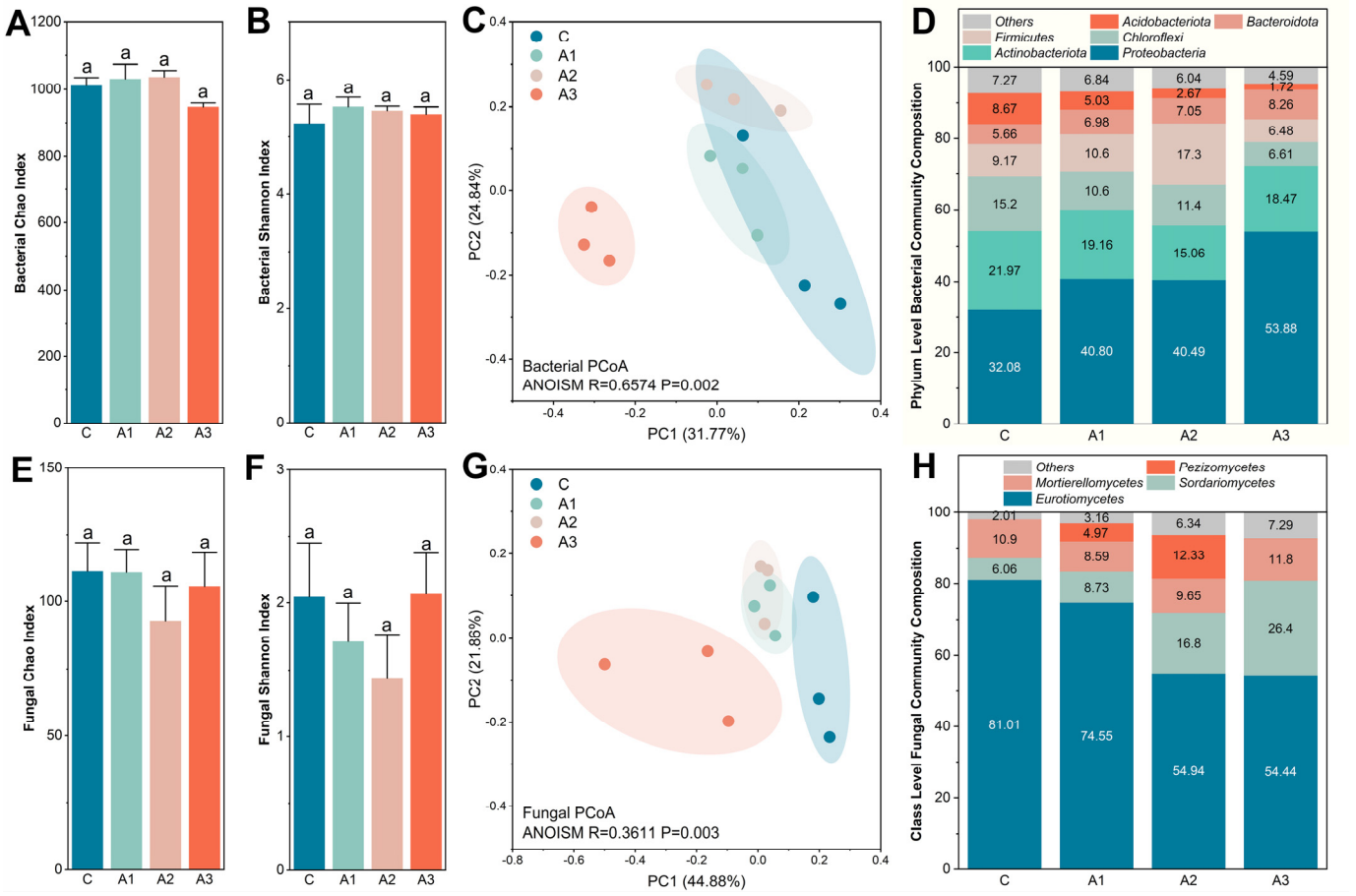

Figure 2. The microbial community diversity and composition differences of the different treatments. The different letters above the bars in (**A**,**B**,**E**,**F**) indicate no significant differences among treatments, using one-way ANOVA Turkey's HSD ($p < 0.05$). C indicates the control, while A1, A2, and A3 indicate 1%, 2%, and 3% *Cinnamomum-camphora*-biomass-added treatment, respectively. The subfigure (**A**,**B**) depict the variation on Chao and Shannon index of bacterial community, respectively. The subfigure (**C**) depict the PCoA analysis results of bacterial community and subfigure (**D**) depict the