Plant Soil (2017) 418:507–521
DOI 10.1007/s11104-017-3313-y

REGULAR ARTICLE

Bamboo invasion of broadleaf forests altered soil fungal community closely linked to changes in soil organic C chemical composition and mineral N production

Yongchun Li · Yongfu Li · Scott X. Chang · Qiufang Xu · Zhiying Guo · Qun Gao · Ziyan Qin · Yunfeng Yang · Junhui Chen · Xue Liang

Received: 15 January 2017 / Accepted: 7 June 2017 / Published online: 19 June 2017

Abstract
Aims Soil fungi play an important role in decomposing soil organic matter and facilitating nutrient uptake by plants, however, the relationship between fungal community and soil biogeochemical cycling during plant invasion is poorly understood. The objective of this study was to investigate the effects of Moso bamboo (*Phyllostachys edulis*) invasion into broadleaf forests on the soil organic C (SOC) chemical composition, fungal community and mineral N production.
Methods We collected soil samples in evergreen broadleaf forests, mixed bamboo-broadleaf forests and bamboo forests. Soil fungal community and SOC chemical composition were determined.
Results Bamboo invasion decreased alkyl C but increased *O*-alkyl C contents. Soil fungal abundance (18S rRNA) was decreased, while their alpha diversity was increased by bamboo invasion. Additionally, bamboo invasion enhanced net N mineralization rate but reduced gross nitrification rate. The fungal community composition strongly correlated with alkyl C content, and alkyl C content explained 32% of the variation in the fungal abundance. Fungal community composition correlated with gross nitrification rate, with 43% of the variation in gross nitrification rate attributable to soil fungal abundance.
Conclusions Changes in soil fungal community caused by bamboo invasion into broadleaf forests were closely linked to changed soil organic C chemical composition and decelerated nitrate production.

Keywords Bamboo forest · ^{13}C NMR · Fungal community · Gross nitrification rate · Illumina MiSeq sequencing · Plant invasion

Responsible Editor: Liz Shaw.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-017-3313-y) contains supplementary material, which is available to authorized users.

Y. Li · Y. Li (✉) · Q. Xu · J. Chen · X. Liang
State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Lin'an 311300, China
e-mail: yongfuli@zafu.edu.cn
S. X. Chang
Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton, AB T6G 2E3, Canada

Z. Guo
State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, China

Q. Gao · Z. Qin · Y. Yang (✉)
State Key Joint Laboratory of Environment Simulation and Pollution Control, School of Environment, Tsinghua University, Beijing 100084, China
e-mail: yangyf@tsinghua.edu.cn

Introduction

Plant invasion has dramatic effects on plant and soil microbial community compositions (Callaway et al. 2004; Hawkes et al. 2005). Through affecting litter quality, root exudates, and nutrient uptake by plants, plant invasion can alter the biogeochemical cycling of C and soil supplied plant nutrients (Ushio et al. 2010). Most soil organic C (SOC) is derived from root

exudates, decomposition of plant litter and root turnover (Kalbitz et al. 2003). The SOC chemical composition in forest soils is strongly affected by the vegetation type at a given site (Stewart et al. 2011). For example, converting natural forests to hoop pine (*Araucaria cunninghamii*) plantations decreased the proportion of *O*-alkyl C (reflecting relatively labile C forms) and increased the proportion of alkyl C (reflecting relatively stable C forms) in SOC (Chen et al. 2004). The process of plant invasion leads to accelerating the biogeochemical cycling in forest ecosystems, due to the high decomposition rate frequently invovled in invaded ecosystems in a previous meta-analysis (Liao et al. 2008). The chemical nature of organic compounds largely determines the intensity of decomposer activities and rates of degradation (Fontaine et al. 2007). However, it remains uncertain about how SOC chemical nature responds to plant invasion as the vegetation type is altered.

Moso bamboo (*Phyllostachys edulis*) is a fast-growing species and can easily invade natural and secondary forests throughout subtropical China (Li et al. 2013; Xu et al. 2015; Song et al. 2016). Invasion of Moso bamboo into other forest types imposes a serious threat on ecosystem function and stability (Song et al. 2016). However, research on changes in litter quality and decomposition associated with SOC fraction after bamboo invasion is scarce and sometimes with contradictory results. For example, bamboo invasion has been shown to increase the input of relatively decomposable litter, and consequently the labile soil organic matter (SOM) fraction in the ecosystem increased (Chang and Chiu 2015; Wang et al. 2016); others showed that bamboo invasion decreased rates of litter decomposition and soil nitrogen (N) mineralization, and ultimately retarded N cycling (Song et al. 2016).

Plant species composition plays a vital role in governing soil microbial community composition (Grayston et al. 2004). Previous studies found that Bamboo invasion into a Japanese cedar (*Cryptomeria japonica*) plantation caused significant changes in soil microbial community structure and increased bacterial diversity (Chang and Chiu 2015; Lin et al. 2014). Much less attention has been paid to fungi except an isolated study that reported that bamboo invasion into natural evergreen broadleaf forests decreased the relative abundance of fungi in the microbial community, resulting in decreased fungal to bacterial (F/B) ratio (Xu et al. 2015).

Fungi play a dominant role in the decomposition of a wide variety of complex and recalcitrant plant-derived organic matter (Baptist et al. 2008; Hanson et al. 2008), and addition of different types of organic matter would markedly influence the structure and composition of the soil fungal community (Sun et al. 2016). Native forests invaded by Moso bamboo experienced a dramatic decline in plant species richness and diversity (Bai et al. 2013), which would be expected to induce the shift of soil fungal community due to the close relationship between soil fungal community composition and plant community diversity in forest ecosystems (Peay et al. 2013). Moso bamboo invasion into a Japanese cedar plantation accelerated the degradation of SOM and decreased the ratio of recalcitrant C to SOC (Wang et al. 2016). However, the role of fungi on the change in the SOC chemical nature caused by Moso bamboo invasion is still unclear.

In addition, fungi play an important role in soil N cycling due to their ability to adapt to a wide range of microsites and secrete exoenzymes that lead to the depolymerization of N-containing compounds (Schimel and Bennett 2004; Nemergut et al. 2008). It has been observed that heterotrophic fungi, such as *Absidia cylindospora* (zygomycetal saprotroph), possess the ability to produce nitrate (Stroo et al. 1986) and contribute to nitrification in acidic forest soils (De Boer and Kowalchuk 2001). Moso bamboo invasion of evergreen broadleaf forests in subtropical China generally occurs in the region with low capacity for the microbiological oxidation of ammonium (NH_4^+) to nitrate (NO_3^-) due to the high soil acidity (pH < 5) (Xu and Cai 2007; Zhang et al. 2013b). Zhu et al. (2013) found that heterotrophic nitrification may be an important N transformation pathway in acidic subtropical forest ecosystems, and fungi are likely to play an important role in heterotrophic nitrification. The question remains, however, whether soil mineral N production will be affected by shifts in soil fungal community caused by Moso bamboo invasion.

To address these questions, SOC chemical composition, fungal community and mineral N production were examined in evergreen broadleaf forests (broadleaf forests), mixed Moso bamboo-broadleaf forests (mix forests; formed after Moso bamboo invasion) and Moso bamboo forests (bamboo forests) in a natural ecosystem located in Tianmushan National Nature Reserve, Zhejiang Province, China. The objective of this study was to investigate the impact of bamboo invasion into broadleaf forests on the SOC chemical composition, fungal community and mineral N production. Specifically, we hypothesize that bamboo invasion into broadleaf forests will result in (1) changes in soil C

forms, with a decrease in alkyl C and an increase in *O*-alkyl C; (2) changes in soil fungal community, with a decrease in fungal abundance and an increase in fungal diversity; (3) changes in the pattern of mineral N production closely linked to shifts in composition and abundance of soil fungal community caused by bamboo invasion.

Materials and methods

Site description

The study site is located in Tianmushan National Nature Reserve (30°18′30″-30°21′37″N, 119°24′11″-119°27′11″ E), in Zhejiang Province in southeastern China. The region wherein this study was conducted has one of the greatest plant species richness in subtropical ecosystems in China. The Nature Reserve is a United Nations Educational Scientific and Cultural Organization (UNESCO) Biosphere Reserve under the UNESCO Man and the Biosphere Program. This area has a typical central subtropical monsoon climate with an annual mean temperature of 15.8 °C during the period from 2004 to 2013. The precipitation and frost-free period per year are 1630 mm and 235 days, respectively, for the same period. The soil at the experimental site was derived from a silt stone and was classified as a Ferralsol in the FAO soil classification system (WRB 2006).

