



Spatial distributions of tree species in a subtropical forest of China

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The spatial dispersion of individuals in a species is an important pattern that is controlled by many mechanisms. In this study we analyzed spatial distributions of tree species in a large-scale (20 ha) stem-mapping plot in a species-rich subtropical forest of China. O-ring statistic was used to measure spatial patterns of species with abundance >10 . Ω_{0-10} , the mean conspecific density within 10 m of a tree, was used as a measure of the intensity of aggregation of a species. Our results showed: (1) aggregated distribution was the dominant pattern in the plot. The percentage of aggregated species decreased with increased spatial scale. (2) The percentages of significantly aggregated species decreased from abundant to intermediate and to rare species. Rare species was more strongly aggregated than common species. Aggregation was weaker in larger diameter classes. (3) Seed traits determined the spatial patterns of trees. Seed dispersal mode can influence spatial patterns of species, with species dispersed by both modes being less clumped than species dispersed by animal or wind, respectively. Considering these results, we concluded that seed dispersal limitation, self-thinning and habitat heterogeneity primarily contributed to spatial patterns and species coexistence in the forest.

Aggregated distribution in species is a widespread pattern in nature. Of the numerous mechanisms that contribute to aggregation, the major mechanisms include niche segregation (Pielou 1961), habitat heterogeneity (Harms et al. 2001), reproductive or foraging behavior, differential predation (Janzen 1970, Connell 1971), neighborhood competition (Firbank and Watkinson 1987, Kenkel 1988, He and Duncan 2000) and dispersal limitation (Thioulouse et al. 1997, Hubbell 2001). Despite the fact that pattern alone is insufficient to disentangle these mechanisms (unless there is additional information, e.g. habitat conditions or dispersal mode), spatial distribution of species provides fundamental information for understanding species coexistence in communities. The importance of spatial pattern lies in two reasons. One is that it is an outcome of the interactions of biological and ecological processes. Spatial pattern combined with other aspects of data can be very useful to infer mechanisms generating the pattern (Janzen 1970, Connell 1971, Sterner et al. 1986, Kenkel 1988, He and Duncan 2000). A classic example is the Janzen–Connell spacing hypothesis that predicts more regular spatial pattern of adult trees than juveniles due to the differential attack rates between adults and juveniles by distance/frequency-responsive predators (Janzen 1970, Connell 1971). Tree distribution pattern is a useful testimony of this mechanism (Hubbell 1980). The second reason is that spatial distribution of species is essential for understanding and modeling

biodiversity patterns over space (Hubbell 1979, Condit et al. 2000, 2002, Plotkin et al. 2000, He and Legendre 2002, Wright 2002, Wills et al. 2006). An example of this is He and Legendre (2002) and Green and Ostling (2003) who show that spatial patterns of individual species would significantly affect species–area and endemics–area relationships, respectively.

Current knowledge about tree distributions in species rich communities is almost exclusively derived from tropical rain forests (Condit et al. 2002). This tradition stems from the historical observation of Wallace (1853) that tropical tree species are highly sparsely distributed. Important but challenging questions have been raised from such pattern. For example, how individuals of a spatially sparse population interact, how the viability of the population is maintained, and how the sparse populations on different trophic levels (e.g. plant–herbivores or host–pollinators) co-evolve? Large-scale plots containing detailed information about tree distributions in the plots are essential to address these questions and to the sustainable extraction of tropical tree species (Condit et al. 1994, Condit 1995). One of the first large scale studies was the 13 ha dry forest in Costa Rica studied by Hubbell (1979) who proposed that dispersal limitation and ecological drift are primary mechanisms controlling for tree diversity in tropical forests. This seminal work has laid a foundation for the establishment of the 18 stem-mapping plots coordinated by the

Smithsonian Tropical Research Institute (<<http://www.ctfs.si.edu/doc/index.php>>). This large plot network has profoundly improved our knowledge about spatial distributions, diversity patterns, conservation and management of tropical forests (Condit et al. 2000, Losos et al. 2004).

