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REGULAR ARTICLE

Degradation of litter quality and decline of soil nitrogen mineralization after moso bamboo (*Phyllostachys pubscens*) expansion to neighboring broadleaved forest in subtropical China

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Abstract
Aims Moso bamboo (*Phyllostachys pubescens*) is a typical native invasive plant imposing serious threats on ecosystem processes and functions. A primary concern is alterations of litter and soil N mineralization in evergreen broadleaved forests coupled with bamboo population expansion.
Methods We conducted a field study to determine the litter production, quality, N resorption efficiency, and soil N mineralization rates in bamboo-dominated forest (BDF) and adjacent uninvaded evergreen broadleaved forest (EBF) in subtropical China.
Results The mean annual litter production for BDF was 5.82 Mg ha^{-1}, 36.0 % lower than that for EBF (9.09 Mg ha^{-1}). Litter N concentration was also lower, but C: N was higher after bamboo expansion, coupled with higher N resorption efficiency for Moso bamboo and lower litterfall, resulting in potential N return decreasing as much as 60.41 kg N ha^{-1} yr^{-1} to the soil. The soil N net nitrification and mineralization rates exhibited lower values in BDF than in EBF. In addition, annual soil N mineralization rate was positively correlated with litter production but negatively with C: N ratio of litter.
Conclusions Expansion of bamboo into neighboring EBF decreased litter production and quality, reduced soil N mineralization rate, and ultimately retarded N cycling. These effects should be carefully considered in the design of restoration strategies for ecosystems impacted by bamboo species.

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Keywords Moso bamboo expansion · Litter quality · Soil N mineralization · N resorption efficiency · Evergreen broadleaved forest · Subtropical China

Abbreviations

BDF	Bamboo-dominated forest
C. fargesii	*Castanopsis fargesii*
C. sclerophylla	*Castanopsis sclerophylla*
EBF	Evergreen broadleaved forest
P. pubescens	*Phyllostachys pubescens*
Q. chenii	*Quercus chenii*
S. laurina	*Symploco slaurina*

Introduction

Moso bamboo (*Phyllostachys pubescens* Mazel ex J. Houz.), a tree-like bamboo species of Poaceae with height of 10–20 m, is naturally distributed in subtropical China (Yi et al. 2008). The uses of this bamboo species for humans are remarkable, such as young edible shoots for popular delicacy, and the timber (adult culms) for construction, floor decoration, furniture and charcoal making, and so on. Like other bamboos, Moso bamboo has active clonal reproduction with a leptomorph rhizome system which can run horizontally belowground. Furthermore, this bamboo displays prodigious growth rate, increases by 10–20 m height in only 2–3 months under suitable conditions (Li et al. 1998), reaching a height comparable with surrounding well-developed canopy trees. These intrinsic strengths facilitate its expansion into adjacent forests. Evergreen broadleaved forest, the native vegetation of subtropical China, which houses high level of diversity, are undergoing much of Moso bamboo expansion due to anthropogenic disturbances such as cultivation and logging (Yang et al. 2015). And the abundance and cover of bamboo-dominated forest has significantly increased both locally and regionally throughout subtropical China in past decades (Ding et al. 2006; Yang et al. 2015).

Unconstrained bamboo expansion can cause dramatic changes in community structure and function, such as declined species richness and diversity (Bai et al. 2013; Touyama et al. 1998), simplified community structure (Okutomi et al. 1996), reduced seedling regeneration (Isagi and Torii 1998), and changed hydrological cycle (Shinohara and Otsuki 2015). Although *P. pubescens* expansion is a widespread phenomenon, there are only few studies on its biogeochemical impacts on the invaded ecosystems. Wu et al. (2008) observed that the size of soil labile N pool increased, but the total N content did not change after *P. pubescens* invasion to *Pinus massoniana*-broadleaved mixed forest. Liu et al. (2013) found that soil total N content of bamboo forest was greater than that of adjacent evergreen broadleaved forest. Fukushima et al. (2015) assumed that *P. pubescens* expansion into broadleaved forests changed the distribution pattern of N stored in plants and soil. However, little is known about the effects of *P. pubescens* expansion on litter and soil N mineralization, two important components of N cycling, which would be crucial for better understanding about the ecological consequences and mechanisms of bamboo expansion.

Litter and soil N mineralization are strongly influenced by changes in vegetation, that is, species composition and community structure (Sundarapandian and Swamy 1999; Yan et al. 2009). The shift from a tree- to a bamboo-dominated ecosystem is likely to have significant effects on production and quality of plant litter, which in turn controls the soil N mineralization since litter input is the major source for soil organic matter accumulation to sustain soil N transformations. In order to assess the effects of bamboo expansion on nitrogen cycling, it is necessary for us to quantify the characteristics of litter parameters (production, quality and timing) and soil N mineralization (including ammonification and nitrification). Space-for-time substitution is always used as an evaluation method (Yan et al. 2008). Generally, along the direction of bamboo expansion, secondary evergreen broadleaved forest (EBF, hereafter) was chosen to represent a reference condition, and bamboo-dominated forest (BDF, hereafter) was recognized as the experimental unit. Our specific objectives were: (1) to examine the production of litter and their seasonal patterns; (2) to assess the chemical quality of litter and potential N return to soil; (3) to determine soil N mineralization rates in BDF and EBF.

