Mycorrhiza (2007) 17:271–278
DOI 10.1007/s00572-006-0096-z

ORIGINAL PAPER

Spatial structure and diversity of woody plants and ectomycorrhizal fungus sporocarps in a natural subtropical forest

Yu Liang · Liang-Dong Guo · Xiao-Jun Du · Ke-Ping Ma

Received: 26 August 2006 / Accepted: 28 November 2006 / Published online: 19 April 2007

Abstract Spatial patterns of ectomycorrhizal fungi, ectomycorrhizal plants, and non-ectomycorrhizal plants were investigated in a natural subtropical forest using second-order analysis. The results of spatial pattern analysis showed that the degree of clumping of woody plants and ectomycorrhizal sporocarps were correlated. There was a significantly positive correlation of relative aggregation indices between ectomycorrhizal fungi and both non-ectomycorrhizal trees and ectomycorrhizal saplings. Correlations between percentage of ectomycorrhizal trees and sporocarp occurrence of ectomycorrhizal fungi and between diversities of woody plants and ectomycorrhizal fungi were distance-dependent or scale-related. A significantly high percentage of ectomycorrhizal trees was found only at relatively short distance from ectomycorrhizal fungal sporocarps, and significantly positive correlation of the diversity between woody plants and ectomycorrhizal fungi was found only at relative long distance, which implied that ectomycorrhizal sporocarps prefer ectomycorrhizal-tree-dominant micro-sites at near distances and at relatively large scales, diverse ectomycorrhizal sporocarps could be found in woodlands with high diversity of woody plants. Important factors affecting the spatial distribution, occurrence, and diversity of ectomycorrhizal fungi include spatial pattern of ectomycorrhizal plants and non-ectomycorrhizal plants, percentage of ectomycorrhizal plants, and plant diversity in a natural forest.

Keywords Community · Ectomycorrhizal fungi · Second-order analysis · Spatial pattern · Woody plants

Y. Liang · X.-J. Du · K.-P. Ma
Laboratory of Quantitative Vegetation Ecology,
Institute of Botany, Chinese Academy of Sciences,
Beijing 100093, China
e-mail: makp@brim.ac.cn

L.-D. Guo (✉)
Systematic Mycology and Lichenology Laboratory,
Institute of Microbiology, Chinese Academy of Sciences,
Beijing 100080, China
e-mail: guold@im.ac.cn

Y. Liang
Key Laboratory of Photosynthesis
and Environmental Molecular Physiology,
Institute of Botany,
Chinese Academy of Sciences,
Beijing 100093, China

Introduction

Ectomycorrhizas are symbiotic structures formed between soil fungi and plant roots. Many ectomycorrhizal plants are dominant or common species in temperate and boreal forests, and ectomycorrhizal fungi play important ecological roles in nutrient transportation, inter-or intra-specific interactions, and maintenance of biodiversity in ecosystems (Read 1991, 1997; Simard et al. 1997, 2002).

The structure of ectomycorrhizal fungal communities, including species composition, diversity, and spatio-temporal distribution of above-ground (fruit bodies) and below-ground parts (mycelia and mycorrhizas), is influenced by multiple factors. For example, climate factors (Gong et al. 1997), soil parameters (Tedersoo et al. 2003), natural and human disturbances (Visser 1995; Nillson and Wallander 2003; Smith et al. 2005), species interactions within the fungal community (Toide et al. 2005), and plant community compositions (Molina et al. 1992; Dahlberg 2001) all have been shown to affect ectomycorrhizal community structure.

Although host specificity of different ectomycorrhizal fungi and fungal symbiont receptivity of different tree

species have been studied (Molina et al. 1992) and spatial relations between host plants and ectomycorrhizal sporocarps or ectomycorrhizas have been reported (Ford et al. 1980; Last et al. 1984, 1992; Liang et al. 2004a), spatial interactions between plant community and ectomycorrhizal fungi are still poorly understood. In natural forests, it is difficult to study the plant–ectomycorrhizal fungi interactions due to the following reasons: (a) the complex and interlaced root systems which make it difficult to trace the ectomycorrhizal fungus–host relations from ectomycorrhizal fungal sporocarps; (b) the unclear influence of non-ectomycorrhizal plants on the formation of ectomycorrhizal fungal sporocarps; and (c) plants with different age influence plant–fungus interactions.

Second-order analyses are used for point pattern analysis, that is, for analyzing the mapped positions of objects in the plane, such as the stems of trees, and assume a complete census of the objects of interest in the area under study (Dale 1999; Dale et al. 2002). In second-order analyses, based on neighbors counting within the circle of radius t (a series of distances) centered on each individual, spatial pattern of a population or community could be evaluated. Compared to analysis based on first-order parameter (i.e., QQ-plots), second-order analysis is often preferable in studies of spatial pattern and is more sensitive to small sample size (Andersen 1992; Haase 1995). It has been widely applied in plant ecological studies (Haase 1995) and recently has been used to analyze the spatial pattern of ectomycorrhizal fungal populations (Liang et al. 2004a, b). We expected second-order analysis on ectomycorrhizal and non-ectomycorrhizal plants, including saplings and mature trees, as well as on ectomycorrhizal fungi to be useful in studying spatial interactions between plants and ectomycorrhizal fungi in natural forests.