In contrast to studies in tropical forests, similar work in other species rich forests such as subtropical forests either is conducted at small scales (ranging from a few hundred m² to a few ha) (Quigley and Platt 2003) or does not exist. Consequently, the spatial structure, species–habitat association, diversity patterns and the mechanisms of species coexistence in these forests are still poorly understood. To fill in this knowledge gap, we proposed to establish five large (20–25 ha in size) stem-mapping plots in China along a latitudinal gradient from temperate, subtropical to tropical forests in 2004. The field census for four of the five plots has been completed. Here we report the spatial pattern analysis for a 20 ha subtropical forest in south China.

Our objectives are: (1) to analyze and explain the spatial distributions of conspecific trees in the 20 ha subtropical forest and to compare the distributions between this forest and tropical forests as reported in Condit et al. (2000), (2) to investigate the change in patterns at different spatial scales, and (3) to test the similarity (or dissimilarity) in spatial pattern between rare and common species, between trees at different size classes, and between different functional groups. We also discuss various possible mechanisms that may contribute to the spatial patterns of the tree species in the plot. This analysis contributes to understanding species coexistence and diversity maintenance in subtropical forests.

Material and methods

Study site

The study site is located in the Dinghushan Mountain (112°30'39"-112°33'41"E, 23°09'21"-23°11'30"N) in Guangdong Province. Dinghushan is the first Nature Reserve established in China in 1956 and has significant importance in the conservation of forest ecosystems over the past 50 years. The reserve comprises low mountains and hilly landscapes. Its total area is 1155 ha, with altitude of 14–1000 m, covered by tropical–subtropical forests. Dinghushan has a south subtropical monsoon climate with a mean annual temperature of 20.9°C, and the mean monthly temperature of 12.6°C in January and 28.0°C in July. Average annual precipitation is 1929 mm, with most of precipitation occurring between April and September. Annual evaporation is 1115 mm and relative humidity 82%.

Data collection

A permanent 20 ha (400 × 500 m) plot was established in the Dinghushan reserve in November 2004, called Dinghu plot hereafter. For stem mapping, the plot was subdivided into 500 20 × 20 m subplots and each of the subplots was further divided into 16 5 × 5 m quadrats. The survey consisted of enumerating all free standing trees and shrubs

at least 1 cm in diameter at breast height (DBH), positioning each one by geographic coordinates on a reference map and identifying it to species. The mapping mainly took place from January to March, but was completed in October 2005. The plot features rough terrain with a steep hillside in the southeast corner. Topography varies with ridge and valley in the plot and the elevation ranges from 240 to 470 m (Fig. 1).

Data analysis

The relative neighborhood density index

Second order point pattern analyses are the most widely used methods to quantify stem-mapped tree distributions. These include using Ripley's K function (Ripley 1977) and the pair correlation g function (Stoyan and Stoyan 1994, Stoyan and Penttinen 2000). K and g functions are related. The former is a cumulative distribution function of distances between pairs of points while the latter is the derivative of the former and thus is a probability density function (Stoyan and Penttinen 2000, Diggle 2003). The K function is computed based on the number of trees located within a circle centered on a focal tree, while the g function is computed based on the number of trees within an annulus (i.e. a ring) centered on the focal tree. Wiegand and Moloney (2004) demonstrate that large-scale heterogeneity of a point-pattern biases Ripley's K-function at smaller scales. This bias is difficult to detect without explicitly testing for homogeneity (Wiegand and Moloney 2004). Using rings instead of circles has the advantage of isolating specific distance classes, whereas the cumulative K-function confounds the effect at larger distances with that at smaller distances (Getis and Franklin 1987, Penttinen et al. 1992, Condit et al. 2000). For better interpretation, a transformation $O(r) = \lambda g(r)$, called O-ring, is sometimes used instead of the g function, where r is distance from the focal tree and λ is the mean density of a species in the whole plot. The O-ring has an intuitive interpretation as local neighborhood density (Condit et al. 2000, Wiegand and Moloney 2004).

