

Spatial distribution patterns of *Symplocos* congeners in a subtropical evergreen broad-leaf forest of southern China

Xiuqing Yang¹ · Haibing Yan¹ · Buhang Li² · Youzhi Han¹ · Bo Song³

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Abstract Studies on spatial distribution of congeneric species can supplement our understanding of species ecological processes. We analyzed population structure, spatial distribution, intra- and interspecific associations among six *Symplocos* tree species on a large (50 ha) plot in a subtropical, evergreen broad-leaf forest in southern China using spatial point pattern analysis methods. Our results suggested that the six *Symplocos* tree species were all clustered at small scales. The aggregation intensity of *S. wikstroemiifolia* with low abundance but relatively numerous large-diameter trees was much higher than that of the other five *Symplocos* species that occurred at high abundance but included few large-diameter trees. Spatial associations among the six congeners showed that 12 of 30 pairs were associated positively at small scales, and 13 of 30 pairs were unrelated. For species among different size

classes, 79 of 120 pairs were not correlated, and 17 of 120 pairs were associated positively. These results showed insufficient evidence for interspecific competition and congeneric *Symplocos* species commonly coexist within subtropical plant communities. The spatial patterns of *Symplocos* species and their correlations changed with size (DBH) class and were simultaneously affected by spatial scales; the intensity of their aggregation and association decreased with increasing area of the sample plot.

Keywords Population structure · Spatial patterns · Spatial associations · *Symplocos*

Introduction

Species spatial distribution is the focus of attention by ecologists because of its importance to understanding ecological processes (Bunyavejchewin et al. 2003; Gao et al. 2014). Analyses of the spatial distributions of tree species and their associations shed light on the underlying ecological processes of species and can explain mechanisms that facilitate species coexistence, while contributing to the prediction of future forest community structures as determined by the underlying processes (Wiegand and Moloney 2004; Wiegand et al. 2007; Lan et al. 2012; Liao et al. 2015).

In many cases, comparative studies of the spatial distribution of tree species indicated that most conspecifics are clustered in space in naturally regenerated tropical (He et al. 1997; Condit et al. 2000) and temperate plant communities (Zhang et al. 2010). This phenomenon may be broadly attributed to three factors: (1) environmental factors such as habitat heterogeneity or niche differences (Harms et al. 2000; Queenborough et al. 2007; Inman-

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✉ Xiuqing Yang
Xiuqingy2002@126.com

- ¹ College of Forestry, Shanxi Agricultural University, Taigu, Shanxi 030801, People's Republic of China
- ² SYSU-Alberta Joint Lab for Biodiversity Conservation, State Key Laboratory of Biocontrol, School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, People's Republic of China
- ³ Belle W. Baruch Institute of Coastal Ecology and Forest Science, Clemson University, Georgetown, SC 29442, USA

Narahari et al. 2014); (2) ecological processes of populations and communities such as dispersal limitation (Grubb 1977; Hubbell et al. 2001), seed deposition (Howe 1989), facilitation (Kikvidze et al. 2005), succession (Felinks and Wiegand 2008), and gap dynamics (Nagel et al. 2006); and (3) phylogenetic differences (Wang et al. 2013, 2015) and stochastic processes that build one cornerstone of neutral theory (Hubbell et al. 2001). Meanwhile, negative feedback responses to the clustered distribution of a species are important for explaining patterns of species coexistence such as negative density dependence (Seri and Shnerb 2015). Negative density dependence can arise because attacks by density-responsive natural enemies (such as host-specialized pathogens) increase disproportionately with local conspecific density (Janzen 1970; Connell 1971; Augspurger and Kelly 1984; Hammond and Brown 1998; Bell et al. 2006; Alvarez-Loayza and Terborgh 2011; Terborgh 2012; Bagchi et al. 2014) or because competition for natural resources (e.g., competition for seed dispersers) is more intense between conspecifics than heterospecifics (Jansen et al. 2014). These direct or indirect factors lead to “repulsion” between individuals or clusters (which induces self-thinning of the same species and decrease of recruitment in its neighborhood), thus increasing the chance that other species will occupy the vacated habitats and hence providing an important theoretical foundation to explain species coexistence (Comita et al. 2010; Bagchi et al. 2014; Jansen et al. 2014).

Previous comparative spatial pattern studies focused mostly on many species of different families/genera and occupying different habitats (He et al. 1997; Lan et al. 2012; Li et al. 2014). Nonpartitioning between habitat heterogeneity and phylogenetic difference has led to confusion about the relative importance of abiotic versus biotic factors on species spatial patterns and has hindered development of theory relating abiotic/biotic factors with patterns of distribution and coexistence. Research on congeners helps to exclude the ambiguous impact caused by phylogenetic differences (Bevill and Louda 1999; Lloyd et al. 2002; Swenson et al. 2006), and might elucidate factors that induce species distribution patterns such as weak scatter abilities (Cowling 2001; Simon and Hay 2003) or specialized habitat requirements (Queenborough et al. 2007). Therefore, analysis of the distributions of congeneric pairs in space offers special opportunities to explain species coexistence in a more scientific and rigorous manner (Li et al. 2014). Alternatively, there exists much fiercer interspecific competition among congeneric species since they have similar phenotypic and ecological characteristics and probably use resources in similar ways (Ackerly and Donoghue 1998; Mooney et al. 2008), which, in principle, should discourage their coexistence (Webb et al. 2002; Mooney et al. 2008). Then, are these

congeners still mainly clustered? Are there differences between the spatial distributions of abundant versus scarce species, and what are the spatial associations among them? How do they coexist in the same communities? Zhang et al. (2010) analyzed the spatial pattern of congeneric *Acer* species in a temperate forest in northeastern China and revealed new species spatial patterns and coexistence. Their research focused on temperate forests but did not address plant communities at other latitudes.

In this study, we compared the spatial distribution and correlations of six sympatric *Symplocos* tree species in a 50-ha subtropical evergreen broad-leaf forest of southern China. A method of the pair-correlation function analysis was used to address the following questions: (1) How are these six congeners distributed in a multispecies southern subtropical forest? (2) Are there detectable differences in distribution patterns among them? (3) What is the correlation among these coexistent congeneric trees in terms of their spatial distribution within a community?

Materials and methods

Study site

Our study site, a subtropical evergreen broad-leaf forest at the Heishiding Nature Reserve, Guangdong Province, southern China (23°26'N, 111°53'E) had a complex plant composition including 1070 species in 527 genera in 162 families. The dominant tree genera are *Castanopsis* and *Lithocarpus* (Fagaceae), *Machilus* and *Lindera* (Lauraceae), *Altingia chinensis* (Hamamelidaceae), and *Camellia* (Theaceae). A subtropical moist monsoon climate characterizes this vegetation distribution area, and average annual temperature is 19.6 °C, with an average of 10.6 °C in January and 28.4 °C in July. Average annual precipitation is 1744 mm, falling as rain from April to September. Average relative humidity is 80–85%. Soil is classified as red acidic forest soil (Xu and Yu 2014; Shuai et al. 2014).