Our study site is located at an elevation of 300–450 m, and the native evergreen broadleaf forest has experienced invasion by Moso bamboo, which was originally planted by local farmers in the 1970s (Xu et al. 2015). Across the Tianmushan National Nature Reserve, some patches of bamboo invasion have developed. In this study, one large (about 50 ha) and old (ca. 45 years) patch, which included broadleaf forests, mixed forests and bamboo forests, was selected for the investigation. According to the records of the local land-use history, the whole region was originally covered by evergreen broadleaf forests before bamboo invasion. Currently three distinct forest types of the broadleaf forests, mixed forests and bamboo forests have been developed.

Experimental design and soil sampling

In October 2014, we selected a large slope with a gradient of 15°, including broadleaf forests, mixed forests and bamboo forests, for sampling in this study. Six transects along the invasion path from the bamboo forests to the broadleaf forests, were set up, with >50 m intervals between adjacent transects. All of the six transects are going parallel to the contour. Within each transect, three plots (20 × 20 m), at least 30 m apart, were established, with one plot in each of the three forest types, resulting in a total of 18 plots. Along the slope, these transects were separated by approximately 30 m in elevation, i.e., at about 300, 330, 360, 390, 420 and 450 m elevation. Horizontally along the contour, plots were separated at 30 m distance from each other.

In the broadleaf forest, the dominant tree species were *Cyclobalanopsis glauca*, *Castanopsis sclerophylla* and *Schima superba* with a mean tree density of 1284 culm ha^{-1}, a height of 13.7 m, diameter at breast height of 18.2 cm, with an overall canopy cover of 70%. The main shrub species included *Camellia fraterna*, *Symplocos caudate* and *Rhododendron ovatum* with a mean height of 1.4 m and 85% ground cover. The stocking density in the bamboo forest was ~4310 culm ha^{-1}, and the mean diameter at breast height of the bamboo plants was 10.6 cm. Compared with broadleaf forests and mixed forests, the bamboo forests were unique in having no overstory species other than bamboo and a much lower diversity in the shrub and herb layers, but had some dead bamboo plants in the stand. The mixed forest approximately has a 1:1 ratio of bamboo plants to broadleaf trees.

In each plot, surface soil (0–20 cm) samples were collected from five randomly selected points, and mixed and homogenized to form a composite sample, with roots and stones removed. Prior to the soil sampling, the litter cover on the soil surface was removed. The samples were placed on ice in a cooler and transported to the laboratory on the same day, and were passed through a 2.0 mm sieve. After sieving, a set of subsamples was stored at 4 °C before soil chemical analysis and another set of subsamples was stored at −80 °C before DNA extraction. In addition, within each plot, a set of six intact soil cores (5 cm diameter) were collected from six randomly selected points for the determination of soil gross nitrification rate.

Soil chemical and physical properties

A subsample of each soil was air-dried and analyzed for chemical and physical properties. Soil pH was determined with a 1:2.5 (w:v) soil-to-water extract. The SOC

and total N (TN) concentrations were measured using an elemental analyzer (model CHN-O-RAPID, Heraeus Co., Hanau, Germany). Available N was determined using a diffusion method (Lu 1999). Briefly, 10 mL of NaOH solution (1 mol L^{-1}) was added into the soil samples, and the NH_3 released from the mixture was absorbed by a H_3BO_3 solution. The amount of NH_3 in the H_3BO_3 solution was measured through a titration method. Available N content was calculated by the amount of NH_3 released from the mixture of soil sample and NaOH solution. Available phosphorus (P) was determined by the Bray procedure (Bray and Kurtz 1945). Available potassium (K) was determined by the flame photometric method (extracted by 1 mol L^{-1} NH_4OAc) (Zhang et al. 2014). Samples were extracted with a 2 mol L^{-1} KCl solution. After being diluted, concentrations of NH_4^+-N and NO_3^--N in each extract were then determined using a Dionex ICS 1500 ion chromatograph (Dionex Co., Sunnyvale, CA) (Zhang et al. 2014).

Solid-state ^{13}C NMR spectroscopy analysis

For the NMR spectroscopy analysis, soil samples were pretreated with 10% (*v*/v) hydrofluoric acid (HF) to remove Fe^{3+} and Mn^{2+} from the soil to increase the signal to noise ratio as described in Li et al. (2010). The ^{13}C cross polarization/total sideband suppression (CP/TOSS) analysis was conducted on a Bruker AVANCE 400 NMR spectrometer using 4-mm diameter sample rotors, with using magic angle spinning (MAS). Data acquisition conditions were as follows: spectrometer frequency of 100 MHz for ^{13}C, a spinning speed of 5 kHz, a CP time of 1 ms, a ^1H 90° pulse-length of 4 μs, and a recycle delay of 0.8 s. Four-pulse TOSS was employed before detection, and two-pulse phase-modulated (TPPM) decoupling was applied for optimum resolution during detection (Mao et al. 2008). The external standard used for chemical shift determination was hexamethylbenzene (methyl at 17.33 ppm). Based on the literature (Huang et al. 2008; Zhang et al. 2013a), each NMR spectrum was divided into the following four regions representing the different chemical environments of a ^{13}C nucleus: 0–46 ppm, alkyl C (lipids, cutin, and suberin); 46–114 ppm, *O*-alkyl C (carbohydrates, cellulose, hemicellulose, and methoxyl C); 114–164 ppm, aromatic C (lignin, tannin, olefins, and aromatic compounds); and 164–220 ppm, carbonyl C (carboxylic acid, amide, and ketone groups). Through measuring the area under the curve in each region, we obtained the relative content of the different C fractions. The ratio of alkyl C region intensity (0–46 ppm) to *O*-alkyl C region intensity (46–114 ppm) (A/*O*-A) was representing the extent of decomposition or substrate quality for microbes, and used as an indicator of the quality of SOC (Huang et al. 2008).

Measurements of soil net N mineralization and gross nitrification rates

Soil net N mineralization was determined according to the method of Wang et al. (2006) with minor modifications. Briefly, two fresh subsamples (10 g) were taken from each soil sample. One was used to determine the concentrations of NH_4^+-N and NO_3^--N right away following extraction with 2 mol L^{-1} KCl. The other was incubated in the laboratory at 25 °C in the dark with four replicates for 21 days. During the incubation, the soil water content was adjusted to 60% of water-holding capacity. Soil net N mineralization was calculated by the difference in NH_4^+-N and NO_3^--N between the incubated and initial sample (Wang et al. 2006).

The soil gross nitrification rate was determined using the Barometric Process Separation (BaPS) technique (Ingwersen et al. 1999; Breuer et al. 2002; Rosenkranz et al. 2006), which is based on the dynamic determination of the total gas pressure during the soil incubation in an isothermal and gas tight system. The basic principle for BaPS technique is that in an isothermal and gas tight space where the soil is incubated, the gas pressure is changed mainly due to the dynamic changes in the processes of soil respiration, nitrification and denitrification. Therefore, the values of soil respiration, gross nitrification rate and denitrification rate can be obtained by the BaPS technique. The detailed principle and calculation process are described in the literatures published previously (Ingwersen et al. 1999; Breuer et al. 2002). A series of previously published experimental data concerning the soil gross nitrification rate in forest soils demonstrate that the data obtained by the BaPS technique were in good agreement with the data obtained by the ^{15}N pool dilution method (Ingwersen et al. 1999; Breuer et al. 2002; Rosenkranz et al. 2006). In brief, for each soil sample, a set of six intact soil cores were directly filled into the BaPS instrument and the system was gas-tight closed and incubated at the same temperature as the soil temperature measured in the bamboo forest in this study. Determination of soil gross

nitrification rate using the BaPS technique lasted for 24 h (Ingwersen et al. 1999).

DNA extraction, Illumina MiSeq sequencing and real-time quantative PCR

Soil DNA was extracted from 0.5 g of soil sample using a PowerSoil Total DNA Isolation Kit (MoBio Labs, Solana Beach, CA) according to the manufacturer's instruction. DNA concentration and quality were checked using a NanoDrop spectrophotometer. Extracted DNA was diluted to 10 ng μL^{-1} and stored at −40 °C for downstream use.

