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Native Bamboo Invasions into Subtropical Forests Alter Microbial Communities in Litter and Soil

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Abstract: Both exotic and native plant invasions can have profound impacts on ecosystems. While many studies have examined the effects of exotic plant invasions on soil properties, relatively few have tested the effects of native plant invasions on soil microbial communities. Furthermore, we know little about the effects of native plant invasions on microbial communities in litter. In subtropical forests in southern China, we sampled litter at three decomposition stages and top soil in three forest sands representing three stages of the invasion (not invaded, moderately and heavily invaded) by the Moso bamboo (*Phyllostachys edulis* (Carriere) J. Houzeau), a native species in China. We measured chemical properties (concentrations of C, N, P, Mg, Al, K, Ca, Mn, Cu, and Zn, and concentrations of cellulose and lignin) and microbial communities in litter and/or soil. The bamboo invasion, in general, decreased the element concentrations in litter and soil and also decreased total microbial abundance and diversity. Considering bacteria and fungi separately, the bamboo invasion decreased fungal diversity in litter and soil, but had little impact on bacterial diversity, suggesting that fungi are more sensitive and vulnerable to the bamboo invasion than bacteria. We conclude that native Moso bamboo invasions into subtropical forests may lead to a complex biogeochemical process in the litter–soil system, which may threaten local forest ecosystems by affecting microbial communities and, thus, litter decomposition and nutrient cycling.

Keywords: bacteria; forest types; fungi; microorganisms; plant invasion; *Phyllostachys edulis* (Carriere) J. Houzeau

1. Introduction

Invasions of exotic plant species, from their native ranges into new regions or countries where they did not occur historically, havebecome common worldwide and are receiving increasing attention [1–5]. It is well known thatexotic plant invasions can decrease native species diversity [6,7], changespecies composition [8,9], alterphysio-chemical properties in soil [10–12] and litter [13–15], and modify soil microbial communities [16–18]. Similarly, native plant invasions, i.e., invasions of native species into a new ecosystem located in the same region or country, may also cause significant ecological impacts on

physio-chemical properties in soil [19–21] and litter [22,23] and soil microbial communities [24–26]. While the effects of exotic plant invasions have received much attention, relatively few studies have considered the impacts of native plant invasions [27–29], in particular on microbial communities in litter. Understanding the impacts on litter microbial communities is important as the quantity, diversity, and activity of soil microbes in litter play key roles in litter decomposition and, thus, nutrient cycling [13–15].

The invasion of native Moso bamboos (*Phyllostachys edulis* (Carriere) J. Houzeau) into subtropical evergreen forests has become a big problem in many areas in southern China [30]. In the past, the management of pure Moso bamboo forests for harvesting bamboo shoots and wood was profitable. Therefore, a large area of subtropical evergreen forests in southern China was turned into Moso bamboo forests by farmers [31]. However, with increasing labor costs and decreasing use of bamboo products, many Moso bamboo forests have been abandoned because they are no longer profitable [32]. After thiscease inmanagement, Moso bamboos started to invade adjacent evergreen forests, gradually replacing local species [33]. Previous studies have shown that Moso bamboo invasions could affect the diversity and composition of local plant species [34] and alter concentrationsof carbon (C), nitrogen (N), phosphorus (P), and organic matter in the soil [35–38]. However, little is known regarding the effect of Moso bamboo invasions on microbial communities in litter.

Plant invasions can greatly alter the structure and function of microbial communities [25,39,40]. For instance, both exotic and native plant invasions were found to increase bacterial and/or fungal diversity in soil and change soil microbial competition [17,18,24,41]. Exotic plant invasions could increase the abundance of nitrogen-fixing bacteria in the rhizosphere, resulting in increased nitrogen availability for plant growth [18]. Furthermore, exotic plant invasions canalter the diversity and composition of microbial communities in litter [42–45]. There is also evidence that exotic or native plant invasions haveno impact on litter microbial communitiesin the short term [46]. Thus, more studies are needed to test the generality of plant invasion impacts on microbial communities, especially those of native plant invasions, on the diversity and composition of litter microbial communities.

We sampled litter and soil in a secondary broadleaved forest (representing the forest stage not invaded by Moso bamboos), a mixed forest of broadleaved trees and bamboos (representing the forest stage moderately invaded by Moso bamboos), and a Moso bamboo forest (representing the forest stage heavily invaded by Moso bamboos). We measured their chemical properties and microbial communities. Specifically, we address the following questions: (1) Does the Moso bamboo invasion alter chemical properties in soil and litter? (2) Does the Moso bamboo invasion alter diversity and composition of microbial communities in soil and litter? We expected that the bamboo invasion would decrease nutrient element concentrations in soil and litter and thus lead to changes in microbial diversity and composition in soil and litter.

