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Aggregated spatial distributions of species in a subtropical karst forest, southwestern China

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Abstract

Aims

Spatial distribution patterns of species reflect not only the ecological processes but also the habitat features that are related to species distribution. In karst topography, species distribution patterns provide more specific information about their environments. The objectives of this study are as follows: (i) to analyse and explain the spatial distribution patterns of conspecific trees in an old-growth subtropical karst forest; (ii) to investigate pattern changes at different spatial scales; (iii) to test the spatial pattern similarity (or dissimilarity) between trees at different abundances, diameter at breast height classes, canopy layers and different functional groups (shade tolerance and seed dispersal mode); (iv) to examine whether habitat heterogeneity has an important effect on the species spatial distribution.

Methods

The spatial distributions of woody species with ≥20 individuals in a 1-ha subtropical karst forest plot at Maolan in southwestern China were quantified using the relative neighbourhood density Ω based on the average density of conspecific species in a circular neighbourhood around each species.

Important Findings

Aggregated distribution is the dominant pattern in the karst forest, but the ratio of aggregated species in total species number decreases with an increase in spatial scale. Less abundant species are more aggregated than most abundant species. Aggregation is weaker in larger diameter classes, which is consistent with the prediction of self-thinning. Seed dispersal mode influences spatial patterns, with species dispersed by animals being less aggregated than those dispersed by wind and gravity. Other species functional traits (e.g. shade tolerance) also influence the species spatial distributions. Moreover, differences among species habitat associations, e.g. with rocky outcrops, play a significant role in species spatial distributions. These results indicate that habitat heterogeneity, seed dispersal limitation and self-thinning primarily contribute to the species spatial distributions in this subtropical karst forest.

Keywords: functional trait • habitat heterogeneity • karst forest • relative neighbourhood density • spatial distribution • species coexistence.

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INTRODUCTION

The species spatial distribution in forest stands is of particular interest in ecological studies because it reveals information about the stand history, population dynamics and species competition (Haase 1995). Furthermore, it infers the underlying ecological processes or mechanisms (Manabe *et al.* 2000; Nishimura *et al.* 2008; Wiegand *et al.* 2007). Species often distribute aggregately in natural forests (Condit *et al.* 2000; Hardy and Sonké 2004; He *et al.* 1997). In recent decades, numerous mechanisms were proposed to explain the formation of species aggregation in forests. For example, many ecologists successfully demonstrated that plant species are restricted to a more or less wide range of habitats (Itoh *et al*. 2003; Takyu and Kitayama 2002). Large forest plots worldwide show that tree species are closely associated with habitat factors (e.g. topographic and edaphic) and microhabitat heterogeneity created by such factors at local scales in the tropics (e.g. Gunatilleke *et al*. 2006; Lai *et al*. 2009; Queenborough *et al*. 2007; Sri-Ngernyuang *et al*. 2003; Yamada *et al*. 2006). Habitat heterogeneity is an important factor in the regulation of species distributions (Harms *et al*. 2001; Yamada *et al*. 2006). Species-specific differences in functional traits and ecological strategies also affect the spatial distribution and dynamics of species (Condit *et al*. 2006; Lortie *et al*. 2004; Murrell 2009). For example, the seed dispersal ability affects species distributions, with poorly dispersed species being more aggregated than well-dispersed ones (Condit *et al*. 2000; Li *et al*. 2009). However, ecologists argued that a single dominant mechanism may not drive patterns of tree species distribution, especially in species-rich forests. Several researchers found that species distributions in plant communities are determined by both habitat heterogeneity and dispersal limitation (Lin *et al*. 2011; Plotkin *et al*. 2002; Shen *et al*. 2009; Wiegand *et al*. 2007). He *et al*. (1997) suggested that the distribution patterns of tree species in tropical forests are subjected to multiple controlling factors, e.g. topography, spacing effect, density-dependent processes and species rarity. Therefore, multiple controlling mechanisms may work together to organize the structure and to maintain the high diversity of species-rich forests. Identifying the multiple factors affecting species spatial distribution in various forest ecosystems is essential because it provides valuable insights into processes that structure communities and permit species coexistence.

Existing knowledge about species spatial distributions and underlying mechanisms in species-rich communities is insufficient because most of the research are mainly derived from tropical (Condit *et al*. 2002; Nishimura *et al*. 2008; Queenborough *et al*. 2007; Seidler and Plotkin 2006) and subtropical forests worldwide (e.g. Lai *et al*. 2009; Legendre *et al*. 2009; Li *et al*. 2009). Furthermore, forests in other bioclimatic zones and specific forests within tropical and subtropical zones should be considered in testing the applicability of these theories or hypotheses developed from tropical and subtropical forests. The karst forest in the subtropics, which is characterized by a hyper-diverse habitat heterogeneity and a hyper-complex species composition (e.g. in the subtropical southwestern China; Zhang *et al*. 2010), is an alternative example. The spatial patterns of tree distributions and their underlying formation mechanisms in such few reported forests can improve our understanding of the mechanisms of species diversity (He *et al*. 1996) and stable species coexistence (Gunatilleke *et al*. 2006).