Spatial patterns of ectomycorrhizal sporocarps, ectomycorrhizal plants, and non-ectomycorrhizal plants were investigated using second-order analysis in a natural subtropical forest in the present study. Our objectives were to (1) find the spatial relationships between ectomycorrhizal sporocarps and both ectomycorrhizal and non-ectomycorrhizal woody plants and (2) evaluate the effects of woody plant composition and distribution pattern on diversity and spatial structure of ectomycorrhizal sporocarps in a natural subtropical forest in southwestern China.

Materials and methods

Study site

The study site was 6.4 ha of natural, subtropical woodlands on a low hill in Dujiangyan at the western edge of the Sichuan Basin in southwestern China (103°27′E, 30°44′N). The site has a mean annual precipitation of 1,244 mm, a mean annual temperature of 15.2°C (Fig. 1), and an altitude of about 780 m. Temperatures and precipitations are high in July and August, and most macrofungal sporocarps are found from July to September. Three 30×15-m plots (I, II, and III) were selected, and each was divided into 18 subplots (5×5 m; Fig. 1). Leaf area index (LAI) of each subplot was determined using a CI-110 digital plant canopy imager (CID, USA).

Woody plants

All woody plants present in each plot were identified. Woody plants were divided into trees (>3 m high), saplings (0.5–3 m), and seedlings (<0.5 m). All trees and saplings were mapped by field measurement. Seedlings were recorded but not mapped. We calculated importance values (IV) for trees and saplings as the mean of relative abundance (RA), relative coverage (RC), and relative frequency (RF), and for seedlings as the mean of RA and RF.

$$IV_{i(trees,saplings)} = \left(\underset{i}{RA} + \underset{i}{RC} + \underset{i}{RF}\right) \Big/ 3$$

$$IV_{i(seedlings)} = \left(\underset{i}{RA} + \underset{i}{RF}\right) \Big/ 2$$

$$RA_i = N_i \Big/ \sum N_i$$

$$RC_i = C_i \Big/ \sum C_i$$

$$RF_i = F_i \Big/ \sum F_i$$

where N_i, C_i, and F_i are number, coverage, and frequency of species i, respectively.

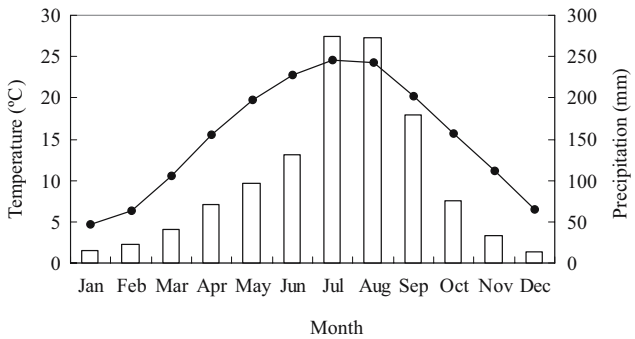

Fig. 1 Monthly temperature and precipitation of the study site

Ectomycorrhizal sporocarps

From July to September 2002, all fungal sporocarps appearing in the plots were mapped, collected, and identified. We calculated importance values (IV) for fungal species as the mean of relative abundance (RA) and relative frequency (RF; see the equations in the IV calculation for seedlings).

Shannon–Wiener biodiversity index (H') of ectomycorrhizal fungi was calculated as $H' = \sum_{i=1}^{n} P_i \ln P_i$, where P_i indicates importance value of species i and n indicates the number of species (Pielou 1985).

Second-order analysis

Spatial patterns were determined by second-order analysis based on Ripley's (1976) K-function. A circle of radius t was centered on each sporocarp or plant, and the number or neighbors within the circle was counted. $K(t)$ is a function of t, with the expected value of πt^2 in randomly arranged points. Ripley (1976) gave an approximately unbiased estimator for $K(t)$ as:

$$\widehat{K}(t) = An^{-2} \sum \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij}),$$

where n is the number of sporocarps in the plot, A is the area (m^2) of the plot, w_{ij} is a weighting factor to correct for edge effects, u_{ij} is the distance between sporocarp i and j, $I_t(u_{ij})$ is a counter variable, which is set to 1 if $u_{ij} \leq t$ and 0 if $u_{ij} > t$, and w_{ij} is obtained according to edge correction methods of Getis and Franklin (1987) and Goreaud and Pélissier (1999). A parameter, $L(t)$, was also used to determine the spatial pattern of a population or community. *L(t) was estimated as* $\widehat{L}(t) = \sqrt{\widehat{k}(t)/\pi} - t$, according to a series of t, from 0 to 15 m in this study. Large negative values of $L(t)$ indicate regular distribution, and large positive values indicate clumped distribution (Thioulouse et al. 1997; Dale 1999).