2. Materials and Methods

2.1. Study Site

The study was carried out at Miaoshanwu Nature Reserve (119°56′~120°02′ E; 30°03′~30°06′ N) in Fuyang, Zhejiang Province, China. The area has a subtropical monsoon climate, with a mean annual temperature of 16.1°C and an annual precipitation of 1000 to 1964 mm. The mean annual sunshine duration is 1995 h, and the frost-free period is approximately 232 days per year [47]. The zonal vegetation is subtropical evergreen broadleaved forests, and dominant tree species include *Cyclobalanopsis glauca* (Thunb.) Oerst., *Lithocarpusglaber* (Thunb.) Nakai., *Quercus fabri* Hance., *Liquidambar formosana* Hance., *Schimasuperba* Gardn. et Champ., *Phoebe chekiangensis* C. B. Shang., *Cinnamomum camphora* (L.) Sieb., and *Machilus leptophylla* Hand. -Mazz.

2.2. Sampling Design

In August 2018, we selected three transects spanning from a secondary broadleaved evergreen forest, via a transition zone, to a Moso bamboo forest, representing three typical stages of the Moso bamboo invasion into subtropical forests. The secondary broadleaved forest (SF, representing the forest stage not invaded by Moso bamboos) included mainly *Phoebe chekiangensis* C. B. Shang, *Machilus leptophylla* Hand.-Mazz., and a few herbs such as *Dryopteris sparsa* (Buch.-Ham. ex D. Don) O. Ktze. In the forest at the transition zone (TF, representing the forest stage moderately invaded by Moso bamboos), 60% of the area is covered by the bamboos and 40% by broadleaved evergreen trees. In the Moso bamboo forest (MB, representing the forest stage heavily invaded by Moso bamboos), the bamboos are the only species at both tree and shrub layers, and the common herbs include *D.sparsa*.

We established a 10×10 m plot in each of the three invasion stages (i.e., SF, TF, and MB) along each of the three transects. There were three replicates per invasion stage and nine plots in total. Within each of the nine plots, we randomly selected five subplots of 1×1 m. In each subplot, we separately collected three litter samples at three different decomposition stages (coded as Stage I, II and III) and a soil sample at 0–10 cm depth (coded as IV for simplicity). In Stage I, the litter sample had not been decomposed; in Stage II, the litter sample had been partially decomposed; and in Stage III, the litter sample had been completely decomposed [48]. Five samples at the same stage and collected in the five subplots of the same plot were pooled into a composite sample.

After collection in the field, the soil samples were sieved to pass a 2-mm mesh, and the litter samples were cut into 0.25 cm^2 pieces after removing small particles. One part of each sample was kept in an icebox, transported to the laboratory, and then stored at $-80°$C for microbial analyses. The other part of each soil sample was air-dried, sieved to pass a 0.15-mm mesh, and then finely ground for measuring concentrations of total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP). The remained part of each litter sample was dried at 65°C for 72 h, sieved to pass a 0.425-mm mesh, and then finely ground for measuring concentrations of cellulose, lignin, total carbon (TC), TN, TP, Al, Ca, Cu, Fe, K, Mg, Mn, and Zn.

2.3. Chemical Analyses

To compare the carbon content in soil and litter, we measured soil TOC, but not soil inorganic carbon. The concentrations of TOC in soil, TC in litter, and TN in both soil and litter were measured by a Multi N/C 3000 analyzer (Analytik Jena AG, Jena, Germany) [49]. The concentrations of TP in both soil and litter were measured by the Mo-Sb antispetrophotography method after the samples were digested with nitric acid.The concentrations of K in litter samples were measured by flamephotometry. The concentrations of Al, Ca, Cu, Fe, Mg, Mn, and Zn in litter samples were determined by inductively coupled plasma–optical emission spectroscopy (ICP–OES, iCAP 7400, Thermo Fisher Scientific, Waltham, MA，USA) after complete digestion.

To measure the concentrations of lignin and cellulose, litter samples were firstly hydrolyzed by the sulphuric acid. Next, the acid-soluble cellulose and lignin were measured by anthrone colorimetry and ultraviolet spectrophotometer, respectively. Then the acid-insoluble lignin after acid hydrolysis was determined as the mass of insoluble residue [50].

2.4. Microbial Analysis

Total genomic DNA was extracted from 500 mg of each soil and litter sample using the E.Z.N.A.® Stool DNA Kit (D4015, Omega, Inc., Norcross, GA, USA). The V3–V4 region of the prokaryotic (bacterial and archaeal) small-subunit (16S) rRNA gene was amplified with slightly modified versions of the primers of 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′). The ITS2 region of the eukaryotic (fungi) small-subunit rRNA gene was amplified with slightly modified versions of the primers of fITS7 (5′-GTGARTCAT

CGAATCTTTG-3′) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′). The 5′ ends of the primers were sequencing universal primers tagged with specific barcodes.