We used the relative neighborhood density Ω_r (Condit et al. 2000) to characterize tree distributions in the plot. The Ω_r is the O-ring scaled by abundance of the species evaluated, as formulated by $\Omega_r = D_r/\lambda$ (Condit et al. 2000), where $D_r = \sum N_r/\sum A_r$, A_r is the area in each annulus at distance r, N_r is the number of conspecifics within the annulus. In this study the annulus width is 10 m. Therefore, D_r is the density of conspecifics as a function of distance. For a random distribution, $\Omega_r = 1$ at all distances r. $\Omega_r > 1$ indicates aggregation at distances $< r$, while $\Omega_r < 1$ suggests regular distribution at distances $< r$. Monte Carlo simulation was used to test the hypothesis that a species is not significantly different from random distribution, i.e. $\Omega_r = 1$. Ninety-nine distributions were simulated by randomly labeling all the trees in the plot while keeping the abundance of each species the same as the observed. Ω_r was calculated each time, thus there are 99 Ω_r 's. If the observed Ω_r falls within the 2.5th and 97.5th quartiles, the null hypothesis cannot be rejected. Otherwise, we would conclude that the species in Dinghu plot is significantly different from random distribution.

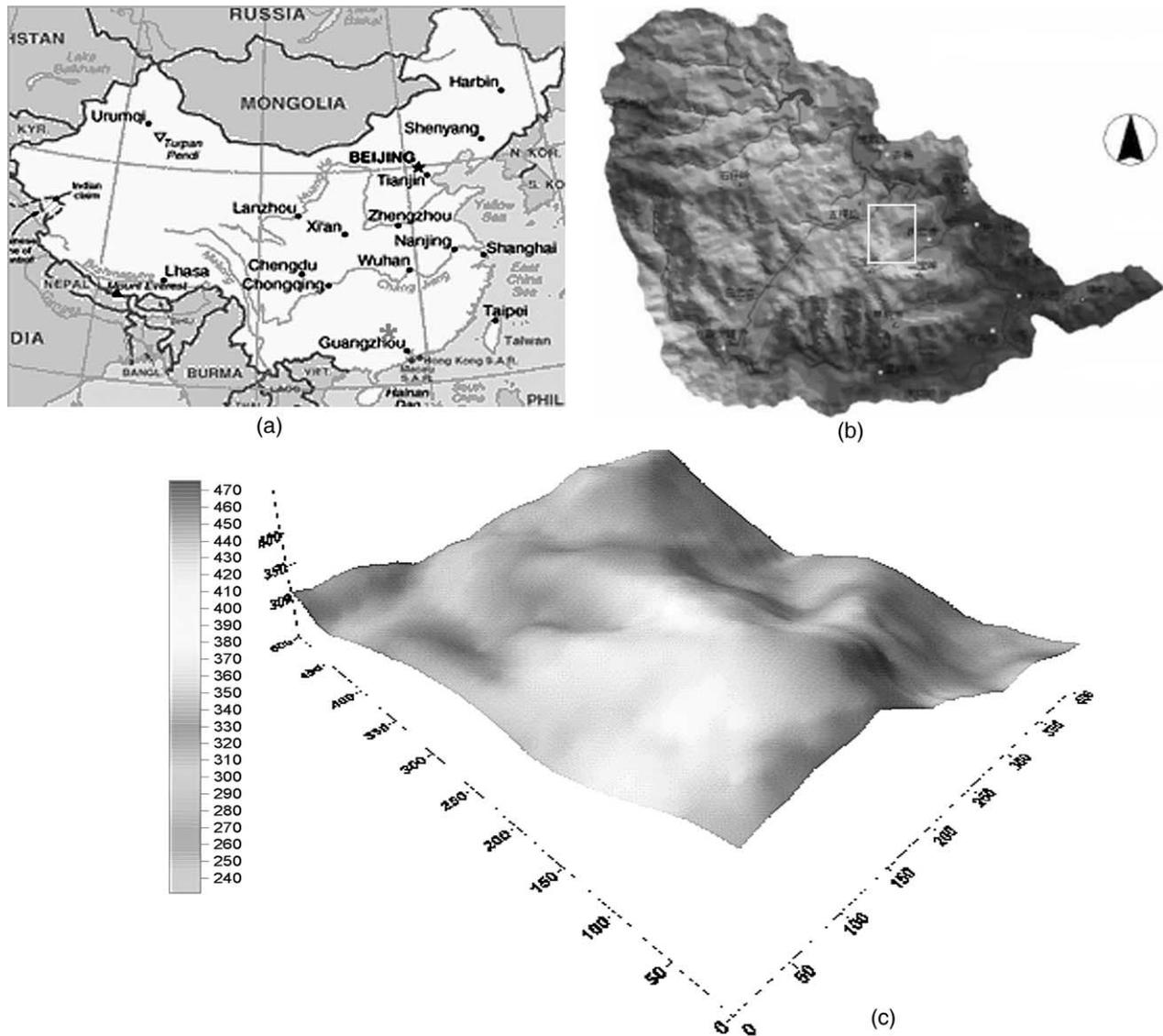


Figure 1. Location of the Dinghu plot in Dinghushan Biosphere Reserve, south China. (a) China, (b) Dinghu Mountain, (c) Dinghu plot (highest point = 470 m, lowest point = 240 m).

