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ORIGINAL ARTICLE

Changes in soil microbial community and activity in warm temperate forests invaded by moso bamboo (*Phyllostachys pubescens*)

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Abstract In the past few decades, moso bamboo (*Phyllostachys pubescens*) forests in Japan have rapidly expanded, and moso bamboo is now invading nearby native forests. In this study, we assessed the effects of moso bamboo invasion on the soil microbial community and activity in warm temperate forests in western Japan. We sampled soil, measured soil microbial respiration, and used phospholipid fatty acid (PLFA) analysis to examine changes in microbial community composition. We found that the invasion of bamboo into the native secondary forest of Japan can cause changes to some soil properties. We also observed a significant difference in soil microbial community composition between the bamboo and native forests. The ratio of bacterial PLFA to fungal PLFA was significantly higher after bamboo invasion, while bacterial PLFA contents were significantly lower in the organic layer. Soil microbial respiration rates significantly decreased in the organic layer, and significantly increased in the mineral layer. Microbial respiration activity, as indicated by soil microbial respiration rates per total PLFA content, decreased in the organic layer but increased in the mineral layer after bamboo invasion. These results indicate that bamboo invasion significantly affects associated soil microbial communities and decomposition patterns of soil organic matter.

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Introduction

Invasions by exotic plants have been recognized as one of the main causes of declining species diversity (Keane and Crawley 2002), native habit degradation (Wilcove et al. 1998), and interference with tree regeneration (Chornesky et al. 2005). In the past few decades, moso bamboo (*Phyllostachys pubescens*), which originated in China and was introduced to Japan about 300 years ago, has rapidly expanded throughout the Japanese archipelago (Torii 2003; Shibata 2010). Recent research showed that bamboo-dominated forested areas doubled in the western part of Japan between the late 1970s and 1990s (Kobayashi and Tada 2010), and that replacement of native forest by bamboo results in landslides (Shinohara and Kyoichi 2015), reduced species diversity (Isagi and Torii 1998), and altered nutrient dynamics (Fukushima et al. 2015).

In addition, bamboo invasion also has significant impacts on forest C dynamics. Kobayashi and Tada (2010) indicated that aboveground C storage in broadleaved forests decreased due to the invasion of bamboo and shifted a potential C sink to a source. Ishiga et al. (2001) indicated that most C allocation in bamboo was in the belowground root system, which is connected to belowground culms, enabling C and nutrient transport from mature to young culms. However, information on the effects of bamboo invasion on soil C dynamics is scarce.

One of the mechanisms by which an exotic plant may affect ecosystem C dynamics is alteration of the soil microbial community. Several studies have indicated that

exotic plants affect the activity and composition of soil microbial communities by altering the soil environment during root growth, substrate availability through root exudation, and nutrient availability through plant uptake (Kourtev et al. 2002, 2003; Wolfe and Klironomos 2005; Li et al. 2006; Batten et al. 2006; Bardgett et al. 2008). Soil microbial communities play an important role in C and nutrient cycles and in soil formation through the decomposition and mineralization of soil organic matter (SOM) (Yoshitake and Nakatsubo 2008). Kourtev et al. (2002) found that two exotic plant species [Japanese barberry (*Berberis thunbergii*) and Japanese stilt grass (*Microstegium vimineum*)] affect the soil microbial community structure and function in hardwood forests in northern New Jersey, USA.

Two recent papers (Chang and Chiu 2015; Xu et al. 2015) clarified the impact of bamboo invasion on the structure and activity of the soil microbial community. However, little is known about its effects on soil C flow in soil layers. Here, we assess the SOM, soil total C and N, soil microbial respiration, and community composition of both organic and mineral layers in non-invaded native evergreen broadleaved forests and adjacent bamboo forests.

Materials and methods

Study site

The study was conducted in forested areas in Higashi-Hiroshima City, Hiroshima Prefecture, western Japan (34°41′N, 132°72′E; 226–278 m a.s.l.). The area is in a warm climate region with an annual mean air temperature of 13.5 °C and annual average precipitation of 1446 mm recorded for 1981–2010 (general weather archives of the Japan Meteorological Agency, http://www.jma.go.jp/jma/index.html). The soils in this area are classified as coarse-textured, residual, immature with a parent rock of granite (Japan National Land Survey Division, Land and Water Bureau, Ministry of Land, Infrastructure and Transport and Tourism).