A 50-ha (1000 × 500 m) permanent forest plot was established in this evergreen broad-leaf forest in 2011 following the field protocol of the Center for Tropical Forest Science (CTFS) (Condit 1998). The first plot survey to record species presence and position, label trees, and record diameter at breast height (DBH) for trees of DBH ≥ 1 cm was completed in 2012. We recorded 273,000 living plants of 245 species, 160 genera, and 71 families. The five most abundant species were *Xanthophyllum hainanense*, *Cryptocarya concinna*, *Litsea acuminata*, *Neolitsea phanerophlebia* and *Itea chinensis*. There were 86 species (accounting for 35% of all species) represented by fewer than 50 plants. Average density and basal area of the stand was 5460 individuals and 39.02 m² per hectare,

respectively. Elevation range of the plot was from 435 to 698 m, asl. Convexity at the 20 m scale range was from -24.53 to 17.63 . Slope span of the plot was from 6.89° to 74.6° (Fig. 1).

Study species

The genus *Symplocos* (Symplocaceae) contains about 318 species, most of which are native to the tropics and subtropics of Asia, Oceania and America (Fritsch et al. 2008). There are 77 *Symplocos* species reported for China (Editorial Board for Flora of China, Chinese Academy of Sciences 1974). These are mainly distributed in southwestern China, but some occur in southeastern China and only one species (*Symplocos paniculata*) in northeastern China. In our plot, individual *Symplocos* trees numbered 7500 but were not the most abundant. However, the genus *Symplocos* was represented by more species (nine) than any other genus recorded in the plot. The nine species varied in habit from shade-tolerant understory shrubs to mid-story trees, and even some canopy species (the maximum height was 30 m).

Six main *Symplocos* species were selected for analysis of their DBH structure, spatial patterns, and intra- and interspecific correlations. These were *Symplocos adenophylla*, *S. anomala*, *S. congesta*, *S. lancifolia*, *S. laurina*, and *S. wikstroemiifolia* (Fig. 2). The remaining three *Symplocos* species (*S. denopus*, *S. pseudobarberina*, *S. stellaris*) were not included in this study because of their low abundance.

All the six closely related *Symplocos* species with tryma are shade-tolerant, and their seeds are dispersed by birds. But their seed shape, size and season of production differ. *S. wikstroemiifolia* and *S. adenophylla* bear oval seeds of 6–12 mm long in July–August, *S. anomala* and *S. congesta* bear cylindrical seeds of 8–13 mm long in June–December (*S. anomala*) and January–February (*S. congesta*), but *S. lancifolia* and *S. laurina* bear round seeds of 4–6 mm diameter long in June–December (*S. lancifolia*) and

March–June (*S. laurina*) (Fig. 2). Moreover, *S. anomala*, *S. congesta* and *S. lancifolia* are understory species, *S. wikstroemiifolia* and *S. adenophylla* are midstory species, while *S. laurina* is a midstory or canopy species.

Data analysis

The pair-correlation function $g(r)$, which combines univariate and bivariate statistics as one method of point pattern analysis, was used to explore the spatial distributions and correlations of the six *Symplocos* species at multiple scales (Wiegand and Moloney 2004; Wiegand et al. 2007, 2012). Univariate statistics were used to evaluate the spatial distribution of a single population and to decide whether the patterns of the six *Symplocos* species in different size classes were random, aggregated, or regular in space, and to describe the spatial scale range in which these patterns occurred. Bivariate statistics were used to evaluate spatial associations between two different populations and to determine whether intraspecific and interspecific correlations among species and DBH were positive, negative or unrelated in space.

In point pattern analysis, an aggregated distribution of species and positive interaction between two patterns at a given distance r will be assumed, respectively, for univariate and bivariate analysis when $g(r)$ exceeds the upper confidence limit, while a regularly dispersed distribution and negative interaction will be assumed when $g(r)$ fails to reach the lower confidence limit. Random dispersal and insignificant correlation are assumed when $g(r)$ lies within the confidence interval (Zhang et al. 2010).

To avoid error in estimating the spatial pattern of species, heterogeneous Poisson null models were used to explain probable environmental heterogeneity. In the model analysis, the emergence of all points is assumed independent of each other, the distribution of the points conform to an intensity function that changes with location (Wiegand and Moloney 2004; Wiegand et al. 2007). One intensity function was established for the pattern analysis in the univariate statistics based on the distribution of the six congeners. A second intensity function was established for the correlation analysis in the bivariate statistics by fixing the trees of the first species and randomizing the locations of the trees of the second species. A bandwidth of 30 m and a spatial resolution of 2 m were chosen for all analyses (Wiegand and Moloney 2004; Zhang et al. 2010). Here we analyzed all species pairs by testing not only species 1 versus species 2 but also species 2 versus species 1 of all pairs to avoid nonsymmetric interaction (Wiegand et al. 2007). We further analyzed the species pairs with $DBH \geq 5$ cm, pairs with $DBH < 5$ cm, and pairs between $DBH \geq 5$ cm and $DBH < 5$ cm (Cipriotti and Aguiar 2005; Zhang et al. 2010).

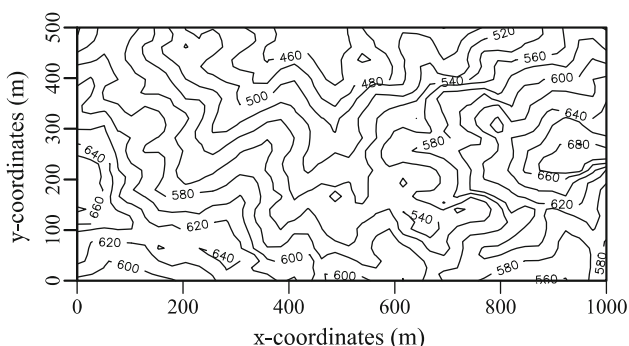


Fig. 1 Topography map of the plot at the Heishiding nature reserve, Guangdong Province, southern China