To amplify the prokaryotic 16S and ITS fragments, the PCR conditions included an initial denaturation at 98 °Cfor 30 s, 35 cycles of denaturation at 98 °C for 10 s, annealing at 54 °C/52 °C for 30 s, and extension at 72 °C for 45 s, and then final extension at 72 °C for 10 min. PCR amplification was performed in a 25-μL reaction mixture consisting of 25 ng template DNA, 12.5 μL PCR premix, 2.5 μL of each primer, and PCR-grade water to adjust the volume. The PCR crude products were purified and quantified. The amplicon pools were prepared for sequencing. The libraries were sequenced on 300PE MiSeq runs, and one library was sequenced with both protocols using the standard Illumina sequencing primers to eliminate the need for a third (or fourth) index read.

2.5. Bioinformatics and Statistical Analysis

Microbial samples were sequenced on an Illumina MiSeq platform according to the manufacturer's recommendations, provided by LC-Bio. Paired-end reads were assigned to samples based on their unique barcode and truncated by cutting off the barcode and primer sequence. They were merged using FLASH (Fast length adjustment of short reads). Quality filtering on the raw tags was performed under specific filtering conditions to obtain high-quality clean tags according to the fqtrim (v0.94). Chimeric sequences were filtered using Vsearch software (v2.3.4). Sequences with ≥97% similarity were assigned to the same operational taxonomic units (OTUs) by Vsearch (v2.3.4) [51–53].

For bacteria, a total of 1, 167, 540 and 396, 976 valid sequencing reads were obtained from the 27 litter samples and the ninesoil samples, respectively. The sequences were clustered into 1,020,078 and 347,410 reads for litter and soil, respectively. Based on the sequences, 7363 and 4498 OTUs were obtained for the litter and soil samples, respectively, and were used for downstream analysis after filtration. For fungi, a total of 812,759 and 168,759 valid sequencing reads were obtained from the 27 litter and 9 soil samples, respectively. The sequences were clustered into 787,458 and 164,611 reads for the litter and soil samples, respectively. A total of 2623 and 987 OTUs for the litter and soilsamples, respectively, were used for downstream analysis.

Representative sequences were chosen for each OTU, and taxonomic data were then assigned to each representative sequence using the Ribosomal Database Project classifier. The differences of the dominant species between different groups and multiple sequence alignments were conducted using the mafft software (v7.310) to study the phylogenetic relationship between different OTUs. OTU abundance information was normalized using the standard of sequence number corresponding to the sample with the least sequences. Alpha diversity was applied in analyzing the complexity of species diversity for a sample through four indices, including the Chao1, Shannon, Simpson, and the observed species indices, which were calculated with QIIME (v1.8.0).

We used two-way ANOVA to examine effects of forest types (no invasion (SF), intermediate invasion (TF) and heavy invasion (MB)) and litter decomposition stages (I, II, III, and/or VI) on the concentrations of macro-elements (C, N, P, and K) and meso- and micro-elements (Al, Ca, Cu, Fe, K, Mg, Mn, and Zn), the concentrations of cellulose and lignin, and microbial diversity (observed OTUs, Chao1 and Shannon indices). When a significant effect was detected, Duncan's tests were used for multiple comparisons. Before ANOVA, data were checked for homogeneity of variance (by the Bartlett test). Data on concentrations of C, Mn, and Zn and Fe were logarithmically transformed, and data on the concentration of Mg were reciprocally transformed. SPSS (v19.0; IBM, Armonk, NY, USA) was used for ANOVA.

To examine whether microbial communities of the three forest types (SF, TF, and MB) and/or the four litter decomposition stages (I, II, III, and IV) could be distinguished, we analyzed microbial community data (OTUs with relative abundances >1% and occurringin >2 samples on the genus level) by principal coordinate analysis (PCoA). This analysis was done for the bacterial and fungus communities separately. The Bray–Curtis distance was used as a dissimilarity measure in PCoA. The

analyses were conducted using CANOCOv5 (Biometrics Plant Research International, Wageningen, Netherlands) [54–56].