The spatial pattern of woody plants and ectomycorrhizal fungi was analyzed using ADS in ADE-4 (a free software for spatial data analysis, ver. 2001, available online: http://pbil.univ-lyon1.fr/ADE-4/ADSWebUS.html). Ectomycorrhizal fungi and four groups of plants, i.e., ectomycorrhizal trees, non-ectomycorrhizal trees, ectomycorrhizal saplings, and non-ectomycorrhizal saplings, in the three plots, were subjected to second-order analysis.

To evaluate the degree of aggregation of plants or ectomycorrhizal fungi, relative aggregation index (RAI) was calculated as $RAI\,(t) = L(t)/L_u(t)$, where $L(t)$ was estimated by above equation and $L_u(t)$ was the upper boundary of 99% confidence interval at distance t. Large RAIs indicate higher degree of aggregation and RAIs>1 indicate significantly clumped spatial patterns. Pearson correlations between RAIs of ectomycorrhizal fungi, ectomycorrhizal trees, non-ectomycorrhizal trees, ectomycorrhizal saplings, and non-ectomycorrhizal saplings were calculated.

Percentage of ectomycorrhizal plant and biodiversity of plants and ectomycorrhizal sporocarps

Twenty points were randomly selected in each plot. In each circle of radius t (1–10 m) centered on these points, percentage of ectomycorrhizal trees and saplings, as well as diversity (H) of trees, saplings, and ectomycorrhizal sporocarps were calculated.

Pearson's correlation coefficients between diversities of trees, saplings, and ectomycorrhizal sporocarps at each distance t (2–10 m) were calculated. In each circle of radius t (1–10 m) centered on each sporocarp, percentages of ectomycorrhizal trees and saplings were calculated. Percentages of ectomycorrhizal trees and saplings were compared between circles centered on sporocarps and those centered on randomly selected points. To avoid sampling error from low numbers of individuals in the circle, circles in which there were less than five plants were excluded from the calculation of percentage of ectomycorrhizal plants.

Statistical analysis

Statistical analyses were performed using SPSS 10.0 for Windows (SPSS, Cary, NC). Pearson's correlation coefficients were calculated using the bivariate correlation program. Percentage of ectomycorrhizal plants around random selected points and ectomycorrhizal fungal sporocarps at different distance, t, were compared using Student's t test. Regression curves of Shannon–Wiener index and Pearson's correlation coefficient along distance t were performed using the regression program.

Results

Composition and spatial distribution of woody plants

Relative importance values and Shannon–Weiner diversity index (H') of plants in the three plots are listed in Table 1. Three ectomycorrhizal tree species (height >3 m) were found in each plot, accounting for 45.4, 34.4, and 55.0% of the importance values in plots I, II, and III, respectively. There were seven, eight, and ten non-ectomycorrhizal tree species in plots I, II, and III, respectively. There were two, three, and one ectomycorrhizal sapling species and 14, 13, and 14 non-ectomycorrhizal sapling species in plots I, II, and III, respectively. The total importance values of ectomycorrhizal saplings were <9% in each plot. Shannon–Wiener biodiver-

Table 1 Importance values (IV) and Shannon–Weiner diversity index (H') of plants in the three plots[a]

Plant species	Trees			Saplings			Seedlings		
	I	II	III	I	II	III	I	II	III
Non-ECM plant									
Cunninghamia lanceolata	20.4	3.7	3.1	17.1	3.2	5.7	1.4	0.3	5.1
Symplocos stellaris	13.4	1.7	3.9	8.9	7.5	2.3	0.4	1.8	0.0
Camellia gaudichaudii	12.2	33.0	16.5	34.1	47.5	45.8	13.0	20.3	18.3
Elaeocarpus japonicus	7.0	15.1	0.0	2.4	4.9	0.0	1.1	3.6	0.0
Symplocos setchuensis	0.7	3.0	0.7	12.1	8.6	11.4	9.6	8.9	9.9
Eurya sp.	0.4	6.8	1.4	3.4	6.4	1.3	3.5	2.8	1.9
Symplocos laurina	0.0	0.0	5.5	5.0	3.6	3.8	3.9	3.6	5.8
Vaccinium sprengelii	0.0	1.5	5.4	3.1	4.7	6.9	2.2	1.4	2.0
Sinocalamus sp.	0.0	0.0	0.0	0.4	0.0	0.0	7.2	3.2	1.8
Zanthoxylum sp.	0.0	0.0	0.0	0.0	0.0	3.1	0.4	0.0	7.2
Viburnum sp.	0.0	0.0	0.0	0.0	0.0	0.0	18.3	7	8
Smilax china	0.0	0.0	0.0	0.0	0.0	0.0	7.1	8.6	5.7
ECM plant									
Castanopsis fargesii	31.4	26.5	46.3	8.2	5.4	8.2	15.5	23.5	13.5
Pinus massoniana	10.8	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0
Quercus varibilis	3.3	3.6	1.2	0.5	0.0	0.0	6.1	5.1	3.9
H'	1.83	1.84	1.85	2.06	1.93	1.94	2.53	2.47	2.67

[a] Only common plant species (IV>5) were listed.

sity index (H') of saplings were slightly higher in plot I than those in plots II and III. There were four ectomycorrhizal seedling species in plots I and II and three in plot III, and 17, 20, and 19 non-ectomycorrhizal seedling species were found in plots I, II, and III, respectively. Diversities of seedlings were similar in the three plots.