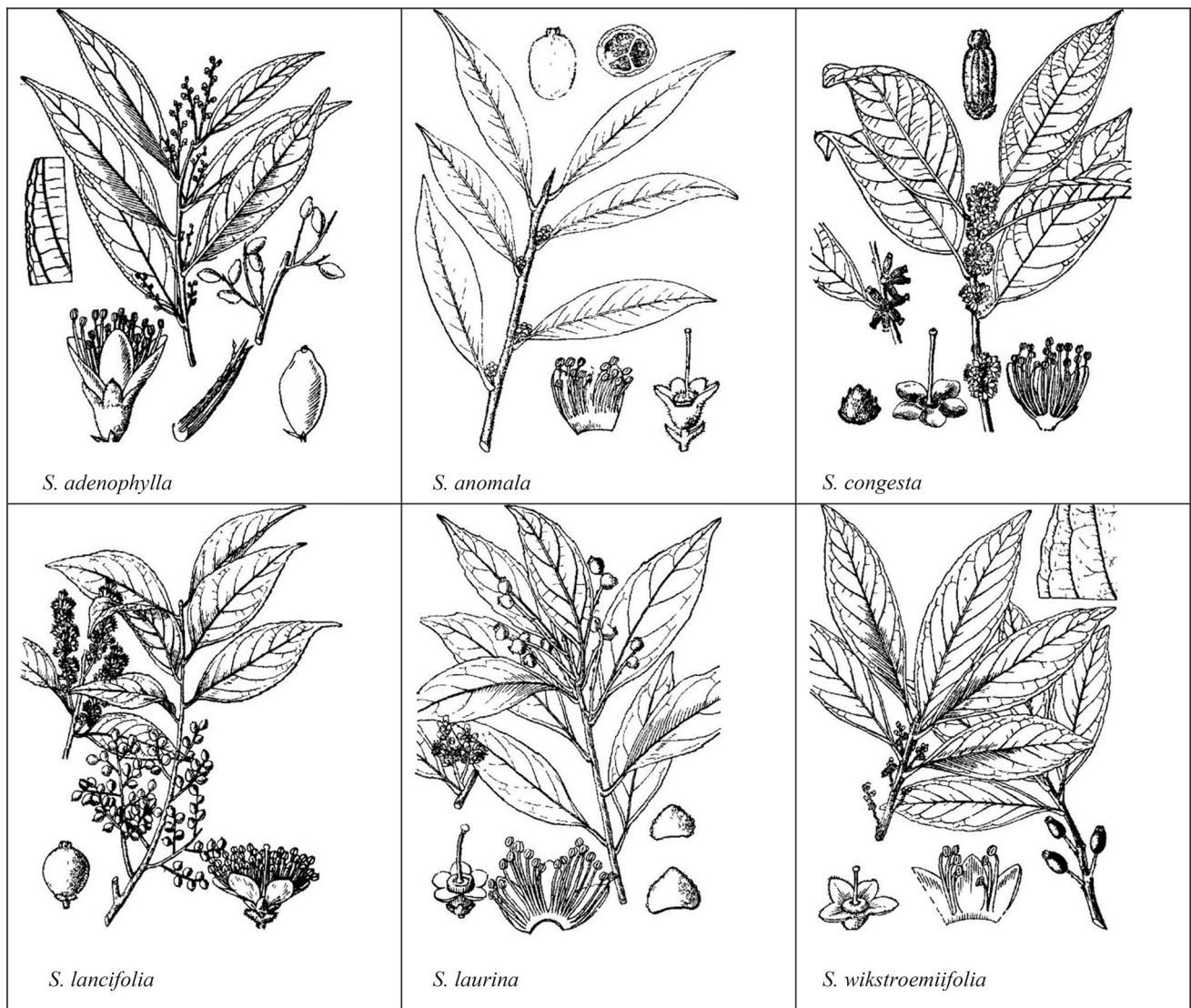


Fig. 2 Morphological traits of six *Symplocos* species. Source: Editorial Board for Flora of China, Chinese Academy of Sciences (1974)

Table 1 Population structure of six *Symplocos* species in a 50-ha subtropical evergreen broad-leaf forest in southern China

Species	Growth type	Abundance (living)		Basal area (m ² /ha)		Mean DBH (cm)	
		WTB	WB	WTB	WB	WTB	WB
<i>S. adenophylla</i>	Midstory	1247	1351	0.0082	0.0085	4.9277	4.8134
<i>S. wikstroemiifolia</i>	Midstory	238	254	0.0089	0.0094	13.6601	13.6188
<i>S. congesta</i>	Understory	1305	1403	0.0062	0.0065	3.9368	3.8693
<i>S. laurina</i>	Midstory/canopy	1749	1964	0.0270	0.0318	6.5131	6.7961
<i>S. lancifolia</i>	Understory	1171	1280	0.0055	0.0061	3.9924	4.0137
<i>S. anomala</i>	Understory	933	1118	0.0036	0.0043	3.6002	3.6071

WTB is abundance without branches, WB is abundance with branches

Data were processed using the grid-based estimators in the Programita software package (Wiegand and Moloney 2004). The spatial scale of 20 m was adopted for the goodness-of-fit (GoF) test, and results were

further analysed when $p \leq 0.05$. Confidence intervals (99%) were determined using the extreme values of $g(r)$ derived from 199 Monte Carlo simulations of the null model.

Results

Population structure

Individual plants of the six selected *Symplocos* species ranged in number from 254 (*S. wikstroemiifolia*) to 1964 (*S. laurina*, Table 1). The abundance of *S. wikstroemiifolia* was lowest of the six species. Abundance ranked in decreasing order as: *S. laurina* (1964) > *S. congesta*

(1403) > *S. adenophylla* (1351) > *S. lancifolia* (1280) > *S. anomala* (1118). *S. laurina* and *S. anomala* had the most branches, while *S. wikstroemiifolia* had the fewest. Total basal area of *S. laurina* was significantly larger than that of the other five species, and mean DBH of *S. wikstroemiifolia* was notably largest.

The five species with abundance over 1000 (*S. adenophylla*, *S. congesta*, *S. lancifolia*, *S. anomala*, and *S. laurina*) had distinct L-shaped distributions, while *S.*