In 2013, three experimental sites (A, B, C), each of which included a native broadleaved forest stand (An, Bn, Cn) and an adjacent bamboo forest stand (Ab, Bb, Cb), were selected. A 10-m × 10-m plot was established in each stand. From aerial photos (Geospatial Information Authority of Japan) of the study area taken in 1975, 1981 and 2013, bamboo appeared to have invaded the native forest approximately 30 years before our study. A vegetation survey was conducted in all plots in 2014. Dominant tree species, tree density, and diameter at breast height in each plot are summarized in Table 1.

Soil sampling and analysis

Three sampling points (15 cm × 15 cm) were randomly selected in each plot. In late August 2013, litter and organic layers (FH layer) were sampled separately, and a mineral soil sample of the 0- to 5-cm layer (under the FH layer) was obtained using a stainless steel cylinder (diameter = 5.0 cm, height = 5.0 cm) at each point. The total number of soil samples is 54 (3 replicates × 3 sites × 2 forest types × 3 soil layers). Samples were placed in plastic bags and transported back to the laboratory. Plant roots and gravel in the soil samples were removed using a 2-mm-mesh sieve and tweezers; each layer was divided into three subsamples for soil characteristic analysis, soil microbial respiration measurement, and phospholipid fatty acid (PLFA) analysis.

For this study, the water contents of the litter layer samples and other layer samples were determined gravimetrically after drying at 80 °C for 48 h and at 105 °C for 24 h, respectively; these were used to calculate the initial samples' dry weight per area. Soil pH (H_2O) (air-dried soil, H_2O 1:5 w/v) was measured using a pH meter fitted with a glass electrode (D-24, no. 9621-10D; Horiba, Kyoto, Japan). SOM was determined by loss in weight on ignition (550 °C, 12 h). Total C and N contents were measured using a CN analyzer (2400 II; PerkinElmer, Wellesley, MA) and the C/N ratio was calculated.

Microbial biomass and community structure

Soil microbial biomass and community composition were examined using PLFA analysis. PLFAs are the major components of the membranes of living cells, so the amount and composition of PLFAs in soils have been used as an index of the total microbial biomass and as a fingerprint of the microbial community structure, respectively (e.g., Frostegård et al. 1993).

We measured the PLFA content of all organic and mineral layer soil samples. The samples for PLFA measurement were freeze-dried and stored at −80 °C until analysis. Total lipids were extracted from moist soil using a chloroform–methanol extraction approach (Bligh and Dyer 1959), as modified by White et al. (1979) and Frostegård et al. (1993). An aliquot of 1–2 g (dry weight) of soil was extracted using a chloroform–methanol-citrate buffer mixture (1:2:0.8 by volume), and the lipids were separated into neutral lipids, glycolipids, and phospholipids on a silicic acid column (Sep-Pak Silica Plus; Waters, Milford, MA), as described by Arao et al. (2001). Phospholipids were esterified using an HCl-methanol reagent (Tokyo Kasei Kogyo, Tokyo) (Stoffel et al. 1959), and the PLFAs were then purified from the lipid extracts, quantified, and identified using a gas chromatograph (GC-2014; Shimadzu,

Table 1 The dominant tree species, tree density, and mean diameter at breast height (*DBH*) (mean ± SD) in our study plots

Site	Stand	Tree density (stems (10 m × 10 m)$^{-1}$)	Mean DBH (cm)	Dominant species
A	Native (An)	35	9.6 ± 7.4	*Symplocos kuroki, Eurya japonica, Chamaecyparis obtusa*
	Bamboo (Ab)	132	6.1 ± 1.2	*Phyllostachys pubescens*
B	Native (Bn)	33	9.0 ± 6.9	*Symplocos kuroki, Eurya japonica*
	Bamboo (Bb)	124	8.3 ± 1.3	*Phyllostachys pubescens*
C	Native (Cn)	34	7.3 ± 2.9	*Symplocos kuroki, Quercus glauca*
	Bamboo (Cb)	116	6.9 ± 1.2	*Phyllostachys pubescens*

Kyoto) equipped with a capillary column (30 m DB-5 ms, phenyl-methyl/silicone; J&W Scientific, Folsom, CA). He was used as the carrier gas, and peak areas were quantified by adding methyl nonadecanoate fatty acid (19:0) as an internal standard; we used the fatty acid nomenclature described by Frostegård et al. (1993). Total content of 26 major PLFAs (TotPLFAs) was used as an indicator of total microbial biomass in the soil sample (Frostegård et al. 1993). The fatty acids i15:0, a15:0, 15:0, i16:0, 17:0, i17:0, cy17:0, 18:1ω7c, and cy19:0 were chosen to represent bacterial PLFAs (BactPLFAs) (Frostegård et al. 1993). The amount of 18:2ω6,9 was used as a metric of fungal biomass (FungPLFA) (Frostegård and Bååth 1996; Yoshitake et al. 2006; Xue et al. 2008). We calculated the ratio of BactPLFAs to FungPLFA (F/B ratio).