3. Results

3.1. Macro-Elements, Cellulose, and Lignin

The concentrations of C, N, P, K, and lignin varied significantly among the three forest types (Figure 1), showing an order of SF > TF > MB for the C, N, P and lignin concentrations, and an order of TF > SF > MB for the K concentration (Figure 1). The concentrations of C, N, P, K, cellulose, and lignin decreased with the decomposition stage from I to IV (all $p < 0.01$) in the three forest types, except for the P and K concentrations in MB (Figure 1). Significant interactions between forest types and decomposition stages were detected for the concentrations of C, N, P, and K, but not for those of cellulose and lignin, indicating that variations of the C, N, P, and K concentrations among the decomposition stages depended on forest types (Figure 1). Forest types had no effect on the cellulose concentration ($p > 0.05$; Figure 1g).
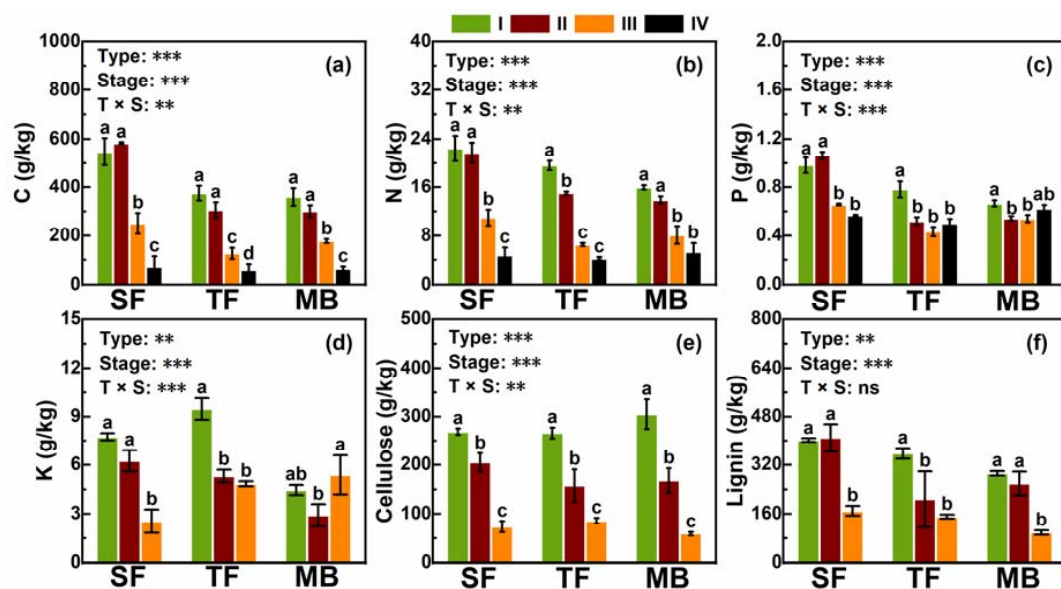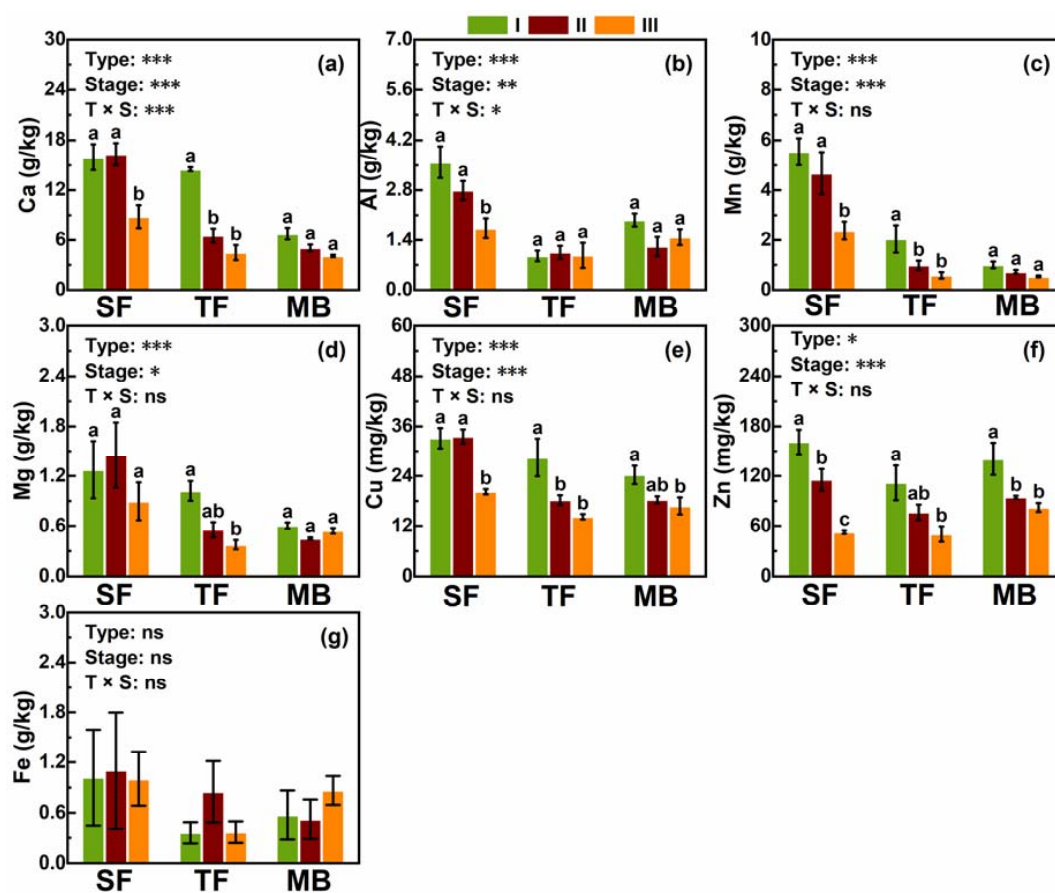

