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Effects of exotic species *Larix kaempferi* on diversity and activity of soil microorganisms in Dalaoling National Forest Park

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Abstract

Introduction: Soil microbial community plays a crucial role in the ecological processes of soil ecosystem. Forest species introduction often changes profoundly soil ecological processes in the forest. *Larix kaempferi* (Lam.) was introduced to China from Japan as a timber tree species in the 1960s. The activity and functional diversity of soil microorganisms in the *L. kaempferi* forest in Dalaoling National Forest Park in Hubei Province, China, was studied to evaluate the effects of this exotic species on the local soil ecosystems.

Methods: Quadrates were set up randomly in the *L. kaempferi* forests cultivated in 1990 and 1996 and the surrounding *Pinus armandii* forest cultivated in 1990. Soil samples were collected using a soil corer at five locations along the diagonals in each quadrat. The activity and functional diversity of soil microorganisms were tested using the BIOLOG technique in laboratory.

Results: The diversity, activity, and carbon utilization pattern of soil microorganism community and soil physicochemical properties were all impacted by the introduced species. The average well color development (AWCD) and Shannon's richness index (*H*) of the soil microorganism community in the *L. kaempferi* forest decreased with the increase in forest age and were significantly lower than those in the surrounding native *P. armandii* forest. The carbon source utilization pattern of soil microorganism community in a 23-year-old *L. kaempferi* forest differed significantly from a 17-year-old *L. kaempferi* forest and the *P. armandii* forest. The introduced species also resulted in the changes of soil physicochemical properties. The organic material content, total nitrogen, available nitrogen, and total phosphorus in the soil of *L. kaempferi* forest were significantly lower than those in the soil of *P. armandii* forest.

Conclusions: Introduction and long-time cultivation of *L. kaempferi* significantly altered the soil microbial functional diversity and activity and the soil physicochemical properties. The alteration increased with the increase of forest age.

Introduction

Soil microbial community is an essential component of the soil ecosystem. Soil microorganisms participate directly in the soil ecological processes including litter decomposition, humus formation, nutrient transformation and recycle, and waste degradation (De Deyn et al. 2004; Maila et al. 2005; Noah and Robert 2006). Soil microbial diversity and function are considered as important indicators for the assessment of soil quality as

the microbial effects on soil ecological processes could further influence soil physicochemical properties, seedling regeneration, plant community development, and biodiversity (Onaindiaa et al. 2013; Owen et al. 2013; Sharma et al. 2011). The change of plant community in composition and structure often leads to the changes of soil microbial community in diversity and function. These changes would have certain impact on the ecological process of soil system that caused the change of plant community in turn (Mummey and Rillig 2006; Patrick 2006; Boudiaf et al. 2013). An introduction of forest species often changes obviously the composition, structure, species diversity, and productivity of plant community (Davies 2011; Omoro et al. 2010; Powell et al. 2013). As a result, the biomass, structure, and function of

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soil microorganism community are also influenced (Kourtev et al. 2002; Ravit et al. 2003; Chen et al. 2013). However, the effects of introduced forest species on soil microbial diversity and related ecological processes displayed inconsistent patterns as the effects were determined by many factors including plant growth characteristic, litter quality and quantity, roots and root secretions, phenology, climate condition, etc. (Ehrenfeld 2003; Chen et al. 2005; Steinlein 2013). Determining the effects of specific exotic plants in detail is critical to the sustainable forest management.

The global need for wood production has led to the increase of forest species introduction on the basis of their ability to adapt to local conditions and of their rapid growth. In 2010, planted forests accounted for 264 million hectares (7 % of the total forest area worldwide), an increase of 5 million hectares per year since 2005. A quarter of planted forests are composed of introduced species (Dodet and Collet 2012). A number of forest tree species, including *Pinus elliottii*, *Acacia mangium*, *Thuja occidentalis*, *Abies firma*, and *Larix kaempferi*, also have been introduced to China from abroad for forestry production in the last century. The introduction has promoted Chinese timber production in general and also caused a few ecological problems in some ecosystems, such as diversity loss and soil degradation (Yang et al. 2010). *L. kaempferi*, a cold-wet temperate tree species indigenous to Japan, was introduced to China in the 1960s and has become an important timber tree species distributed in Heilongjiang, Jilin, Liaoning, Hebei, Shandong, Henan, Jiangxi, and Hubei Province. *L. kaempferi* was introduced to Dalaoling National Forest Park (longitude 110° 43′ 42″–111° 22′ 2″, latitude 30° 58′ 50″–31° 07′ 23″), located in the southwestern Hubei Province in the late 1970s. Currently, there are over 700 hectares of *L. kaempferi* forests within the park as a result of its rapid growth and expansion. However, there is a report on biodiversity decline and seedling regeneration failure on local species (Xiao and Zeng 2005). The objectives of this study were to (1) determine the effect of the introduction and cultivation of *L. kaempferi* on the functional diversity and activity of the soil microbial community, (2) evaluate the changes in physicochemical proprieties of soil in the *L. kaempferi* forest, and (3) analyze the relationship between the functional diversity and activity of the soil microbial community and the physicochemical proprieties of soil in the *L. kaempferi* forest. The findings from this study may gain important scientific insights for forest management in the park.