Soil microbial respiration

Samples for measuring soil microbial respiration rate were stored in a plant growth chamber at 20 °C for 10 days. Before measurement, the samples were weighed to determine their in situ water content. We conducted a preliminary experiment in which the soil microbial respiration rates were measured for 10 days (measurements were made on days 0, 2, 5, 7 and 10) to determine whether they change; we found that soil microbial respiration rates stabilize after 7 days, so we measured the soil microbial respiration rate between the 7th and 10th days after sampling.

Soil microbial respiration rates of samples were measured at 20 °C using an open-flow system with an infrared gas analyzer (LI-6252; LI-COR, Lincoln, NE), as detailed by Bekku et al. (1997). Litter layer samples were placed in a cylindrical plastic chamber (diameter = 15.0 cm, height = 5.0 cm) that was connected to the system. The samples of the organic and mineral soil layers were placed in stainless steel cylinders for field soil density measurement, and then in cylindrical plastic chambers for the measurement of soil microbial respiration (diameter = 5.3 cm, height = 6.4 cm). Ambient air containing approximately 400 p.p.m. CO_2 flowed into the system at a rate of 150 ml min^{-1}. During the measurement, the chamber was placed in a water bath to maintain the sample temperature at 20 °C; the sample temperature was monitored with a thermocouple sensor (D717; Technol Seven, Tokyo).

Data analysis

We used two-way ANOVA to analyze the effects of vegetation (native vs. bamboo) and site (A, B, C) on soil properties, microbial respiration rates, activity, and PLFA contents in organic and mineral layers, respectively. In addition, to clarify the difference in microbial community composition, we performed a nonmetric multidimensional scaling (NMDS), based on the Bray-Curtis dissimilarity index. The contents of the major PLFAs were arcsine square root transformed prior to analysis, and the resulting dissimilarity matrices were subjected to NMDS. We obtained two-dimensional ordination graphs for organic (Fig. 2a, stress value = 0.15) and mineral layers (Fig. 2b, stress value = 0.11), respectively. The closer the points on a graph, the more similar they are in composition. To assess the statistical compositional dissimilarity of microbial communities between the native and bamboo forests, the Euclidean distance was calculated. The significance of the difference in the Euclidean distances was determined by permutation tests (999 permutations). All statistical analyses were carried out using R version 3.2.0 (R Core Team 2015).

Results

Soil characteristics

The forest type (native vs. bamboo) had significant effects on some of the soil characteristics, while the study site (A, B, C) had no significant effects on any of the soil characteristics examined (Table 2). In the litter layer, water

Table 2 Results of the two-way ANOVA showing the effects of vegetation (native vs. bamboo) and site (A, B, C) on the soil physicochemical properties (mean ± SD) in organic and mineral layers

Forest type	Native forest	Bamboo forest	Two-way ANOVA *P*-values		
			Vegetation	Site	Vegetation × site
Water content					
Litter	44.7 ± 8.4	60.7 ± 10.5	0.02*	0.39	0.27
Organic	38.3 ± 2.2	28.1 ± 4.1	0.02*	0.26	0.38
Mineral	11.7 ± 3.9	19.3 ± 3.8	0.01**	0.32	0.13
pH (H_2O)					
Litter	4.8 ± 0.2	4.6 ± 0.2	0.93	0.18	0.79
Organic	4.5 ± 0.2	4.4 ± 0.2	0.66	0.36	0.48
Mineral	4.3 ± 0.1	4.3 ± 0.1	0.67	0.61	0.21
SOM (mg g^{-1})					
Organic	391.7 ± 75.8	123.7 ± 45.8	0.001**	0.99	0.74
Mineral	46.0 ± 5.3	77.1 ± 17.4	0.02*	0.32	0.69
Total C (%)					
Litter	49.2 ± 2.0	39.3 ± 2.5	<0.001***	0.49	0.38
Organic	30.1 ± 2.7	7.9 ± 4.2	<0.001***	0.13	0.26
Mineral	2.3 ± 0.6	3.5 ± 0.8	0.02*	0.27	0.04*
Total *n* (%)					
Litter	1.5 ± 0.6	1.6 ± 0.1	0.793	0.36	0.95
Organic	1.5 ± 0.3	0.4 ± 0.2	<0.001***	0.89	0.23
Mineral	0.1 ± 0.02	0.2 ± 0.03	<0.001***	0.66	0.04*
C/N ratio					
Litter	35.5 ± 10.9	24.9 ± 1.4	0.02*	0.08	0.19
Organic	21.0 ± 2.7	17.8 ± 2.0	0.425	0.12	0.84
Mineral	21.1 ± 1.7	14.3 ± 2.1	<0.001***	0.51	0.023*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

