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Spatial dispersion patterns of trees in a tropical rainforest in Xishuangbanna, southwest China

Received: 29 October 2008 / Accepted: 9 January 2009 / Published online: 7 March 2009
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Abstract Spatial dispersion patterns of trees at different life stages are an important aspect to investigate in understanding the mechanisms that facilitate species coexistence. In this paper, Ripley's univariate $L(r)$ and bivariate $L_{12}(r)$ functions were used to analyze spatial distribution patterns and spatial associations across different life stages of 131 tree species in a 20-ha plot of a tropical rainforest in Xishuangbanna, southwest China. Our results show that: (1) Saplings of 109 (83.2%) species have a significant clumped distribution, which confirms the ubiquity of clumped spatial distributions among tropical tree species. (2) Adults of 126 (96.2%) species have a random distribution suggesting that density-dependent mortality can make the spatial pattern of tropical trees more regular with time. (3) At small scales (0–10 m), 95 (72.5%) species have a neutral or negative sapling-adult association, implying that there is recruitment limitation within the vicinity of their conspecific adults. The reduction in spatial clumping in going from younger to older life stages and the neutral or negative sapling-adult association imply density-dependent mortality in the vicinity of adult trees. In accordance with the Janzen–Connell hypothesis, such

density-dependent mortality can free up space for other species to colonize, contributing to the maintenance of species diversity.

Keywords Janzen–Connell effects · Spatial distribution · Species diversity · Tropical rainforest · Xishuangbanna

Introduction

In recent decades, many ecological investigations have focused on identifying potential mechanisms for the maintenance of diversity in species-rich communities (Ashton 1998; Bunyavejchewin et al. 2003; Cadotte and Fukami 2005; Hubbell 2005). Numerous mechanisms have been proposed to explain tropical tree species coexistence at local scales, and many of these hypotheses invoke density- and frequency-dependent mechanisms (Volkov et al. 2005). One of these hypotheses is the Janzen–Connell (J–C) hypothesis (Volkov et al. 2005). Janzen and Connell noticed that seedlings of tropical trees found close to conspecific adults often suffer higher mortality than seedlings further away (Condit et al. 1992) and explained how this pattern can maintain diversity in a community (Condit 1995). Hubbell et al. (1990) concluded that density-dependence contributed a limited role to the maintenance of tree species diversity in Barro Colorado Island (BCI) forest and Condit et al. (1994) suggested that the role of density-dependence may only be important among those species with the highest population densities. However, later research showed that density-dependence was rather common in tropical forests (Wills et al. 1997; Harms et al. 2000; Peters 2003).

The major objective of our study was to enhance our knowledge about the spatial patterns of tree species in the tropical dipterocarp rainforest of Xishuangbanna (southwest China), and to improve the understanding of how spatial dispersion patterns contribute to the interpretation of tropical tree diversity. In 2007, we

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established a 20-ha dynamics plot in Xishuangbanna in order to monitor long-term changes in tree populations and to test theories and hypotheses related to the biodiversity of tropical rain forests. Compared to most CTFS permanent plots, the Xishuangbanna plot has greater habitat heterogeneity: elevation in our plot ranges from 709 to 869 m, with three creeks (Lan et al. 2008), whereas elevation ranges from 70 to 90 m in Pasoh (Malaysia), and from 120 to 160 m in BCI (Panama). The Sinharaja plot also has large habitat heterogeneity, and about 79% of species positively or negatively associate with different habitats (Gunatilleke et al. 2006). We therefore predicted that habitat heterogeneity is probably responsible for the high diversity of the Xishuangbanna rain forest. Habitat heterogeneity always makes species have a clumped distribution. In this case, there will be more saplings within the vicinity of their conspecific adults, habitat heterogeneity will make the sapling-adult association to be positive, whereas the J–C effects have the opposite effect.