The primer pair ITS3_KYO2 (5′- GATGAAGA ACGYAGYRAA-3′) and reverse primer ITS4 (5′- TCCTCCGCTTATTGATATGC-3′) with unique 12 nt barcode was used to amplify the ITS2 region (Toju et al. 2012). The average lengths of fragments amplified were 327 ± 40 bp. The PCR reaction mixture contained 2.5 μL of 10 × PCR buffer, 1.5 mM $MgCl_2$, 0.4 μM of each deoxynucleoside triphosphate, 1.0 μM of each primer, 0.5 U of Ex Taq (TaKaRa Inc., Dalian, China) and 10 ng DNA template in a final volume of 25 μL. The PCR amplification program included initial denaturation at 94 °C for 3 min, followed by 30 cycles of 94 °C for 40 s, 50 °C for 60 s, and 72 °C for 60 s, and a final extension at 72 °C for 10 min. Three PCR reactions were conduct for each sample, and they were combined after PCR amplification. The PCR products were subject to electrophoresis using 1.0% agarose gel. The band with a correct size was excised and purified using TaKaRa MiniBEST Agarose Gel DNA Extraction Kit (TaKaRa Inc., Dalian, China) and quantified with Nanodrop spectrophotometer. All samples were pooled together with equal molar amount from each sample. The sequencing samples were prepared using TruSeq DNA kit according to the manufacturer's instruction. The purified library was diluted, denatured, re-diluted, mixed with PhiX (equal to 30% of final DNA amount) as described in the Illumina library preparation protocols, and then applied to an Illumina Miseq system for sequencing with the Reagent Kit v2 2 × 250 bp as described in the manual. Sequencing data were deposited in the DNA Data Bank of Japan (DDBJ) under the accession number DRA005308.

The gene copy numbers of fungal 18S rRNA were detected in triplicates using primers NS1-F/FungR (May et al. 2001). Each PCR reaction contained 25 μL of SYBR® Premix Ex Taq™ (2×) (Takara Bio Inc., Shiga, Japan), 0.2 μM of each primer, 1 μL of ROX Reference Dye, and 1 μL diluted DNA (1–10 ng) template in a final volume of 50 μL. Real-time PCR was conducted using an ABI7100 (Applied Biosystem, Foster City, CA) in the following thermal profile for amplification: 2 min at 50 °C; 2 min at 95 °C; 40 cycles of 15 s at 95 °C, 30 s at 55 °C. Product specificity was checked by melt curve analysis at the end of the PCR runs and visualization by agarose gel electrophoresis. Copy numbers of the 18S rRNA gene in soil samples were determined using a standard curve generated using purified template plasmid DNA with a log-linear effect of target concentration ($R^2 = 0.99$).

Sequencing data processing

Processing of the raw sequences obtained through Illumina sequencing was performed using the Quantitative Insights into Microbial Ecology (QIIME) pipeline (Caporaso et al. 2010). We assembled paired-end reads using FLASH (Magoč and Salzberg 2011). Reads with average quality score lower than 20, ambiguous bases and improper primers were discarded before clustering. The resultant high-quality sequences were then clustered into operational taxonomic units (OTUs) at 97% similarity using UPARSE algorithm (Edgar 2013). Simultaneously, chimeras were checked and eliminated during clustering. Taxonomic classification of representative sequences from individual OTU was performed by BLASTing against the QIIME-compatible versions of the UNITE ITS database. In order to compare relative differences between samples, a subset of 8200 sequences per sample was randomly selected for down-stream analyses.

Statistical analysis

All soil properties were expressed on an oven-dry weight basis. The forest type effect on the soil physical and chemical properties, and parameters of soil fungal community were analyzed by a one-way analysis of variance (ANOVA) and the least significant difference (LSD) test was used to separate the means when a significant treatment effect was found. Before performing ANOVA, the normality of distribution and homogeneity of the variance were tested, and the data were log-transformed if the assumption of homogeneity was violated. Correlation analyses were carried out with the Spearman's correlation method. All of the above statistical analyses were performed

using SPSS version 18.0 (SPSS, Chicago, IL). The downstream analysis of the sequence data was performed in QIIME and R (Team 2013). Alpha diversity indices, including the Shannon index (Shannon 1948), Faith's phylogenetic diversity (PD) (Faith 1992) and Chao1 index (Chao 1984), were calculated. Significance tests of the effects of bamboo invasion on the overall fungal community composition with multi-response permutation procedures (MRPP) were carried out using the R package vegan (Oksanen et al. 2007). Principal coordinates analysis (PCoA) was used to analyze beta diversity across three forest types based on the Bray-Curtis distance matrix (Sun et al. 2016). To identify fungal OTUs that are specifically associated with three forest types, indicator species were determined by the Dufrene-Legendre indicator species analysis method (Dufrene and Legendre 1997) using the R package labdsv (Roberts 2007), and visualized using the Cytoscape software (Version 3.2.1) (Shannon et al. 2003). Mantel tests were used to determine environmental factors significantly correlated with beta diversity of soil fungal community, which were used to construct the soil property matrix for canonical correspondence analysis (CCA) in the vegan package (Sun et al. 2015). The statistical significance was determined at the 5% level.

Results

Soil properties, SOC chemical composition and mineral N production

The soil pH, SOC, C/N ratio, NH_4^+-N and available P were significantly ($P < 0.05$) higher by 13.4, 33.5, 52.9, 58.6 and 140.4%, respectively, in the bamboo forest compared to the broadleaf forest. The NO_3^--N and available K concentrations were lower by 14.1 and 26.3%, respectively, in the bamboo forest compared to the broadleaf forest (Table 1). Total N concentrations were 24.5% lower ($P < 0.05$) in the mixed forest than in the broadleaf forest, but were similar between the broadleaf and bamboo forests. Soil net N mineralization rate was higher by 21.3%, and soil gross nitrification rate was lower by 32.9% in the bamboo forest, compared to the broadleaf forest (Table 1).

The *O*-alkyl C (47.4–52.0%) dominated among the four C fractions regardless of the forest type, followed by alkyl C (23.3–26.0%) (Table 2). The *O*-alkyl C content in the bamboo forest soil was higher than that in the broadleaf forest soil, whereas the alkyl C content and A/*O*-A ratio in the bamboo forest soil were lower than that in the broadleaf-associated (broadleaf forest and mixed forest) soils ($P < 0.05$) (Table 2), indicating that the chemical composition of SOC was substantially changed by bamboo invasion.

Table 1 Selected soil chemical and physical properties in the three different forest types

Soil property	Broadleaf forest	Mixed forest†	Bamboo forest
pH	4.41(0.34) b‡	4.44(0.34) b	5.00(0.21) a
Soil organic C (g kg^{-1})	23.13(3.69) b	25.2(3.29) ab	30.87(7.31) a
Total N (g kg^{-1})	2.37(0.34) a	1.79(0.35) b	2.11(0.49) ab
C/N ratio	9.91(2.06) b	14.42(3.12) a	15.15(4.24) a
NH_4^+-N (mg kg^{-1})	9.13(2.87) b	10.43(2.89) ab	14.48(4.64) a
NO_3^--N (mg kg^{-1})	19.19(1.33) a	17.58(1.77) ab	16.48(0.97) b
Available N (mg kg^{-1})	110.25(17.69) a	121.62(10.77) a	125.77(21.31) a
Available P (mg kg^{-1})	13.08(3.33) c	18.99(4.78) b	31.44(8.40) a
Available K (mg kg^{-1})	61.33(13.28) a	39.17(4.17) b	45.20(10.26) b
Net N mineralization (μg N g^{-1} d^{-1})	3.28(0.38) b	3.42(0.44) b	3.98(0.47) a
Gross nitrification (μg N g^{-1} d^{-1})	3.43(0.28) a	2.82(0.23) b	2.30(0.22) c

Data were presented as means of six replicates with standard deviation in the brackets

† Mixed forest: mixed bamboo-broadleaf forest

‡ Different letters within a row indicate significant differences among the different forest types at the $P = 0.05$ level

Table 2 Distribution (percent) of different chemical shift ranges in total signal intensity in ^{13}C NMR spectra, as well as alkyl C to *O*-alkyl C ratio (A/*O*-A), in soils of the three forest types

Forest type	Alkyl C	*O*-alkyl C	Aromatic C	Carbonyl C	A/*O*-A
Broadleaf forest	26.0 (1.5) a‡	47.4 (3.0) b	15.1 (2.6) a	11.5 (1.5) a	54.9 (4.6) a
Mixed forest†	25.4 (0.9) a	49.6 (2.0) ab	13.6 (1.4) a	11.4 (0.8) a	51.2 (3.4) a
Bamboo forest	23.3 (1.1) b	52.0 (1.6) a	14.0 (1.3) a	10.7 (0.9) a	44.8 (2.1) b