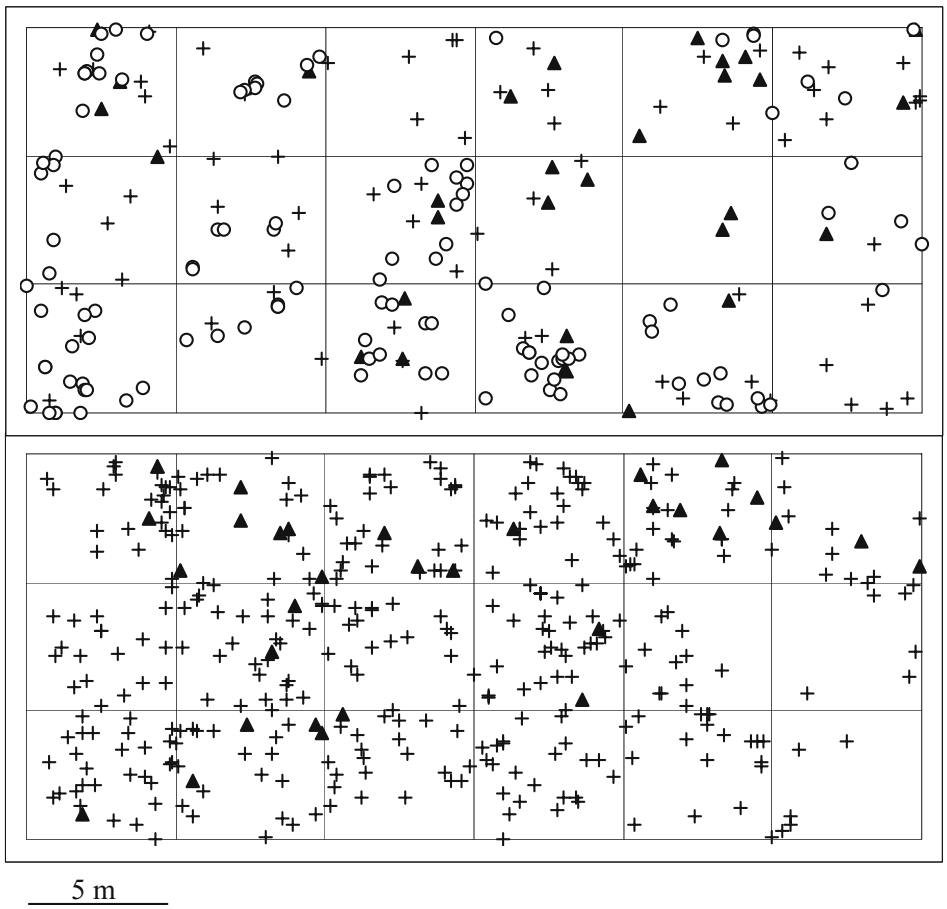

Fig. 2 Spatial distribution of trees and ectomycorrhizal fungal sporocarps (**a**) and saplings (**b**) in plot I (*filled triangle*) ectomycorrhizal (ECM) plants,+ (*open circle*) non-ECM plants, ECM fungal sporocarps