In this study, we investigate whether there is any evidence that J–C effects might be contributing to the maintenance of diversity in this forest. Previous studies focusing on detecting J–C effects have analyzed the mortality or growth (recruitment or survival) of individual species (Hubbell et al. 1990; Condit et al. 1992, 1994; Peters 2003), or have analyzed the density after (or before) predation of naturally occurring seeds at different distances from the parent tree (Burkey 1994). In this paper, we test the J–C hypothesis by using Ripley's L-function in two ways: (1) By dividing the tree species into three life stages (saplings, poles, and adults) and examining how the spatial patterns change across the life stages; (2) By analyzing spatial associations among saplings, poles, and adults. Density-dependent mortality should produce less aggregated distributions as cohorts become older. Reduction of spatial aggregation of species for older life stages could therefore indicate the presence of J–C effects. A negative sapling-adult association would indicate recruitment limitation near adults, possibly indicating J–C effects on early seeds and seedlings.

Study site and methods

Study site

The study was conducted in the tropical rainforest of Xishuangbanna National Nature Reserve (101°34'26"–47" E, 21°36'42"–58" N), located in southwest China. The dry season is from November to April (Cao et al. 2006). Mean annual rainfall (recorded at Mengla County, 14 km from the study site) is 1,531.9 mm and annual mean temperature is 21.0°C (Zhu 2006). Mean temperatures of the hottest and coldest months are 24.6 and 15.2°C, respectively. The forest of our study site reaches up to 60 m high, and is dominated by *Parashorea chinensis* Hsie Wang of Dipterocarpaceae (Zhang

and Cao 1995). The thickest tree is *P. chinensis* with DBH 191.10 cm. Other canopy species, such as *Pometia tomentosa* (Blume) Teijsm. & Binn., *Semecarpus reticulatus* Lecomte, *Sloanea tomentosa* (Benth.) Rehder & E. H. Wilson, are very common and usually constitute the tree layers between 30 and 45 m. *Pittosporopsis kerrii* Craib is the most abundant species dominating the treelet layer. Other species, such as *Mezzettiopsis creaghii* Ridl., *Saprosma ternata* Hook. f., *Leea compactiflora* Kurz are also very common in the treelet layer. Due to the development of rubber plantations in the area, the remaining areas of this primary forest are decreasing, and only occur in 16 patches along the gullies of some rivers with a total cover of ca. 800 ha (Zhu 1992).

Methods

A permanent plot of 20 ha was established in the tropical dipterocarp rainforest in Xishuangbanna, southwest China, in 2007, following existing methodology for large forest dynamics plots, such as the one on Barro Colorado Island, Panama (Condit 1998). The plot measures 400 × 500 m, and covers an elevation gradient from 709 to 869 m a.s.l. with the highest elevation located in the northwest. Three perennial streams join southwest of the plot. Free-standing trees of ≥1 cm in diameter at breast height (DBH) in the 20-ha plot, were tagged with sequentially numbered aluminium tags. Tree diameter was measured at 1.3 m from the ground, unless there were abnormalities on the trunk, in which case the measurement was taken at the nearest lower or upper point where the stem was cylindrical (Condit et al. 1996; Ayyappan and Parthasarathy 1999). Trees with multiple stems were counted as a single individual, but each stem was tagged and measured (Condit 1998). All free-standing trees ≥1 cm DBH were identified to species. The identification of plant species were based on the English version of "Flora of China". Furthermore, we collected specimens from every species, and these vouchers were stored at the herbarium of the Xishuangbanna Tropical Botanical Garden.

In order to test how widespread Janzen–Connell effects are in our plot, we only considered species with more than 80 individuals. Those species having less than five adults were also excluded. We finally selected 131 species, which account for 28.1% of total species and 92.6% of the total individuals. Individuals of each of these species were classified into three life stages: saplings (1 to ≤ 5 cm DBH), poles (5 to ≤ D_{95,0.1} cm DBH) and adults (> D_{95,0.1} cm DBH). Here, D_{95,0.1} is the 95th percentile of diameter of all trees ≥0.1 × D_{max}, and D_{max} is the diameter of the thickest tree (King et al. 2006). For treelets (with maximum DBH no more than 20 cm), stems between 1 and 3 cm in diameter were classified as saplings, and poles included stem diameters between 3 and D_{95,0.1} cm.