Figure 1. Concentrations of macro-elements, cellulose, and lignin at the four stages of litter decomposition (I, II, III and IV) in the three forest types. (**a**–**f**) a–e, in turn, is the concentration of C, N, P, K, Celllose, and Lignin in the litter and soil. SF—secondary broadleaved forest, representing the stage not invaded by Moso bamboos; TF—forest at the transition zone, representing the stage moderately invaded by Moso bamboos; MB—pure Moso bamboo forest, representing the stage heavily invaded by Moso bamboos. Mean, SE ($n = 9$) and the significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and [ns] $p > 0.05$) of two-way ANOVAs are also given. Different letters indicate significant differences between the four stages within a forest type. Concentrations of K, cellulose, and lignin were measured only for litter (I, II, and III), but not for soil (IV).

3.2. Meso- and Micro-Elements

Except for Fe (Figure 2g), the meso- and micro-elements measured significantly varied with both forest type and decomposition stage (Figure 2). However, only Ca and Al were influenced by the interaction between forest type and decomposition stage (Figure 2a–c). Fe in all the three forest types (Figure 2g) and Al in MB and TF (Figure 2b) did not change with the decomposition stage; all other elements in other cases showed a decreasing trend with increasingdecomposition stage from I to IV (Figure 2). Except for Fe (MB = TF = SF), SF had the highest levels of those meso- and micro-elements (Figure 2).

Figure 2. Concentrations of meso- and micro-elements at the three stages of litter decomposition (I, II, and III) in the three forest types. (**a**–**g**) a–g, in turn, is the concentration of Ca, Al, Mn, Mg, Cu, Zn, and Fe in the litter. The codes for forest types are described as in Figure 1. Mean, SE ($n = 9$), and the significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and ns $p > 0.05$) of two-way ANOVAs are also given. Different letters indicate significant differences between the four stages within a forest type.

3.3. Bacteria

The total number of bacterial OTUs was 6489 in SF, 6652 in MB, and 6727 in TF. Averaging across the four stages, the number of OTUs, Chao1 and Shannon indices of bacteria were not affected by forest types (Figure 3a–c; all $p > 0.05$). Decomposition stages had significant effects on bacteria, and bacteria were, in general, more abundant and diverse in Stages II and III than in Stages I and IV (Figure 3a–c; all $p < 0.001$).

In the bacterial communities, for the 20 genera with the highest abundance, there was a shift in the relative abundance of, e.g., *Burkholderia*, *Sphingomonas*, *Enterobacteriaceae*, *Luteibacter*, and *Acidisphaera* from SF to TF (Figure4). At Stage I, from SF to TF, the abundance of *Burkholderia*, *Sphingomonas,* and *Enterobacteriaceae* decreased by 8.92, 3.66, and 4.22%, respectively, but that of *Luteibacter* and *Acidisphaera* increased (Figure 4a). At Stage II, the relative abundance of *Burkholderia* increased by 10.41% from SF to TF, but that of *Enterobacteriaceae* decreased by 7.89% (Figure 4b). At Stage III, the relative abundance of *WPS-2_genera* decreased by 10.4% from SF to TF (Figure 4c). At Stage IV, no change was found between forest types in the first 20 genera (Figure 4c). The remaining taxa (labeled as "others") increased from SF to TF at all four stages (Figure 4).