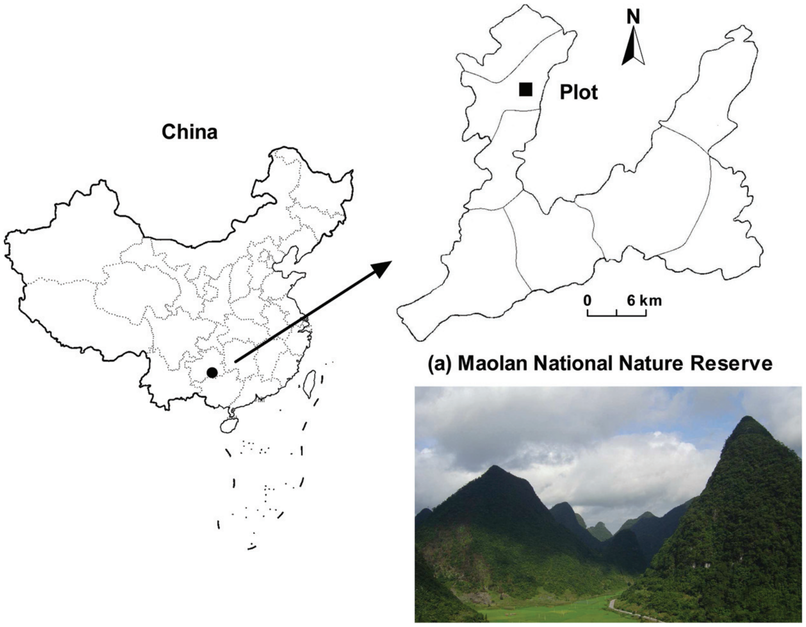
On the other hand, the karst forest in China is mainly distributed in the southwest mountainous regions, where the continuous, largest karst landscape in the world is located (Yuan 1991). The representative subtropical mixed evergreen–deciduous broad-leaved forest in southern Guizhou Province has a specific habitat, a complex community structure and a rich biodiversity (Hou and Jiang 2006; Long *et al*. 2005; Zhu and Wei 1993). The spatial patterns of eight dominant tree species in two forest plots (Zhang *et al*. 2010) showed that six species have significant aggregations at the majority of the scales, whereas the other two species show a random distribution pattern at most scales. Habitat heterogeneity is the key factor in determining the spatial distributions of eight tree species, implying the existence of niche theory in species-rich karst forests. However, the spatial distribution patterns of other woody species are still unclear.

The large plot size containing detailed information about plant distributions is essential to address species spatial patterns and sustainable extraction of tree species, especially in tropical forests (Condit *et al*. 1994; Condit 1995). However, studies of the species spatial patterns at a relatively small scale (0–100 m) also helped to identify the relative importance of ecological processes in structuring tree-dominated communities (Getzin *et al*. 2006; Moeur 1993; Salas *et al*. 2006; Strasberg 1996; Yasuhiro *et al*. 2004), especially in places where it is not possible to set-up large-sized plots. This article reports on all of the 43 species spatial distributions with ≥20 individuals in a 1-ha karst forest plot at Maolan, southern Guizhou Province. The objectives of this study were as follows: (i) to analyse and explain the spatial distribution patterns of conspecific trees in an old-growth subtropical karst forest; (ii) to investigate the pattern changes at different spatial scales; (iii) to test the spatial pattern similarity (or dissimilarity) between trees at different abundances, diameter at breast height (DBH) classes, canopy layers and different functional groups (shade tolerance and seed dispersal mode); (iv) to examine whether habitat heterogeneity has an important effect on the species spatial distributions. This study is expected to provide important insights into the possible mechanisms that maintain the assemblage of species in a karst forest.

MATERIALS AND METHODS

Study site

The study was conducted in a Man and the Biosphere reserve, namely, the Maolan National Natural Reserve (MNNR) (25°09′20′′–25°20′50″N, 107°52′10″–108°05′04″E) located in Libo County, southwestern China's Guizhou Province (Fig. 1a). In this ~20 000-ha reserve, the elevation ranges from 430 to 1078.6 m with an average of 800 m, but the relative peak elevations are generally from 100 to 300 m. Topography is characterized by the typical karst fengcong depression (a combination of clustered peaks, cylindrical and cone-shaped towers, with a common rocky base) (Fig. 1b). Carbonate rocks (mainly of pure limestone and dolomite) are usually exposed on the surface. Therefore, soils are thin and discontinuous in the karst terrain. However, the shallow black limestone soil is rich in organic matter, nutrients (N, P and K) and Ca. This region has a subtropical monsoon climate with plateau climate features such as mild temperature and plenty of rainfall



(a) Maolan National Nature Reserve

(b) Karst fengcong-depression landscape

Figure 1: location of the 1 ha plot (a) and the typical karst landscape (b) in the Maolan National Natural Reserve, southwestern China.

throughout the year, but with humid air and cloudy sky. The mean temperature ranges from 8.3°C in January to 26.4°C in July, with an annual mean of 15.3°C. The mean annual frost-free period lasts 315 days. The average annual precipitation is 1320.5 mm. The mean annual relative humidity is 83%. The mean sunshine percentage is only ~20%.