Data were presented as means of six replicates with standard deviations in the brackets

† Mixed forest: mixed bamboo-broadleaf forest

‡ Different letters within a column indicate significant differences between the different forest types at the $P = 0.05$ level

Soil fungal community abundance and composition

The 18S rRNA gene copy number in the bamboo forest soil was lower by 59.9% ($P < 0.01$) as compared to broadleaf forest soil, while it was similar between the bamboo and mixed forest soils (Table 3). Fungal OTU numbers ($P < 0.01$), the Shannon Index, Chao1 and PD indices in bamboo and mixed forest soils were higher ($P < 0.05$) than those in the broadleaf forest (Fig. 1a; Table 3). The three axes in the PCoA explained 42.6% of the observed variance in total, and fungal community from the same forest stand tended to cluster together (Fig. 1b). PCoA showed that samples in broadleaf forest were separated from those in bamboo and mixed forests along the PC1 accounting for 18.3% of the variation, while samples in the mixed forest were separated from those in bamboo forest along the PC2 accounting for 15.0%. The result of MRPP confirmed significant effects of forest type on the overall fungal community composition (bamboo forest vs mixed forests: $\delta = 0.74$, $P = 0.005$; bamboo forest vs broadleaf forest: $\delta = 0.65$, $P = 0.001$; mixed forests vs broadleaf forest: $\delta = 0.69$, $P = 0.003$).

The phyla Basidiomycota (16.8–36.8%), Ascomycota (7.7–33.6%) and Zygomycota (6.4–23.0%) dominated the assigned fungal phyla of all OTU sequences (Fig. 2). The Archaeorhizomycetales, Eurotiales, Helotiales, Hypocreales, Sordariales (Ascomycota), Agaricales, Russulales (Basidiomycota) and Mortierellales (Zygomycota) were the most abundant orders with average relative abundance >1% across three forest types soils (Fig. 2). The relative abundance of Hypocreales and Sordariales was higher but that of Mortierellales was lower after bamboo invasion ($P < 0.05$). The relative abundance of Ascomycota was higher in bamboo (27.1%) and mixed forest (33.6%) soils as compare to broadleaf (7.7%) forest soil. The proportions of other members, such as Glomeromycota, Chytridiomycota and Blastocladiomycota, were relative low (<1%) regardless of the forest type.

Indicator species were surveyed to identify fungal OTUs specifically associated with the different forest types (Fig. 3). The most abundant indicator species in the broadleaf forest were OTU186 (8.3%) and OTU33 (3.1%), which were closely related to *Mortierella elongate* and *Hygrocybe intermedia,* respectively. The most abundant indicator species in the mixed forest were OTU60 (0.9%) and OTU69 (0.8%), followed by OTU99 (0.7%) closely related to *Clitopilus prunulus*. For bamboo forest, OTU22 belonging to Agaricomycetes with a relative abundance of 2.0%

Table 3 Diversity and abundance of soil fungal community in the soils of three forest types

	No. of OTUs	The Shannon Index	Chao1	Phylogenetic diversity (PD)	Abundance (10^7 copies g^{-1} soil)
Broadleaf forest	360 (123.0) b‡	3.68 (0.6) b	549 (158.9) b	67.0 (20.9) b	4.07 (1.19) a
Mixed forest†	722 (99.7) a	5.91 (1.0) a	963 (117.0) a	157.5 (28.4) a	2.18 (0.64) b
Moso bamboo forest	639 (100.3) a	5.63 (0.9) a	894 (163.5) a	134.9 (26.7) a	1.63 (0.47) b

Data were presented as means of six replicates with standard deviations in the brackets

† Mixed forest: mixed bamboo-broadleaf forest

‡ Different letters within a column indicate significant differences between the different forest types at the $P = 0.05$ level

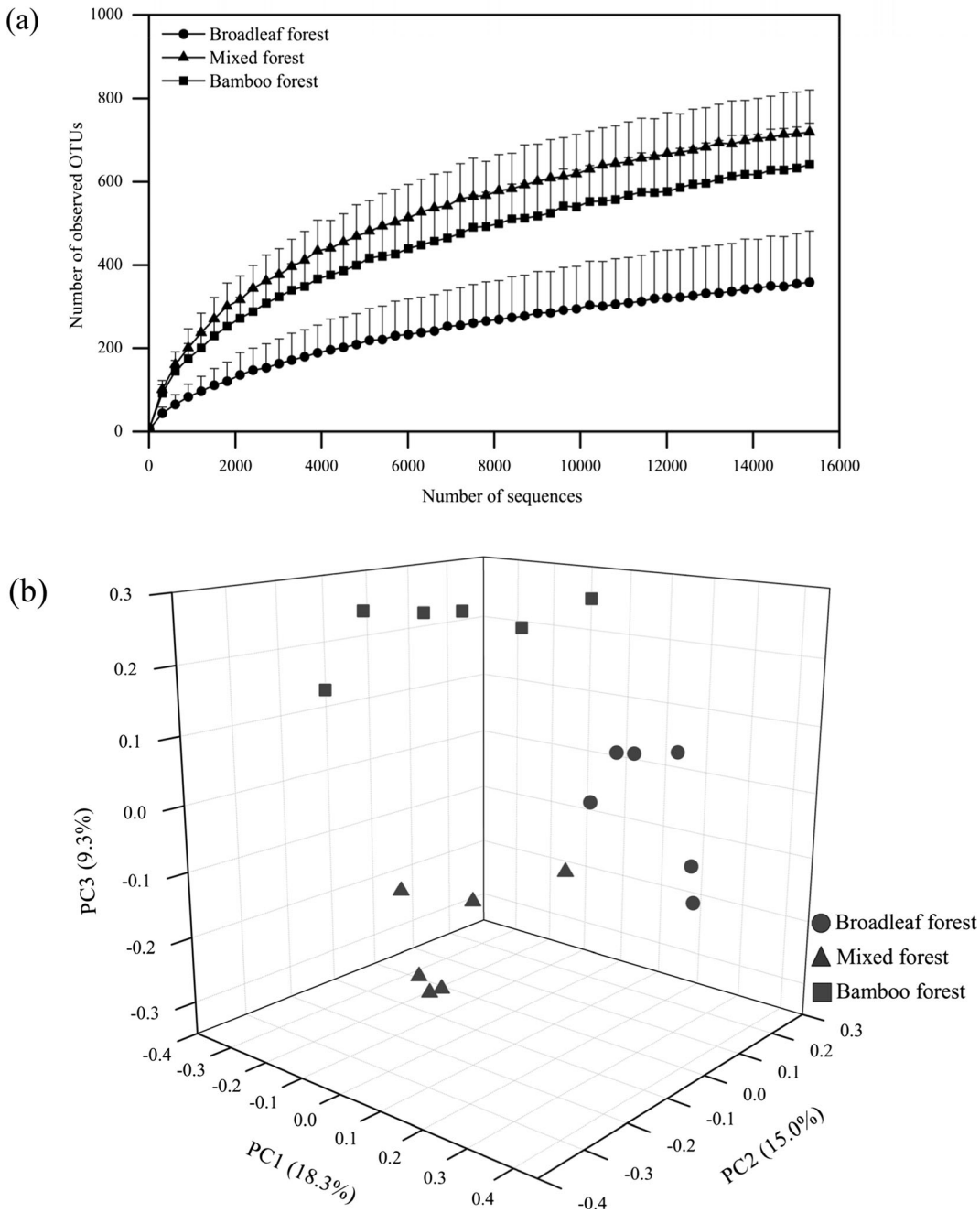

Fig. 1 (**a**) Rarefaction curves of the number of OTUs against the total number of sequence reads and (**b**) PCoA ordination based on Bray-curtis distances showing the changes in fungal community composition in the soils of three forest types. Mixed forest: mixed bamboo-broadleaf forest. Error bars are standard deviations ($n = 6$)

was the most abundant indicator species, which had no close match in these databases and as such may represent a novel fungal taxon. In addition, indicator species OTU61 closely related to *Hygrocybe intermedia* showed a relative abundance of 1.8% in the bamboo forest soil, which was significantly lower than that of OTU33 (3.1%), also closely related to *Hygrocybe intermedia*, in the broadleaf forest soil.