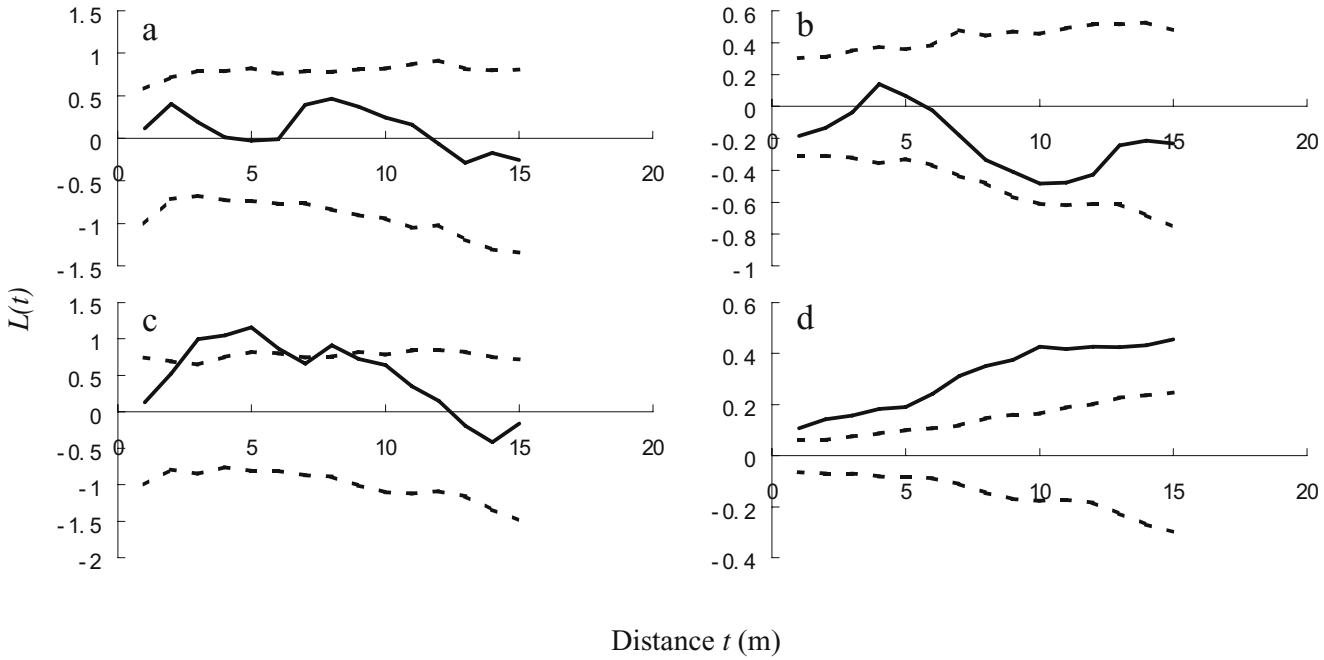

Fig. 3 Second-order analysis of trees and saplings in plot I. The *dashed lines* indicate boundaries of 99% confidence interval. $L(t)$ higher than the upper boundary indicates a significantly clumped distribution; $L(t)$ lower than the lower boundary indicates a significantly regular distribution; and $L(t)$ between two boundaries indicates a random distribution at distance t. **a** Ectomycorrhizal trees, **b** non-ectomycorrhizal trees. **c** Ectomycorrhizal saplings, **d** non-ectomycorrhizal saplings

The relative positions of trees and saplings in the three plots are shown in Fig. 2. The spatial distributions of ectomycorrhizal and non-ectomycorrhizal trees are shown in Fig. 2a. The spatial patterns of trees, no matter their mycorrhizal status, were random in the three plots (Fig. 3a and b).

The density of non-ectomycorrhizal saplings was much higher than ectomycorrhizal saplings in the three plots (Fig. 2b). In plot I, ectomycorrhizal saplings were clumped at the distances of 3–6 and 8 m, whereas the non-ectomycorrhizal saplings were clumped at all distances tested (Fig. 3c and d). In plot II, ectomycorrhizal saplings were not clumped, whereas non-ectomycorrhizal saplings were clumped at 2 m (data not shown). In plot III, both types of saplings had a random distribution (data not shown).

Canopy LAI (mean±SE) was 1.743±0.041, 1.795±0.050, and 1.802±0.028 in plots I, II, and III, respectively. Whereas these values are not significantly different, F-tests showed that LAI variances of plots I and II were significantly higher than that of plot III ($p<0.05$).

Composition and spatial distribution of ectomycorrhizal fungi

There were 16, 17, and 8 ectomycorrhizal fungal species based on sporocarp identification in plots I, II, and III, respectively (Table 2). Although sporocarp numbers were 132, 53, and 9 in plots I, II, and III, respectively, the diversity of ectomycorrhizal fungi was greatest in plot II, followed by plot I and then plot III. A sample of spatial distributions of ectomycorrhizal fungi (plot I) are shown in Fig. 2a. The results of second-order analysis indicated that sporocarps of ectomycorrhizal fungi appeared in clumped

Table 2 The importance values (IV) and Shannon–Weiner diversity index (H') of ectomycorrhizal sporocarps in the three plots[a]

Taxa	Plot I	Plot II	Plot III
Russula nigricans	20.7	8.1	0.0
Xerocomus badius	16.7	5.2	11.5
Amanita manginiana	11.6	9.7	22.9
Leccinum sp.1	7.8	2.6	0.0
Boletus sp.1	6.9	2.6	0.0
B. sp.2	6.1	9.9	0.0
R. azurea	5.2	0.0	0.0
Gyroporus purpurinus	5.2	3.6	0.0
B. impolitus	5.2	0.0	0.0
A. virgineoides	3.8	9.7	0.0
Suillus sp.1	0.0	15.9	11.5
R. vinosa	0.0	5.4	0.0
Phylloporus rhodoxanthus	0.0	6.2	0.0
Lactarius sanguifluus	0.0	5.2	0.0
R. veternosa	0.0	4.5	19.5
A. caesarea var. *alba*	0.0	2.6	11.5
B. sp.3	0.0	0.0	22.9
H'	2.419	2.668	1.742

[a] Rare taxa (IV<5): *Russula turci*, *Tylopilus felleus*, *T. nigerrimus*, *Amanita longistriata*, *A. ceciliae*, *Strobilomyces* sp.1, *Phylloporus* sp.1

patterns in all three plots, but the clumped distances were different: 1–6 m in plot I, 1–4 and 7–8 m in plot II, and 1–2 m in plot III (Fig. 4).

Correlation between woody plants and ectomycorrhizal fungi

Significant positive correlations were found between ectomycorrhizal sporocarps and both non-ectomycorrhizal trees and ectomycorrhizal saplings, as well as between ectomycorrhizal saplings and both ectomycorrhizal trees or non-ectomycorrhizal trees (Table 3).