bacterial community composition on phylum level. The subfigure (**E**,**F**) depict the variation on Chao and Shannon index of fungal community, respectively. The subfigure (**G**) depict the PCoA analysis results of fungal community and subfigure (**H**) depict the fungal community composition on Class level.

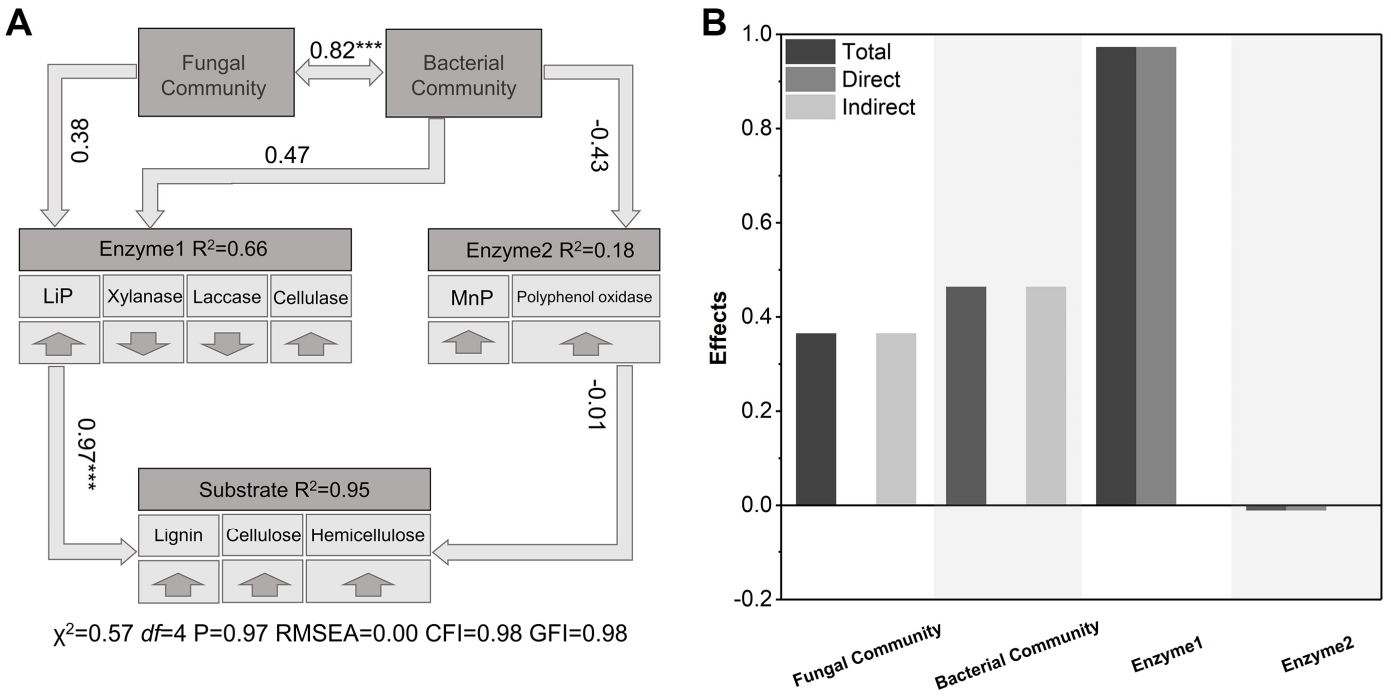

Figure 3. The structural modelling equation resolving the relationship among microbial community composition and substrate composition. The *** indicates significant correlation on the $p < 0.001$ level. Subfigure (**A**) depict the model and subfigure (**B**) depict the standard effects contributed by the factors.