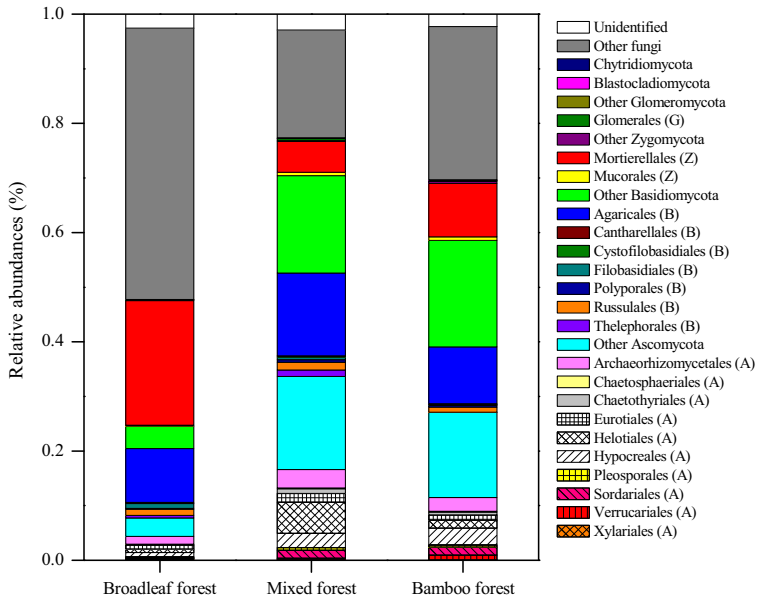

Fig. 2 Fungal community composition in the soils of three different forest types based on Illumina MiSeq sequencing of fungal ITS. Order names are provided for the order with average relative abundance >0.1% across three forest types soils

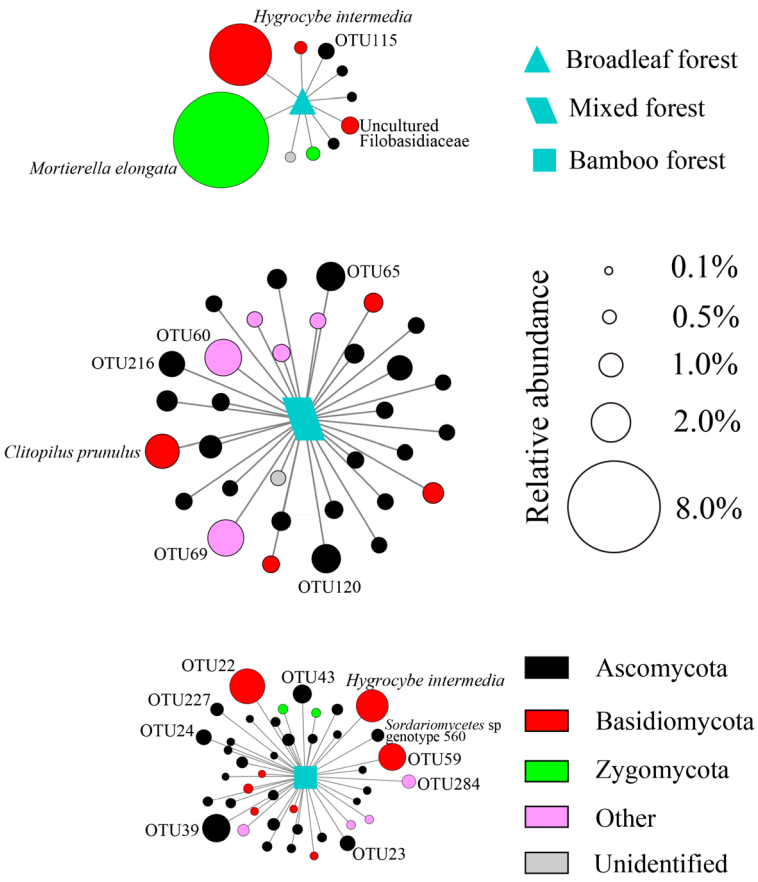

Fig. 3 Indicator species associated with three different forest types. Circles represent OTUs, and the other shapes represent the different forest types. The size of each circle represents its relative abundance

Linkage between fungal community composition and soil properties

Across all treatments, we found that the Shannon Index ($r = -0.51$, $P = 0.032$) and Chao1 ($r = -0.48$, $P = 0.042$) were negatively correlated with the A/*O*-A ratio. In addition, total number of OTU ($r = -0.47$, $P = 0.049$), the Shannon Index ($r = -0.57$, $P = 0.013$) and PD ($r = -0.49$, $P = 0.035$) were negatively correlated with the gross nitrification rate (Table S1).

Fungal abundance was positively correlated with the alkyl C content ($r = 0.52$, $P = 0.028$), A/*O*-A ratio ($r = 0.67$, $P = 0.003$) and gross rate of nitrification ($r = 0.71$, $P = 0.001$), but negatively correlated with the *O*-alkyl C content ($r = -0.68$, $P = 0.002$) and net rate of N mineralization ($r = -0.55$, $P = 0.017$) (Table S1). Linear regression analysis showed that the content of alkyl C explained 32% of the variation in the fungal abundance ($P < 0.05$) (Fig. 4a), and the abundance of fungi explained 43% of the variation in the gross nitrification rate ($P < 0.01$) (Fig. 4b).

Results of the Mantel test revealed that fungal community composition was positively correlated with gross nitrification rate, NO_3^--N, alkyl C ($P < 0.01$) and pH ($P < 0.05$) (Table S2). Then, factors significantly correlated with the fungal community composition were selected to perform CCA, which showed that gross nitrification rate ($P = 0.01$) and NO_3^--N ($P = 0.07$) had stronger effects on fungal community composition by permutation test (Fig. 5). The first two axes of the

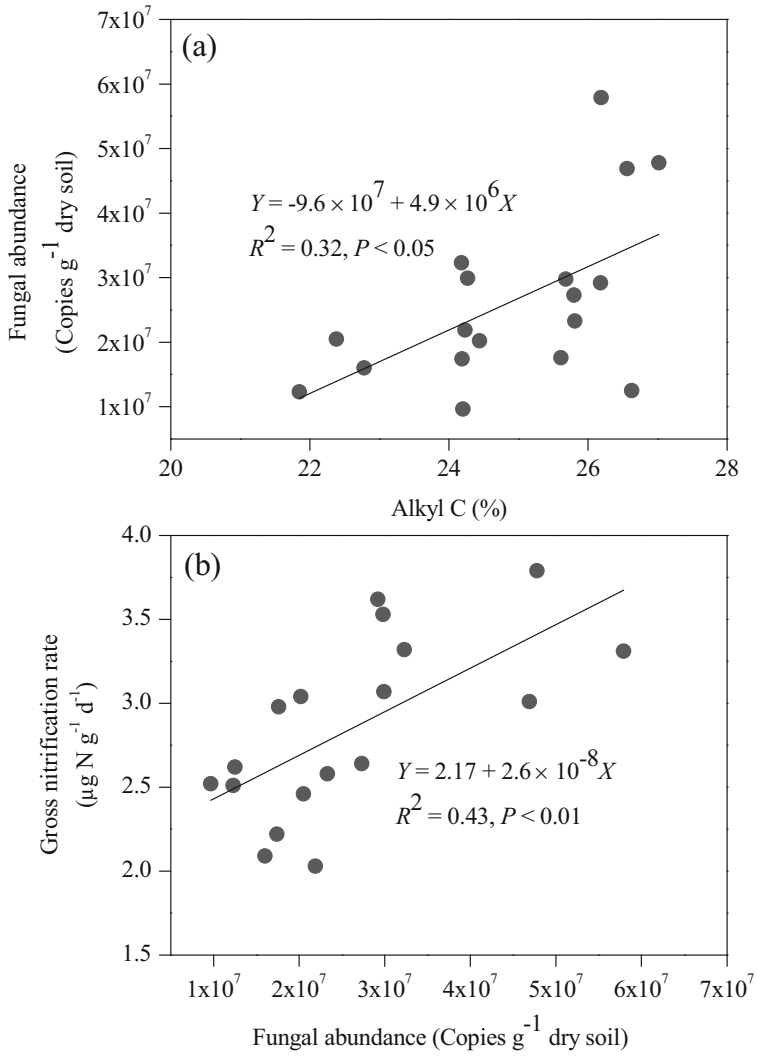

Fig. 4 Relationships (**a**) between soil alkyl C content and fungal abundance and (**b**) between soil fungal abundance and gross nitrification rate in the soils of three forest types