Materials and methods

Study area and site description

Fieldwork was conducted at Dagang Mountain National Forest Ecological Station in Jiangxi Province, China (latitude 27°30′–27°50′ N and longitude 114°30′–114°45′ E). This region has a humid mid-subtropical monsoon climate with a hot, humid summer and a dry, cold winter. The annual mean temperature is 17.7 °C. July is the warmest month with a mean temperature of 28 °C and January is the coldest month with a mean temperature of 1.9 °C. The annual mean precipitation is 1 591 mm concentrated from March to August. The rainfall and air temperature in the study year were showed in Fig. 1. The soil is predominantly derived from slate and shale, classified as Oxisol with reference to US Taxonomy (Wang et al. 2005). In the study region, the climax vegetation is EBFs. However, due to human activities, many of these EBFs have converted to the secondary forests. Moso bamboo forests are also widely distributed here for the suitable climate condition (Yang et al. 2011).

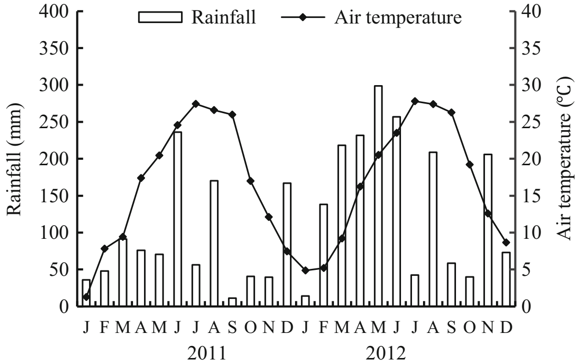

Fig. 1 Average monthly rainfall and air temperature during 2011–2012 in Dagangshan Mountain, Forest Ecological Station, in Jiangxi Province, China

Table 1 Structural characteristics for bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF), in Dagang Mountain National Forest Ecological Station, Jiangxi Province, China

	BDF	EBF
Tree density (stems ha^{-1})	5366 ± 824	1011 ± 356
DBH (cm)	10.8 ± 1.8	17.8 ± 9.4
Plant height (m)	13.5 ± 1.7	15.0 ± 2.7
BA (m^2 ha^{-1})	53.9 ± 6.3	27.3 ± 4.3
Mean age of stand (yr)	30	50
Dominant species	*Phyllostachy pubescens*	*Castanopsis fargesii*
Associated species	*Castanopsis fargesii*	*Castanopsis sclerophylla*
	Castanopsis sclerophylla	*Symplocos laurina*
	Symplocos laurina	*Quercus chenii*
	Quercus chenii	*Schima superba*

Data are means ± SE. DBH is diameter at breast height. BA is stand basal area

We continuously selected BDF and uninvaded secondary EBF to examine the effects of bamboo invasion on litter dynamics and soil N transformation rates. Three pairs of plots straddling BDF and EBF were established in January, 2011. The plots were 20 m × 20 m located on the same position of slope, ranging from 280 to 320 m above mean sea level. The soils were developed from the same parent material (Wang et al. 2005).

BDF was occupied by *P. pubescens*, with some resident broadleaved trees including *C. fargasii*, *C. sclerophylla*, *S. laurina and Q. chenii*. The stand density was 5366 stems ha^{-1}, with 9:1 ratio of *P. pubescens* over broadleaved trees. The height and basal area were 13.5 m and 53.9 m^2 ha^{-1}, respectively (Table 1). BDF was about 30 years old. It formed by expanding into area which was EBF in history (personal communication with local forest managers). No forest management practices such as fertilizing and harvesting were performed in BDF.

EBF, was about 50 years old, located in frontier of BDF, mainly dominated by broadleaved species of *C. fargasii*, *C. sclerophylla*, *S. laurina*, *Q. chenii and S. superba*. Its measured tree density, height and basal area were 1011 stems ha^{-1}, 15.0 m and 27.3 m^2 ha^{-1}, respectively, of which *C. fargasii* shared about 54.8 % of the total tree density (Table 1).

Determination of litter production and quality

Five litter traps (1 × 1 m) constructed with nylon netting (1-mm mesh), were randomly laid out in each plot, suspended approximately 0.2 m above the ground with four bamboo stakes (15 traps in each stand). Litter was collected monthly from January, 2011 to December, 2012 (24 sampling periods). Samples were taken to the laboratory and sorted into leaves, small wood (e.g., branches and bark ≤2.0 cm in diameter) and other parts (e.g., reproductive parts and miscellaneous materials). Leaf litter samples were further subdivided by species to determine the individual species contribution to total litter. All fractions were oven-dried at 70 °C to constant weight to determine the dry mass. The annual mass of each litter component produced in each plot was expressed as litter dry weight per hectare (Mg ha^{-1}). The same litter sub-samples from each plot in each month were mixed, ground and sieved through a 0.25-mm mesh to measure the C, N and lignin concentration.