Table 2. The OTUs directly linked to carbon sources and enzymes.

ID	Phylum	Genus	Network Zi-Pi Roles			Interactions					
			Zi	Pi	Functional Roles	LiP	Laccase	Protein	Lignin	Cellulose	Hemicellulose
BOTU399	*Proteobacteria*	*Camelimonas*	0.57	0.00	Peripherals			+			
BOTU247	*Proteobacteria*	*Bradyrhizobium*	−0.13	0.22	Peripherals		+				
BOTU2392	*Proteobacteria*	*Acinetobacter*	0.00	0.00	Peripherals	–		–			
BOTU223	*Proteobacteria*	*Unclassified*	0.04	0.50	Peripherals	–				–	–
BOTU2207	*Proteobacteria*	*Azospirillum*	−0.55	0.50	Peripherals				–	–	–
BOTU214	*Proteobacteria*	*Prosthecomicrobium*	0.00	0.61	Peripherals	–					
BOTU2099	*Proteobacteria*	*Burkholderia*	−0.13	0.22	Peripherals	–					–
BOTU1339	*Proteobacteria*	*Acinetobacter*	2.87	0.00	Module hubs	+					
BOTU1425	*Myxococcota*	*Anaeromyxobacter*	0.92	0.24	Peripherals			–			
BOTU3773	*Firmicutes*	*Unclassified*	−1.19	0.00	Peripherals				+	+	
BOTU3669	*Firmicutes*	*Lysinibacillus*	0.04	0.20	Peripherals			–			
BOTU3643	*Firmicutes*	*Oxobacter*	0.22	0.30	Peripherals			–			
BOTU3581	*Firmicutes*	*Brevibacillus*	1.46	0.41	Peripherals			–	+		
BOTU3563	*Firmicutes*	*Symbiobacterium*	0.73	0.44	Peripherals		-			+	
BOTU2329	*Firmicutes*	*Clostridium*	0.73	0.49	Peripherals	+			+		
BOTU1613	*Firmicutes*	*Ammoniphilus*	−0.06	0.67	Connectors				+		
BOTU1371	*Firmicutes*	*Unclassified*	1.89	0.22	Peripherals	–		–	+		
FOTU1032	*Ascomycota*	*Candida*	0.43	0.00	Peripherals		+				
BOTU2370	*Actinobacteriota*	*Kribbella*	2.68	0.21	Module hubs	+		+			
BOTU2354	*Actinobacteriota*	*Actinophytocola*	3.03	0.14	Module hubs			+			
BOTU2338	*Acidobacteriota*	*Bryobacter*	0.40	0.17	Peripherals						–

Note: the minus and plus indicate negative and positive links, respectively.