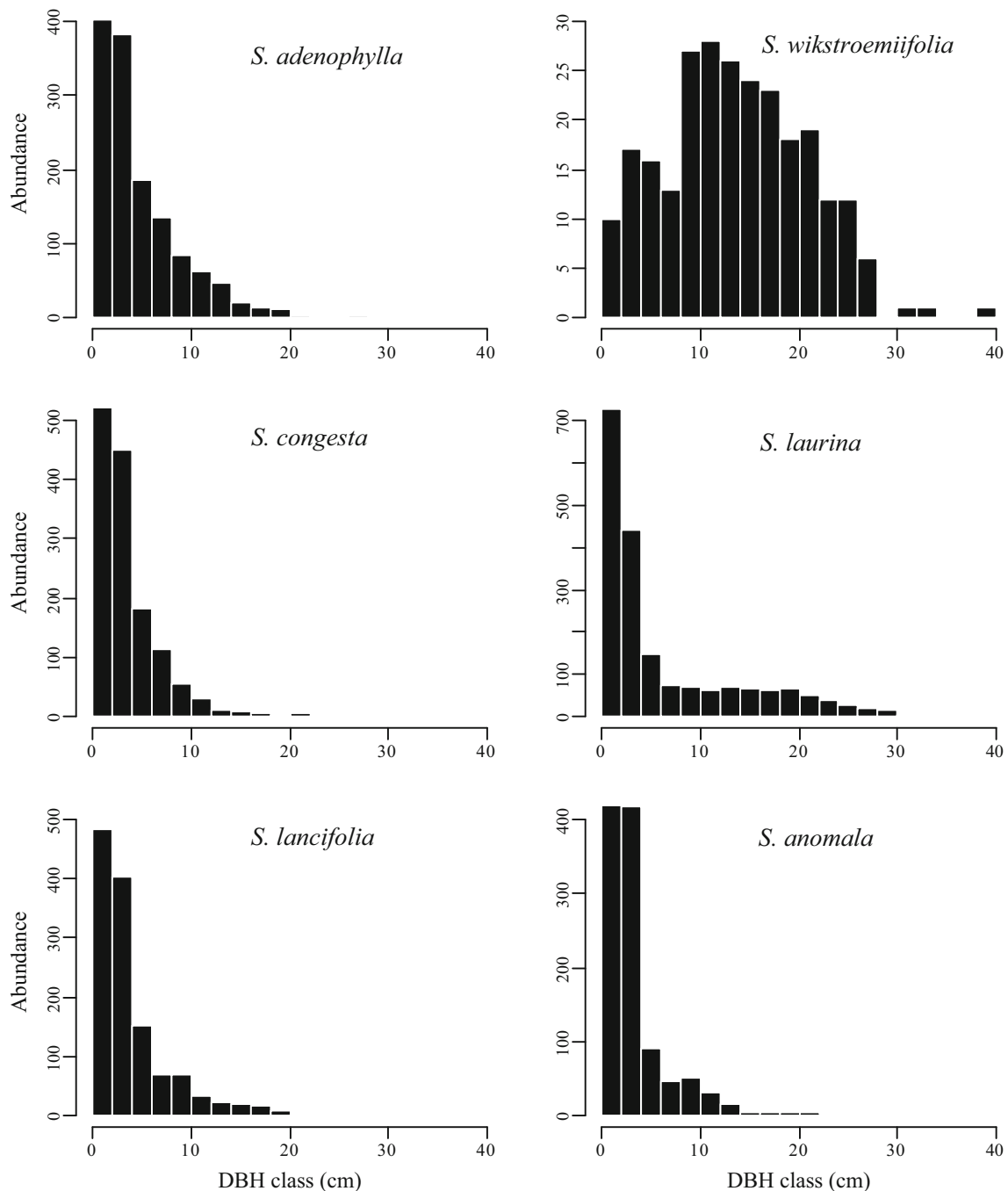


Fig. 3 Abundance by DBH size of class of the six *Symplocos* species in the study plot

wikstroemiifolia with few individuals showed a unimodal-shaped size class distribution (Fig. 3). Few individuals had a DBH >10 cm among the high-abundance species (*S. adenophylla*, *S. congesta*, *S. lancifolia*, *S. anomala*, and *S. laurina*). There were relatively more large specimens of the low-abundance species *S. wikstroemiifolia* compared with the other species.

Spatial patterns

The spatial distributions of the six *Symplocos* tree species differed. *S. adenophylla* was mainly distributed in the middle of the plot from north to south. *S. laurina* was centralized in the northwestern corner and southern part

Fig. 5 Univariate point pattern analysis of six *Symplocos* species. (The *insertions* indicate the point pattern analysis of two size classes (DBH <5 cm and DBH ≥5 cm). *Black lines* indicate $g_{11}(r)$ function; *dotted lines* indicate the upper and lower limits of the 99% confidence interval. Points above the upper limits indicate aggregation distribution, within the intervals random, and below the lower limits regular. The 99% confidence level were calculated using the highest and the lowest values of $g_{11}(r)$ derived from 199 Monte Carlo simulations of the heterogeneous Poisson null model with bandwidth $h = 30$ m; ring width for estimation of the pair-correlation function was 4 m; cell size was 2×2 m)

of the plot. *S. lancifolia* and *S. anomala* were spread out nearly over the entire plot. *S. congesta* occurred everywhere but the northeastern corner. *S. wikstroemiifolia* was only found in the southwestern corner of the plot (Fig. 4).