Total C was determined by the oil bath-K_2CrO_7 titration method (Nelson and Sommers 1975). Total N concentration was measured by the micro-Kjeldahl method of 0.25 g litter sample digesting in 5 ml concentrated H_2SO_4 with a catalyst mixture ($CuSO_4$, K_2SO_4 and selenium powder) and then distillation (Nelson and Sommers 1982). Lignin was analyzed by modified gravimetry according to a standardized method of hot sulfuric acid digestion (King and Heath 1967). Each sample was conducted in triplicate and the average of each triplicate was taken.

The monthly litter production was the sum of all litter components mass in each month, and the annual litter production was summed by the monthly production in each year. The value of C (N or lignin) concentration of each litter component was the means of all months in each year. Litter C (N or lignin) concentration at ecosystem level was calculated using the following formula (1). The annual N return was multiplying annual litter production by initial N concentration of each year.

$$\overline{X} = \sum (P_i \times X_i) / \sum P_i \quad (1)$$

where $\overline{X}$ is the weighted average value of C (N or lignin) concentration (g kg^{-1}), P_i is the production of litter component i (kg ha^{-1} a^{-1}) in each plot, X_i is the corresponding C (N or lignin) concentration (g kg^{-1}) of litter component i.

Determination of litter layer and decomposition

Standing litter crop was sampled from soil surface in April, August, October and December of 2011 and 2012 (eight times). Ten random samples of 0.25 m^2 were collected in the vicinity of the litter traps at each plot. Then the samples were taken to the laboratory, removed of sand, separated into leaf, small wood and other parts. All samples were oven-dry at 70 °C to constant weight. Turnover rate (k) was estimated for each litter component according to Scott et al. (1992).

$$k = A/F \quad (2)$$

where k is the turnover rate (yr^{-1}), A is the annual litter production (Mg ha^{-1} yr^{-1}) and F is the mean litter standing crop (Mg ha^{-1}) in each plot.

Determination of leaf N resorption efficiency

Green and mature leaves of *P. Pubescens*, *C. fargesii*, *C. sclerophylla*, *Q. chenii* and *S. laurina*, whose leaf litter contributed over 2 % to total litter dry mass, were collected from each field plot in August and October in 2011. Their leaf litter were collected from each selected species. Samples were washed with distilled water to clear dust, oven-dried at 60 °C, finely grounded and analyzed for N content. N-resorption efficiency was estimated according to Killingbeck (1996).

$$\text{NRE} = \left(\text{N}_{\text{green}} - \text{N}_{\text{sen}}\right) / \text{N}_{\text{green}} \times 100 \quad (3)$$

where NRE is leaf N resorption efficiency (%), N_{green} and N_{sen} are the average N concentration in green and litter leaves (g kg^{-1}), respectively.

Determinations of soil properties

Ten soil samples were taken with a soil auger (6 cm diameter × 20 cm height) from randomly chosen spots in each plot in January 2011. The litter layer was removed before soil was taken. 5 soil cores per plot were oven at 105 °C for over 48 h to estimate soil bulk density (2 stands × 3 plots × 5 spots). The remaining soil cores per plot were air-dried for about 30 days, and passed through a 0.5 mm sieve to determine soil C, N and pH. Total C was measured by oil bath-K_2CrO_7 titration method (Nelson and Sommers 1975) and N concentration by semimicro-Kjeldahl method (Nelson and Sommers 1982). Soil pH was determined by using a Metterler-S20P-K pH meter (1: 2.5, H_2O).

Determination of soil N mineralization rates

Soil net N mineralization (including ammonification and nitrification) rates were measured in situ incubations using PVC method (Binkley and Hart 1989; Yan et al. 2008). In each plot, five pairs of sharpened PVC cores (5 cm diameter × 17 cm length) were driven 15 cm into the chosen spots. One of each pipe pair (initial sample) was removed and taken to the laboratory to measure initial concentrations of extractable ammonium (NH_4^+-N) and nitrate (NO_3^--N). The second pipe of each pair (incubated sample) was covered with low density polyethene on the top and with gauze under the bottom, and then inserted into its original position for 30 days. 24 successive in situ incubations were established from January 2011 to the end of December 2012. The incubated samples were pulled out and the accumulation of mineral N was determined after field incubation. In the laboratory, after removal of the stones and roots, each sample was well blended by hand to avoid the heterogeneity of soil. Subsamples of ~20 g were weighted to extract mineral N with 100 ml of 2 M KCl during 2 h in a shaker. Mineral NH_4^+-N and NO_3^--N were determined by methods of alkaline phenol and cadmium reduction, respectively (Yan et al. 2008).

The soil NH_4^+-N and NO_3^--N concentration were the means of the initial sample of NH_4^+-N and NO_3^--N concentration of all months in each stand, respectively. Soil net ammonification of a sample was calculated by the incubated sample of NH_4^+-N concentration minus that of the initial sample. Soil net nitrification of a sample was obtained by the incubated sample of NO_3^-−N concentration minus that of the initial sample.