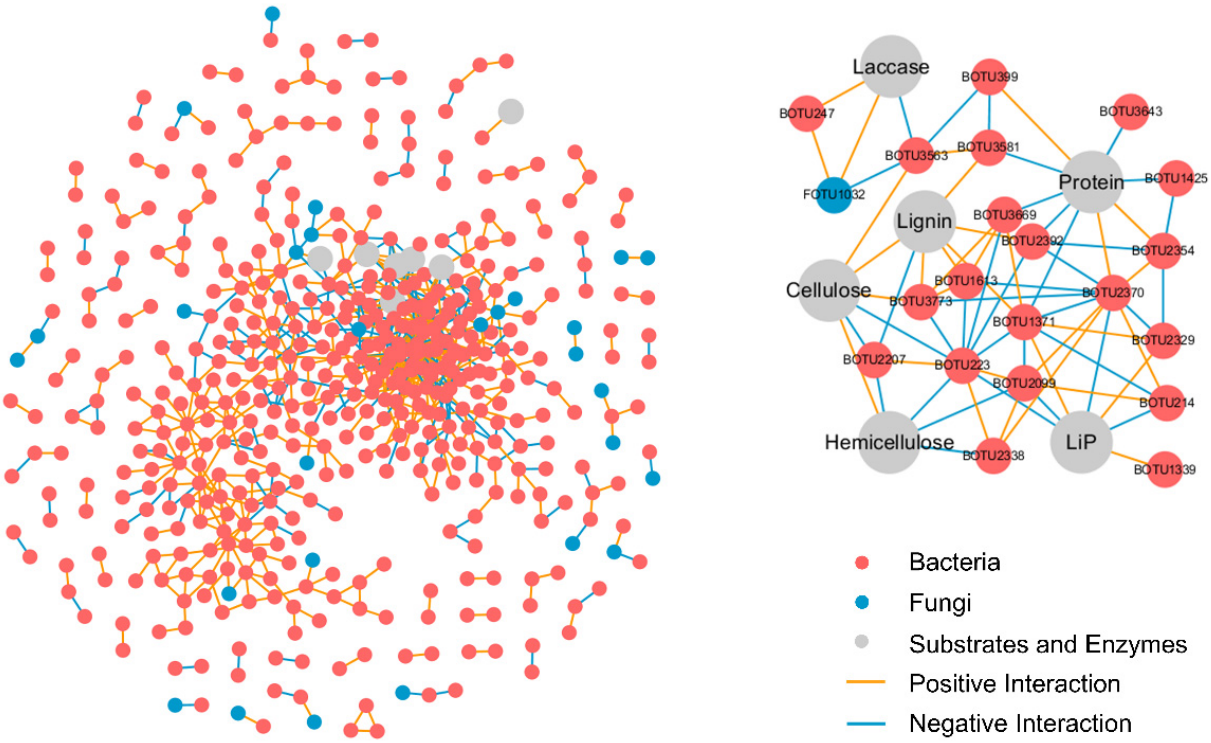

Figure 4. The co-occurrence network of OTUs, carbon sources, and enzymes. The red, blue, and gray dots indicate bacterial OUT, fungal OUT, and the carbon sources and enzymes, respectively. The orange and blue lines indicate positive and negative correlations, respectively. The left part depicts the total network, while the right part depicts the subnetwork OTUs directly linked to carbon sources and enzymes.

4. Discussion

The present results show that the *Cinnamomum camphora* biomass addition to the compost significantly enhanced the degradation of lignocellulose, especially the lignin degradation, of which the content in A3 was only one-sixth of the control. Lignin comprises highly phenolic monomers, and offers less energy to microorganisms after been decomposed, compared to the equivalent mass of cellulose and hemicellulose [38–40]. In addition, lignin always forms crystalline domains with cellulose and hemicellulose, and acts as a protective shelter that prevents enzymes from accessing cellulose and hemicellulose [38–40]. Thus, the cultivation materials with a high lignin content are unfriendly to the nutrient assimilation and growth of the *Stropharia rugosoannulata* mycelium [38,41]. Meanwhile, the results show that the contents of both soluble sugar and starch were not significantly altered by the addition of *Cinnamomum camphora* biomass. Labile carbon sources are readily absorbed and utilized by the mycelium, and the contents of soluble sugar and starch are closely related to the activity and subsequent growth of the mycelium during cultivation [7], especially in the early stages of cultivation. The lack of labile carbon sources leads to limited mycelial development [42], which increases the risk of disease, and greatly affects the yield and quality of subsequent mushrooms products. This research supports the theory that *Cinnamomum camphora* biomass addition promotes the degradation of lignocellulose, but does not negatively affect labile carbon fractions.

The activities of xylanase, laccase, and LiP significantly changed with the addition of *Cinnamomum camphora* biomass. The activities of xylanase and laccase were enhanced by the addition, while LiP decreased, which indicates that the *Cinnamomum camphora* biomass addition altered the substrate preference of the microbial community, mainly by regulating metabolic enzyme activities. This may be caused by the stresses from the *Cinnamomum camphora*, which contains a variety of secondary metabolite compounds, such as vanillyl alcohol and camphora [26]. These substances have been reported to influence microbial cell signal-