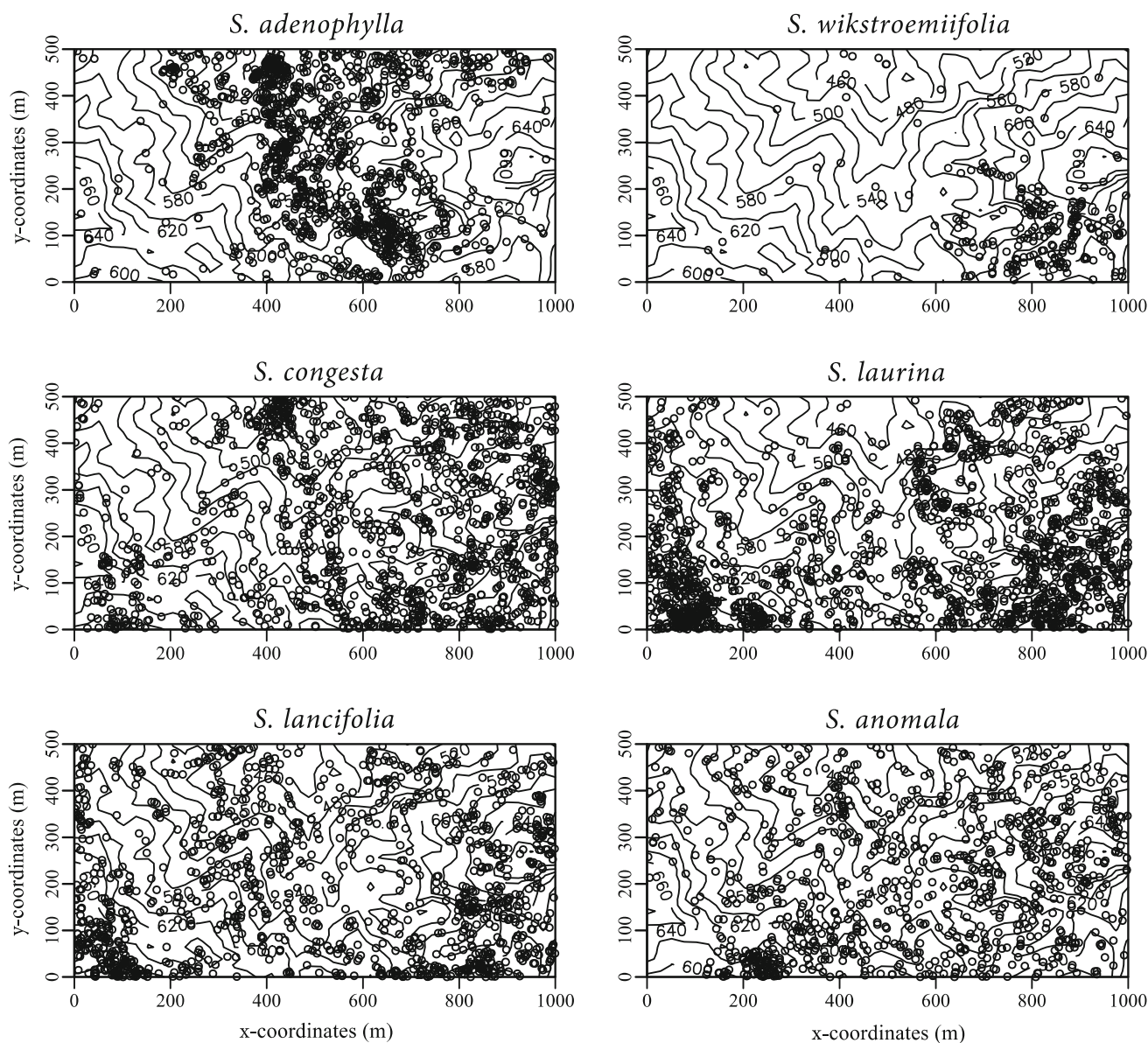
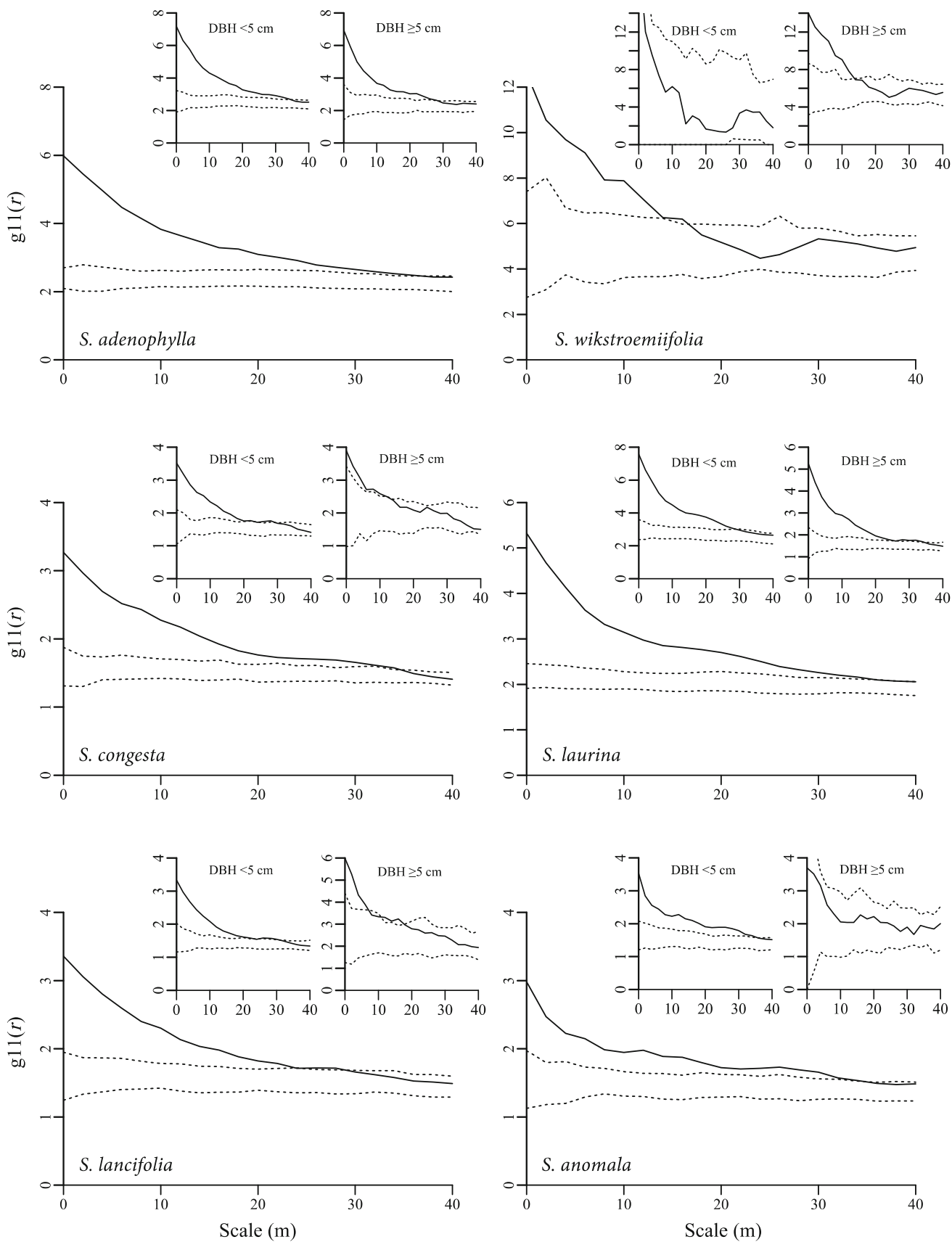


Fig. 4 Spatial distribution of six *Symplocos* species in relation to the topography of the study plot



The six congeners were notably aggregated (Fig. 4). The GoF test indicated deviation from the Poisson null model (at 0–20 m scale range). Two species (*S. adenophylla* and *S. laurina*) had a high cluster intensity at 0–35 m scale range. The other three species also occurred in aggregated distributions at 0–35 m (*S. congesta* and *S. anomala*) or 0–30 m (*S. lancifolia*) scale ranges, but were less aggregated than *S. adenophylla* and *S. laurina* (Fig. 5). *S. wikstroemiifolia* was more highly aggregated than the other five species (Figs. 4, 5). The degree of aggregation of all six species decreased as the scale increased, which conformed to their natural distributions in the plot (Fig. 4).

Five mid-story species (*S. adenophylla*, *S. congesta*, *S. laurina*, *S. lancifolia*, and *S. anomala*) had individuals with DBH <5 cm, and they all notably aggregated at 0–20 m scale range. Among these species, *S. adenophylla* and *S. laurina* had a much higher clustering intensity than that of the other three species (Fig. 5). For individuals with DBH \geq 5 cm, two species (*S. adenophylla* and *S. laurina*) were notably aggregated at 0–20 m scale range, while *S. wikstroemiifolia* and *S. congesta* were aggregated at 0–13 m but random at >13 m scale range. Additionally, *S. lancifolia* was aggregated at 0–7 and 10–17 m, and random at 7–10 and >17 m scale ranges; *S. anomala* was randomly distributed at all study scales (Fig. 5).