content increased significantly after moso bamboo invasion, while the total C and the C/N ratio decreased. In the organic layer, lower water content, SOM, total C, and N were observed in the bamboo forest compared to the native forest. Conversely, in the mineral layer, we found higher water content, SOM, and total C and N, and lower C/N ratio, in the bamboo forest compared to the native forest. Significant interaction effects between forest type and site were detected on the total C, N and C/N ratio in the mineral layer (Table 2).

Soil microbial community composition

Twenty-five major PLFAs were detected in the organic layer, while 26 major PLFAs were detected in the mineral layer (Table 3). In the native forests, cy17:0 and 18:3ω3 were not detected in the organic layer, while in the mineral layer 15:0, 17:1ω7, 2OH16:0 and 20:0 were not detected. In contrast, in the bamboo forests, i17:0, a17:0, cy17:0, 17:0 and 2OH16:0 were not detected in the organic layer, while in the mineral layer 14:0, 15:0, 2OH14:0, 18:3ω3, 18:3ω6 and 20:0 were not detected. The TotPLFA content, an index of soil microbial biomass, did not differ in either organic or mineral layers between the bamboo and native forests (Table 4; Fig. 1a). In contrast, the BactPLFA content of the organic layer decreased and the FungPLFA content of the mineral layer increased in the bamboo forests (Table 4; Fig. 1b, c). As a result, the F/B ratios in both organic and mineral layers were higher in bamboo forests than in native forests (Table 4, organic layer, $P < 0.001$; mineral layer, $P < 0.05$). No significant interaction effect of forest type and site was detected (Table 4).

There was a significant difference in composition of the major PLFAs in both organic and mineral layers between bamboo forests and native forests. Using plant type as an explanatory variable, composition of the major PLFAs in both organic (Fig. 2a, $P < 0.05$) and mineral layers (Fig. 2b, $P < 0.001$) between bamboo and native forests significantly differ.

Soil microbial respiration

The microbial respiration rates per soil weight of the organic layer in the bamboo forest (27.7 ± 9.5 μg C g^{-1} h^{-1}) were approximately one-third of that in the native forest (70.2 ± 14.3 μg C g^{-1} h^{-1}) (Fig. 3a). However, in

Table 3 Composition of 26 major phospholipid fatty acids (mol %) between native and bamboo-invaded forests

	14:0	i15:0	a15:0	15:0	2OH14:0	i16:0	16:1ω7	16:1	16:0	Br17:0	17:1ω7	i17:0	a17:0
No	2.9	5.6	2.6	2.0	2.3	4.5	5.0	2.7	24.2	5.6	1.7	2.0	4.3
Bo	0.0	4.4	2.1	0.0	1.5	2.6	4.0	2.7	10.1	3.9	0.0	1.9	3.1
	cy17:0	2OH16:0	18:3ω3	18:3ω6	18:2ω6c	18:1ω9c	18:1ω9t	18:0	cy19:0	20:3ω6	20:3ω3	20:0	
No	0.0	2.0	0.0	3.4	13.0	15.9	9.3	4.4	6.2	4.6	2.3	1.4	
Bo	1.2	0.0	18.5	1.9	6.0	10.6	7.6	3.2	8.2	3.8	2.5	0.0	
	14:0	i15:0	a15:0	15:0	2OH14:0	i16:0	16:1ω7	16:1	16:0	Br17:0	17:1ω7	i17:0	a17:0
Nm	2.0	5.0	5.0	3.1	1.3	3.8	2.6	2.6	8.5	6.0	1.8	0.0	0.0
Bm	0.0	6.4	4.3	0.0	0.0	5.0	2.9	3.9	15.2	5.5	2.0	2.5	6.0
	cy17:0	2OH16:0	18:3ω3	18:3ω6	18:2ω6c	18:1ω9c	18:1ω9t	18:0	cy19:0	20:3ω6	20:3ω3	20:0	17:0
Nm	0.0	0.0	2.4	2.3	4.4	8.4	4.6	2.9	27.8	1.1	3.0	1.4	0.0
Bm	0.8	1.6	0.0	0.0	5.9	10.6	9.0	4.5	8.5	1.2	2.9	0.0	1.3