Methods
Study sites and soil sampling
Experimental plots were established in field sites of three types of forest in the Dalaoling National Forest Park.

The forests with close altitude, slope, and aspect included *L. kaempferi* forests cultivated in 1990 and 1996 and the surrounding *P. armandii* forest cultivated in 1990. *P. armandii* is a native species which has similar altitude adaptation with *L. kaempferi* in the Dalaoling National Forest Park. Soil samples were collected on 5 August 2013. Five quadrats (5×5 m^2) were set up randomly at each of the four plot corners and in the center in a plot. Soil within the top 20-cm depth was collected using a soil corer at five locations along the diagonals in each quadrat and mixed thoroughly as a sample within each quadrat. Half an amount of each sample was placed directly into a sterile bag and sent to the laboratory, homogenized, sieved through a 2-mm filter, and stored in an icebox at 4 °C for microbial analysis. The other half of the sample was dried in air for physicochemical analysis.

BIOLOG analysis
A BIOLOG Microstation System (BIOLOG Inc., Hayward, CA, USA) was used to study the metabolic function of the soil microbial community. The BIOLOG technique proposes a simple and sensitive way to compare potential metabolic diversity of soil microbial communities and has been widely used in assessing microbial metabolic diversity in agricultural soils, forest soils, and under various vegetations as it represents certain metabolic functions in the microplates; the outcomes reflected the patterns of carbon source utilization (Grayston et al. 1998; Preston-Mafham et al. 2002; Zheng et al. 2005; Chen et al. 2013). We used ECO microplates to compare potential metabolic diversity of soil microbial communities among the three plantations. One ECO microplate contained three replicates of 31 different substrates to discriminate the heterotrophic microbial community. Five grams of fresh soil from each sample were suspended in 45 mL of sterile distilled water in a flask and sealed with silver paper. The flask containing the soil solution was shaken at 190 rpm for 20 min at 22 °C. Then, the soil suspension was allowed to settle for 10 min. Five milliliters of supernatant liquid was transferred to 45 mL of sterile distilled water in a flask. The procedure was repeated three times. Five milliliters of suspension was diluted 1000 times in a tenfold dilution series, from which 150 μL of the supernatant was inoculated to each well of the microplate. The microplates were incubated in the dark at 28 °C for 10 days, during which period color development in each well was measured at the wavelengths of 595 and 750 nm, respectively, every 24 h using an automated microplate reader (BIOLOG, Hayward, USA) (Classen et al. 2003; Chen et al. 2013).

The number of carbon substrates used by soil microorganisms (S), average well color development (AWCD), Shannon's richness index (H), Simpson's dominance

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index (D), and relative use efficiency of carbon resources (RUE) were evaluated and used as indicators to assess the soil microbial functional diversity and activity (Chen et al. 2013; Boudiaf et al. 2013). The average well color development reflecting the total ability of microorganisms to use carbon resource was determined using the method reported by Classen et al. (2003):

$$AWCD = \sum (C_i - R)/n$$

where C_i represents the difference of optical density (OD) of a sample well recorded at the wavelengths of 590 and 750 nm. R is the optical density of the control well, and n is the total number of the sole carbon substrates (ECO plates $n = 31$). AWCD was treated as 0 when its value was below 0.06.

The number of carbon substrates used by soil microorganisms was derived by counting the wells with color development. Biodiversity was evaluated using Shannon's richness index (H) and Simpson's dominance index (D) (Wei et al. 2008; Chen et al. 2011):

$$H = -\sum P_i \ln P_i,$$
$$D = 1 - \sum P_i^2$$

where P_i is the proportional color development of the ith well over the total color development of all wells in a plate.