Net N mineralization of a sample was obtained based on the sum of the increases of NH_4^+-N and NO_3^-−N concentration in the field incubation. Net N ammonification rate, nitrification rate and mineralization rate were expressed mg kg^{-1} $(30d)^{-1}$ on an oven-dried-soil basis.

Statistical analyses

Data were analyzed through one-way ANOVA by SPSS 17.0 for windows. Means were compared using Tukey's Honestly Significant Difference in litter production, litter quality, litter N return, standing litter crop, litter turnover rate, soil properties and soil net mineralization rates between BDF and EBF. Least Significant Difference (LSD) test was used to determine the differences in litter quality and leaf N-resorption efficiency of species in the same stand. In all statistical analyses, $P < 0.05$ was the criterion for significant difference. Pearson correlation was used to assess the relationship between soil N mineralization rates and litter properties.

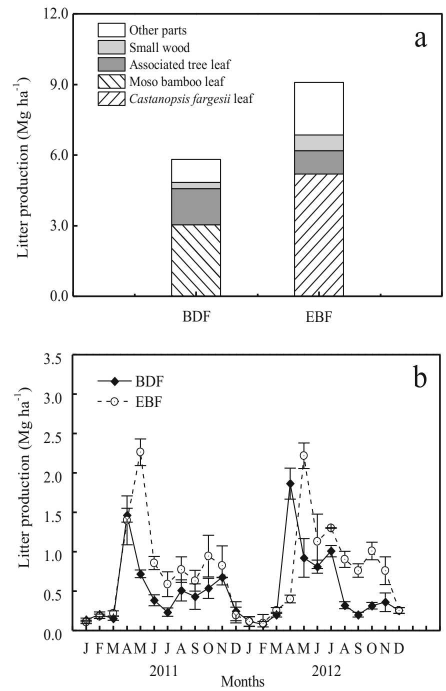

Fig. 2 The production (**a**) and seasonality (**b**) of litter for bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF) in Dagang Mountain National Forest Ecological Station, Jiangxi Province, China

Results

Litter production and seasonality

There were significant differences between BDF and EBF ($F_{1,\ 10} = 42.42$, $P = 0.003$) in the litter production during the 2-year period. The annual total litter production in BDF was 5.82 Mg ha^{-1}, 36.0 % lower than that in EBF (9.09 Mg ha^{-1}, Fig. 2a). Leaf litter occupied 80.1 % of the total annual litter for BDF, with corresponding value of 68.2 % for EBF. Leaf litter from *P. pubescens* (3.04 Mg ha^{-1}) contributed about 52.3 % of the total litter at the BDF sites, less than leaf litter from *C. fargasii* (5.19 Mg ha^{-1}) who accounting for 57.1 % of the total litter at the EBF sites (Fig. 2a).

Litterfall demonstrated a bimodal distribution pattern for both BDF and EBF, with an obvious peak in later spring period (April–June) and an inconspicuous peak in autumn (October-November) every year (Fig. 2b). About 46.0 % of total litter at the BDF site occurred in first peak, whereas about 50.8 % at the EBF site. The peak of BDF was a month earlier than that of EBF, with the highest value in April and May for BDF and EBF, respectively. In addition, the production of litter in BDF fluctuated significantly ($F_{1,\ 4} = 9.33$, $P < 0.001$) in studying years. In 2011 the production of litter in BDF was 5.39 Mg ha^{-1}, 0.85 Mg ha^{-1} lower than that in 2012.

Litter quality and N resorption efficiency

There were significant differences in litter quality between BDF and EBF stands (Table 2). The weighted average N and lignin concentration of litter in BDF were all lower than those in EBF, while weighted litter C concentration for BDF (475.7 g kg^{-1}) was close in value to that of EBF (491.4 g kg^{-1}). The C/N was greater in BDF than in EBF, but not for lignin/N ratio which was similar in two stands. Species showed strong variations in leaf litter quality. *P. pubescens* had the lowest N concentration but the highest C/N among all species. In contrast, *C. fargasii* exhibited the highest N concentration while almost the lowest C/N. In addition, the common species (*C. fargasii*, *Q. chenii* and *S. laurina*) generally had lower N concentration in BDF than in EBF.

With respect to NRE, there were substantial differences among species in BDF. *P. pubescens* had the greatest NRE (39.7 %), followed by *C. sclerophylla* (22.5 %), *S. laurina* (21.6 %) and *Q. chenii* (17.9 %),

Table 2 The litter quality and N-resportion efficiency for main species in bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF)