Values are means ($n = 9$)

No organic layer sample in native forest, *Bo* organic layer sample in bamboo forest, *Nm* mineral layer sample in native forest, *Bm* mineral layer sample in bamboo forest

Table 4 Results of two-way ANOVA showing the effects of vegetation and site on phospholipid fatty acid (PLFA) contents and soil microbial respiration rate and activity in organic and mineral layers

Parameter	Organic layer			Mineral layer		
	Vegetation	Site	Vegetation × site	Vegetation	Site	Vegetation × site
TotPLFA						
F	7.206	0.882	2.267	4.155	0.107	0.69
P	0.363	0.462	0.185	0.076	0.899	0.529
BactPLFA						
F	91.691	0.718	2.373	0.602	0.496	3.669
P	0.023*	525	0.174	0.46	0.627	0.074
FungPLFA						
F	2.526	1.338	2.012	73.178	3.223	9.419
P	0.093	0.331	0.214	0.001***	0.094	0.079
F/B ratio						
F	9.587	0.147	0.31	68.119	0.126	0.005
P	0.021*	0.867	0.745	<0.001***	0.884	0.995
Respiration rate						
F	85.276	2.744	0.441	65.879	0.726	0.442
P	<0.001***	0.104	0.654	<0.001***	0.513	0.658
Activity[a]						
F	10.1	0.103	0.99	3.15	3.28	0.287
P	0.003**	0.748	0.445	0.023*	0.078	0.885

BactPLFA Bacterial PLFA, *FungPLFA* fungal PLFA, *F/B ratio* BactPLFA:FungPLFA ratio * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] As indicated by microbial respiration rate per total content of 26 major PLFAs [*TotPLFA*; ng CO_2-C (nmol PLFA)$^{-1}$ h^{-1}]

the mineral layer, the microbial respiration rates per soil weight in the bamboo forest (1.26 ± 0.2 μg C g^{-1} h^{-1}) were approximately three times higher than those in the native forest (0.44 ± 0.09 μg C g^{-1} h^{-1}) (Fig. 3b). The microbial respiration rates per unit weight in the organic layer were significantly lower after the bamboo invasion