Spatial associations

There were positive associations for 12 pairs of species and negative associations for five pairs at the small scale range (Table 2). Ten of 12 pairs with positive associations proved symmetrical in *S. lancifolia* and *S. wikstroemiifolia*, *S. laurina* and *S. wikstroemiifolia*, *S. congesta* and *S. wikstroemiifolia*, *S. congesta* and *S. lancifolia*, and *S. lancifolia* and *S. laurina*. *S. lancifolia* and *S. wikstroemiifolia* were associated positively at the 0–4 m scale range, *S. laurina* and *S. wikstroemiifolia* at 0–6 m, *S. congesta* and *S. wikstroemiifolia* at 0–8 m, *S. congesta* and *S. lancifolia* at 0–14 m, and *S. lancifolia* and *S. laurina* at 0–18 m scale range. *S. adenophylla* had a positive association with *S. congesta* at 0–2 m scale range, and *S. lancifolia* had a positive association with *S. adenophylla* at 0–2 m scale range. Five pairs with negative associations proved symmetrical in *S. adenophylla* and *S. laurina*, *S. adenophylla* and *S. wikstroemiifolia* at scales of the entire study plot. *S. adenophylla* and *S. lancifolia* were negatively correlated at all scales in the entire study plot. The remaining 13 pairs had no significant spatial associations.

The spatial correlations between large DBH (\geq 5 cm) plants and small DBH (<5 cm) plants of the same species were further tested. Eight of 12 species pairs had positive associations at 0–18 m scale range, and none were

negatively associated at any scale (Fig. 6). For the correlations for different species pairs with large DBH (\geq 5 cm), 8 of 30 species pairs had symmetrical negative associations with *S. adenophylla* and 4 other species (*S. anomala*, *S. lancifolia*, *S. laurina* and *S. wikstroemiifolia*), 4 of 30 species pairs had symmetrical positive associations among *S. lancifolia* and 2 other species (*S. congesta* and *S. wikstroemiifolia*) at the small scale (<4 m), and the remaining 18 species pairs were not correlated (Fig. 6). For the correlations of different species pairs with small DBH (<5 cm), 21 of 30 species pairs were not correlated, five species pairs (*S. lancifolia* symmetrically vs *S. congesta*, *S. lancifolia* symmetrically vs *S. laurina*, *S. congesta* vs *S. adenophylla*) had positive associations at small scales, and four species pairs (*S. adenophylla* symmetrically vs *S. lancifolia*, *S. adenophylla* symmetrically vs *S. laurina*) had negative associations (Fig. 6). For the correlations between large DBH (\geq 5 cm) individuals and small DBH (<5 cm) individuals of different species, six of 60 species pairs were positively associated at small scales and 14 of 60 species pairs were negatively associated at 0–20 m scale range. The remaining 40 species pairs were not notably associated (Fig. 6).

Discussion

The distribution patterns of tree species in space provide fundamental information for comprehending underlying ecological process and species coexistence mechanisms (Li et al. 2014). Similar species occupying one ecological area theoretically repel sibling species because of the similarity between their strategies for resource use. Thus, obstacles to coexistence often occur among congeners. Our analysis of the spatial associations among six congeners found that 12 of 30 pairs were associated positively at small scales, and 13 of 30 pairs were unrelated. For species with different size classes, 79 of 120 pairs were not correlated, and 17 of 120 pairs were associated positively. These results suggest that coexistence of *Symplocos* species within subtropical plant communities is common and that interspecific competition among them is not very common. Consistent co-occurrence patterns of congeneric tree species were reported for other plant communities (Zhang et al. 2010; Li et al. 2014). What determines the relative distribution of congeneric species in a community? Previous studies suggested that divergence of traits within a genus can reduce niche overlap and relax competition, thus permitting the co-occurrence of congeners (Beltrán et al. 2012). The six *Symplocos* species varied in habit from shade-tolerant understorey shrubs to mid-storey trees, and even to canopy trees (maximum height of 30 m). The distinct functional traits characteristic of these growth

Table 2 Bivariate point pattern analysis of the spatial associations of six *Symplocos* species in the study plot

Species A	Species B	<i>p</i>	Scales (m)																				
			0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40
<i>S. adenophylla</i>	<i>S. anomala</i>	0.01	r	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. adenophylla</i>	<i>S. congesta</i>	0.01	+	+	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. adenophylla</i>	<i>S. lancifolia</i>	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. adenophylla</i>	<i>S. laurina</i>	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. adenophylla</i>	<i>S. wikstroemiifolia</i>	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. anomala</i>	<i>S. adenophylla</i>	0.01	r	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. anomala</i>	<i>S. congesta</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. anomala</i>	<i>S. lancifolia</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. anomala</i>	<i>S. laurina</i>	0.01	r	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. anomala</i>	<i>S. wikstroemiifolia</i>	0.02	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. congesta</i>	<i>S. adenophylla</i>	0.01	+	+	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. congesta</i>	<i>S. anomala</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. congesta</i>	<i>S. lancifolia</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. congesta</i>	<i>S. laurina</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. congesta</i>	<i>S. wikstroemiifolia</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. lancifolia</i>	<i>S. adenophylla</i>	0.01	+	+	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. lancifolia</i>	<i>S. anomala</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. lancifolia</i>	<i>S. congesta</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. lancifolia</i>	<i>S. laurina</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. lancifolia</i>	<i>S. wikstroemiifolia</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. laurina</i>	<i>S. adenophylla</i>	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. laurina</i>	<i>S. anomala</i>	0.01	r	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. laurina</i>	<i>S. congesta</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. laurina</i>	<i>S. lancifolia</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. laurina</i>	<i>S. wikstroemiifolia</i>	0.02	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. wikstroemiifolia</i>	<i>S. adenophylla</i>	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. wikstroemiifolia</i>	<i>S. anomala</i>	0.01	r	r	r	r	r	r	r	r	r	r	r	-	-	-	-	-	-	-	-	-	-
<i>S. wikstroemiifolia</i>	<i>S. congesta</i>	0.01	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. wikstroemiifolia</i>	<i>S. lancifolia</i>	0.05	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>S. wikstroemiifolia</i>	<i>S. laurina</i>	0.03	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-

The intensity function was constructed based on the pattern of species B in the bivariate statistic under the heterogeneous Poisson null model with the bandwidth $h = 30$ m. Ring width for estimation of the pair-correlation function was 4 m; cell size was 2×2 m; “+” means positive correlation, “r” means no correlation, and “-” means negative correlation. Scale = 0, the points are within the cells. Monte Carlo confidence was constructed at the 99% confidence level (199 simulations). The *p* values were derived from the goodness-of-fit (GOF) test. Only species pairs with $p < 0.05$ are shown in the table