The RUE reflects the degree of microorganisms to use a carbon resource. RUE was derived from the ratio of the optical density of one kind of carbon substrate with the total optical density of all other carbon substrates among the seven major carbon substrates including monosaccharides and glycosides, amino acids, alcohols, amines, polymerization saccharides, lipids, and organic acids (Wei et al. 2008).

Determination of soil physicochemical properties

Soil water content (SWC) was determined gravimetrically by weighing the soil sample, drying it in an oven at 105 °C for 24 h, and then re-weighing the sample. Soil organic matter (OM) was measured using the potassium dichromate melting method, total nitrogen (TN) by the semi-micro Kjeldahl nitrogen determination apparatus, total phosphate (TP) by the NaOH alkali melting method, total potassium (TK) by the flame photometer method, available nitrogen (AN) by the diffusion method, and pH by the precision acidity meter, respectively (Bao 2000). Five replicates were tested for each forest type.

Data analysis

One-way analysis of variance (ANOVA) was performed to determine the effects of the introduction and cultivation of *L. kaempferi* on the soil microbial diversity and

function. The parameters used in the analysis included forest type as an independent factor, the average well color development, Shannon's richness index, Simpson's dominance index, number of carbon substrates used by soil microorganisms, and indicators for measuring the physicochemical properties such as soil organic matter, total nitrogen, total phosphorus, total potassium, available nitrogen, and pH as dependent factors, respectively. All values were expressed as mean ± SE. The forest types included the 23-year-old and 17-year-old *L. kaempferi* forests and the *P. armandii* forest. The Duncan test method was conducted for multiple comparisons to assess the significance level of each parameter among treatments when the main effect was significant.

The structure of the bacterial community was characterized by classifying treatments according to their substrate utilization patterns using the principal component analysis (PCA) (Kourtev et al. 2003). The first and second principal component variances contained the information of carbon type and their contribution. The difference in principal component variances was used to represent the pattern of carbon utilization. The PCA results were presented as factor loading plots (Choi and Dobbs 1999). The relationship between microorganism diversity and function and soil physicochemical properties was determined by the correlation analysis of the average well color development, Shannon's richness index, Simpson's dominance index, number of carbon substrates used by soil microorganisms with soil organic matter, total nitrogen, total phosphorus, total potassium, available nitrogen, and pH, respectively. All above analyses were conducted using SPSS software (13.0).

Results

Functional diversity and activity of soil microorganism community

The introduction and long-time cultivation of *L. kaempferi* caused a significant change of microorganism community in diversity and activity (Table 1). The average well color development (AWCD) and richness index (H) used by microorganisms in soil microorganism community in the 23-year-old *L. kaempferi* forest decreased by 7.6 and 1.6 % in contrast with those in the 17-year-old *L. kaempferi* forest. Both of these indicators and the number of carbon substrates (S) in the 23-year-old *L. kaempferi* forest were significantly lower than those in the *P. armandii* forest ($P < 0.05$). However, the dominance index (D) did not differ significantly among forests ($P > 0.05$).

Principal component analysis of carbon source utilization

The principal component analysis indicated that the introduction and cultivation of *L. kaempferi* also induced changes in the soil microorganism community and the pattern of carbon utilization (Fig. 1). The

Table 1 Changes of function diversity and activity of the soil microbial community

Forest types	AWCD	H	D	S
23-year-old *L. kaempferi* forest	1.10 ± 0.02 a	3.23 ± 0.02 a	0.96 ± 0.00 a	26.76 ± 0.32 a
17-year-old *L. kaempferi* forest	1.19 ± 0.01 b	3.28 ± 0.01 b	0.96 ± 0.00 a	27.43 ± 0.29 ab
Pinus armandii forest	1.22 ± 0.02 b	3.29 ± 0.01 b	0.96 ± 0.00 a	27.79 ± 0.28 b

Note: Values are expressed as mean ± SE. Significance of the statistical test is reported at $P < 0.05$
AWCD average well color development, *H* Shannon's richness index, *D* Simpson's dominance index, *S* the number of carbon substrates used by soil microorganisms

percent contribution from the first and second principal component variances were 83.94 and 8.82 %, respectively. The three plant communities differed significantly in the principal component 1 (PC1) and principal component 2 (PC2) ($F = 95.998$, $P < 0.01$; $F = 195.998$, $P < 0.001$), respectively. The 23-year-old *L. kaempferi* forest differed significantly from the 17-year-old *L. kaempferi* forest and the *P. armandii* forest in the carbon substrate utilization pattern; meanwhile, the difference was not significant between the 17-year-old *L. kaempferi* forest and the *P. armandii* forest.