The percentage of ectomycorrhizal trees was significantly higher at distances 2 and 3 m around ectomycorrhizal sporocarps than around randomly selected points, whereas the percentage of ectomycorrhizal saplings around ectomycorrhizal fungal sporocarps was similar to that around randomly selected points (Fig. 5). These results implied that at short distances, ectomycorrhizal sporocarps prefer microsites where ectomycorrhizal trees were dominant.

The diversity of trees and saplings around randomly selected points showed a similar trend (Fig. 6): (a) diversities of both trees and saplings along distance t fit

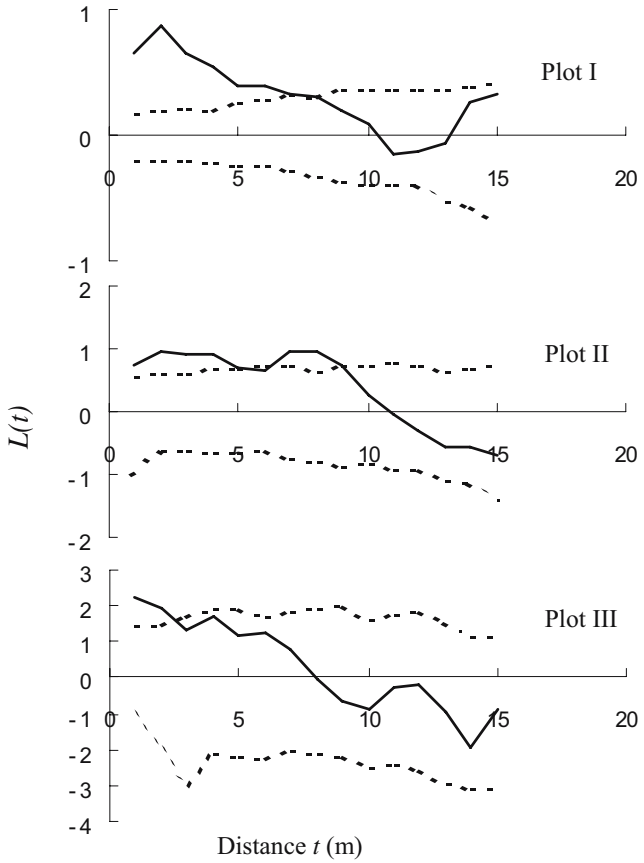

Fig. 4 Second-order analysis of the ECM fungal sporocarps in the three plots (see Fig. 3 for interpretation of figure)

Table 3 Correlation of relative aggregation indices (RAI) between ectomycorrhizal fungi and plants from July to September, 2002

	ECM fungi	ECM tree	Non-ECM tree	ECM sapling	Non-ECM sapling
ECM fungi	1				
ECM tree	0.097	1			
Non-ECM tree	0.494[b]	−0.013	1		
ECM sapling	0.359[a]	0.542[b]	0.402[b]	1	
Non-ECM sapling	0.203	0.128	−0.122	−0.01	1

Superscripts "a" and "b" indicate significant correlations at 0.05 and 0.01 level, respectively.

S-curve equations $\left(y = e^{(ax+b)}\right)$ and (b) diversity increased relatively sharply at short distance t, but was relatively constant when t was >4 to 5 m. Diversity of ectomycorrhizal fungal sporocarps along distance t fit the S-curve equation, but the increase was much sharper than those of trees and saplings.

Pearson's correlation coefficients of the diversities of ectomycorrhizal fungi and trees increased linearly with the increasing of distance t (Fig. 7). These results indicated that at relatively long distances (>8 m) or large scales, there were significantly positive correlations between diversities of trees and ectomycorrhizal sporocarps, but no positive correlations at short distances or small scales. Pearson's correlation coefficients of the diversities of ectomycorrhizal sporocarps and saplings along distance t fit a logarithmic curve ($y=a\times\ln(x)+b$). Comparing with trees, significantly positive correlations between diversities of ectomycorrhizal sporocarps and saplings were found at relatively shorter distances (>4 m).

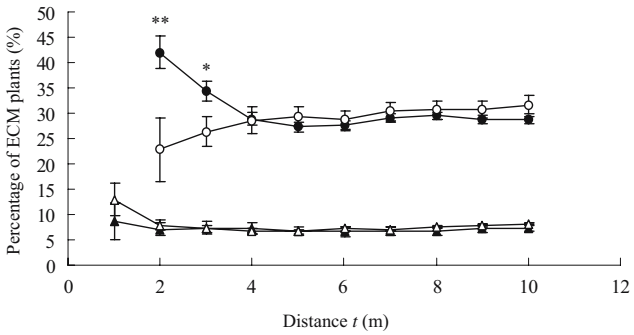

Fig. 5 Percentage of the ECM plants along distance t around random selected points and ECM fungal sporocarps from July to September 2002. Percentage of ECM trees around random selected points Percentage of ECM trees around ECM fungal sporocarps Percentage of ECM saplings around random selected points Percentage of ECM saplings around ECM fungal sporocarps. The *bars* indicate SE; ** and * indicate significant differences at the 0.01 and 0.05 levels, respectively