We also used Ω_{0-10} , the mean conspecific density within 10 m of a tree, as a measure of the intensity of aggregation of a species (Condit et al. 2000), to compare spatial patterns of species belonging to different characteristic groups. We first divided species into three groups according to abundance: rare (with abundance < 50), intermediate (50–500), and abundant (≥ 500) species. We then compared spatial patterns of trees at different DBH classes. The DBH classes were grouped at every 5 cm interval. The third comparison was done between species of different seed dispersal modes: wind or explosively dispersed versus animal dispersed species. To sort out the effects of abundance, DBH and dispersal modes on spatial patterns, we conducted a multiple regression for the 124 species of abundance > 10 using Ω_{0-10} as dependent variable and abundance, dispersal, maximum DBH and average DBH as independent variables.

Results

Stand structure

There are 56 families, 119 genera, 210 species and 71617 individuals with DBH ≥ 1 cm in the 20 ha Dinghu plot. Fifteen of the 210 species dominate the plot, accounting for 62.3% (2230.75 stem ha^{-1}) of total density and 80.3% (22.67 $\text{m}^2 \text{ha}^{-1}$) of the total basal area (Table 1). Lauraceae and Euphorbiaceae are the two most abundant families, having 21 and 20 species respectively. *Aidia canthioides* is the most abundant species with 5996 individuals in the plot but its basal area is small (0.2 $\text{m}^2 \text{ha}^{-1}$) as it is an understory/midstory species. *Castanopsis chinensis* is an intermediate abundant species with 2311 individuals in the plot but has the highest basal area (8.66 $\text{m}^2 \text{ha}^{-1}$). The species has the oldest individual over one thousand years in

Table 1. Density, basal area, and maximum diameter of live trees ≥ 1.0 cm DBH in the 20 ha Dinghu plot.