Stands/Species	C (g kg^{-1})	N (g kg^{-1})	Lignin (g kg^{-1})	C/N	Lignin/N	NRE
BDF	475.5 ± 6.9 A	11.2 ± 1.1 A	256.6 ± 16.8 A	41.8 ± 4.9 A	22.7 ± 5.7 A	
Phyllostachys pubescens	469.3 ± 16.7a	10.8 ± 0.7b	233.4 ± 16.7c	43.5 ± 3.0a	21.6 ± 4.6b	39.7 ± 4.6a
Castanopsis fargesii	475.0 ± 10.8a	12.5 ± 1.0a	311.2 ± 17.9b	37.9 ± 3.3b	24.8 ± 2.8b	15.5 ± 1.3c
Castanopsis sclerophylla	487.4 ± 10.7a	11.7 ± 1.0a	275.6 ± 19.1bc	41.6 ± 4.4ab	23.6 ± 4.1b	22.5 ± 1.9b
Symploco slaurina	392.2 ± 14.8b	10.9 ± 1.1b	142.4 ± 16.5d	36.0 ± 5.8b	13.1 ± 6.7c	21.6 ± 2.8b
Quercus chenii	496.8 ± 22.2a	11.5 ± 1.8ab	408.5 ± 23.4a	43.2 ± 5.8a	35.5 ± 5.6a	17.9 ± 1.7bc
EBF	491.4 ± 9.7 A	14.0 ± 1.3B	312.7 ± 16.5B	35.1 ± 3.6B	22.4 ± 4.6 A	
Castanopsis fargesii	492.7 ± 10.3a	14.3 ± 1.3a	310.2 ± 26.5b	34.6 ± 5.3b	21.7 ± 3.6b	14.7 ± 2.1b
Castanopsis sclerophylla	503.8 ± 29.4a	11.4 ± 0.9b	328.1 ± 14.1b	44.2 ± 4.6a	28.8 ± 6.7b	20.3 ± 2.4a
Symploco slaurina	401.5 ± 23.3b	13.3 ± 1.8a	132.8 ± 15.6c	30.2 ± 2.8b	10.0 ± 2.2c	7.0 ± 1.8c
Quercus chenii	500.1 ± 11.0a	12.1 ± 0.4ab	394.0 ± 17.1a	41.3 ± 7.5ab	32.6 ± 7.7a	18.2 ± 2.2a

Data are means ± SE. SE is standard error. $n = 6$ for litter quality and $n = 3$ for N-resorption efficiency (NRE). Uppercase letters in the same column indicate significant differences between two stands. Lowercase letters in the same column indicate significant differences among species in each stand at $P = 0.05$

C. fargesii (15.5 %) being the lowest, indicating the highest N use efficiency for *P. pubescens* (Table 2).

Potential N return and decomposition

Using litter production data (from Fig. 2) and initial N concentration (from Table 2), the annual potential N return via litter in BDF was 59.0 kg N ha^{-1}, nearly two times lower ($F_{1,10} = 38.71$, $P < 0.001$) than that in EBF stand (119.4 kg N ha^{-1}, Table 3). Leaf litter contributed 82.5 % and 67.8 % to the total N return for BDF and EBF, respectively.

The standing litter crop was higher in BDF (2.87 Mg ha^{-1}) than in EBF (2.26 Mg ha^{-1}), with all the litter components showing the same pattern (Table 3). In terms of litter turnover rates (Table 3), BDF showed an annual turnover rate of 2.06, nearly two times lower than EBF (4.05), indicating that the decomposition rate of litter was reduced after bamboo expansion. Furthermore, the turnover rates for all litter components were also lower for BDF than for EBF.

Soil physical and chemistry properties

Total organic C, N, and C/N in BDF was slightly, but not significantly, higher than that in EBF, however, EBF had slightly higher NH_4^+-N and NO_3^--N concentration than BDF (Table 4). Significant difference ($p < 0.05$) of pH

Table 3 Annual potential N return (kg N ha^{-1} yr.$^{-1}$), standing litter crop (Mg ha^{-1}) and turnover rates (yr^{-1}) for bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF)

	Leaf	Small wood	Other parts	Total
N return				
BDF	48.7 ± 7.9a	2.1 ± 0.6a	8.2 ± 2.5a	59.0 ± 8.2a
EBF	81.0 ± 12.0b	5.7 ± 1.3b	32.7 ± 1.5b	119.4 ± 10.3b
Standing litter crop				
BDF	1.54 ± 0.13a	0.84 ± 0.07a	0.40 ± 0.06a	2.87 ± 0.17b
EBF	1.36 ± 0.12a	0.63 ± 0.08a	0.27 ± 0.04b	2.26 ± 0.12a
Turnover rates				
BDF	3.04 ± 0.39b	0.31 ± 0.12b	1.99 ± 0.24b	2.06 ± 0.34b
EBF	4.54 ± 0.43a	1.06 ± 0.23a	8.28 ± 0.14a	4.05 ± 0.47a

Data are means ± SE. SE is standard error ($n = 6$). Lowercase letters in the same column indicate significant differences between BDF and EBF at $P = 0.05$

was found between the two stands, with pH of BDF being 3.7, 0.36 lower than that of EBF (4.1).

Soil net N ammonification and nitrification

The annual net ammonification rate was slightly higher in BDF (105.1 kg N ha^{-1}) than in EBF (87.4 kg N ha^{-1}, Table 5). However, there were significant differences in soil annual net nitrification rates between BDF and EBF, and that was much lower in BDF (1.2 kg N ha^{-1}) than in EBF (57.7 kg N ha^{-1}), leading to low total net N mineralization (including ammonification and nitrification) rates in BDF (Table 5).