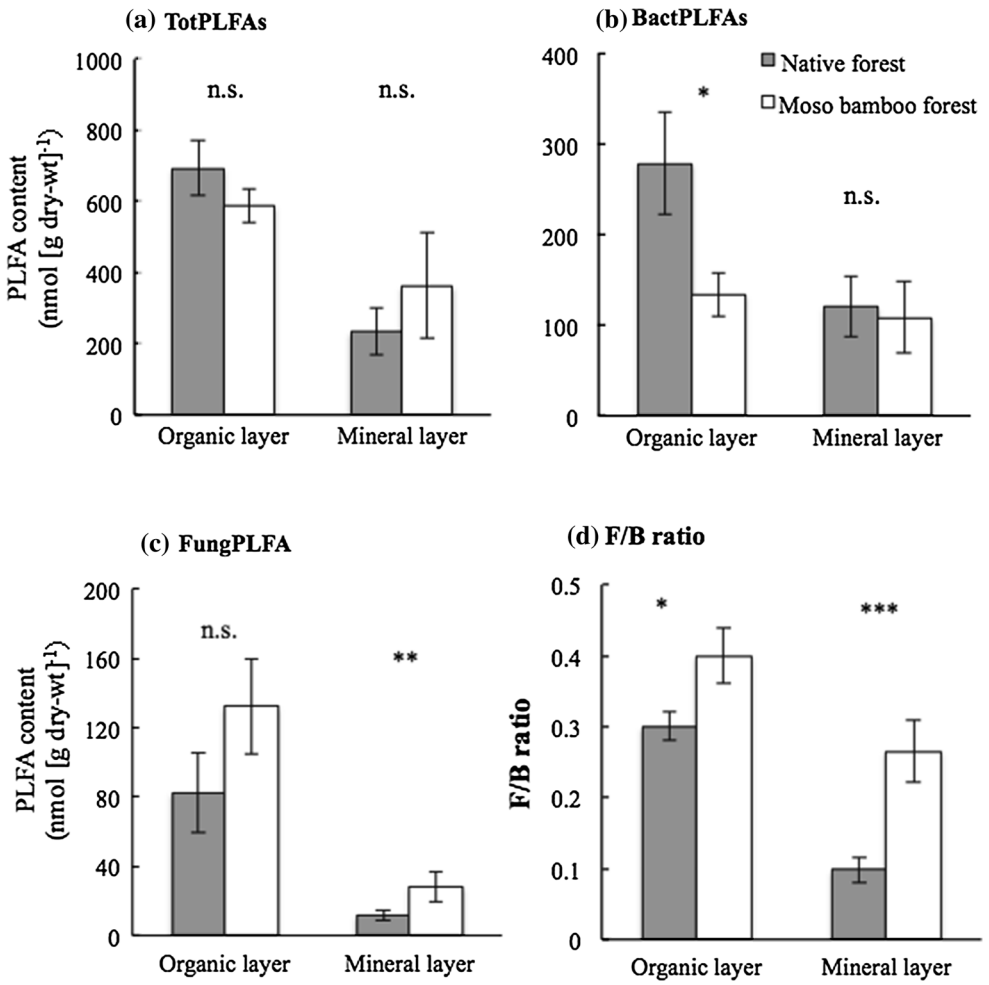

Fig. 1 **a** Total (*TotPLFA*), **b** bacterial (*BactPLFA*), and **c** fungal (*FungPLFA*) phospholipid fatty acid (PLFA) contents of organic and mineral layers in moso bamboo and native forests. **d** Ratio of fungal to bacterial PLFAs (*F/B*). *Vertical bars* represent the SD ($n = 9$). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, *n.s.* not significant (statistically significant differences between moso bamboo and native forests; two-way ANOVA)

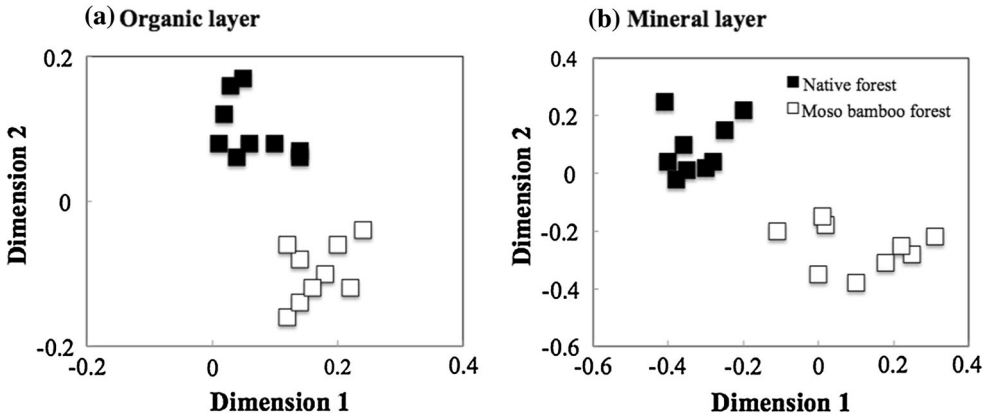

Fig. 2 Soil microbial communities show differences between moso bamboo (*open symbols*) and native forests (*closed symbols*) in both organic (**a**) and mineral (**b**) layers. Nonmetric multi-dimensional scaling ordination of soil microbial communities sampled over the course of this study, based on a Bray-Curtis similarity matrix calculated from a square-root transformation

(Table 4, $P < 0.001$; Fig. 3a), but were higher in the mineral layer (Table 4, $P < 0.001$; Fig. 3b).

Microbial respiration activity, as indicated by microbial respiration rate per TotPLFA contents in both organic and mineral layers, were significantly affected by bamboo invasion (Fig. 4): the microbial respiration activity was lower in the organic layer (Table 4, $P < 0.01$; Fig. 4a), but higher in the mineral layer (Table 4, $P < 0.05$; Fig. 4b).