Data collection

The karst terrain is too complex and steep (Fig. 1b) to find a relatively flat area for setting up a bigger forest plot of 16–50 ha similar with many permanent forest plots in the world. Thus, a 1-ha (100 × 100 m) plot in the summer of 2008 was established in a typical old-growth mixed evergreen–deciduous broad-leaved forest of MNNR (Fig. 1a). To our knowledge, there is no large plot bigger than 1 ha in the subtropical karst forest in the world. This plot is situated near the top of a hill (25°18′07″N, 107°57′21″E), spanning an altitudinal range of 895–938 m. Two slopes facing southeast and northeast are included. The plot is gently flat in the lower and higher parts, rather moderate or steep in the middle, and with numerous outcrop rocks in the mid-lower part. The mean slope is ~30°. The whole-plot slope ranges from 5° to 48°. The soils are slightly acidic to neutral.

The plot was divided into 100 contiguous 10 × 10 m subplots using the DQL-1 forest compass (Harbin Optical Instrument Factory, China). Each subplot was further divided into four 5 × 5 m quadrats. All free-standing woody plants with ≥1-cm DBH were investigated, with each quadrat as the basic unit of vegetation survey. The species names, relative geographic coordinates of each individual and DBH were recorded. Meanwhile, the rock-bareness (basement rock was exposed on the ground surface and not covered by soils) percentage within each quadrat was visually estimated. Vertically, the old-growth karst forest is typically stratified into three vegetation layers and species that occupy different canopy levels at maturity. Thus, the species guilds (groups) were easily distinguished as overstory, midstory and understory tree species (Table 1). The shade tolerance and seed dispersal mode were identified according to the Editorial Board for Flora of Guizhou (1982). A total of 3857 individuals belonging to 58 families, 121 genera and 191 species were documented. The basal area was 23.62 m^2 ha^{-1}. The plot is dominated by *Castanopsis carlesii* var. *spinulosa*, *Cyclobalanopsis myrsinifolia*, *Distylium myricoides*, *Rhododendron latoucheae*, *Osmanthus fragrans*, *Platycarya longipes*, *Engelhardtia roxburghiana*, *Rapanea neriifolia* and *Cyclobalanopsis glauca*. The spatial patterns of 43 species with ≥20 individuals (Table 1) were analysed to obtain a sufficiently large sample size. These species comprised 86.4% of the stems in the plot.

Data analysis

Second-order point pattern analyses are the most widely used methods in quantifying stem-mapped tree distributions. These analyses include the Ripley's K function (Ripley 1977) and the relative neighbourhood density function Ω (Condit *et al.* 2000; Wiegand and Moloney 2004), which have been commonly applied to detect individual spatial arrangements within communities and to generate hypotheses regarding the underlying processes controlling the observed patterns (Stoyan and Stoyan 1994; Wiegand *et al.* 2007). The Ripley's K function and index Ω are closely related. K is the cumulative distribution function of distances between pairs of points, whereas Ω is the derivative of the K function and is, thus, a probability density function

Table 1. properties of 43 woody species with ≥20 individuals in a subtropical, mixed evergreen–deciduous broad-leaved karst forest in Maolan, southern Guizhou Province