The first two axes of PCoA explained 72.36% and 8.96% of the variance, respectively. The bacterial communities of the four decomposition stages were well separated along the first axis of PCoA, but those of the three forests types (SF, TF, and MB) could not be distinguished in the ordination space (Figure S1A).
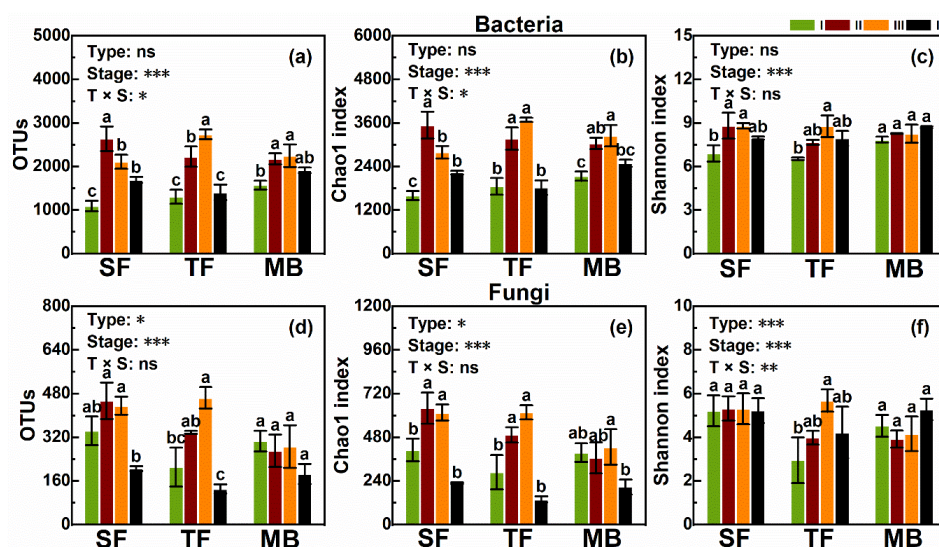
Figure 3. Community diversity of bacteria (**a**–**c**) and fungi (**e**,**f**) at the four stages of litter decomposition (I, II, III and IV) in the three forest types. The codes for forest types are described as in Figure 1. Mean, SE (*n* = 9) and the significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and [ns] $p > 0.05$) of two-way ANOVAs are also given. Different letters indicate significant differences between the four stages within a forest type.
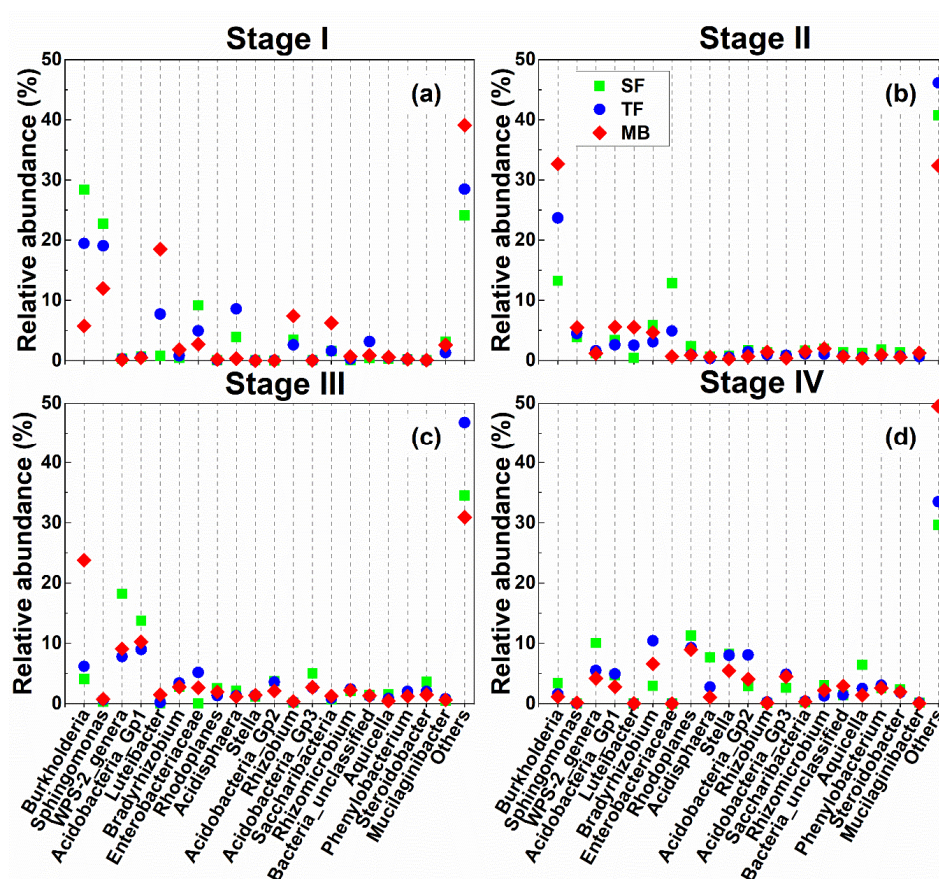
Figure 4. Relative abundances of bacterial OTU clusters at the genus level from the four litter decomposition stages (I, II, III, and IV) in the three forest types. (**a**–**d**) a–d, in turn, is the litter decomposition stages I, II, III, IV. The codes for forest types are described as in Figure 1. The data shown are the 20 taxa with the highest abundances, as well as the summed abundance of the remaining taxa (labeled as "others").

3.4. Fungi

The total number of fungal OTUs was 1853 in TF, 1650 in SF, and 1495 in MB. The forest type significantly affectedthe number of OTUs, Chao1 and Shannon indices of fungi (Figure 3d–f; all *p*< 0.05). The number of OTUs, Chao1 index, and Shannon index were higher in SF than in MB and TF, but did not differ between MB and SF (Figure 3d–e). Decomposition stages highly and significantly affected the abundance and diversity of fungi (all *p*< 0.001), and fungi were, in general, more abundant and diverse in Stages II and III as compared to Stages I and IV (Figure 3e–f).