Soil net N mineralization rates also showed remarkable seasonal dynamics (Fig. 3). Both for BDF and EBF stands, soil net N ammonification rates were highest in early summer and lowest in winter. Soil net nitrification rate of BDF was constantly low all the year round, on the other hand, that of EBF showed a parabola trend peaking in the early summer and decreasing afterwards. Additionally, there was a consistent seasonal pattern of net N mineralization rates in both BDF and EBF.

Correlation of litter with soil net N mineralization rates

We evaluated the importance of litter parameters as potential factors regulating net N mineralization rates. The coefficients of determination for these tests were shown in Table 6. Annual litter production, N concentration and turnover rate were positively correlated with the soil N ammonification and nitrification rate. The average C: N ratio of litter showed negative correlations with the soil N ammonification, nitrification and mineralization. The litter standing crop was significant negatively related to the soil nitrification rate.

Table 4 Soil properties for bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF), Dagang Mountain National Forest Ecological Station, Jiangxi Province, China

	BDF	EBF
C (g kg^{-1})	25.18 ± 2.93a	22.42 ± 1.72a
Total N (g kg^{-1})	1.99 ± 0.21a	1.89 ± 0.32a
C/N	17.99 ± 0.51a	15.06 ± 0.90a
NH_4^+-N (mg kg^{-1})	3.99 ± 1.32a	4.43 ± 0.94a
NO_3^-–N (mg kg^{-1})	1.65 ± 0.46a	2.54 ± 3.89a
Mineral-N (mg kg^{-1})	5.64 ± 1.82a	6.97 ± 3.54a
pH value	3.70 ± 0.10a	4.06 ± 0.05b
Bulk density (g cm^{-3})	1.01 ± 0.07a	1.12 ± 0.06a

Data are means ± SE. SE is standard error (n = 3). Lowercase letters in the same row indicate significant differences between BDF and EBF at $P = 0.05$

Discussion

Moso bamboo plays a crucial important role in economy and culture in eastern Asia. However, recent years this species can overwhelmingly expand to adjacent forest ecosystems, displaced many of treess, and ultimately become the dominant species in subtropical China. Like other alien invasive plants, bamboo invasion would cause profound changes in community composition and structure, and may have legacy effects on ecosystem processes including litter input and soil N mineralization rate.

Litter production and dynamics

In the present study the mean annual litter production in BDF stand was 5.82 kg ha^{-1} (Fig. 2a), which was higher than that in two subtropical bamboo plantations (4.34–4.94 Mg ha^{-1} a^{-1}) reported by Tu et al. (2014) and lower than that in a Moso bamboo forest in Japan (7.17 Mg ha^{-1} a^{-1}) investigated by Isagi et al. (1997). The annual litter production in EBF stand was 9.09 Mg ha^{-1} (Fig. 2a), which was close to those recorded in other broadleaved forests of neighboring subtropical region [6.69–11.01 Mg ha^{-1} a^{-1} (Yang et al. 2004; Wang et al. 2010)]. These results showed that the expansion of bamboo remarkably decreased the litter production in adjacent ecosystem, which was in contrast to the previous findings that invasive species generally increased the litter quantity (Lindsay and French 2005; Liao et al. 2008; Brantley and Young 2008; Zhang et al. 2013).

Table 5 Annual soil N ammonification, nitrification and mineralization rate (kg N ha^{-1} yr^{-1}) in the top 15 cm soil in bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF)

	Ammonification	Nitrification	Mineralization
BDF	105.1 ± 15.6a	1.4 ± 0.4a	106.5 ± 11.3a
EBF	87.4 ± 9.2a	57.7 ± 12.1b	145.1 ± 16.2b

Data are means ± SE. SE is standard error (n = 6). Lowercase letters in the same column indicate significant differences between BDF and EBF at $P = 0.05$