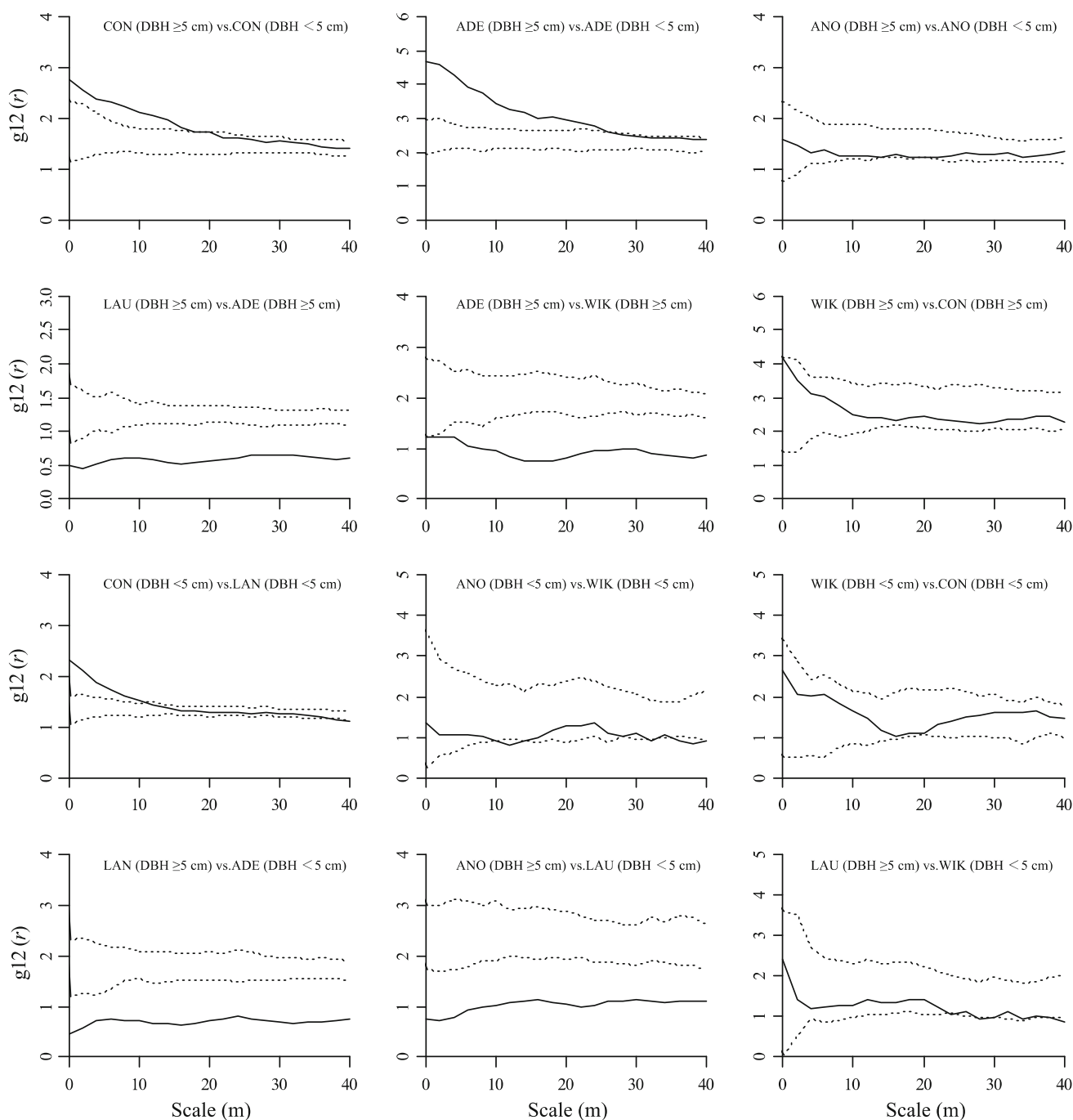


Fig. 6 Bivariate point pattern analysis examples for intra- and interspecies associations among two size classes (DBH <5 cm and DBH \geq 5 cm) of six *Symplocos* species. CON: *S. congesta*, ADE: *S. adenophylla*, ANO: *S. anomala*, LAU: *S. laurina*, WIK: *S. wiktstroemiifolia*, LAN: *S. lancifolia*. Black lines indicate $g_{12}(r)$ function;

dotted lines indicate the upper and lower limits of the 99% confidence interval. Points above the upper limits indicate a positive correlation, within the intervals indicate no correlation, and below the lower limits negative correlation

habits might explain the coexistence of *Symplocos* species within this subtropical forest.

Specialized habitat is also an important impact factor contributing to the coexistence of congeneric species (Davies et al. 1998). In our plot, elevation varied from 435.4 to 698.4 m asl. These congeneric species distributed

in different parts of the heterogeneous topography. Hence, we suggest that topographical differences may contribute to species traits divergence and thus maintain the coexistence of species within a genus.

Significant difference of size (DBH) class structure distinguished the congeners. *S. wiktstroemiifolia* with few

individuals had a unimodal shaped size-class structure with many large trees. The five other congeners were more abundant and had a distinct L-shaped size-class structure with few large individuals. The distribution patterns of some species changed with size-class. For example, *S. anomala* at DBH <5 cm had significant aggregation at small scales. In contrast, *S. anomala* at DBH \geq 5 cm was randomly distributed at all study scales. For small plants of DBH <5 cm, the degree of aggregation of *S. adenophylla* and *S. laurina* was much higher than that of the other congeners, but for large individuals of DBH \geq 5 cm, *S. wikstroemiifolia* had the highest degree of aggregation of all six congeners. The spatial associations between some species pairs also varied by size-class. For example, the GoF test detected a symmetrically positive association between small–small trees at scales of 0–10 m, but no correlation between large–large trees or large–small trees. The observed size-dependent changes in the distribution pattern of the six congeners and their associations are possibly due to the changes of functional traits of species with increasing tree size. Because tree functional traits such as stem diameter, leaf mass, specific leaf area, and N/P ratio in leaf usually have underlying effects on species survival and competitive ability, such traits typically vary with tree size (Iida et al. 2014). Moreover, the spatial patterns of the congeners and their associations were found to change with spatial scales, and the intensity of aggregation and association decreased as scaling increased as a whole.