The relative abundance of the first 20 genera varied with both forest types and decomposition stages (Figure 5). At Stage I, from SF to TF, the relative abundance of an unclassified genus of *Ascomycota*, *Sordariomycetes*, and *Pleosporales* decreased by 11.95%, 7.27%, and 7.21%, respectively, but that of *Dothideomycetes*, *Capnodiales*, and *Amphisphaeriaceae* increased by 11.99%, 29.6%, and 20.09%, respectively (Figure 5a). At Stage II, from SF to TF, the relative abundance of the unclassified genus of *Ascomycota* and *Basidiomycota* decreased by 24.51% and 12.74%, respectively, but that of *Trechispora*, *Dothideomycetes*, *Hypocrea,* and *Geastrum* increased by 15.08%, 11.42%, 13.05%, and 8.26%, respectively (Figure 5b). At Stage III, the relative abundance of *Russula* decreased by 16.03%, but that of *Mycena* increased by 14.77% (Figure 5c). At Stage IV, the relative abundance of *Trechispora* decreased by 17.01%, but the unclassified genus of *Ascomycota* and *Tomentella* increased by 8.09% and 26.47%, respectively (Figure 5d). The remaining unclassified fungal taxa (labeled as "others") decreased from SF to TF at all four stages (Figure 5).
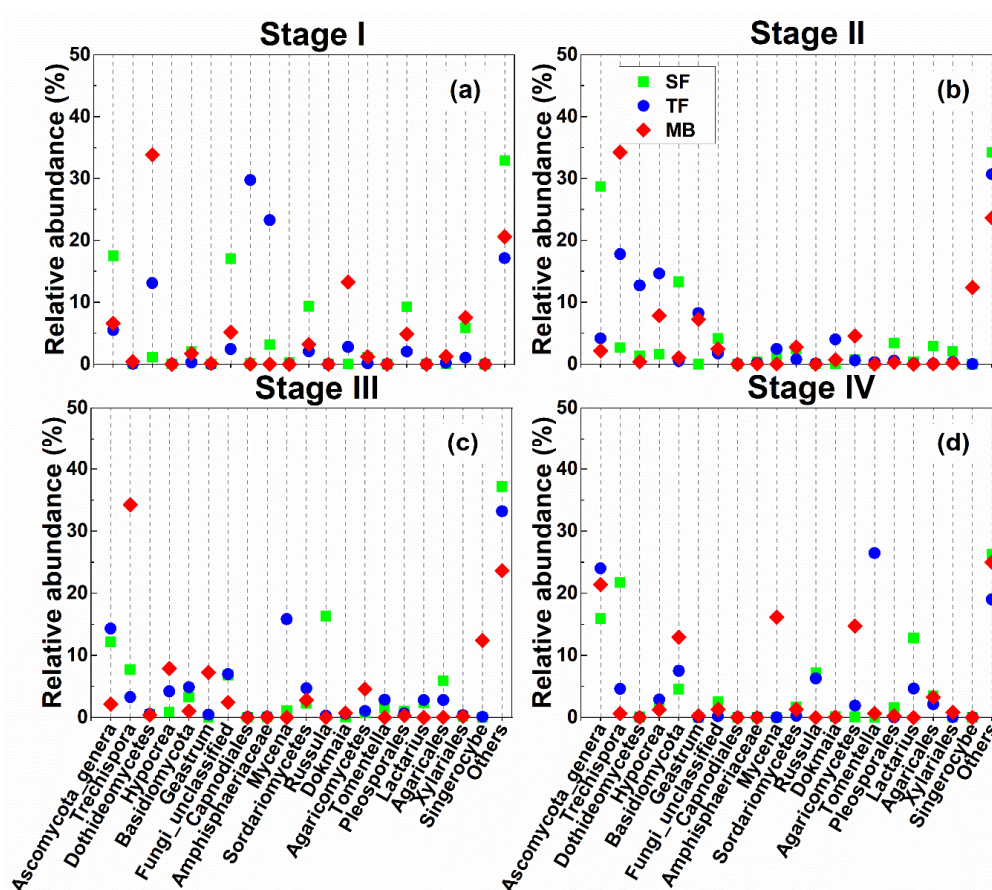
Figure 5. Relative abundances of fungal OTU clusters at the genus level from the four litter decomposition stages (I, II, III, and IV) in the three forest types. (**a**–**d**) a–d, in turn, is the litter decomposition stages I, II, III, IV. The codes for forest types are described as in Figure 1. The data shown are the 20 taxa with the highest abundances, as well as the summed abundance of the remaining taxa (labeled as "others").

The first two axes of PCoA explained 39.9% and 22.7% of the variance, respectively. The fungal communities of the four decomposition stages were well separated along the first axis of PCoA, but those of the three forest types (SF, TF, and MB) could not be distinguished in the ordination space (Figure S1B).