All calculations and simulations were computed using R software and spatstat package. Ripley's *K*-function

characterizes spatial patterns at a range of distances for both univariate and bivariate analysis (Perry et al. 2006). Mathematically, the edge-corrected estimated Ripley's K -function for detecting departures from complete spatial randomness is defined as (Cressie 1993; Woodall and Graham 2004):

$$\hat{K}(r) = \frac{1}{\hat{\lambda}} \frac{1}{N} \sum_{i=1}^N \sum_{\substack{j=1 \\ j \neq i}}^N \frac{1}{w(S_i, S_j)} I(\|S_i - S_j\| \leq r) \quad (1)$$

where r is the step-size, N the number of trees in the study area, $|A|$ the size of the study area, $\hat{\lambda} = N/|A|$, the estimated tree density, $w(S_i, S_j)$, the proportion of the circumference of a circle centered at S_i , passing through S_j , and that is inside the study region. A. Larger Ripley's $K(r)$ values at a certain (r) may indicate attractive properties (clustering) among individual trees, while smaller Ripley's $K(r)$ values at the same (r) may indicate dispersive spatial properties (regularity) among individual trees. The transformation of Ripley's K -function to $L(r)$

$$L(r) = \sqrt{K(r)/\pi} - r \quad (2)$$

can simplify the interpretation of $K(r)$ (Hou et al. 2004). By using the $L(r)$ function, the univariate spatial patterns of the 131 species at different growth stages were analyzed. Our null hypothesis is that distributions are random, and we test for significant deviations from this null-model. Values of $L(r) < 0$ indicate a regular distribution and $L(r) > 0$ indicates clumping at scale r . A Monte-Carlo simulation was used to test the statistical significance of deviations of $L(r)$ from zero under the null hypothesis of complete spatial randomness (CSR) (Besag and Diggle 1977; Hou et al. 2004). If the distribution pattern of the object species was heterogeneous, then a heterogeneous Poisson process was chosen as the alternative to CSR. Confidence intervals of 99% were generated using high and low values of $L(r)$ obtained from 99 simulations of random permutations (Ripley 1977).

Similar to the univariate case, the K -function can be extended to the bivariate case to quantify the relationship between the two species, defined as (Lotwick and Silverman 1982):

$$\tilde{K}_{12}(r) = \frac{1}{\lambda_2} \frac{1}{N_1} \sum_{i=1}^{N_1} \sum_{j=1}^{N_2} \frac{1}{w(S_i^{(1)}, S_j^{(2)})} I(\|S_i^{(1)} - S_j^{(2)}\| \leq r) \quad (3)$$

where N_1 and N_2 are the number of two species, respectively, in the study area, $w(S_i^{(1)}, S_j^{(2)})$ is the proportion of the circumference of the circle with center $S_j^{(1)}$ and radius r that lies within the study region A . To analyze spatial relationships among different life stages of these species, we used Ripley's $K_{12}(r)$ bivariate analysis's transformation $L_{12}(r)$:

$$L_{12}(r) = \sqrt{K_{12}(r)/\pi} - r \quad (4)$$

(Diggle 1983; Upton and Fingleton 1985; Hou et al. 2004, 2006). Values of $L_{12}(r)$ within the confidence intervals indicate that there is no interaction between saplings and adults (or poles and adults), while values of $L_{12}(r)$ above (or below) the upper (or lower) confidence interval indicate a positive (or negative) association at scale r , respectively.