Twelve of the 31 carbon sources in the BIOLOG ECO microplates contributed to the PC1. These carbon sources included 6 organic acid, 2 monosaccharides and glycosides, 2 amino acids, 1 lipid, and 1 polymeric carbohydrate (Table 2). Seven carbon sources mainly contributed to the PC2 and included 2 lipids, 2 monosaccharides and glycosides, 1 amino acid, 1 amine, and 1 alcohol. The important carbon sources contributing to both PC1 and PC2 were organic acid, monosaccharide, and glycoside, respectively (Table 2). The relative use efficiency of carbon source (RUE) changed with the type of carbon source and forest. A high relative use efficiency was found for organic acids and amino acids ranging from 22.78 to 25.41 %. By contrast, the relative use efficiency for other five carbon sources was relatively

low ranging from 6.09 to 13.72 %. There was significant difference in the use efficiency for monosaccharides and glycosides, amines, and polymerization saccharides among the 23-year-old *L. kaempferi* forest, 17-year-old *L. kaempferi* forest, and the *P. armandii* forest ($P < 0.05$) (Fig. 2)

Soil physicochemical properties
Soil physicochemical properties were also influenced significantly by the introduction of *L. kaempferi* (Table 3). The soil organic matter (OM), total nitrogen (TN), total phosphate (TP), available nitrogen (AN), and soil water content (SWC) in the *P. armandii* forest were all significantly higher than those in the *L. kaempferi* forest ($P < 0.05$). All physicochemical values of these indicators decreased with the increase of cultivation time. However, the difference of total potassium (TK) did not reach significant level among the three forests ($P > 0.05$).
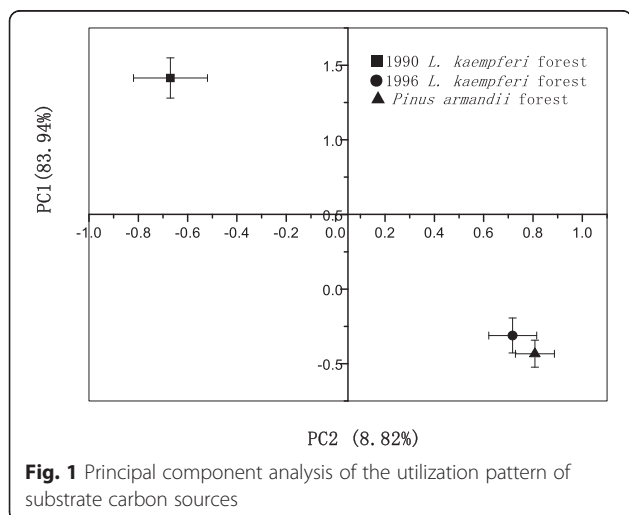
Relationship between activity and diversity of microorganism community and soil physicochemical properties
The average well color development (AWCD) had a very significant positive correlation with available nitrogen (AN) and pH ($P < 0.05$). However, there was no strong correlation among other physicochemical properties and microbial metabolic activity and function ($P > 0.05$) (Table 4).

Discussion
Diversity and activity of soil microorganism community
Introduction of exotic plant species not only influenced plant community structure but also led to the changes of soil microbial diversity and function and the soil physicochemical properties (Kourtev et al. 2003; Mummey and Rillig 2006). Previous reports showed that the introduction of exotic species displayed two patterns, either increased or decreased soil microbial activity and diversity (Saggar et al. 1999; Callaway et al. 2004). Duda et al. (2003) found that the soil bacterial diversity in the *Halogeton glomeratus* community, an invasive species in the western United States, was significantly higher than that in native community. However, many other studies supported the decreasing

Fig. 1 Principal component analysis of the utilization pattern of substrate carbon sources

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Table 2 The loading matrix of principal components