4. Discussion

4.1. Effects of Moso Bamboo Invasions on Nutrients in Litter and Soil

Plant invasions may affect ecosystems through multiple processes, including the alteration ofenvironmental factors (light and soil nutrients), soil physio-chemical properties, and soil microbial abundance, diversity, and composition [57,58]. Previous studies have shown that bamboo invasions can change C, N, and P concentrations in the soil layer [35–38,59]. In this study, C, N, P, and lignin concentrations decreased after the bamboo invasion, which is consistent with previous findings [35–38,59]. In addition, some other studies have shown that the concentrations of soil-exchangeable K, Ca, and Mg changed after the invasion of bamboos, which were close to those in the pure forest of bamboos [60]. In this study, Mg, Al, Ca, Mn, Cu, and Zn concentrations were lower in TF than in SF. The mechanisms of litter decomposition and soil nutrient dynamics are still not clear, but recent studies have shown that it may be closely related to the composition of bacterial and fungal communities [61].

4.2. Effects of Bamboo Invasion on Bacteria and Fungi in Litter and Soil

A previous study showed that the invasion of Moso bamboos increased the diversity of soil bacterial communities [41]. Our results showed that the invasion of Moso bamboo increased microbial diversity in litter and soil, but some bacteria or fungi exhibited different responses to the bamboo invasion. The proportion of bacteria (*Burkholderia*, *Luteibacter,* and *Acidisphaera*) and fungi (*Trechispora*, *Capnodales*, *Amphisphaeriaceae*, *Dothideomycetes*, and *Hypocrea*) in litter in TF increased after the bamboo invasion. The increase of these microorganisms may promote litter decomposition [62–64]. Conversely, the bamboo invasion led to a decrease in the proportion of some bacteria, such as *Sphingomonas* and *Enterobacteriaceae*, which may be due to the inhibition of the growth of some microorganisms in bamboo forests. Such a decrease in microbial diversity also occurred after invasions by plants other than Moso bamboos [55,65].

Given that there were different microbial communities in different litter and soil layers, more definitive results were obtained by stratifying litter into different stages under the three forest types. Litter at Stage I is easily exposed to tissue leaching, initial colonization, and decay; litter at stage II is composed of rich "soil fungi"; and litter at Stage III possesses low mass-loss rates [48]. Litter in the soil layer (at Stage IV) has the largest microbial abundance, which directly affects the composition of microbial communities [56,66]. In this study, microbes were more abundant in Stages II and III than in Stages I and IV. An increase in fungal abundance and diversity mainly occurred during Stage III. This indicates that the bamboo invasion has different effects at different litter decomposition stages.

Compared with bacteria, fungi showed different responses to bamboo invasions because of their low diversity and abundance. It has been proposed that fungal communities in litter are mainly influenced by dominant plant species, while fungal communities in soil are influenced by both dominant plant species and soil physio-chemical properties [67]. In this study, fungi were more susceptible to the bamboo invasion than bacteria, which may be caused by different physiological metabolisms of bacteria and fungi themselves. It is also found that fungal communities are more vulnerable to changes in dominant vegetation than bacterial communities [42]. These findings may explain why fungal communities were more affected by the Moso bamboo invasion in our study.

4.3. Litter Microbial Communities in Relation to Litter Characteristics

Litter nutrients have an important effect on the decomposition of litter and the growth of microorganisms, and the invasive species can influence the growth of the microorganisms and the decomposition of litter by changing the nutrient composition of mixed litter [67–69]. Although many studies have reported that changes in tree species affect the composition of microbial communities, it is not clear how microbial communities respond to tree species changes [59,70,71]. Litter with a high concentration of N and a low concentration of lignin is generally considered to be susceptible to microbial decomposition. The heterogeneity and interaction of litter can promote the mobility of microbes and improve the utilization of C and N by microbes [72]. For example, compared to coniferous forests, broadleaved forests produce a smaller amount of litter with high N, thereby releasing a larger amount of cations such as Ca^{2+} and Mg^{2+}, promoting the soil to become acidic, and affecting the growth and activity of the microbes [70]. Lignin is mainly degraded by a specific fungal community [72]. In our study, bacterial diversity in litter was significantly negatively correlated with the concentration of cellulose, lignin, N, C, and P in litter, as well as with the concentration of metal elements such as Zn, Cu, Ca, K, and Al in litter (Figures S2 and S3). The fungal diversity in litter was significantly negatively correlated with the cellulose concentration in litter (Figure S3). We show that changes in nutrients in litter can affect the structure of microbial communities in the litter and soil [21,63].

5. Conclusions

We found that native Moso bamboo invasions could decrease soil nutrient concentrations and modify fungal abundance, diversity, and composition. Also, fungi were more sensitive to native Moso bamboo invasions than bacteria. These findings suggest that native Moso bamboo invasions into subtropical forests may lead to a complex biogeochemical process in the litter–soil system, which can further threaten the local forest ecosystems by affecting microbial communities and, thus, litter decomposition and nutrient cycling. Further studies are needed to better understand how these changes will affect the litter decomposition processes and, thus, soil quality and plant–soil feedback processes.

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