ing, and to alter microbial extracellular enzyme secretion and metabolic pathways [19,26]. Faced with low-extent stresses, organisms prone to enhanced substrate consumption and respiration produce more energy to overcome the stress. This is a potential reason why the degradation of lignocellulose was increased [43]. The cellulase showed a significant but weak decrease caused by the *Cinnamomum camphora* biomass addition, which was only from 1479 ± 13.4 μg min^{-1} g^{-1} (C) to 1403 ± 8.74 μg min^{-1} g^{-1} (A3). This suggests that the cellulose degradation was mainly driven by the lignin and hemicellulose degradation, as the lignocellulose crystals were destroyed, and the cellulose became more accessible to cellulase, but the cellulase activity itself might not be sensitive to the *Cinnamomum camphora* biomass addition. The MnP and polyphenol oxidase activities were also not significantly affected by the *Cinnamomum camphora* biomass addition. LiP, MnP, and laccase are the main mediating enzymes responsible for lignin degradation in nature, and each of them is released by certain microbial taxa in the community [6,38,40]. The results show that LiP, MnP, and laccase responded differently to the *Cinnamomum camphora* biomass addition, which indicated that the *Cinnamomum camphora* biomass addition specifically selected a certain subset of functional microbial taxa, and this were also consistent with the results of the microbial community composition analysis.

Significant variations were found in both the bacterial and fungal community structure, caused by the different levels of *Cinnamomum camphora* biomass addition. The RA of *Proteobacteria* was significantly enhanced. The members of the phylum *Proteobacteria* were reported to have a strong metabolic transformation capacity, and a strong tolerance to stresses [44,45]. They were capable of rapidly changing metabolic strategies in response to environmental changes, and degrading recalcitrant carbon through functional specification and cooperation. *Proteobacteria* were widely reported as the dominant taxon in agricultural composting [44,45] and municipal waste composting [46]. *Proteobacteria* were also tolerant to secondary plant metabolites, such as camphor. The *Proteobacteria* RA was enhanced by the addition of camphor in ruminal fermentation [23,24,47], which was consistent with our results. The RA of *Sordariomycetes* also significantly increased with the *Cinnamomum camphora* biomass addition. *Sordariomycetes* were previously reported as the main contributor to carbon degradation in mango leaf compost under a high plant secondary metabolite concentration [40,48], and was also reported to have a higher RA in hardwood-based substrate composts, rather than grass-based substrates, due to its higher capability to degrade lignin [8]. Thus, the variation in the *Proteobacteria* and *Sordariomycetes* RA was potentially the main cause for the compost carbon degradation altered by the *Cinnamomum camphora* biomass addition.

SEM found that the change in the bacterial community composition caused higher impacts on lignocellulose degradation than the fungal community did. Fungal communities are more responsible for lignocellulose decomposition in nature, while bacteria are prone to decompose substrates with a higher nitrogen content [38]. However, previous studies showed that bacterial communities and bacterial-originated laccase played more important roles than their fungal counterpart in a compost based on the industrial extracted waste of *Cinnamomum camphora* [49]. Meanwhile, bacterial communities have a higher richness and higher functionally redundant community members, which makes it easier to reshape the community composition, and maintain functional stability in the face of environment changes [50,51]. Bacterial-originated laccase is also less sensitive to fluctuations in environmental factors such as temperature and pH than fungal laccase, which might also further increase the bacterial contribution to lignocellulose degradation in compost [52,53].

Co-occurrence network analysis found that lignin, cellulose, hemicellulose, protein, LiP, and laccase appeared in the network, which suggests that LiP and laccase were the main enzymes driving lignocellulose degradation and biomass synthesis during composting. The substrates and enzymes mentioned above were all clustered in one large central module, which indicates that they were closely related to each other functionally [35]. Among the OUTs directly interacting with them, *Firmicutes* occupied nearly 1/3 RA, which significantly exceeded their RA in the bacterial community composition, and implied that they may