PC1			PC2		
Carbon sources	Classification	r	Carbon sources	Classification	r
4-Hydroxybenzoic acid	Acids	1.00	D-Xylose	Monosaccharides and glycosides	0.97
D-Malic acid	Acids	1.00	L-Asparagine	Amino acids	0.97
Pyruvic acid methyl ester	Lipids	1.00	Tween 80	Lipids	0.95
β-Methyl-D-glucose	Monosaccharides and glycosides	0.98	Tween 40	Lipids	0.94
L-Serine	Amino acids	0.97	Phenylethylamine	Amines	0.86
D-Galactonic acid γ-lactone	Polymerization saccharides	0.96	D,L-α-Glycerol	Alcohols	0.79
α-Ketobutyric acid	Acids	0.93	Glucose-1-phosphate	Monosaccharides and glycosides	0.75
2-Hydroxybenzoic acid	Acids	0.87			
α-D-Lactose	Monosaccharides and glycosides	0.86			
L-Arginine	Amino acids	0.85			
Itaconic acid	Acids	0.83			
D-Glucosaminic acid	Acids	0.80			

Note: *r* represents for the loading value of principal components

pattern (Lindsay and French 2004; Valéry et al. 2004; Li et al. 2006). Chen et al. (2011) reported that the introduction and cultivation of *Pinus elliottii* significantly reduced the soil microbial diversity and function compared to those in the native *Pinus massoniana* forest in the same region. Yang et al. (2008) found that the soil bacterial diversity in the *L. kaempferi* forest was significantly lower than that in the surrounding native *Pinus tabulaeformis* forest. In this study, we found that the activity and functional diversity of soil microbial communities in the 23-year-old *L. kaempferi* forest were significantly lower than the 17-year-old *L. kaempferi* forests and the surrounding *P. armandii* forest. Therefore, we concluded that the introduction and cultivation of

Fig. 2 Relative use efficiency of the seven carbon sources including monosaccharides and glycosides, amino acids, alcohols, amines, polymerization saccharides, lipids, and organic acids

L. kaempferi negatively influenced the local microbial activity and diversity. Under this circumstance, this type of impact increased as the forest stand aged.

Carbon source utilization and soil physicochemical properties

The cultivation of exotic species often affects soil ecological processes, especially the litter composition process (Lindsay and French 2004; Standish et al. 2004; Rodgers et al. 2008). The biochemical composition of exotic plant litter significantly differed from that of native species. The change of soil physicochemical properties resulting from the litter decomposition would affect the presence and activity of local microorganisms in the soil ecosystem, which in turn affected the soil ecological processes and soil physicochemical properties (Bilgo et al. 2012; Bragazza et al. 2007; Owen et al. 2013). Compared to the indigenous plants, the presence of exotic plants typically leads to the increase in net forest primary productivity or biomass (Ehrenfeld 2003). However, the influence pattern of exotic plant on soil ecological processes was not consistent as exotic plants affected the soil ecosystem processes through a variety of mechanisms (Hedge and Kriwoken 2000; Yeates and Williams 2001; Mack and D'Antonio 2003; van der Putten et al. 2007). The inhibition of exotic plant species on soil ecological processes depended on litter quantity, litter degradation, litter biochemical characteristics, and species ecological characteristics (Allison and Vitousek 2004; Valéry et al. 2004; Scott et al. 2001; Wolfe et al. 2008).

The introduction of *L. kaempferi* forest significantly changed the carbon source utilization pattern of the soil microorganism community in Dalaoling National Forest

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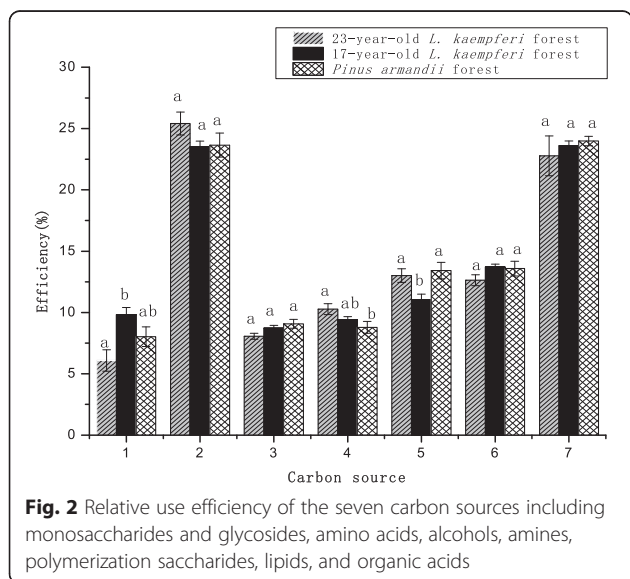
Table 3 Changes in soil physicochemical properties under different forests