Species	Family	No. of individuals	Canopy layer	Shade tolerance	Dispersal mode
Acer fabri	Aceraceae	57	Midstory	Shade tolerant	Wind
Adina pilulifera	Rubiaceae	30	Understory	Shade tolerant	Wind
Aidia canthioides	Rubiaceae	168	Understory	Shade tolerant	Gravity
Alniphyllum fortunei	Styracaceae	22	Overstory	Light demanding	Wind
Beilschmiedia kweichowensis	Lauraceae	31	Midstory	Shade tolerant	Gravity
Castanopsis carlesii var. *spinulosa*	Fagaceae	206	Overstory	Shade tolerant	Gravity
Carpinus pubescens	Betulaceae	34	Overstory	Light demanding	Gravity
Camellia furfuracea	Theaceae	39	Understory	Shade tolerant	Wind
Celtis biondii	Ulmaceae	27	Overstory	Light demanding	Animal
Cinnamomum wilsonii	Lauraceae	62	Midstory	Shade tolerant	Gravity
Clausena dunniana	Rutaceae	92	Understory	Shade tolerant	Gravity
Cyclobalanopsis myrsinifolia	Fagaceae	86	Overstory	Midtolerant	Gravity
Cyclobalanopsis glauca	Fagaceae	84	Overstory	Midtolerant	Gravity
Cyclobalanopsis sessilifolia	Fagaceae	27	Overstory	Midtolerant	Gravity
Daphniphyllum oldhami	Daphniphyllaceae	40	Understory	Shade tolerant	Gravity
Distylium myricoides	Hamamelidaceae	201	Midstory	Light demanding	Wind
Engelhardtia roxburghiana	Juglandaceae	221	Midstory	Light demanding	Wind
Eriobotrya henryi	Rosaceae	34	Midstory	Midtolerant	Wind
Euonymus myrianthus	Celastraceae	60	Understory	Shade tolerant	Gravity
Gardenia jasminoides	Rubiaceae	33	Understory	Shade tolerant	Wind
Ilex ficoidea	Aquifoliaceae	39	Midstory	Shade tolerant	Gravity
Lasianthus japonicus var. *lancilimbus*	Rubiaceae	97	Understory	Shade tolerant	Gravity
Lindera communis	Lauraceae	157	Understory	Shade tolerant	Wind
Lindera nacusua	Lauraceae	62	Understory	Shade tolerant	Wind
Lindera pulcherrima var. *hemsleyana*	Lauraceae	33	Understory	Shade tolerant	Animal
Lithocarpus henryi	Fagaceae	61	Overstory	Light demanding	Gravity
Litsea subcoriacea	Lauraceae	24	Midstory	Light demanding	Gravity
Machilus microcarpa	Lauraceae	26	Midstory	Shade tolerant	Animal
Meliosma fordii	Sabiaceae	36	Midstory	Midtolerant	Gravity
Neolitsea aurata	Lauraceae	52	Midstory	Shade tolerant	Animal
Osmanthus fragrans	Oleaceae	183	Midstory	Light demanding	Gravity
Pittosporum crispulum	Pittosporaceae	36	Understory	Shade tolerant	Wind
Pittosporum podocarpum	Pittosporaceae	28	Understory	Shade tolerant	Wind
Platycarya longipes	Juglandaceae	74	Overstory	Light demanding	Wind
Rapanea neriifolia	Myrsinaceae	205	Understory	Shade tolerant	Gravity
Reevesia glaucophylla	Sterculiaceae	73	Midstory	Light demanding	Wind
Rhododendron latoucheae	Ericaceae	174	Midstory	Shade tolerant	Wind
Sloanea sinensis	Elaeocarpaceae	97	Midstory	Midtolerant	Wind
Symplocos lancifolia	Symplocaceae	85	Understory	Shade tolerant	Gravity
Symplocos sumuntia	Symplocaceae	29	Midstory	Shade tolerant	Gravity
Swida austrosinensis	Cornaceae	20	Midstory	Light demanding	Gravity
Tarenna mollissima	Rubiaceae	22	Understory	Light demanding	Gravity
Vaccinium mandarinorum	Ericaceae	21	Understory	Shade tolerant	Animal

(Diggle 2003; Stoyan and Penttinen 2000). The *K* function confounds the effects of large scales with small scales because it is a cumulative measurement and each larger scale includes information from all smaller scales (George *et al.* 2006; Schurr *et al.* 2004; Wiegand *et al.* 2007). Ω isolates specific distance classes by replacing the Ripley's *K* function circles with rings and using the mean number of neighbours in a ring of radius and width around an individual (Wiegand and Moloney 2004). Thus, the index Ω has an intuitive biological interpretation as a local neighbourhood density (Condit *et al.* 2000).

Therefore, the relative neighbourhood density Ω (Condit *et al.* 2000) was used in this study to characterize the tree distributions in the plot. For a given species, Ω is equivalent to the average density of conspecifics in the neighbourhood of individuals, which is normalized by the density of the individual species in the entire plot:

$$\Omega_{\chi1,\chi2} = D_{\chi1,\chi2}/\lambda$$

where $D_{\chi1,\chi2} = \sum N_{\chi1,\chi2} \big/ \sum A_{\chi1,\chi2}$. $N_{\chi1,\chi2}$ is the number of conspecifics located between distances χ^1 and χ^2 from each individual, averaged by the overall individuals of the species, $A_{\chi1,\chi2}$ is the area of the annulus, and λ is the mean density of a given species in the entire plot. For a random distribution, $\Omega_{\chi1,\chi2} = 1$ within an annulus between χ^1 and χ^2 meters. $\Omega_{\chi1,\chi2} > 1$ indicates aggregation, whereas $\Omega_{\chi1,\chi2} < 1$ suggests regular distribution. Complete spatial randomness null models were chosen for analyses. The 99% statistical confidence limit was estimated by performing Monte Carlo procedure with 499 replicates. These calculations were analysed using software SpPack 1.38 (Perry 2004).

$\Omega_{0\text{–}10}$, which refers to the mean conspecific density within 10 m of a tree, was used as the intensity of species aggregation measurement (Condit *et al.* 2000) to compare species spatial patterns belonging to different characteristic groups. DBH was first used to divide species into six size classes (0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm and 40–50 cm). Second, species were classified into overstory, midstory and understory species. The third comparison was performed between species of different seed dispersal modes: wind, gravity and animal-dispersed species. Data were tested for normal distributions. The non-normal distributed data were log-transformed to achieve normalization. The differences between groups were then compared using the Student's *t*-test. A multiple regression for these 43 species of abundance ≥20 was conducted to analyse the effects of abundance, DBH, canopy layer, shade tolerance and dispersal mode on spatial patterns using $\Omega_{0\text{–}10}$ as the dependent variable. Abundance, maximum DBH, average DBH, canopy layer, shade tolerance and dispersal mode were used as the independent variables.

RESULTS

Most of the 43 species in the plot were aggregated at a scale of <50 m (Table 2). Although aggregation was a dominant pattern when all the DBH classes ≥1 cm were included in the analysis, the percentage of aggregated species decreased with the increase in spatial scale. For example, 93.0% of the species were significantly aggregated from 0 to 10 m, 81.3% of the species from 10 to 20 m and 69.8% of the species from 20 to 30 m (Table 2). The value of Ω invariably decreased with the spatial scale, and the Ω of the less abundant species decreased faster than that of the most abundant species at the smaller scales (<10 m) (Fig. 2).