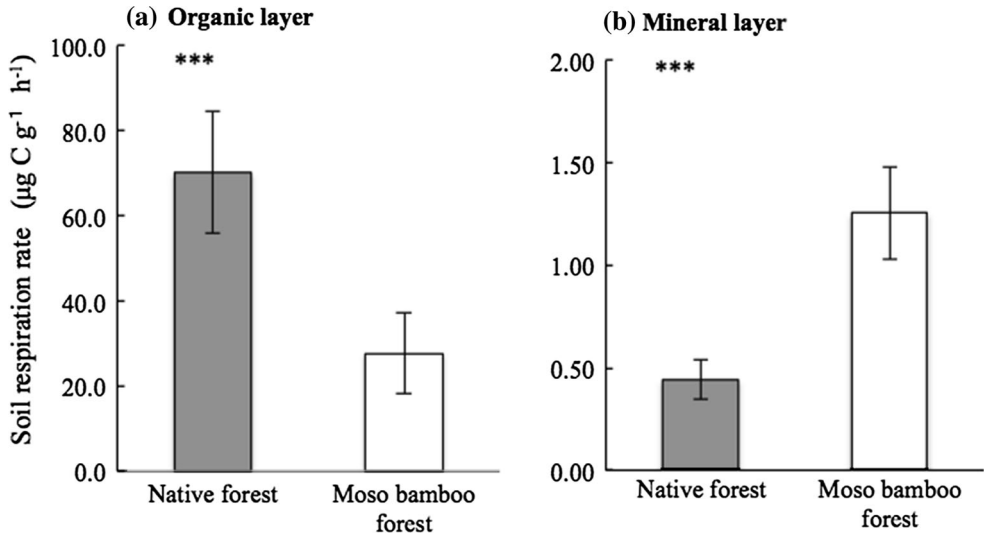

Fig. 3 Soil microbial respiration rates per unit weight of the organic layer (**a**) and mineral layer (**b**) in moso bamboo and native forests. *Vertical bars* represent the SD ($n = 9$). ***$P < 0.001$ (statistically significant differences between moso bamboo and native forests; two-way ANOVA)

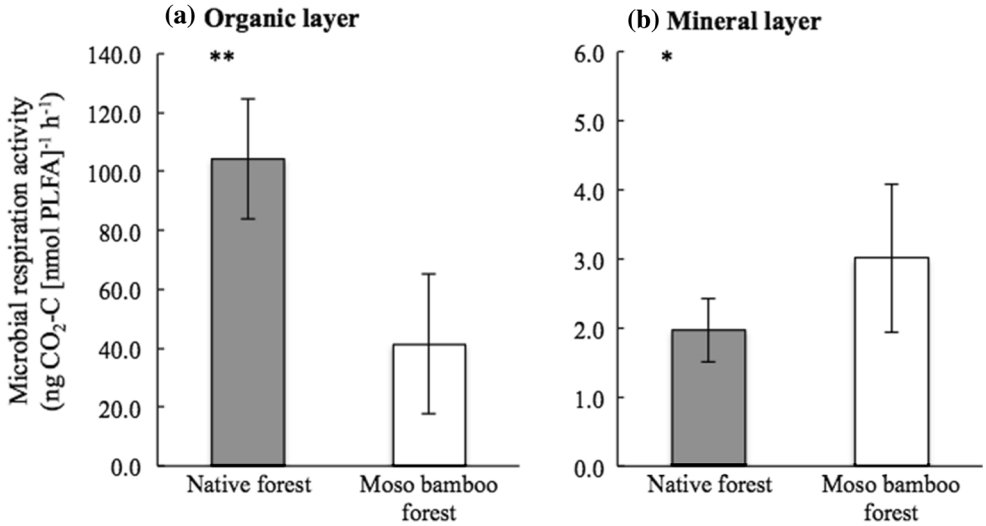

Fig. 4 Microbial respiration activity (CO_2 emission rate per total PLFA content) of the organic layer (**a**) and mineral layer (**b**) in moso bamboo and native forests. *Vertical bars* represent the SD ($n = 9$). *$P < 0.05$, **$P < 0.01$ (statistically significant differences between moso bamboo and native forests; two-way ANOVA)

No significant interaction effect between forest types (native vs. bamboo) and site (A, B, C) was detected on the soil microbial respiration rates and microbial respiration activity (Table 4).

Discussion

In contrast with our study, the results of previous studies have shown that after bamboo invasion, the total individual fatty acids (as a measure of microbial biomass) of the broadleaved forest increased, which was suggested to be caused by increased plant productivity (Xu et al. 2015). Conversely, Chang and Chiu (2015) observed a significant reduction in TotPLFA contents in bamboo-invaded soil compared to adjacent Japanese cedar-plantation soil and suggested that this was caused by allelopathy and antibacterial activity, exhibited by the bamboo itself, which results in lower soil bacterial biomass and/or activities in bamboo-invaded soils. These results suggest that the effects of bamboo invasion on soil microbial community biomass differ according to the native forest type.