Forests	OM	TN	TP	TK	AN	pH	SWC
	(g/kg)	(g/kg)	(g/kg)	(g/kg)	(mg/kg)		(%)
23-year-old *L. kaempferi* forest	67.32 ± 1.79 a	3.76 ± 0.07 a	0.74 ± 0.02 a	1.81 ± 0.07 a	0.30 ± 0.01 a	4.96 ± 0.06 a	66.06 ± 5.53 a
17-year-old *L. kaempferi* forest	72.38 ± 2.96 ab	3.95 ± 0.12 ab	0.64 ± 0.03 b	1.83 ± 0.11 a	0.32 ± 0.01 ab	5.39 ± 0.05 b	63.49 ± 4.64 a
Pinus armandii forest	76.22 ± 3.14 b	4.10 ± 0.12 b	0.97 ± 0.03 c	1.91 ± 0.12 a	0.36 ± 0.02 b	5.35 ± 0.08 b	85.03 ± 2.59 b

Note: Values are expressed as mean ± SE. Means followed by the same letter(s) within each column are not significant at $P > 0.05$

Park. The use efficiency of some carbon sources in the soil microorganism community in the *L. kaempferi* forest differed from those in the *P. armandii* forest and decreased with the increases in stand age. *L. kaempferi* also caused significant changes in soil physicochemical properties. Therefore, we concluded that the introduction and cultivation of *L. kaempferi* in the Dalaoling National Forest Park resulted in a decline in soil quality and soil fertility. The significant relationship between soil pH and AWCD suggested that *L. kaempferi* influenced soil activity by changing the soil pH. However, the detailed mechanism of introduction of *L. kaempferi* on soil microbial diversity and function is worthwhile for further research, such as how the litter affects specifically the composition of microbial community and soil physicochemical properties and the response of composition and structure of microbial community to the litter of exotic species.

Conclusions

Soil ecological process is an important part in the material cycle and energy flow of terrestrial ecosystem and is closely related with vegetation development and succession (Wardle et al. 2004; Noah and Robert 2006). Most artificial plantations alter soil ecological process and cause soil fertility decline and soil degradation, which is more prominent in exotic species forest because of their significant effect on soil microbial community diversity and physicochemical properties (Lorenzo et al. 2010; Patrick 2006). The long-term cultivation of *L. kaempferi* forest decreased the activity and functional diversity of soil microorganism community in Dalaoling National Forest Park. As a result, the soil physicochemical properties resulted in a decline in soil quality. The plant diversity and seedling regeneration in *L. kaempferi* forest was further impacted (Xiao and Zeng 2005). Modifying the negative effects of introduced forest species on soil ecological process is crucial to the sustainable forest management. Appropriate disturbance could reduce the effects of exotic plants on the local soil microorganism community (Xu et al. 2008; Carvalho et al. 2010). Zhang (2001) reported that thinning plantation stands increased soil microbe quantities, strengthened soil enzyme activities, decreased bulk density, and enhanced soil total porosity degree and available nutrients. Our primary field investigation showed that thinning the *L. kaempferi* forest stands increased the diversity of soil microorganism communities and improved soil texture (Song et al. 2013). The mechanism that thinning improves soil fertility is that the increased understory biodiversity after thinning enhances the increase of quantity and diversity of soil microbe and, therefore, strengthens bioactivity of soil and accelerates nutrient cycling of soil (Zhang 2001). The appropriate thinning approach and frequency and the response of *L. kaempferi* forest to thinning are going to be tested in our future research to provide more information for the sustainable management of the forest.

Authors' contributions
NS and GC were the major persons involved in the field and laboratory experiments. FC and JW have analyzed and interpreted the experimental data and primarily drafted the manuscript. All authors approved the final draft of this manuscript.

Table 4 Pearson correlation analysis of chemical properties and microbial function

PCP	AWCD	H	S
OM	0.03 (0.84)	−0.02 (0.88)	−0.10 (0.54)
TN	0.06 (0.72)	0.16 (0.26)	0.21 (0.15)
TP	−0.03 (0.85)	0.07 (0.64)	0.06 (0.70)
TK	0.02 (0.89)	0.03 (0.82)	0.05 (0.75)
AN	0.09 (0.05)*	−0.01 (0.96)	−0.02 (0.93)
pH	0.50 (0.00)**	0.21 (0.13)	−0.03 (0.84)
SWC	0.03 (0.91)	−0.22 (0.37)	0.09 (0.73)

Note: Pearson correlation coefficients and P values in parentheses
* is significant at $P < 0.05$
** is significant at $P < 0.001$

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