Species	Family	Density (stem ha ⁻¹)	Basal area (m ² ha ⁻¹)	Maximum DBH (cm)
<i>Castanopsis chinensis</i>	Fagaceae	115.55	8.66	175.00
<i>Schima superba</i>	Theaceae	114.80	3.87	89.00
<i>Engelhardtia roxburghiana</i>	Juglandaceae	36.85	3.12	95.00
<i>Acmena acuminatissima</i>	Myrtaceae	74.20	1.03	69.70
<i>Syzygium rehderianum</i>	Myrtaceae	299.50	0.86	51.00
<i>Machilus chinensis</i>	Lauraceae	26.60	0.83	63.00
<i>Aidia canthioides</i>	Rubiaceae	299.80	0.20	31.70
<i>Cryptocarya concinna</i>	Lauraceae	223.90	0.17	47.10
<i>Craibiodendron kwangtungense</i>	Ericaceae	166.25	1.64	59.10
<i>Cryptocarya chinensis</i>	Lauraceae	127.85	1.12	51.00
<i>Aporosa yunnanensis</i>	Euphorbiaceae	187.35	0.42	26.40
<i>Sarcosperma laurinum</i>	Sarcospermaceae	78.80	0.31	56.00
<i>Xanthophyllum hainanense</i>	Polygalaceae	93.65	0.34	54.10
<i>Ardisia quinquegona</i>	Myrsinaceae	185.10	0.07	22.70
<i>Blastus cochinchinensis</i>	Melastomataceae	200.55	0.05	22.30
Others		1350.10	5.57	
Total		3580.85	28.24	

the reserve and the biggest tree in the plot with 175 cm DBH. Six other species in the plot have basal area larger than 1.0 m² ha⁻¹ (Table 1).

Of the 210 species, there are 132 rare species, 46 intermediate species and 32 abundant species. Thirty species are singletons and 110 species have fewer than 20 individuals. The tree size distribution for all the individuals indicates inverse J-shape. There are excessive small trees with 59697 trees of DBH < 10 cm. Abundant species include eight canopy species (average DBH > 8 cm), 11 midstorey species (average DBH 4–8 cm), and 13 understorey species (average DBH < 4 cm). The most abundant species in each layer from canopy to understorey are: *Craibiodendron kwangtungense*, *Syzygium rehderianum* and *Aidia canthioides*.

Spatial pattern analysis

Of the 210 species in the Dinghu plot, 124 species with abundance ≥ 10 are included in spatial pattern analysis. They consist of 32 abundant species, 46 intermediate species and 46 rare species. Most species are aggregated at scale $r < 50$ m. Most regularly distributed species are rare species, while most common (abundant and intermediate) species are aggregated (Table 2).

Although aggregation is a dominant pattern when all DBH classes of ≥ 1 cm are included in the analysis, the percentage of aggregated species overall decreases with the increase in spatial scale (Table 2); the significant aggrega-

tion of the 124 species decreases from 96.8% to 73.4% when scale increases (Table 2).

The percentages of significantly aggregated species decrease from abundant, to intermediate species and to rare species (Table 2). All of the abundant species are significantly aggregated at scale less than 50 m, while the percentages of significantly aggregated intermediate species decrease with distance from 100% ($r = 0-10$ m), 97.8% ($r = 10-20$ m), 93.5% ($r = 20-30$ m), 91.3% ($r = 30-40$ m), to 87% ($r = 40-50$ m), and the percentages of rare species decrease from 91.3% ($r = 0-10$ m), 78.3% ($r = 10-20$ m), 58.7% ($r = 20-30$ m), 47.8% ($r = 30-40$ m) to 41.3% ($r = 40-50$ m) with scale r .

Figure 2 shows the relative neighborhood density Ω_r for species of different abundances (abundant, intermediate and rare species) and different dispersal modes (wind, animals, and wind/animals). It is clear that Ω_r invariably declined with scale, and the Ω_r of rare species declined faster than intermediate species and common species at small scales (< 50 m).