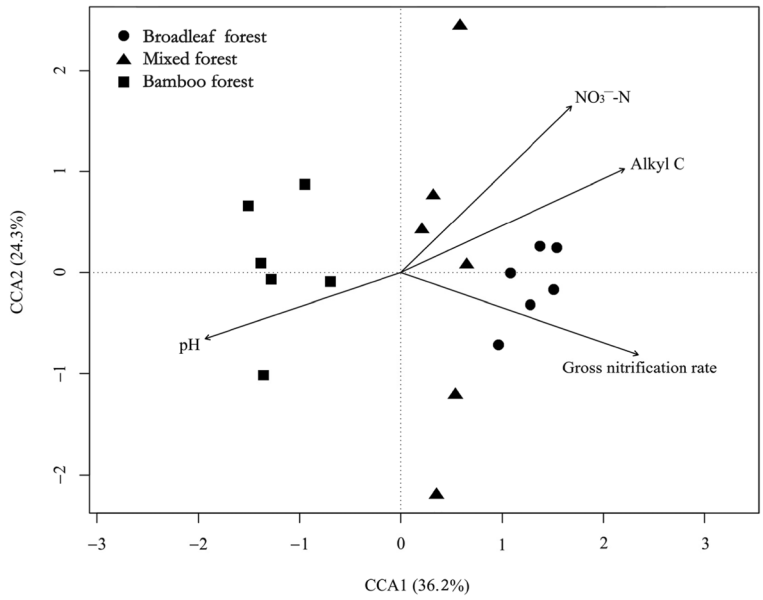

Fig. 5 Canonical correspondence analysis (CCA) of soil fungal community with soil pH, NO_3^--N, gross nitrification rate and alkyl C in three forest types

CCA accounted for 60.5% of the total variance in fungal community composition, with the first axe accounting for 36.2% of the variance.

Regression analysis showed that the proportion of Zygomycota (R^2 = 0.35, P < 0.01) increased exponentially with content of alkyl C, while the proportion of Ascomycota (R^2 = 0.32, P < 0.05) and Basidiomycota (R^2 = 0.31, P < 0.05) increased exponentially with content of *O*-alkyl C (Fig. S1). The gross nitrification rate was significantly correlated with the relative abundance of Mortierellales (R^2 = 0.42, P < 0.01) and Filobasidiales (R^2 = 0.44, P < 0.01) (Fig. S2).

Discussion

Bamboo invasion altered SOC chemical composition

Moso bamboo invasion into neighboring forests can affect plant biodiversity (Bai et al. 2013), decrease litter quality (Song et al. 2016), and consequently alter SOC chemical composition in forest soils (Wang et al. 2016). In this study, the result of higher *O*-alkyl C content but lower alkyl C content and A/*O*-A ratio in the bamboo than in the broadleaf forest soil (Table 2), is consistent with the result of Wang et al. (2016), supporting our first hypothesis. Chang and Chiu (2015) previously assumed that concentration of labile organic C in the bamboo forest soil was higher than that in the neighboring forest soil. This assumption was verified by our results, since *O*-alkyl C compounds (such as carbohydrates) are more labile than alkyl C chains in lipid structure (Baldock et al. 1992; Chen et al. 2004). Plant fine roots provide important C inputs to soil (Mathers et al. 2007), and changes in its chemical characterisitc during vegetation succession can markedly alter the chemical compositon of SOC (Crow et al. 2009; Wang et al. 2010; Wang et al. 2015). Fine root biomass of bamboo forests was found to be much larger than that of bamboo-broadleaf mixed forests and broadleaf forests, and both growth and turnover rates of bamboo fine roots were faster than that of broadleaf trees (Liu et al. 2013). Since the majority of the carbohydrate in all fine roots are attributable to cellulose and hemicelluloses (Mathers et al. 2007), the increased *O*-alkyl C content in the bamboo forest soil in this study (Table 2) could be attributed to much larger biomass of bamboo fine roots as well as faster rates of its growth and turnover than that of broadleaf trees (Liu et al. 2013).

Shifts in fungal community associated with changes in vegetation types and SOC chemistry

The composition and abundance of soil fungal communities in bamboo forests and mixed forests clearly differed from those in broadleaf forests (Fig. 1b; Table 3). Bamboo invasion significantly led to higher soil fungal diversity (Fig. 1a; Table 3) but lower A/*O*-A ratio (Table 2), and

A/*O*-A ratio was negatively correlated to the Shannon Index and Chao1 indices (Table S1). Those findings supported our second hypothesis, and also suggested that fungal diversity increases with the increase in the ratio of relatively easily biodegradable C to SOC, due to lower A/*O*-A ratio indicating that SOC is relatively easy to biodegrade (Baldock et al. 1992; Zhang et al. 2013a). Result of Kubartová et al. (2009) revealed that fungal diversity increases as substrate supply rises because more species met their minimum requirements at low resource availability. Here, we have also demonstrated the significant correlation between fungal community composition and alkyl C content by Mantel test (Table S2), and fungal abundance, as determined by the 18S rRNA gene copy numbers, showed positive correlation to alkyl C content (Fig. 4a). Since changes in content of SOC fraction were closely associated with changes in soil fungal community composition (Li et al. 2017), lower alkyl C content in bamboo invasion sites (Table 2) may partially contribute to alterations in the composition and function of soil fungal community in this study.

The fungal community within the classified OTU group in the broadleaf forest soil was dominated by Zygomycota (Fig. 2; Fig. 3), most of which are considered to be primary colonizers in the earlier stage of litter decomposition and they are ineffective in breaking down recalcitrant organic matter (Hanson et al. 2008). The regression analysis in this study also showed that the proportion of Zygomycota increased exponentially with the alkyl C content (Fig. S1), confirming the close relationship between soil fungal community and relatively stable C forms reported in the previous studies (Ng et al. 2014; Li et al. 2017). After bamboo invasion, the relative abundance of Ascomycota and Basidiomycota significantly increased in bamboo-associated soils compare to the broadleaf forest soil (Fig. 2; Fig. 3). Both the proportion of Ascomycota and Basidiomycota increased with *O*-alkyl C content (Fig. S1), consistent with the finding that cellulose (a type of *O*-alkyl C compound) decomposition by fungi was mainly carried out by Ascomycota and Basidiomycota (Štursová et al. 2012).

Bamboo invasion alters soil mineral N production in association with shifts in soil fungal community

The change in soil N transformation caused by plant invasion has been reported in forests (Song et al. 2016) and grasslands (Hawkes et al. 2005). The increase in soil net mineralization rate after bamboo invasion (Table 1) is inconsistent with a previous study where soil net mineralization rates were much lower in a bamboo dominant forest than that in a broadleaf forest (Song et al. 2016). Increased soil pH caused by bamboo invasion in this study is consistent with previous studies in the same region (Wu et al. 2008; Xu et al. 2015), which might be explained by changes in some chemical characteristics such as cation exchange capacity or root exudates induced by the process of bamboo invasion (Chang and Chiu 2015). The increase of soil pH by bamboo invasion can enhance soil microbial biomass and activity (Xu et al. 2015), resulting in increase in the net mineralization rate, which was documented in a previous study showing that net mineralization rate increased when soil pH increased from 4 to 8 in crop-residue-treated soils (Fu et al. 1987).

In this study, the gross nitrification rate decreased with increasing soil pH, paralleled with fungal abundance decreased and fungal community composition altered after bamboo invasion (Table 1; Table 3; Fig. 2). Soil fungi are considered to play an important role on the soil N transformation in the acidic forest soil (Cheng et al. 2013; Aciego Pietri and Brookes 2009), specially, the process of heterotrophic nitrification mediated by fungi is not inhibited even at pH 3 (De Boer and Kowalchuk 2001; Hayatsu et al. 2008). The CCA result showed that the positive relationships between soil fungal community composition and gross nitrification rate and NO_3^--N content were only observed in the broadleaf forest (Fig. 5), suggesting that heterotrophic nitrification might be driven by soil fungi in the broadleaf forests with lower soil pH. Furthermore, we found that gross nitrification rate was significantly correlated with the relative abundance of Mortierellales and Filobasidiales, respectively ($P < 0.01$) (Fig. S2). Notably, the order of Mortierellales contains mostly saprobic species capable of diverse functions such as cellulose and lignin degradation (Kjøller and Struwe 2002; Wagner et al. 2013), and fungal nitrification, which is linked to degradation of lignin or acetate, can frequently occur in the acidic forest soil (De Boer and Kowalchuk 2001). This finding implied that shifts in composition and abundance of soil fungal community caused by bamboo invasion could alter the relative abundance of fungal species, such as Mortierellales and Filobasidiales, which ultimately change the pattern of mineral N production, supporting our third hypothesis.