The aggregation intensity, as measured by $\Omega_{0\text{–}10}$, clearly decreased with the abundance in the plot (Fig. 3). For example, the less abundant species with higher and more dispersed $\Omega_{0\text{–}10}$ values were more aggregated than the most abundant species having $\Omega_{0\text{–}10} < 5$. The largest $\Omega_{0\text{–}10}$ was 31.1 (*Alniphyllum fortunei*, 22 individuals; Fig. 2a).

Table 2. number of woody species for each spatial distribution pattern and each spatial scale in the Maolan plot, as measured by Ω

r (m)	Aggregated distribution	Random distribution	Regular distribution
0–10	40	3	0
10–20	35	8	0
20–30	30	13	0
30–40	26	13	4
40–50	24	14	5

The aggregation intensity varied for the different DBH size classes. The smaller size classes showed a higher degree of aggregation than the larger size classes. The percentage of significantly aggregated species decreased with the DBH (Table 3). Specifically, 95.3% of the species at the 1–5 cm DBH size class, 75% at the 20–30 cm DBH size class and 33.3% at the 40–50 cm DBH size class were aggregated. Taking the two dominant species *C. carlesii* var. *spinulosa* and *C. glauca* as examples, the aggregation intensity of these species declined with the DBH (Fig. 4), indicating that the larger trees were more dispersed than the smaller trees.

The average $\Omega_{0\text{–}10}$ of the overstory species (5.8, SE = 1.6) was lower than those of the midstory species (6.9, SE = 0.9) and the understory species (9.1, SE = 1.8). The results of the *t*-test only showed a significant difference between the overstory and understory species. The overstory species were less aggregated than the understory species, whereas the midstory species were not significantly different from both the overstory and the understory species.

The average $\Omega_{0\text{–}10}$ of the light-demanding species (6.3, SE = 1.3) was lower than that of shade-tolerant ones (8.2, SE = 1.2), whereas the mid-tolerant species had the lowest average $\Omega_{0\text{–}10}$ (4.3, SE = 0.8). The *t*-test showed that the aggregation intensity of the mid-tolerant species was significantly different from those of the shade-tolerant and light-demanding species. The mid-tolerant species were less aggregated than the shade-tolerant and light-demanding species, whereas the light-demanding species were not significantly different from the shade-tolerant species.

The average $\Omega_{0\text{–}10}$ of the animal-borne species (4.4, SE = 0.7) was lower than that of the gravity-borne species (6.6, SE = 0.9) and the wind-borne species (8.9, SE = 1.8). The *t*-test showed that only the aggregation intensity of the animal-dispersed species was significantly different from those of the gravity-dispersed and wind-dispersed species. The species that are dispersed by animals were less aggregated than those dispersed by gravity or the wind. In contrast, the gravity-dispersed species were not significantly different from the wind-dispersed species.

The multiple regression analysis of $\Omega_{0\text{–}10}$ showed that the regression model was highly significant (analysis of