The relationship between aggregation intensity and abundance

The aggregation intensity as measured by Ω_{0-10} clearly decreases with abundance in the plot (Fig. 3). Rare species are more aggregated than intermediate species and common species. Ω_{0-10} values of rare species are higher and more scattered than intermediate and abundant species. The

Table 2. Tree spatial distribution in the Dinghu plot as tested by Ω_r . Species with < 50 trees were classified as rare species, those with abundance 50–500 were intermediate species, and with ≥ 500 trees were common species. n indicates the total number of species in each category, the number in each cell is the significantly aggregated (or regular) species in each category.

r (m)	Aggregated				Regular			
	Abundant (n=32)	Intermediate (n=46)	Rare (n=46)	Total (n=124)	Abundant (n=32)	Intermediate (n=46)	Rare (n=46)	Total (n=124)
0–10	32	46	42	120	0	0	1	1
10–20	32	45	36	113	0	0	5	5
20–30	32	43	27	102	0	1	5	6
30–40	32	42	22	96	0	1	11	12
40–50	32	40	19	91	0	1	6	7

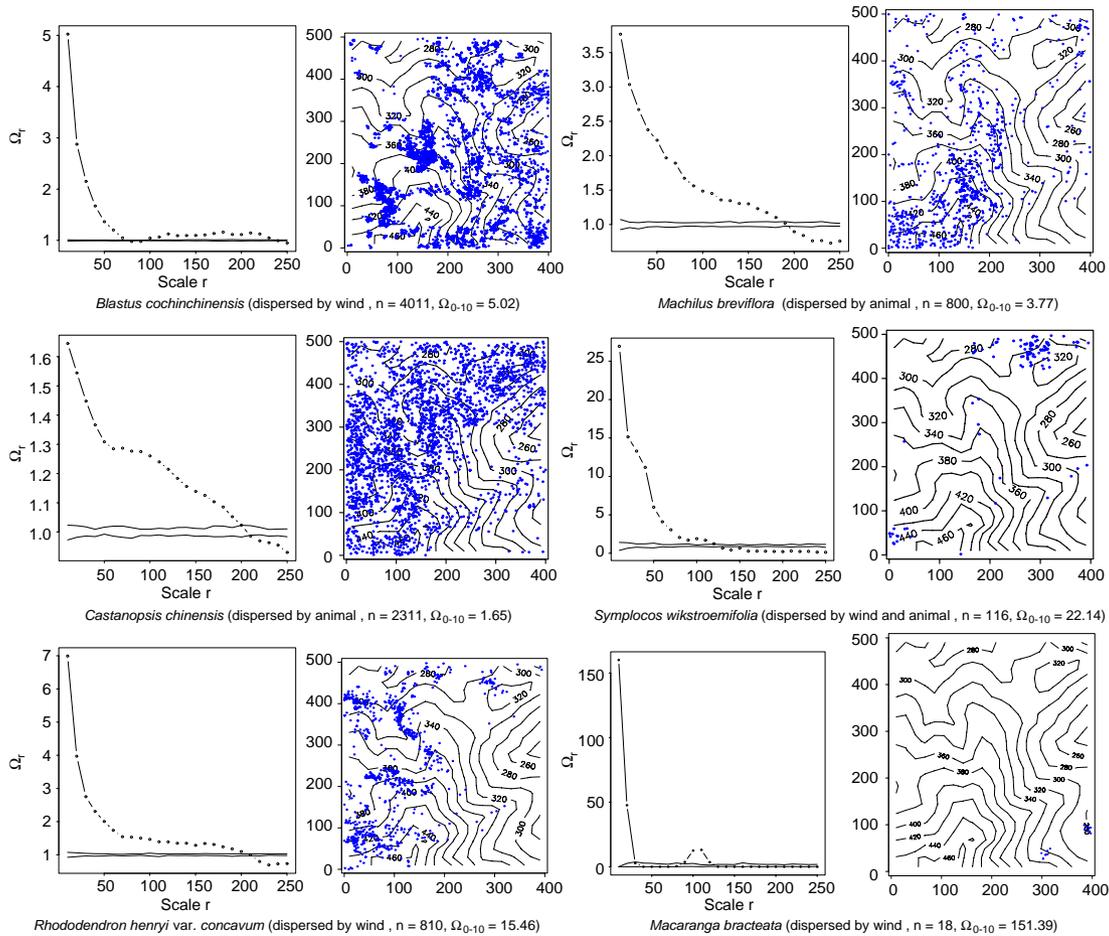


Figure 2. Left column showing the relationship between Ω_r and scale for six species, and right column showing their corresponding distribution patterns. The six species were chosen from high to low abundance having different modes of seed dispersal. Point-line is for Ω_r value. Thin lines correspond to the confidence intervals generated from 99 Monte Carlo simulations under the null hypothesis of complete spatial randomness.