Results

A total of 95,834 trees ≥ 1 cm DBH was enumerated in the 20-ha plot. Ultimately, 95,498 (99.65%) individuals were identified to 468 species or morphospecies, belonging to 213 genera and 70 families (Lan et al. 2008). Most of the studied species have a large number of juveniles, especially for *P. chinensis*, *Garcinia cowa* Roxb., *M. creaghii* and *Knema furfuracea* (Hook. f. & Thomson) Warb., indicating that they have a self-replacing recruitment. Distribution maps of the two abundant species (with individuals greater than 1,000) and two common species (with individuals greater than 100 but less than 1,000) across three life stages were plotted (Fig. 1). These maps clearly show that trees are not uniform across the plot: some species are found in the gullies whereas others are found on the slope. It is interesting that fewer adult trees appear to be found within the vicinity of saplings, especially for *Cinnamomum bejolghota* (Buch.-Ham.) Sweet.

Spatial distribution pattern

The spatial pattern of each life stage of the 131 species was analyzed in the 20-ha plot with univariate spatial analysis. For saplings, 109 (83.2%) species show a significantly clumped distribution at certain scales (Table 1), whereas only 20 (15.3%) species show a random distribution at all study scales. For poles, 66 (50.4%) tree species have a significant clumped distribution and 63 (48.1%) species have a random distribution. However, for adults, 126 (96.2%) tree species have a random distribution at all the study scales. There are only five species whose adults have an aggregated distribution at certain scales. The change in distribution pattern is of the clump-clump (or random)-random from saplings to adults. Figure 2 shows the spatial patterns of two abundant species and two common species.

Spatial association among life stages

Bivariate analysis was used to analyze spatial associations among different life stages within species. At small scales (0–10 m), 85 (64.9%) species have a neutral sapling-adult association and ten (7.6%) species have a

Fig. 1 Distribution maps of the four species in the 20-ha plot of tropical rainforest in Xishuangbanna, southwest China (n is the total abundance of species in the entire plot; $D95_{0.1}$ is the adult size for the species; Green cross saplings, blue circle poles, red square adults)