The higher net mineralization rate and lower gross nitrification rate in the bamboo forest soil, as compared to the broadleaf forest (Table 1), had the potential to decelerate NO_3^--N production and accelerate NH_4^+-N production. A previous study reported that slow nitrification in the bamboo dominant forest could be likely related to the nutrient habit of NH_4^+-N preference for Moso bamboo because of shoot emergence (Song et al. 2013). Therefore, changes in soil mineral N production pattern (mineralization/nitrification) induced by the shifts in soil fungal community and pH would have positive feedback to bamboo invasion by helping maintain fast-growing shoots. In addition, bacteria members have been generally considered as the dominant contributors to the N cycle (Hayatsu et al. 2008), and the gross N mineralization rate has been found to be correlated negatively with F/B ratios in boreal forests soil (Högberg et al. 2007). Bamboo invasion of native broadleaf forests significantly decreased F/B ratio as indicated by Xu et al. (2015), it remains to be tested in further study whether bacteria plays a major role in the N mineralization with increased soil pH in the bamboo forest soil.

Conclusions

The results from this study revealed that Moso bamboo invasion into broadleaf forests markedly altered composition and abundance of soil fungal community, which was closely linked to decreased soil relatively stable C (alkyl C) fraction and nitrification rate, providing valuable insights into the close linkage of fungal community to soil C and N transformations. Generally, the change of soil N transformation caused by plant invasion will affect the growth of native and exotic plants due to their different nutrient preference to NH_4^+-N or NO_3^--N. Therefore, whether the alteration of soil N transformation will in turn promote or inhibit the invasion process and associated mechanisms needs to be elucidated in the future. Additionally, in situ phenotypic traits for most soil fungi are often scarce or inconsistent, rendering it important to analyze fungal abundance or composition. This work revealed close linkages between fungi abundance or composition traits and soil C and N properties, highlighting the potential for using fungal abundance and composition information to begin building a trait-based understanding of fungi in regulating soil C and N transformations during bamboo invasion.

Acknowledgements This work was financially supported by the National Natural Science Foundation of China (31670618, 31470626), the Natural Science Foundation of Zhejiang Province (No. LY15C160006, LY14C160007), and the Science Foundation of the Education Department of Zhejiang Province, China (Y201225759)

Compliance with ethical standards

Funding This work was funded by the National Natural Science Foundation of China (31670618, 31470626), the Natural Science Foundation of Zhejiang Province (No. LY15C160006, LY14C160007), and the Science Foundation of the Education Department of Zhejiang Province, China (Y201225759).

Conflict of interest The authors declare that they have no conflict of interest.

References

Aciego Pietri JC, Brookes PC (2009) Substrate inputs and pH as factors controlling microbial biomass, activity and community structure in an arable soil. Soil Biol Biochem 41:1396–1405

Bai SB, Zhou GM, Wang YX, Liang QQ, Chen J, Cheng YY, Shen R (2013) Plant species diversity and dynamics in forests invaded by Moso bamboo (*Phyllostachys edulis*) in Tianmu Mountain nature Reserve. Biodivers Sci 21:288–295 (in Chinese with an English abstract)

Baldock JA, Oades JM, Waters AG, Peng X, Vassallo AM, Wilson AM (1992) Aspects of the chemical structure of soil organic materials as revealed by solid-state ^{13}C NMR spectroscopy. Biogeochemistry 16:1–42

Baptist F, Zinger L, Clement JC, Gallet C, Guillemin R, Martins JMF, Sage L, Shahnavaz B, Choler P, Geremia R (2008) Tannin impacts on microbial diversity and the functioning of alpine soils: a multidisciplinary approach. Environ Microbiol 10:799–809

Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. Soil Sci 59:39–46

Breuer L, Kiese R, Butterbach-Bahl K (2002) Temperature and moisture effects on nitrification rates in tropical rain-forest soils. Soil Sci Soc Am J 66:834–844

Callaway RM, Thelen GC, Barth S, Ramsey PW, Gannon JE (2004) Soil fungi alter interactions between the invader *Centaurea maculosa* and north American natives. Ecology 85:1062–1071

Caporaso JS, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK et al (2010) QIIME allows analysis of high-throughput community sequencing data. Nat Methods 7:335–336

Chang EH, Chiu CY (2015) Changes in soil microbial community structure and activity in a cedar plantation invaded by moso bamboo. Appl Soil Ecol 91:1–7

Chao A (1984) Nonparametric estimation of the number of classes in a population. Scand J Stat 11:265–270

Chen CR, Xu ZH, Mathers NJ (2004) Soil carbon pools in adjacent natural and plantation forests of subtropical Australia. Soil Sci Soc Am J 68:282–291

Cheng Y, Wang J, Mary B, Zhang JB, Cai ZC, Chang SX (2013) Soil pH has contrasting effects on gross and net nitrogen mineralizations in adjacent forest and grassland soils in central Alberta, Canada. Soil Biol Biochem 57:848–857

Crow SE, Lajtha K, Filley TR, Swanston CW, Bowden RD, Caldwell BA (2009) Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. Glob Chang Biol 15:2003–2019

De Boer W, Kowalchuk GA (2001) Nitrification in acid soils: micro-organisms and mechanisms. Soil Biol Biochem 33: 853–866

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Edgar RC (2013) UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat Methods 10:996–998

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Conserv 61:1–10

Fontaine S, Barot S, Barre P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–280

Fu MH, Xu XC, Tabatabai MA (1987) Effect of pH on nitrogen mineralization in crop-residue-treated soils. Biol Fert Soils 5: 115–119

Grayston SJ, Campbell CD, Bardgett RD, Mawdsley JL, Clegg CD, Ritz K, Griffith BS, Rodwelld JS, Edwardsd SJ, Daviesd WJ, Elstone DJ, Millard P (2004) Assessing shifts in microbial community structure across a range of grasslands of differing management intensity using CLPP, PLFA and community DNA techniques. Appl Soil Ecol 25:63–84

Hanson CA, Allison SD, Bradford MA, Wallenstein MD, Treseder KK (2008) Fungal taxa target different carbon sources in forest soil. Ecosystems 11:1157–1167

Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol Lett 8:976–985

Hayatsu M, Tago K, Saito M (2008) Various players in the nitrogen cycle: diversity and functions of the microorganisms involved in nitrification and denitrification. Soil Sci Plant Nutr 54:33–45

Högberg MN, Chen Y, Högberg P (2007) Gross nitrogen mineralisation and fungi-to-bacteria ratios are negatively correlated in boreal forests. Biol Fert Soils 44:363–366

Huang ZQ, Xu ZH, Chen CR, Boyd S (2008) Changes in soil carbon during the establishment of a hardwood plantation in subtropical Australia. Forest Ecol Manag 254:46–55

Ingwersen J, Butterbach-Bahl K, Gasche R, Richter O, Papen H (1999) Barometric process separation: new method for quantifying nitrification, denitrification, and nitrous oxide sources in soils. Soil Sci Soc Am J 63:117–128

Kalbitz K, Schwesig D, Schmerwitz J, Kaiser K, Haumaier L, Glaser B, Ellerbrockd R, Leinwebere P (2003) Changes in properties of soil-derived dissolved organic matter induced by biodegradation. Soil Biol Biochem 35:1129–1142

Kjøller AH, Struwe S (2002) Fungal communities, succession, enzymes, and decomposition. In: Burns RG, Dick RP (eds) Enzymes in the environment: activity, ecology and applications. CRC, New York, pp 267–284

Kubartová A, Ranger J, Berthelin J, Beguiristain T (2009) Diversity and decomposing ability of saprophytic fungi from temperate forest litter. Microbial Ecol 58:98–107

Li YF, Jiang PK, Chang SX, Wu JS, Lin L (2010) Organic mulch and fertilization affect soil carbon pools and forms under intensively managed bamboo (*Phyllostachys praecox*) forests in southeast China. J Soils Sediments 10:739–747

Li YF, Zhang JJ, Chang SX, Jiang PK, Zhou GM, Fu SL, Yan ER, Wu JS, Lin L (2013) Long-term management effects on soil organic carbon pools and chemical composition in Moso bamboo (*Phyllostachys pubescens*) forests in subtropical China. Forest Ecol Manag 303:121–130