largest Ω_{0-10} is 504 (*Indocalamus longiauritus*, 19 individuals). For the majority of abundant species Ω_{0-10} are less than 20.

Relationship between aggregation intensity and DBH

Almost all the species are aggregated at every DBH class (Table 3). No species are at regular distribution. The median Ω_{0-10} decreased with DBH, except for DBH 20–30 cm. Taking dominant species *Castanopsis chinensis* as example, the aggregation intensity of the species declined with DBH (Fig. 4), indicating large trees are more dispersed than small trees. The aggregation intensity of *Castanopsis chinensis* decreases faster at smaller DBH classes, until not aggregated at DBH 40–50 cm.

Seed dispersal limitation

Among the 124 species having >10 individuals, there are 44 (35.5%) animal-dispersed species, 17 (13.7%) wind or explosively dispersed species, 61 (49.2%) are dispersed by both modes, and the dispersal modes are not known for two species. The average Ω_{0-10} of animal borne species (31.3,

SE = 90.9) is smaller than average Ω_{0-10} of wind borne species (84.7, SE = 119.5), while the average Ω_{0-10} of species dispersed by both modes (16.2, SE = 19.5) is smallest. Results of the τ -test only found statistically

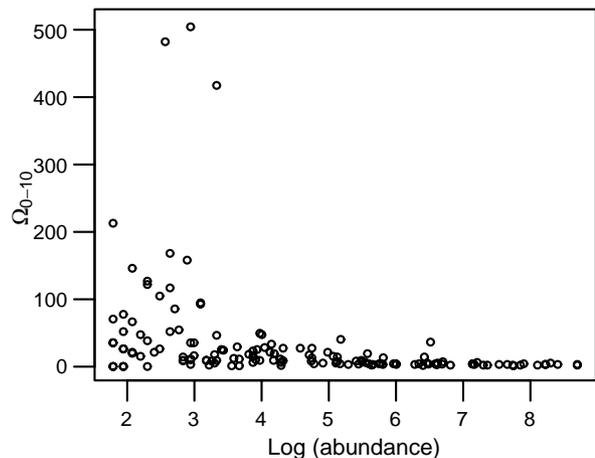


Figure 3. Relationship between abundance and aggregation intensity (Ω_{0-10}) of species with abundance >10 at Dinghu plot. The DBH classes were the same as that of Table 3.

Table 3. Spatial distribution across DBH classes for all species with abundance >10 in the Dinghu plot. The last column shows the number of species out of the total number of species that are significantly aggregated. No species were found to be significantly regularly distributed.

DBH class (cm)	Median Ω_{0-10}	Total no. of species	No. of significant aggregated species
1-5	11.83	133	131
5-10	10.52	83	83
10-15	8.2	56	54
15-20	4.59	29	28
20-30	7.23	23	23
30-40	3.41	10	9
40-50	2.20	3	2
>50	2.16	2	2

significant difference between species dispersed by wind and that dispersed by both modes. Species dispersed by both modes are less clumped than species dispersed by animal or wind, respectively. In contrast, animal borne species are not statistically significantly different from wind borne species and species dispersed by both modes, although the point patterns showed that animal borne species were in general less clumped than wind borne species in Dinghu plot. For example, *Blastus cochinchinensis*, a wind dispersed species, is more abundant than *Castanopsis chinensis*, an animal dispersed species. Their distribution patterns show *Castanopsis chinensis* less clumped than *Blastus cochinchinensis* (Fig. 2). *Rhododendron henryi* var. *concaum* and *Machilus breviflora* have similar abundance. The former is wind dispersed species, while the latter is animal dispersed species. Their distribution patterns show *Machilus breviflora* less clumped than *Rhododendron henryi* (Fig. 2).