In our study, we observed a significant decrease in BactPLFA contents in the organic layer of the stands invaded by bamboo (Fig. 1b), though no significant difference in TotPLFA (Fig. 1a) or FungPLFA contents (Fig. 1c) was detected between the forest types. This could be explained by the decreased water content, which is a

major factor controlling the survival and activity of microorganisms (Table 2). In addition, Chang and Chiu (2015) indicated that bamboo itself has antibacterial activity, which can result in lower soil bacterial biomass in bamboo forest soils compared to adjacent native forest soils; these findings may also support our results. Consequently, bamboo invading a native forest may alter the soil environment and the chemical composition of litter, which would affect the bacterial biomass. Furthermore, the NMDS analysis of the PLFA composition data indicated that samples of bamboo and native forests significantly segregated (Fig. 2). These results show that the quality (composition) of the soil microbial community was altered by bamboo invasion of native forests.

In the organic layer, we found that microbial respiration rates, in terms of both soil weight and microbial biomass (TotPLFA content), also decreased due to bamboo invasion (Figs. 3, 4); this change may be partly explained by the variation in soil microbial community composition and microbial activity. In our study, the F/B ratio was significantly higher in the bamboo forest (Fig. 1d), suggesting that the decreased total C and N observed after bamboo invasion caused a structural shift from a bacteria-dominated to a fungal-dominated microbial community. Such a shift in microbial community structure would lead to changes in physiological activity of the whole soil microbial community. Fungi have lower respiration activity per unit biomass compared to bacteria because they have a large inactive biomass (Ohtonen et al. 1999). In addition, the significantly higher F/B ratio in the organic layer in the bamboo forest (Fig. 1d) might be related to their recalcitrant compounds. Compared with wood species, the rate of lignin degradation and carbonyl formation was lower in bamboo (Wang and Ren 2008). Ueda (1960) indicated that the proportion of Si (SiO_2) is more than 5.0 % in the leaves, and about 0.5 % in the rhizome of bamboo. SOM with a larger percentage of recalcitrant compounds (e.g., lignin and Si) may have a higher F/B ratio (Zhang et al. 2013). Furthermore, soil bacteria are the primary decomposers of simple carbohydrates, organic acids, and amino acids, whereas soil fungi are the primary decomposers of recalcitrant compounds (Myers et al. 2001).

We found that the effects of bamboo invasion on the soil microbial community and on microbial respiration rates extended to the mineral soil layer. The microbial respiration rate per soil weight in the mineral layer increased after the bamboo invasion (Fig. 3b), which correlated with increased microbial respiration activity (Fig. 4b), in spite of the significantly higher F/B ratio (Fig. 1d). The increased microbial respiration and microbial respiration activity in the mineral soil layer of the bamboo forest could be partly attributable to the clearer differences in microbial community composition between bamboo and native forests than in the organic layer (Fig. 2). A previous study reported that the supply of fresh plant-derived C to the deep soil layers stimulated deep SOC decomposition (Fontaine et al. 2007). Although the growth dynamics of belowground plant biomass (roots and rhizomes) were not evaluated in our study, previous studies reported that the belowground biomass in bamboo forests is approximately double that in secondary forest (Fukushima et al. 2015; Tang et al. 2015), even at a depth of 20–40 cm. It is well known that stimulated plant growth increases organic matter input to the soil in the form of root litter and root exudation, thus increasing SOM, soil total C and total N contents. In the present study, we also observed a significant increase in SOM, soil total C and total N contents in the mineral layer of the bamboo forest soil (Table 2). In addition, total C and N were higher in bamboo forest than broadleaved forest at all experimental sites. Thus increased root litter and root exudation may explain the increased soil microbial respiration rates in the mineral layer of the bamboo forest. These results suggest that the pattern of soil C dynamics changed vertically due to bamboo invasion.

In conclusion, the moso bamboo invasion changed litter quality and soil properties, and caused shifts in microbial community composition in both the organic and mineral layers. Such changes in soil properties and microbial community composition contribute to changes in microbial respiration activity. SOM decomposition in the organic layer was reduced, while the deep soil C decomposition in the mineral layer was stimulated by bamboo invasion; these changes can lead to changes in plant growth (positive or negative), leading to feed-back between plants and the soil microbial community (Wolfe and Klironomos 2005). We suggest that these changes may have cascading effects on other species and may affect the potential for forest restoration.

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