have played an auxiliary role in carbon source degradation, although their RA was not as high as that of *Proteobacteria* [54,55]. This might be partially because *Firmicutes* can act as major lignin decomposers under adversary conditions, such as in heavy-metal-contaminated soils [54] and in anoxic environments [55], although their tolerance to plant secondary metabolite in compost is seldom reported. The members of a network module are often highly correlated in terms of their functions, and module hubs generally play a metabolic core role among the module members [35]. There were three module hubs in the network, two of which were *Actinobacteriota*, which is a sign that *Actinobacteriota* potentially coordinated metabolite turnover with other community members. The other mushroom cultivation material compost research also reported the isolation of specific *Actinobacteriota* members, which can accelerate lignocellulose degradation, enhance the carbon turnover rate, and promote a decrease in the C:N in compost products [56]. However, an overly high content of *Actinobacteriota* is also considered potentially risky for human health and needs to be treated cautiously [57]. The only connector in the network was BOTU1613, which belonged to the genus *Ammoniphilus*, and was directly related to lignin. The connector generally serves to combine different modules, as well as different functions of the microbial community [35]. Members of the genus *Ammoniphilus* may be involved in the nitrogen-cycling process of composting, as their activities were previously reported to be closely linked to ammonium content [58]. *Ammoniphilus* were a potential bridge linking the carbon cycle and the nitrogen cycle in our study. Laccase was directly related to FOTU1032, which belonged to *Candida*. Previous research has reported the lipase secretion activity of *Candida* during woody material composting, but their laccase secretion activity has not been reported before [59]. In addition, this genus has been reported to be sensitive to plant secondary metabolites such as salicylic acid, cinnamic acid, benzoic acid, and o-vanillin [60], while our study found that its RA increased with the addition of *Cinnamomum camphora* biomass, suggesting the existence of strains that are insensitive to plant secondary metabolites, which could lead to the genus *Candida* having a potentially high value in aromatic waste compost.

It is noteworthy that although the *Cinnamomum camphora* biomass addition unexpectedly lowered the lignocellulose content of compost product by altering the microbial composition and function, the ideal compost would be the conversion of a macromolecular recalcitrant carbon source into small labile organic molecules, which would greatly enhance the quality of cultivation materials [7,61]. It would be promising to explore whether natural plant aromatic additives can promote the accumulation of labile carbon during cultivation material compost in the future [7,62–64]. We will further investigate the optimal *Cinnamomum camphora* biomass addition ratios, to maximize the lignocellulose degradation and labile carbon accumulation, and analyze the detailed secondary metabolites which affect the microbial communities and lignocellulose transformation, to pave the way for subsequent simplification and optimization of the process.

5. Conclusions

In this study, we investigated the effect of the addition of a low dose of *Cinnamomum camphora* biomass on the carbon source degradation of composted *Stropharia rugosoannulata* cultivation materials. Mainly by decreasing the LiP activity, and enhancing the laccase activity, the *Cinnamomum camphora* biomass addition significantly altered the microbial community composition during compost, and lowered the lignocellulose content of the end compost products. Microbial members in *Proteobacteria*, *Firmicutes* and *Actinobacteriota* may have contributed majorly to the enzyme-activity variation. The research provides a new insight into the reuse of aromatic plant waste, offers valuable information for the further optimization of *Stropharia rugosoannulata* cultivation material compost, and has positive effects on the promotion of the development of the mushroom industry in developing countries.

Author Contributions: Conceptualization, H.Z. and X.W.; methodology, H.Z.; software, H.Z.; validation, H.Z., L.D. and X.H.; formal analysis, H.Z.; investigation, H.Z. and X.W.; resources, X.W.; data curation, H.Z., T.D. and X.W.; writing—original draft preparation, H.Z.; writing—review and editing, H.Z.; visualization, H.Z., L.D. and X.H.; supervision, X.W.; project administration, X.W.; funding acquisition, X.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by Jiangxi Science and Technology Department Major Science and Technology R&D Special Project, grant number 20203ABC28W016, and Jiangxi Forestry Bureau Special Project of Camphor Tree Research, grant number 2020-04-04.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The raw sequences were uploaded to NCBI, and the project numbers are SUB13022549 (fungal) and SUB13022469 (bacterial).

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

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