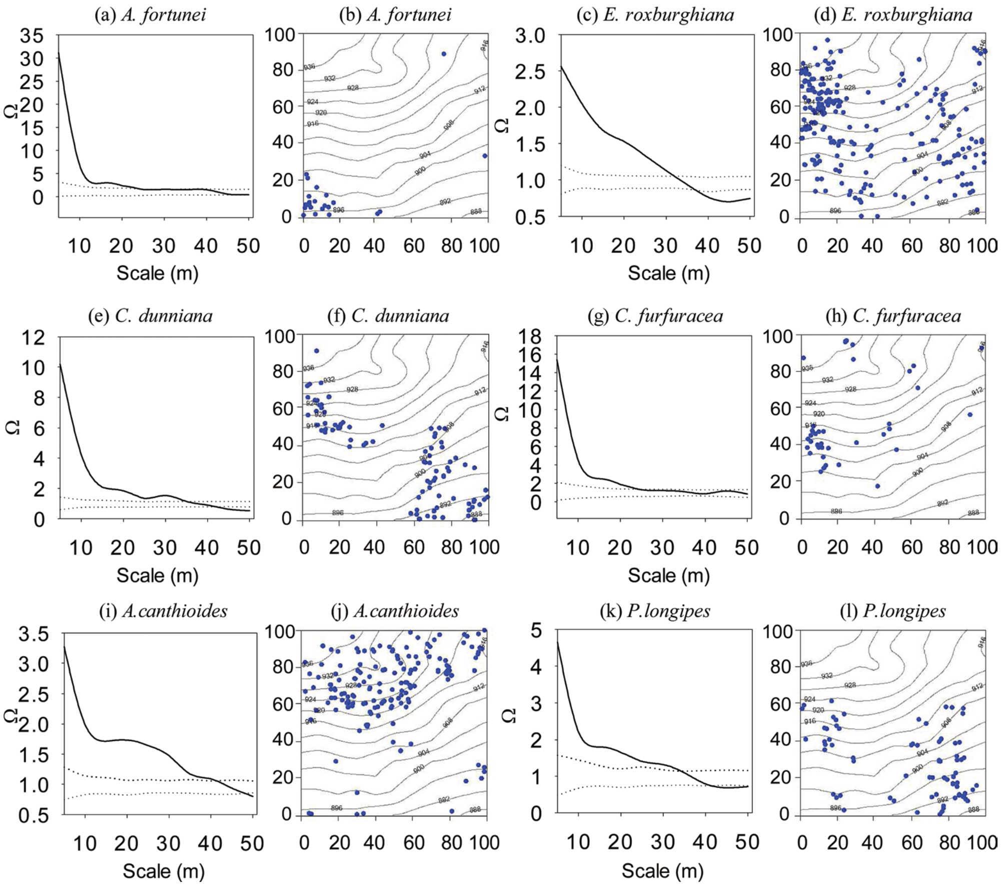


Figure 2: examples of species distribution in the Maolan plot. Left column shows the relationship between Ω and the spatial scale for six species; right column shows their corresponding distribution patterns. The six species were chosen from high to low abundance. The black line represents the Ω value. The thin dashed line corresponds to the confidence intervals generated from 499 Monte Carlo simulations under the null hypothesis of complete spatial randomness.

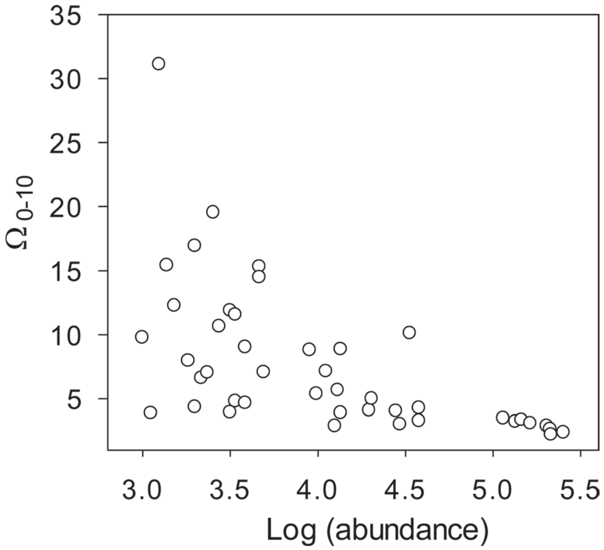


Figure 3: relationship between abundance and Ω_{0-10} of woody species with abundance ≥20 at the Maolan plot with the following DBH classes: (1) 1–5 cm, (2) 5–10 cm, (3) 10–20 cm, (4) 20–30 cm, (5) 30–40 cm, and (6) 40–50 cm.

variance, *F*-test with *P*-value = 0.011). The standardized coefficients indicated that the abundance had the largest effect on the spatial aggregation, followed by the maximum DBH, the average DBH, the dispersal mode, the level of shade tolerance and the canopy layer (Table 4). Except for the average DBH and the dispersal mode, the effects of all factors on aggregation were negative, i.e. the aggregation intensity decreased with an increase in the respective factors.

Table 3. **number of woody species in different DBH classes with significantly aggregated spatial distribution in the Maolan plot**

DBH class (cm)	Median Ω_{0-10}	Total no. of species	No. of significant aggregated species
1–5	9.35	43	41
5–10	8.17	42	38
10–20	6.58	36	31
20–30	4.55	20	15
30–40	2.14	7	4
40–50	1.02	3	1

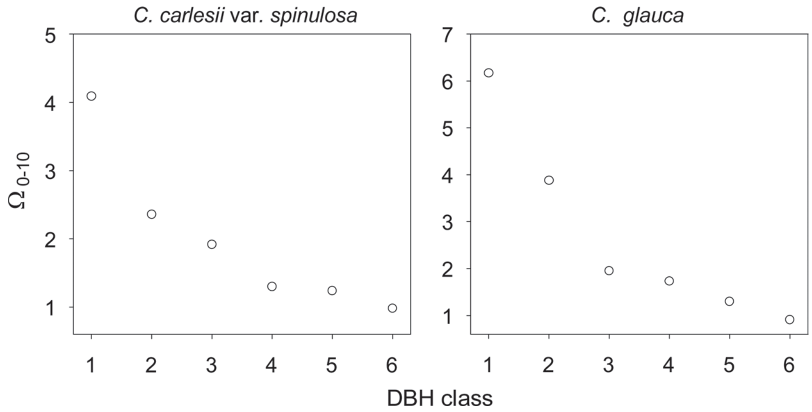


Figure 4: relationship between $\Omega_{0–10}$ and the DBH of *C. carlesii* var. *spinulosa* and *C. glauca* with the following DBH classes: (1) 1–5 cm, (2) 5–10 cm, (3) 10–20 cm, (4) 20–30 cm, (5) 30–40 cm, and (6) 40–50 cm.