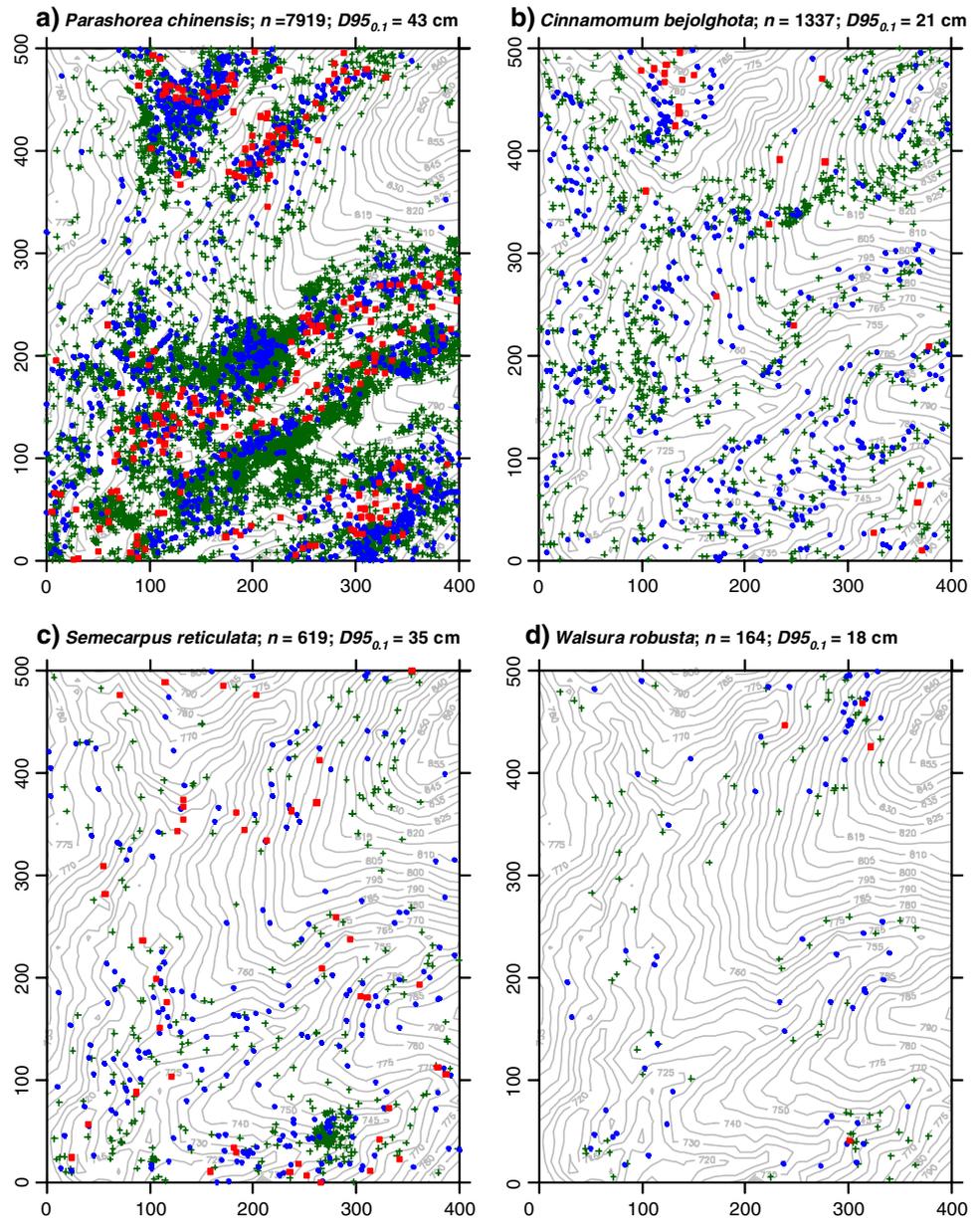


Table 1 Summary of the distribution patterns for the 131 species at different growth stages in the 20-ha plot of tropical rainforest in Xishuangbanna, southwest China

Life stages	No. of species (%)		
	Aggregated	Random	Regular
Saplings	109 (83.2)	20 (15.3)	2 (1.5)
Poles	66 (50.4)	63 (48.1)	2 (1.5)
Adults	5 (3.8)	126 (96.2)	0 (0)

negative association. However, at large scales (30–50 m), more than 104 (73.6%) species have a positive sapling-adult association. For the association between poles and adults, 87 (66.4%) species have a neutral and eight (6.1%) species have a negative association at small scales

(0–10 m). Whereas, at large scales (30–50 m), more than 104 (73.6%) species have a positive pole-adult association. Figure 3 shows the spatial association of two abundant species and two common species.

Discussion

Previous studies of spatial pattern of tropical trees in other CTFS plots (He et al. 1997; Condit et al. 2000; Plotkin et al. 2000, 2002; Bunyavejchewin et al. 2003) have concluded that most species are clumped, and a few are randomly distributed. Spatial patterns shift from high clumping to looser intensity clumping or random distribution when moving from juveniles to adults (He et al. 1997) (Table 2).