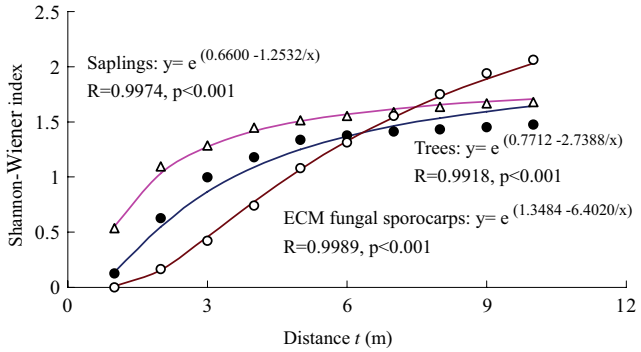

Fig. 6 Diversity of the trees, saplings, and ECM fungi along distance *t* (*filled circle*) trees, (*open triangle*) saplings, (*open circle*) ECM fungi

Discussion

Although the diversity and spatial pattern of ectomycorrhizal fungi in natural forests are affected by multiple factors, e.g., temperature, moisture, soil pH, organic matter, wild fire, pollution, and forest management (Gong et al. 1997; Erland and Taylor 2002), the presence of host plants is an important determinant for the occurrence of ectomycorrhizal fungi. This is the first study of spatial relationship between ectomycorrhizal fungi and ectomycorrhizal and non-ectomycorrhizal plants using spatial data of woody plants and considering tree size.

According to our spatial pattern analysis of mapped plots in a natural forest, the degree of aggregation of ectomycorrhizal fungi was positively correlated with those of non-ectomycorrhizal trees and ectomycorrhizal saplings, implying that ectomycorrhizal and non-ectomycorrhizal plants influenced the spatial distribution of ectomycorrhizal fungal sporocarps. The positive correlations between the aggregation degrees of non-ectomycorrhizal trees and ectomycorrhizal fungi might be due to (1) the indirect influence of non-ectomycorrhizal trees through ectomycorrhizal plants considering the significantly positive correlations between RAIs of non-ectomycorrhizal trees and ectomycorrhizal saplings; or (2) the influence of non-ectomycorrhizal trees in creating suitable microenvironments for ectomycorrhizal sporocarps aggregation.

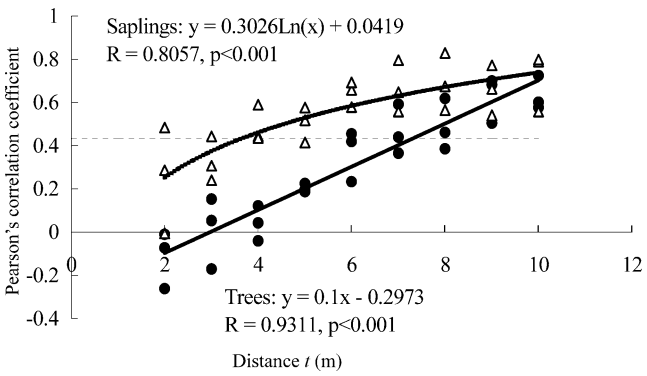

Fig. 7 Correlation of the diversity between plants and ECM fungi along distance *t*. The *dashed line* indicates significant boundaries ($p<0.05$) for Pearson's correlation coefficient. (*open triangle*) Diversity between saplings and ECM fungi, (*filled circle*) diversity between trees and ECM fungi

The correlations between percentage of ectomycorrhizal trees and ectomycorrhizal fungal sporocarp occurrence and between diversity of woody plants and ectomycorrhizal fungi were distance-dependent (scale-related). A significantly high percentage of ectomycorrhizal trees was found only at relatively short distance from ectomycorrhizal fungal sporocarps, and significantly positive correlation of the diversities of woody plants and ectomycorrhizal fungi was found only at relatively long distance. A high percentage of ectomycorrhizal trees in a limited area (short distance) would provide suitable root systems to support ectomycorrhizal sporocarps, and the influence of ectomycorrhizal plants would decrease with increasing distance because the effects of host roots would also decrease at longer distances from the trunk.

The distance-dependent influence of host plants could explain the correlation of the diversities of plants and ectomycorrhizal fungi at different distances. At long distances or within relatively large areas, the high diversity of woody plants would provide more micro-sites with diverse plant compositions and microenvironments (e.g., LAI) suitable for various ectomycorrhizal fungal species, leading to significantly positive correlation between diversity of ectomycorrhizal fungi and woody plants. At short distances within a limited area, high percentage of ectomycorrhizal trees would decrease the plant diversity around ectomycorrhizal fungal sporocarps and, therefore, reduce the correlation between plant and ectomycorrhizal fungal diversities.

Although the interaction between woody plants and ectomycorrhizal fungi is complex in natural forests, our application of spatial pattern analysis, as well as distance-related measurement of percentage of ectomycorrhizal plants and diversity, has clarified the plant–ectomycorrhizal fungus relationship. Our results indicate that there may be multiple interactions between plants and ectomycorrhizal fungi, e.g., the related spatial pattern of plants and ectomycorrhizal fungal sporocarps, the correlation between plant and ectomycorrhizal fungal diversities, and the distance-dependent relationship between percentage of ectomycorrhizal plants and sporocarp occurrence of ectomycorrhizal fungi. Important factors affecting the spatial distribution, occurrence, and diversity of ectomycorrhizal fungi in our study include spatial pattern of ectomycorrhizal and non-ectomycorrhizal plants, distance from ectomycorrhizal plants, percentage of ectomycorrhizal plants, and plant diversity.