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References

- Ackerly DD, Donoghue MJ (1998) Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *Am Nat* 152:767–791
- Alvarez-Loayza P, Terborgh J (2011) Fates of seedling carpets in an Amazonian floodplain forest: Intra-cohort competition or attack by enemies? *J Ecol* 99:1045–1054
- Augspurger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211–217

- Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, Freckleton RP, Lewis OT (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85–88
- Bell T, Freckleton RP, Lewis OT (2006) Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecol Lett* 9:569–574
- Beltrán E, Valiente-Banuet A, Verdú Verd M (2012) Trait divergence and indirect interactions allow facilitation of congeneric species. *Ann Bot* 110:1369–1376
- Bevill RL, Louda SM (1999) Comparisons of related rare and common species in the study of plant rarity. *Conserv Biol* 13:493–498
- Bunyavejchewin S, LaFrankie JV, Baker PJ, Kanzaki M, Ashton PS, Yamakura T (2003) Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. *For Ecol Manag* 175:87–101
- Cipriotti PA, Aguiar MR (2005) Effects of grazing on patch structure in a semi-arid two-phase vegetation mosaic. *J Veg Sci* 16:57–66
- Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332
- Condit R (1998) Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a Comparison with other plots. Springer, Berlin, pp 17–19
- Condit R, Ashton PS, Baker PJ, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP, Foster RB, Itoh A, LaFrankie JV, Lee HS, Losos E, Manokaran N, Sukumar R, Yamakura T (2000) Spatial patterns in the distribution of common and rare tropical tree species. *Science* 288:1414–1418
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer PJ, Gradwell GR (eds) Dynamics of numbers in populations. Center for Agricultural Publication and Documentation, Wageningen, pp 298–312
- Cowling RM (2001) Endemism. In: Levin SA (ed) Encyclopedia of biodiversity. Academic Press, San Diego, pp 497–507
- Davies SJ, Palmiotto PA, Ashton PS, Lee HS, LaFrankie JV (1998) Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *J Ecol* 86:662–673
- Editorial Board for Flora of China, Chinese Academy of Sciences (1974) The sixtieth volumes of Flora of China (second fascicule). Science Press, Beijing, pp 1–8 (in Chinese)
- Felinks B, Wiegand T (2008) Exploring spatiotemporal patterns in early stages of primary succession on former lignite mining sites. *J Veg Sci* 19:267–276
- Fritsch PW, Kelly LM, Wang Y, Almeda F, Kriebel R (2008) Revised infrafamilial classification of *Symplocaceae* based on phylogenetic data from DNA sequences and morphology. *Taxon* 57:823–852
- Gao M, Wang X, Wang D (2014) Species spatial distribution analysis using nearest neighbor methods: aggregation and self-similarity. *Ecol Res* 29:341–349
- Grubb PJ (1977) Maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145
- Hammond DS, Brown VK (1998) Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Dynamics of tropical communities: the 37th symposium of the British Ecological Society, Cambridge University, pp 51–78
- Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495

- He F, Legendre P, LaFrankie JV (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. *J Veg Sci* 8:105–114
- Howe HF (1989) Scatter-and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79:417–426
- Hubbell SP, Ahumada JA, Condit R, Foster RB (2001) Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecol Res* 16:859–875
- Iida Y, Kohyama T, Swenson NG, Su SH, Chen CT, Chiang JM, Sun IF (2014) Linking functional traits and demographic rates in a subtropical tree community: the importance of size dependency. *J Ecol* 102:641–650
- Inman-Narahari F, Ostertag R, Asner GP, Cordell S, Hubbell SP, Sack L (2014) Trade-offs in seedling growth and survival within and across tropical forest microhabitats. *Ecol Evol* 4:3755–3767
- Jansen PA, Visser MD, Wright SJ, Rutten G, Muller-Landau HC (2014) Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecol Lett* 17:1111–1120
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Kikvidze Z, Pugnaire FI, Brooker RW, Choler P, Lortie CJ, Michalet R, Callaway RM (2005) Linking patterns and processes in alpine plant communities: a global study. *Ecology* 86:1395–1400
- Lan G, Getzin S, Wiegand T, Hu Y, Xie G, Zhu H, Cao M (2012) Spatial distribution and interspecific associations of tree species in a tropical seasonal rain forest of China. *PLoS ONE* 7:e46074
- Li L, Ye WH, Wei SG, Lian JY, Huang ZL (2014) Spatial Patterns and Associations between Species Belonging to Four Genera of the Lauraceae Family. *PLoS ONE* 9:e111500
- Liao J, Bogaert J, Nijs I (2015) Species interactions determine the spatial mortality patterns emerging in plant communities after extreme events. *Sci Rep* 5:11229
- Lloyd KM, Lee WG, Wilson JB (2002) Competitive abilities of rare and common plants: comparisons using *Acaena* (Rosaceae) and *Chionochloa* (Poaceae) from New Zealand. *Conserv Biol* 16:975–985
- Mooney KA, Jones P, Agrawal AA (2008) Coexisting congeners: demography, competition, and interactions with cardenolides for two milkweed-feeding aphids. *Oikos* 117:450–458
- Nagel TA, Svobodab M, Diacia J (2006) Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. *For Ecol Manag* 226:268–278
- Queenborough SA, Burslem DFRP, Garwood NC, Valencia R (2007) Habitat niche partitioning by 16 species of Myristicaceae in Amazonian Ecuador. *Plant Ecol* 192:193–207
- Seri E, Shnerb NM (2015) Spatial patterns in the tropical forest reveal connections between negative feedback, aggregation and abundance. *J Theor Biol* 380:247–255
- Shuai F, Wang Y, Yu S (2014) Density dependence in forests is stronger in tropical and subtropical climates among closely related species. *Ecography* 37:659–669
- Simon MF, Hay JD (2003) Comparison of a common and rare species of *Mimosa* (Mimosaceae) in Central Brazil. *Austral Ecol* 28:315–326
- Swenson NG, Enquist BJ, Pither J, Thompson J, Zimmerman J (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology* 87:2418–2424
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *Am Nat* 179:303–314
- Wang X, Swenson NG, Wiegand T, Wolf AT, Howe R, Lin F, Ye J, Yuan Z, Shi S, Bai X, Xing D, Hao Z (2013) Phylogenetic and functional diversity area relationship in two temperate forests. *Ecography* 36:883–893
- Wang X, Wiegand T, Swenson NG, Wolf AT, Howe RW, Hao Z, Lin F, Ye J, Yuan Z (2015) Mechanisms underlying local functional and phylogenetic beta diversity in two temperate forests. *Ecology* 96:1062–1073
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475–505
- Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104:209–229
- Wiegand T, Gunatilleke S, Gunatilleke N (2007) Species associations in a heterogeneous Sri Lankan dipterocarp forest. *Am Nat* 170:e77–e95
- Wiegand T, He F, Hubbell SP (2012) A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography* 35:1–12
- Xu M, Yu S (2014) Elevational variation in density dependence in a subtropical forest. *Ecol Evol* 4:2823–2833
- Zhang J, Song B, Li BH, Ye J, Wang XG, Hao ZQ (2010) Spatial pattern and associations of six congeneric species in an old-growth temperate forest. *Acta Oecol* 36:29–38