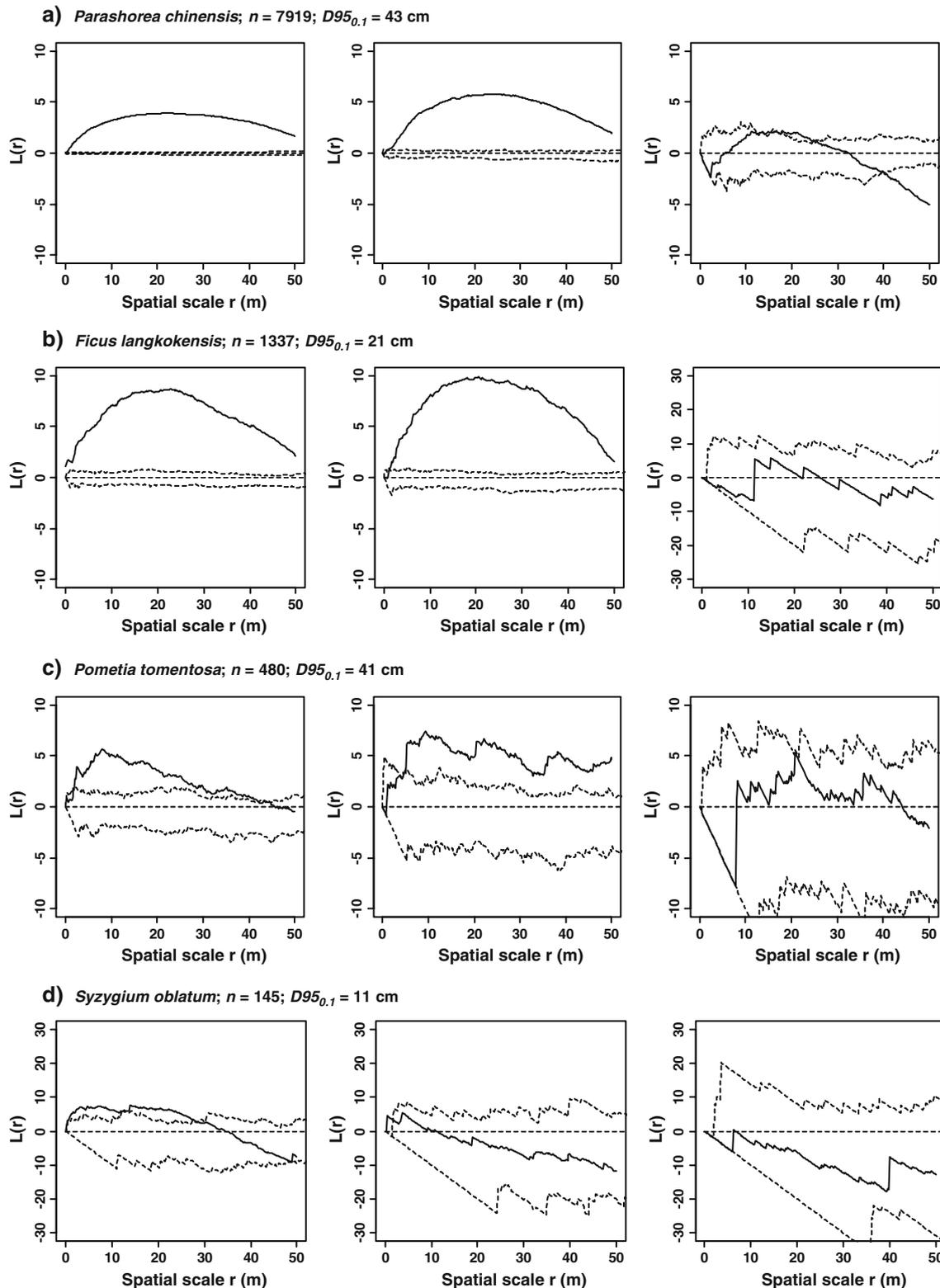


Fig. 2 Plots of $L(r)$ versus scale r (black lines) for different growth stages of four species in the 20-ha plot (dashed lines correspond to 99% confidence intervals generated from 99 Monte Carlo

simulations. $L(r) = 0$ indicates that the spatial pattern at scale r is entirely random; $L(r) < 0$ indicates a regular pattern; $L(r) > 0$ indicates clumped pattern)

In this study, most saplings or poles are significantly clumped at certain scales. Adults of the most species have a random distribution at all scales (0–50 m).