Table 4. **multiple regression of $\Omega_{0–10}$ with the abundance, maximum DBH, average DBH, canopy layer, shade tolerance, and dispersal mode showing the estimated coefficients, standard errors and standardized coefficients**

	Unstandardized coefficients		Standardized (beta) coefficients
	Estimates	SE	
Constant	8.661	5.174	
Abundance	–0.041	0.015	–0.437
Max DBH	–0.178	0.132	–0.374
Average DBH	0.582	0.435	0.346
Canopy layer	–0.130	1.697	–0.017
Shade tolerance	–0.406	1.105	–0.063
Dispersal mode	1.513	1.209	0.173

The standardized coefficients are partial regression coefficients that indicate the relative effects of each variable on $\Omega_{0–10.}$

DISCUSSION

Any population in a community, at a given scale of observation, presents one of three distributions, aggregated, random or regular, depending on the underlying processes (He *et al.* 1997). Few species in nature have a regular distribution. On the contrary, aggregation is a common pattern of species distribution, particularly in species-rich tropical forests (Itoh *et al.* 1997; Plotkin *et al.* 2000). The species in the subtropical karst forest considered in this study followed this general pattern, but the proportion of aggregated species decreased with the increasing spatial scale. Aggregation occurred in 93.0% of the species at 0–10 m, 81.3% at 10–20 m and 69.8% at 20–30 m (Table 2). Similar results were also found in a temperate forest (Wang *et al.* 2010), but a clear decrease in species aggregation accompanying the increased spatial scale was not found in tropical and subtropical forests (Condit *et al.* 2000; Li *et al.* 2009). In an earlier study, the percent aggregation at all scales were all higher than 97.8% in tropical forests, based on counting the aggregation patterns of 1768 species with at least one individual per hectare (Condit *et al.* 2000). In subtropical forests, the aggregation percentages were also all >96.1% at all scales (Li *et al.* 2009).

Numerous factors play important roles in determining the spatial patterns of trees in a plant community. The spatial distribution of tree species can arise from many biotic and abiotic processes such as regeneration, competition, dispersal limitation, habitat heterogeneity, disturbances and other stochastic events (Camarero *et al.* 2000; Hou *et al.* 2004; Houle 1994; Palmiotto *et al.* 2004; Pelissier 1998;). This study showed that the abundance of a species, DBH class, canopy layer, functional traits (shade tolerance and seed dispersal mode) and habitat heterogeneity are important factors affecting the spatial patterns of tree species in a subtropical karst forest.

The degree of aggregation of a species was strongly inversely correlated with its abundance. The clumping intensity decreased as the individual abundance increased (Fig. 3), which is consistent with other forest studies showing that rare species are more clumped than common species (Condit *et al.* 2000). However, not all species have a similar response. In our study, e.g. the abundant species *Clausena dunniana* with 92 individuals had a relatively high $\Omega_{0–10}$ of 10.2 (Fig. 2e). One of the most important reasons for this observation is that the spatial distribution of a species can arise from a strong habitat preference (Zhang *et al.* 2010).

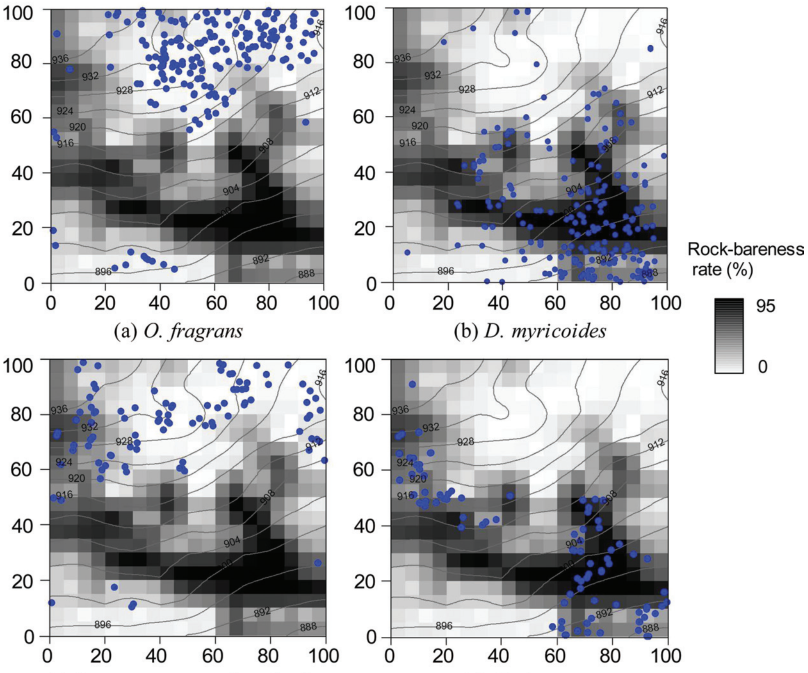
The species aggregation generally decreased with increasing DBH in the plot. The observation that aggregation was weaker in classes with larger diameters may be due to the self-thinning process or their density-dependent mortality. Water and soil have been shown to be limiting resources in karst forests (Zhang *et al.* 2010), and adjacent stems in the studied forest are likely to compete with each other for these resources. A number of studies support that there is less aggregation with increasing DBH (Condit *et al.* 2000; Davis *et al.* 2005; He *et al.* 1997). Our result is consistent with the findings from tropical and subtropical forests (Condit *et al.* 2000; Li *et al.* 2009), which report that small-size classes are more clumped than larger-size classes. This trend suggests that the larger trees competitively inhibit conspecifics over a larger area of influence than the smaller trees. Furthermore, the tree spacing patterns are influenced by the tree size and the tree species.