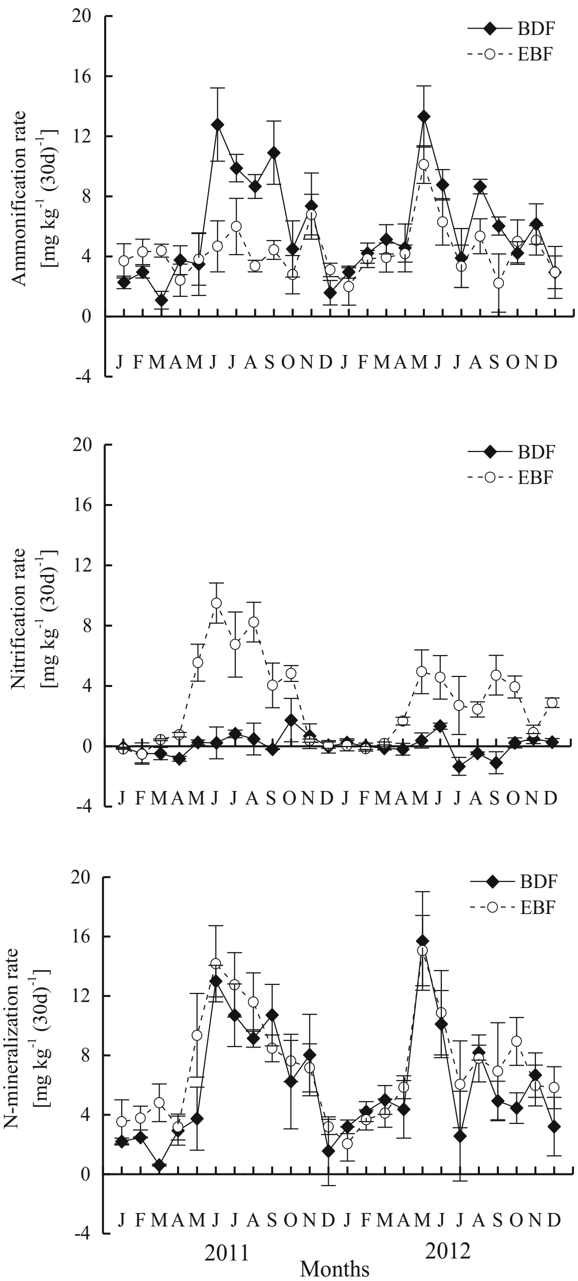

Fig. 3 The dynamics of soil N ammonification, nitrification and mineralization rates for bamboo-dominant forest (BDF) and secondary evergreen broadleaved forest (EBF) in Dagang Mountain National Forest Ecological Station, Jiangxi Province, China

Litter production in forest ecosystems is mostly determined by species composition and characteristics, community structure and biomass under the same climate condition (Sundarapandian and Swamy 1999). In our study, bamboo population defeated the tree species in EBF through competitive exclusion, leading to the species composition significantly changed, which in turn affected the contribution of individual species to the litter production. Leaf litter from Moso bamboo which dominated BDF site was 3.04 Mg ha^{-1} a^{-1}, 41.4 % less than the level found from *C. fargasii* (5.19 Mg ha^{-1} a^{-1}) who dominated EBF site (Fig. 2a), thus, the shift of dominant species could mainly account for the observed decline in litter production after bamboo expansion. Besides, several other factors, such as lower species diversity (Bai et al. 2013), simple community structure (Okutomi et al. 1996; Touyama et al. 1998) and less biomass of vegetation (Yang et al. 2011), could partly explain the effects of bamboo expansion on litter production.

The litter production in BDF and EBF exhibited obvious seasonal dynamics with an evident peak in late spring (Fig. 2b), broadly comparable with other results in subtropical forest ecosystems composed of evergreen tree species (Yang et al. 2005; Wang et al. 2010). However, the highest peak value in BDF stands occurred in April, a month earlier than that in EBF stands, which was related to plant leaf phenology. Before flushing of new leaves for bamboo, 2 years old leaves and leaves on the first-year shoots dropped massively in April (Li et al. 1998), however, broadleaves trees like *C. fargasii* and *C. sclerophylla* generally replace senescent leaves by new leaves mainly in May (Li et al. 2014). Moreover, the litter production of BDF fluctuated obviously between 2011 and 2012. Because there is a biennial cycle in the production of new bamboo shoots among years (Li et al. 1998), the number and size of new shoots in on-year (2011) significantly exceeded those in off-year (2012) in the BDF in our study, yet the leaves of these new shoots all fall in the following year, leading to an increase of litter production in off-year.

Litter quality and decomposition

Previous studies found that invasive plant generally had higher litter quality (i.e., higher N, lower C: N ratio and lower lignin: N ratio) than native species (Allison and Vitousek 2004; Ashton et al. 2005; Liao et al. 2008; Kurokawa et al. 2010), but some papers were not always in accord with this pattern (Evans et al. 2001; Baker and Murray 2012; Williams et al. 2013). In our study, Moso bamboo had lower litter quality with lower N concentration and higher C/N (Table 2), which was consistent with the results from other studies on bamboo (Liu et al. 2000; Tripathi et al. 2006; Fukushima et al. 2015). Litter quality is mainly regulated by plant ecophysiological properties

Table 6 Pearson correlation coefficients for the relationship between soil N ammonification, nitrification, mineralization rates and litter properties in the top 15 cm soil, in Dagang Mountain National Forest Ecological Station, South China

	Annual litter Production	Standing litter crop	C content	N content	C:N ratio	Turnover rate
Annual ammonification rate	0.49	0.40	−0.28	**0.60***	−0.47	**0.65***
Annual nitrification rate	0.50	−0.47	−0.37	0.39	**−0.66***	0.49
Annual N mineralization rate	**0.63***	−0.53	−0.29	0.52	**−0.58***	**0.59***

Note: All the significant correlations indicated in bold. * $P < 0.05$; $n = 12$

(Tong et al. 2011; Van Kleunen et al. 2010). Here, Moso bamboo was charactered by the highest N resorption efficiency in all plants (Table 2), resulting in a low N concentration in litter. In addition, maybe due to the lower soil available N concentration (Table 4) and slightly higher N resorption efficiency (Table 2), the most resident tree species (i.e. *C. fargasii*, *Q. sclerophylla* and *S. laurina*) showed less N concentration in leaf litter in BDF (Table 2). Thus, the overwhelming dominance of *P. pubescens* with low litter quality, combined with declined litter quality of resident tree species, consequently, degraded the litter quality at ecosystem level after Moso bamboo expansion.