However, *P. chinensis* and *Engelhardtia spicata* Lesch. ex Blume adults show a clumped distribution. Clumped distribution patterns can be caused by regeneration

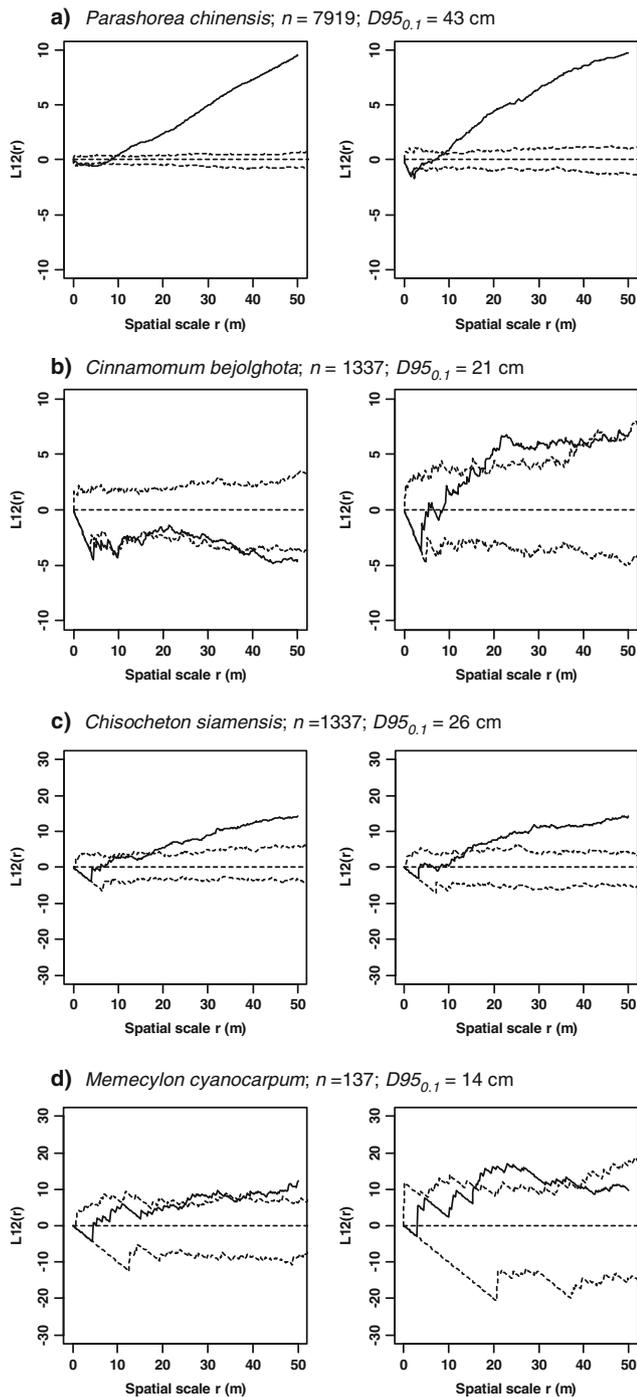


Fig. 3 Plots of $L_{12}(r)$ versus scale r (black lines) for association among different growth stages of four species in the 20-ha plot (dashed lines correspond to 99% confidence intervals generated from 99 Monte Carlo simulations). $L_{12}(r) = 0$ indicates neutral association; $L_{12}(r) < 0$ indicates negative association; $L_{12}(r) > 0$ indicates positive association)

strategies (such as limited seed dispersal or vegetative recruitment), topographical heterogeneity, canopy gaps, and disturbances (Hou et al. 2004). *P. chinensis* and *E. spicata* produce winged seeds and are wind dispersed, however, seeds of other species are mainly dispersed by

animals. The results of our study confirm Condit et al.'s (Condit et al. 2000; Seidler and Plotkin 2007) suggestion that wind-dispersed species are poorly dispersed compared to animal-dispersed species and tend to show an aggregated distribution.

Another important finding here is that most young trees (saplings) of the 131 studied species have a significant clumped distribution, but adults have a random distribution. This is similar to He et al.'s (1997) results. Density-dependent mortality of the offspring can contribute to this change in spatial distribution from clumped to random and promote species diversity (Itoh et al. 1997). Density-dependent mortality might be caused by specific pathogens or enemies or by competition (Getzin et al. 2006).