Several studies suggested that canopy trees usually have well-dispersed seeds relative to the understory treelets; these trees are thus assumed to be less clumped than the treelets (Condit *et al*. 2000; Wang *et al*. 2010). A better dispersal-reducing aggregation was found in the studied forest. There was a significant difference in the aggregation intensity between the overstory and the understory species in the subtropical karst forest. The overstory species tend to be less aggregated than the understory species.

The shade tolerance of a species may also be expected to have a significant effect on distribution pattern. Lorimer (1980) and Wang *et al*. (2009) demonstrated that the mid-tolerant species have almost unimodal distributions with suppressed small trees, whereas the shade-tolerant species tend to have a steeply descending monotonic diameter distribution with a number of suppressed small trees. This observation indicates that the smaller trees are more aggregated than the larger trees. Thus, the shade-tolerant species are expected to be more aggregated than the mid-tolerant species. Light-demanding species also have the tendency to live in gaps created by tree-falls, thereby causing more aggregation than the mid-tolerant species. In this study, the mid-tolerant species were also found to be less aggregated than the shade-tolerant species and the light-demanding species in the subtropical karst forest.

Several studies found that dispersal limitation is commonly regarded as one of the important mechanisms to explain species aggregation (Plotkin *et al.* 2000; Seidler and Plotkin 2006) in tropical forests (Condit *et al*. 2000; He *et al*. 1997), subtropical forest (Li *et al*. 2009) and temperate forests (Hou *et al*. 2004; Wang *et al*. 2010). Several studies showed that the extent and scale of conspecific spatial aggregation is correlated with the mode of seed dispersal. Animal-dispersed species generally have a high dispersal ability compared with either the wind- or gravity-dispersed species; thus, the species dispersed by animals are assumed to be less clumped than species dispersed by gravity or the wind (Condit *et al.* 2000; Li *et al*. 2009). This study also showed that the animal-borne species are better dispersed than both the wind- and gravity-borne species. Furthermore, the animal-dispersed species were less aggregated than the wind- and gravity-dispersed species. Thus, the clustering of these species can be linked to their dispersal properties, which are associated with the random interception and accumulation of seeds by the nearby neighbouring vegetation, including the trees, shrubs and dense understory grasses. The aggregated distributions of numerous species indicate the existence of a dispersal limitation in the subtropical karst forest. However, the karst forest has a rocky outcrop and a steep slope. Therefore, some of the species occurring in small-scale clumps do correspond with the topographic and edaphic factors.

Habitat heterogeneity, which involves topographic, edaphic or other environmental factors, is considered an important factor that controls the distribution of a species (Harms *et al.*



(a) *O. fragrans* (b) *D. myricoides*

(c) *L. japonicus var. lancilimbus* (d) *C. dunniana*

Figure 5: Spatial distribution of *O. fragrans*, *D. myricoides*, *L. japonicus* var. *lancilimbus* and *C. dunniana* in different habitats. The rock-bareness rate in each 5 × 5 m quadrat is shown in different grey levels throughout the entire plot.

2001; Yamada *et al.* 2006). In the study site of this research, the topography such as rocky outcrops, steep slopes, elevation and slope aspect lead to the high habitat heterogeneity of the karst forest. Most tree species in the plot showed significant topographic habitat associations. The prevalence of rock is associated with a low water-holding capacity and shallow soil. Trees on rocky slopes are susceptible to water shortage (Zhou and Pan 2001). Shallow soils interspersed with rocky outcrops limit the availability of nutrients for tree growth (Huang *et al.* 2009). These conditions may lead to habitat specialization. Thus, species in the plot were aggregated due to habitat specificity, and each species had its preferred habitat. For example, *O. fragrans* and *Lasianthus japonicus* var. *lancilimbus* favour habitats with relatively less rocky outcrops and shady slopes. However, *D. myricoides* and *C. dunniana* are established more successfully in habitats with rocky outcrops and sunny slopes (Fig. 5). Habitat specialization that is based on the niche differentiation of resources can explain why different tree species are best suited to different habitats (Harms *et al.* 2001). Therefore, coexisting species are strongly associated with and are adapted to various habitats that are required for their survival and recruitment. Such habitat heterogeneity is another key reason for the spatial patterns observed in the Maolan plot.

CONCLUSIONS

In summary, the results of this study show that aggregation is dominant at the plot scale (1 ha) for tree species in the species-rich subtropical karst forest of the Maolan plot. The aggregation intensity clearly declines with the increase in the spatial scale, and the less abundant species are more aggregated than the most abundant species. The aggregation intensity of a species also declines with increasing DBH, which is consistent with the prediction of self-thinning. The functional traits of a species (such as shade tolerance and seed dispersal mode) also have an effect on the spatial distribution of species. In the karst landscape, the topographic habitat partitioning also plays a significant role in the spatial distribution of a species. Therefore, habitat heterogeneity, seed dispersal limitation and self-thinning may have primarily contributed to the observed spatial distribution of various species in the karst forest.

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