Li YC, Li YF, Chang SX, Liang X, Qin H, Chen JH, Xu QF (2017) Linking soil fungal community structure and function to soil organic carbon chemical composition in intensively managed subtropical bamboo forests. Soil Biol Biochem 107:19–31

Liao CZ, Peng RH, Luo YQ, Zhou XH, Wu XW, Fang CM, Chen JK, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytol 177: 706–714

Lin YT, Tang SL, Pai CW, Whitman WB, Coleman DC, Chiu CY (2014) Changes in the soil bacterial communities in a cedar plantation invaded by Moso bamboo. Microbial Ecol 67: 421–429

Liu J, Yang QP, Yu DK, Song QN, Zhao GD, Wang B (2013) Contribution of fine root to soil nutrient heterogeneity at two sides of the bamboo and broad-leaved forest interface. J Plant Ecol 37:739–749 (in Chinese with an English abstract)

Lu RK (1999) Analytical Methods for soil and agro-chemistry. China Agricultural Science and Technology Press, Beijing (in Chinese)

Magoč T, Salzberg SL (2011) FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics 27:2957–2963

Mao JD, Olk DC, Fang XW, He ZQ, Schmidt-Rohr K (2008) Influence of animal manure application on the chemical structures of soil organic matter as investigated by advanced solid-state NMR and FT-IR spectroscopy. Geoderma 146: 353–362

Mathers NJ, Jalota RK, Dalal RC, Boyd SE (2007) ^{13}C-NMR analysis of decomposing litter and fine roots in the semi-arid Mulga lands of southern Queensland. Soil Biol Biochem 39: 993–1006

May LA, Smiley B, Schmidt MG (2001) Comparative denaturing gradient gel electrophoresis analysis of fungal communities associated with whole plant corn silage. Can J Microbiol 47: 829–841

Nemergut DR, Townsend AR, Sattin SR, Freeman KR, Fierer N, Neff JC, Bowman WD, Schadt CW, Weintraub MN, Schmidt SK (2008) The effects of chronic nitrogen fertilization on alpine tundra soil microbial communities: implications for carbon and nitrogen cycling. Environ Microbiol 10:3093–3105

Ng EL, Patti A, Rose M, Schefe C, Wilkinson K, Smernik R, Cavagnaro T (2014) Does the chemical nature of soil carbon

drive the structure and functioning of soil microbial communities? Soil Biol Biochem 70:54–61

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ, Suggests MASS (2007) The vegan package. Comm Ecol Pack 10

Peay KG, Baraloto C, Fine PV (2013) Strong coupling of plant and fungal community structure across western Amazonian rainforests. ISME J 7:1852–1861

Roberts DW (2007) labdsv: ordination and multivariate analysis for ecology. R package version 1.1

Rosenkranz P, Brüggemann N, Papen H, Xu Z, Horvát L, Butterbach-Bahl K (2006) Soil N and C trace gas fluxes and microbial soil N turnover in a sessile oak (*Quercus petraea* (Matt.) Liebl.) forest in Hungary. Plant Soil 285: 301–322

Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. Ecology 85:591–602

Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27:379–423

Shannon P, Markiel A, Ozier O, Baliga NS, Wang JT, Ramage D, Amin N, Schwikowski B, Ideker T (2003) Cytoscape: a software environment for integrated models of biomolecular interaction networks. Genome Res 13:2498–2504

Song QN, Yang QP, Liu J, Yu DK, Fang K, Xu P, He YJ (2013) Effects of *Phyllostachys edulis* expansion on soil nitrogen mineralization and its availability in evergreen broadleaf forest. Chin J Appl Ecol 24:338–344 (in Chinese with an English abstract)

Song QN, Ming OY, Yang QP, Lu H, Yang GY, Chen FS, Shi JM (2016) Degradation of litter quality and decline of soil nitrogen mineralization after moso bamboo (*Phyllostachys pubscens*) expansion to neighboring broadleaved forest in subtropical China. Plant Soil 404:113–124

Stewart CE, Neff JC, Amatangelo KL, Vitousek PM (2011) Vegetation effects on soil organic matter chemistry of aggregate fractions in a Hawaiian forest. Ecosystems 14:382–397

Stroo HF, Klein TM, Alexander M (1986) Heterotrophic nitrification in an acid forest soil and by an acid-tolerant fungus. Appl Environ Microbiol 52:1107–1111

Štursová M, Žifčáková L, Leigh MB, Burgess R, Baldrian P (2012) Cellulose utilization in forest litter and soil: identification of bacterial and fungal decomposers. FEMS Microbiol Ecol 80:735–746

Sun RB, Zhang XX, Guo XS, Wang DZ, Chu HY (2015) Bacterial diversity in soils subjected to long-term chemical fertilization can be more stably maintained with the addition of livestock manure than wheat straw. Soil Biol Biochem 88:9–18

Sun RB, Dsouza M, Gilbert JA, Guo XS, Wang DZ, Guo ZB, Ni YY, Chu HY (2016) Fungal community composition in soils subjected to long-term chemical fertilization is most influenced by the type of organic matter. Environ Microbiol 18: 5137–5150

Team RC (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Toju H, Tanabe AS, Yamamoto S, Sato H (2012) High-coverage ITS primers for the DNA-based identification of ascomycetes and basidiomycetes in environmental samples. PLoS One 7: e40863

Ushio M, Kitayama K, Balser TC (2010) Tree species-mediated spatial patchiness of the composition of microbial community and physicochemical properties in the topsoils of a tropical montane forest. Soil Biol Biochem 42:1588–1595

Wagner L, Stielow B, Hoffmann K, Petkovits T, Papp T, Vágvölgyi C, de Hoog GS, Verkley G, Voigt K (2013) A comprehensive molecular phylogeny of the *Mortierellales* (*Mortierellomycotina*) based on nuclear ribosomal DNA. Persoonia 30:77–93

Wang CH, Wan SQ, Xing XR, Zhang L, Han XG (2006) Temperature and soil moisture interactively affected soil net N mineralization in temperate grassland in northern China. Soil Biol Biochem 38:1101–1110

Wang H, Liu SR, Mo JM (2010) Correlation between leaf litter and fine root decomposition among subtropical tree species. Plant Soil 335:289–298

Wang H, Liu SR, Chang SX, Wang J, Shi Z, Huang X, Wen Y, Lu LH, Cai DX (2015) Soil microbial community composition rather than litter quality is linked with soil organic carbon chemical composition in plantations in subtropical China. J Soils Sediments 15:1094–1103

Wang HC, Tian G, Chiu CY (2016) Invasion of moso bamboo into a Japanese cedar plantation affects the chemical composition and humification of soil organic matter. Sci Rep 6:32211

World Reference Base for Soil Resources (WRB) (2006) A framework for international classification, correlation and communication. Food and Agriculture Organization of the United Nations, Rome

Wu JS, Jiang PK, Wang ZL (2008) The effects of *Phyllostachys pubescens* expansion on soil fertility in National Nature Reserve of mountain Tianmu. Acta Agric Univ Jiangxiensis 30:689–692 (in Chinese with an English abstract)

Xu YB, Cai ZC (2007) Denitrification characteristics of subtropical soils in China affected by soil parent material and land use. Eur J Soil Sci 58:1293–1303

Xu QF, Jiang PK, Wu JS, Zhou GM, Shen RF, Fuhrmann JJ (2015) Bamboo invasion of native broadleaf forest modified soil microbial communities and diversity. Biol Invasions 17: 433–444

Zhang T, Li YF, Chang SX, Jiang PK, Zhou GM, Liu J, Lin L (2013a) Converting paddy fields to lei bamboo (*Phyllostachys praecox*) stands affected soil nutrient concentrations, labile organic carbon pools, and organic carbon chemical compositions. Plant Soil 367:249–261

Zhang YC, Zhang JB, Meng TZ, Zhu TB, Müller C, Cai ZC (2013b) Heterotrophic nitrification is the predominant NO_3^- production pathway in acid coniferous forest soil in subtropical China. Biol Fert Soils 49:955–957

Zhang JJ, Li YF, Chang SX, Jiang PK, Zhou GM, Liu J, Wu JS, Shen ZM (2014) Understory vegetation management affected greenhouse gas emissions and labile organic carbon pools in an intensively managed Chinese chestnut plantation. Plant Soil 376:363–375

Zhu TB, Meng TZ, Zhang JB, Yin YF, Cai ZC, Yang WY, Zhong WH (2013) Nitrogen mineralization, immobilization turnover, heterotrophic nitrification, and microbial groups in acid forest soils of subtropical China. Biol Fert Soils 49:323–331