The coupling of lower litter production and lower N concentration led to the potential N return to the soil via litter in BDF being only a half of that in EBF (Table 3). This result was in agreement with the finding reported by Wang et al. (2010) that N return through litter in degraded forest was significantly lower than that in subtropical broadleaved forest.

Our results indicated that Moso bamboo expansion decreased litter relative decomposition rate (turnover rate) in expanded ecosystem (Table 3), consistent with the negative impacts of other bamboos expansion on litter decomposition in broadleaved forests of subtropical China (Liu et al. 2000; Tripathi et al. 2006). Litter decomposition rate is primarily controlled by litter quality at a regional scale with similar climatic conditions (Aerts 1997). Plant litter decomposes more quickly usually because of higher chemical quality [higher N, lower C: N and/or lower lignin: N ratios (Liao et al. 2008; Ehrenfeld 2010)]. Considering there were no significant differences in lignin: N between two stands (Table 2), it seems that the initial low litter N concentration and high C: N were the main factors in explaining the slow decomposition rate combined with bamboo expansion in this study. Furthermore, Watanabe et al. (2013) found high silicate concentration in bamboo was a possible controlling factor to explain the slower decomposition rate than that of tree leaf litter. Slower decomposition is prone to accumulate litter on the forest floor compared to EBF (Table 3), and dense and thick litter would modify forest floor microenvironment and thereby influence seed germination and seedling establishment (Larpkern et al. 2011).

Soil N mineralization and litter

Invasive species can cause legacy effects on rates of N transformation by changing litter quantity and quality and soil properties if they equip with significant different ecophysiological properties from native species (Evans et al. 2001; Yan et al. 2009). Our results showed that soil N ammonification rate of BDF was slightly higher, but soil N nitrification was particularly lower when comparing with EBF, especially in growing season (May-October) (Fig. 3). These results indicated that expansion of Moso bamboo to EBF declined soil N mineralization rate and changed soil N transformation pattern (ammonification/nitrification), which was partly in agreement with Yan et al. (2008) who found that both soil N ammonification and nitrification rate declined after EBF converted to Moso bamboo forest in Eastern China.

The changed pattern of soil N mineralization associated with Moso bamboo expansion could be attributed to the following reasons. Firstly, lower quality of litter, and slower litter decomposition in BDF resulted in the decrease in soil N nitrification and mineralization rate. This idea was also showed in the studies of subtropical forests (Yan et al. 2008; Yan et al. 2009; Fukushima et al. 2015). The correlation analysis also demonstrated that soil nitrification significantly negatively correlated with C: N ratio of litter (Table 6). Our results agreed with the generalization that higher litter quality can accelerate soil N mineralization, on the contrary, lower quality can hinder soil N mineralization (Evans et al. 2001; Yan et al. 2009). Secondly, slow soil nitrification in BDF could likely relate to the nutrient habit of NH_4^+-N preference for Moso bamboo (Song et al. 2013). The process that plant uptake of NH_4^+-N from soil is often accompanied by the release of H^+ (Schulze et al. 2006), which probably results in soil pH decreased after Moso bamboo expansion (Table 4). The change in soil pH may greatly affect the soil net N mineralization rate because under low pH some groups of ammonifying bacteria can be activated (Aciego Pietri and Brookes 2008), but some groups of nitrifying bacteria can be deactivate (Nugroho et al. 2007). Moreover, the soil bacterial community was gradually changed in other invaded forests of bamboo invasion (Lin et al. 2014), thus, changes of soil microbes could be one of main reasons for the changes of soil mineralization in EBF after bamboo invasion, which should be verified in further study.

The supply of nitrogen is one of the most important environmental factors determining the dynamics of species composition in many ecosystems (Berendse et al. 1998; Berendse 1990). Decline of soil available N supply in BDF could limit the growth of most tree species which used to relative rich-habitat, but provide chances for Moso bamboo to survive due to its N conservation mechanisms like higher N resorption efficiency (Table 2). Additionally, Moso bamboo in poor-habitat can receive nutrients from rich-habitat by clonal physiological integration (Li et al. 2000), ultimately, it could outcompete tree species and displace broadleaved vegetation in N poor ecosystem. Thus, the decline in N mineralization rate is not only the consequence but also likely to be one of mechanisms for Moso bamboo expansion to its neighboring broadleaved forest.

Conclusion

Though Moso bamboo is of great benefit for people worldwide, the expansion of this species to its neighbor forests has been recently identified as one of serious ecological problems. However, its potential impacts on the ecosystems processes in evergreen broadleaved forest have not been well studied. Our study showed that the expansion of Moso bamboo to adjacent EBF not only decreased litter production, degraded litter quality, but also declined soil net N mineralization rate, especially soil net N nitrification rate. Changes in litter is likely the mechanism for the deceasing supply of plant available N observed with bamboo expansion. To reveal their relationship thoroughly, there is a need to further quantify the N cycling in detail, especially the changes of microbes, to determine the extent and mechanisms of Moso bamboo expansion altering the biogeochemistry cycling of subtropical evergreen broadleaved forest ecosystem.

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