Janzen (1970) and Connell (1971) hypothesized that host-specific pests reduce recruitment near conspecific adults thereby freeing space for other plant species (Wright 2002). The neutral and negative associations between adults and saplings indicate that there is recruitment limitation within the vicinity of the conspecific adults (Bunyavejchewin et al. 2003), which is likely a result of predation of seeds and seedlings. For *P. chinensis*, the dominant canopy species in the forest, nearly 60–70% of the seeds fall within a circle of 1–8 m near the conspecific adults, and most of the seeds (56.95%) suffer from insect pests before germination (Yin and Shuai 1990). Furthermore, *P. chinensis* seedlings also suffer from predation by *Xyleborus formicatus* Eichhoff (Coleoptera) (Yan and Cao 2008).

J–C effects could make the sapling–adult association to be negative at small scales, whereas habitat association can make such association positive because many trees show habitat preference in tropical forests (Yamada et al. 2007). In our study, spatial associations among life stages show that at small scales (0–10 m), most of the studied species have a neutral or negative sapling–adult association, indicating the presence of J–C effects. Since habitat association and J–C effects have opposite effects on the sapling–adult association, the importance of J–C effects in our plot could be stronger than that observed. Our results are very similar to a previous study in the seasonal dry evergreen forest at Kuai Kha Khaeng in western Thailand (Bunyavejchewin et al. 2003).

Concluding, our results clearly show that the degree of spatial clumping decreases from saplings, to poles, to adults in most species. The reduction of spatial aggregation with life stages is indirect evidence of a J–C spacing effects. The negative and neutral associations between saplings and adults at small scales (0–10 m) are further evidence of J–C spacing effects. However, there are other mechanisms for the maintenance of diversity in our plot. For example, some species are confined to the gullies of the plot, whereas some are confined on the slope (Fig. 1), indicating the presence of habitat associations. The positive spatial associations between adults and younger life-history stages at larger spatial scales (> 30 m) suggest that either habitat association or dispersal limitation exists in our plot. These suggest that the tropical rainforest in

Table 2 Summary of the spatial associations for the 131 species at different growth stages in the 20-ha plot of tropical rainforest in Xishuangbanna, southwest China

Scales (m)	No. of spatial association (%)					
	Saplings-adults			Poles-adults		
	Negative	Neutral	Positive	Negative	Neutral	Positive
0–10	10 (7.6)	85 (64.9)	36 (27.5)	8 (6.1)	87 (66.4)	36 (27.5)
10–20	4 (3.1)	43 (32.8)	84 (64.1)	1 (0.8)	52 (39.7)	78 (59.5)
20–30	3 (2.3)	32 (24.4)	96 (73.3)	0 (0)	34 (26.0)	97 (74.0)
30–40	4 (3.1)	23 (17.6)	104 (79.4)	0 (0)	27 (20.6)	104 (79.4)
40–50	3 (2.3)	21(16.0)	107 (81.7)	0 (0)	24 (18.3)	107 (81.7)

Xishuangbanna and its high diversity are subjected to multiple controlling factors, including habitat association, limited seed dispersal, and, as demonstrated here, J–C effects. Further studies are required to understand the relative importance of these different factors in the maintenance of tree diversity in Xishuangbanna.

Acknowledgments This project is supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (KZCW2-YW-430, KSCX2-YW-N-066) and the National Natural Science Foundation of China (30570128). We thank Dr. Fangliang He, Chuck Cannon, Dr. Ferry Slik, Dr. I-fang Sun and Dr. Keping Ma for their helpful suggestions and assistance in establishing the plot and data analysis. We thank Dr. Mahnew William and Dr. Miquel De Cáceres Ainsa for their help in improving the English writing in the article. We also thank two anonymous reviewers who gave us some constructive and helpful comments.

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