Conclusions

The degree of clumping of woody plants and ectomycorrhizal fungi were correlated, and the correlations between percentage of ectomycorrhizal trees and sporocarp occurrence of ectomycorrhizal fungi and between diversities of woody plants and ectomycorrhizal fungi were distance-dependent or scale-related. The spatial structure and diversity of ectomycorrhizal fungi were affected by the spatial pattern and diversity of woody plants. Fine-scale studies based on mapped plots and differentiation of plant size (trees and saplings) and ectomycorrhizal status (ectomycorrhizal or non-ectomycorrhizal) are helpful in better understanding the spatial interactions between woody plants and ectomycorrhizal fungi in natural forests.

Acknowledgment This work was supported by National Natural Science Foundation of China Grants (30370006, 30470006, 30230020, 30499340) and a State Key Basic Research and Development Plan of China Grant (G2000046802). We are grateful to the West China Subalpine Botanical Garden, the Chinese Academy of Sciences for providing climate data for the study site and Dr. X.-M. Gao, Mr. C.-W. Liu, and Dr. P. Zhuang for their assistance in plant identification.

References

Andersen M (1992) Spatial analysis of two-species interactions. Oecologia 91:134–140

Dahlberg A (2001) Community ecology of ectomycorrhizal fungi: an advancing interdisciplinary field. New Phytol 150:555–562

Dale MRT (1999) Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge, UK, pp 206–241

Dale MRT, Dixon P, Fortin MJ, Legendre P, Myers DE, Rosenberg MS (2002) Conceptual and mathematical relationships among methods for spatial analysis. Ecography 25:558–577

Erland S, Taylor AES (2002) Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic environment. In: van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Springer, Berlin Heidelberg New York, pp 163–200

Ford ED, Mason PA, Pelham J (1980) Spatial patterns of sporophore distribution around a young birch tree in three successive years. Trans Br Mycol Soc 75:287–296

Getis A, Franklin J (1987) Second-order neighborhood analysis of mapped point patterns. Ecology 68:473–477

Gong MQ, Chen YL, Zhong CL (1997) Mycorrhizal research and application. China Forestry Publishing House, Beijing, China, pp 35–60

Goreaud F, Pélissier R (1999) On explicit formulas of edge effect correction for Ripley's *K*-function. J Veg Sci 10:433–438

Haase P (1995) Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. J Veg Sci 6:575–582

Last FT, Mason PA, Ingleby K, Fleming LV (1984) Succession of fruitbodies of sheathing mycorrhizal fungi associated with *Betula pedula*. For Ecol Manag 9:229–234

Last FT, Natarajan K, Mohan V, Mason PA (1992) Sequences of sheathing (ecto-) mycorrhizal fungi associated with man-made forests, temperate and tropical. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) Mycorrhizas in ecosystems. CAB International, Wallingford, UK, pp 214–219

Liang Y, Guo LD, Ma KP (2004a) Spatial pattern of the most common late-stage ectomycorrhizal fungi in a subtropical forest in Dujiangyan, southwest of China. Acta Bot Sin 46:29–34

Liang Y, Guo LD, Ma KP (2004b) Genetic structure of a population of the ectomycorrhizal fungus *Russula vinosa* in subtropical woodlands in southwest China. Mycorrhiza 14:235–240

Molina R, Massicotte H, Trappe JM (1992) Specificity phenomena in mycorrhizal symbioses: community–ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning: an integrative plant–fungal process. Chapman & Hall, New York, pp 357–423

Nillson LO, Wallander H (2003) Production of external mycelium by ectomycorrhizal fungi in a Norway spruce forest was reduced in response to nitrogen fertilization. New Phytol 158:409–416

Pielou EC (1985) Mathematical ecology, 2nd edn. Wiley, NY

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47:376–391

Read DJ (1997) Mycorrhizal fungi—the ties that bind. Nature 388:517–518

Ripley BD (1976) The second-order analysis of stationary processes. J Appl Probab 13:255–266

Simard SW, Perry DA, Jones MD, Myrold DD, Durall DM, Molina R (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388:579–582

Simard SW, Jones MD, Durall DM (2002) Carbon and nutrient fluxes within and between mycorrhizal plants. In: van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Springer, Berlin Heidelberg New York, pp 34–74

Smith JE, McKay D, Brenner G, McIver J, Spatafora JW (2005) Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. J Appl Ecol 42:526–535

Tedersoo L, Koljalg U, Hallenberg N, Larsson KH (2003) Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. New Phytol 159:153–165

Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: a multivariate analysis and graphical display software. Stat Comput 7:75–83

Toide R, Xu B, Sharda J, Lekberg Y, Ostiguy N (2005) Evidence of species interactions within an ectomycorrhizal fungal community. New Phytol 165:305–316

Visser S (1995) Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol 129:389–401