The results of the multiple regression for Ω_{0-10} are shown in Table 4. Overall, the regression model is highly significant (ANOVA, F-test with p-value = 0.019). The standardized coefficients shown in Table 4 indicate that maximum DBH has largest effect on spatial aggregation, following by dispersal modes, average DBH and abundance. Except for average abundance, the effects of other factors on aggregation are negative, i.e. aggregation intensity decreases with those factors. Species dispersed by both

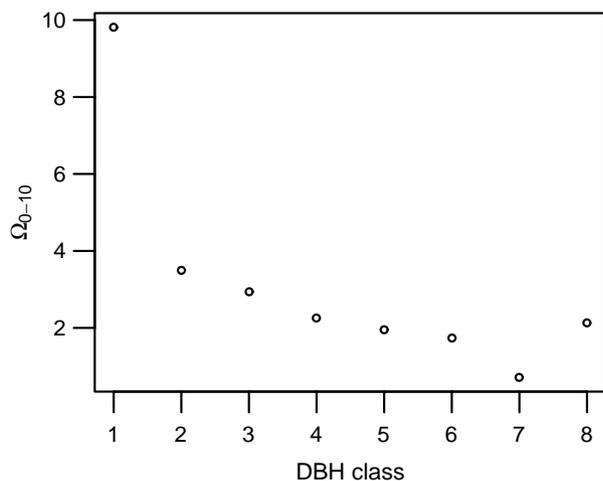


Figure 4. Relationship between Ω_{0-10} and DBH of *Castanopsis chinensis*. DBH classes were the same to that of Table 3.

Table 4. Multiple regression of Ω_{0-10} with abundance, dispersal modes, maximum DBH and average DBH, showing the estimated coefficients, standard errors and standardized coefficients. The standardized coefficients (often called 'beta coefficients') are partial regression coefficients and indicate the relative effects of each variables on Ω_{0-10} .

	Unstandardized Coefficients		Standardized (beta) coefficients
	Estimates	SE	
Constant	60.376	14.951	
Abundance	-3.803×10^{-3}	0.005	-0.078
Dispersal	-10.812	5.582	-0.176
Max dbh	-0.820	0.365	-0.332
Average dbh	1.856	1.491	0.170

modes are less aggregated than species dispersed by animal or wind, respectively.

Discussion

Aggregation is a common pattern of species distribution in nature, particularly in species rich tropical rainforests (Parrish and Edelstein-Keshet 1999, Manabe et al. 2000, Mitsui and Kimura 2000, Plotkin et al. 2000). This study shows aggregation is also a dominant pattern in tree species of subtropical forests. Condit et al. (2000) counted the aggregation patterns of 1768 species based on species with at least one individual per hectare. At scale 0-10 m, aggregation rate is 99.2%, at 10-20 m it is 99.4%, and 20-30 m is 97.8% in tropical rain forests. To compare the aggregation percentage in our 20 ha plot with tropical rain forests, we considered the species with abundance >20, the aggregation percentages are 98%, 98%, and 96.1%, respectively, at the corresponding scales. Tropical rain forests have comparable, but slightly higher aggregated distribution percentage than the Dinghu plot.

Plant species patterns can arise from many biotic and abiotic processes. Because the spatial organization of individuals depends to a great extent on biotic processes (Begon et al. 1986), biotic processes such as regeneration, reproductive behavior, dispersal limitation, and competition can induce spatially heterogeneous patterns (Sternier et al. 1986, Pélissier and Goreaud 2003). In contrast, abiotic processes such as habitat heterogeneity, disturbances or other stochastic events also contribute to nonrandom distributions of trees. The present study shows that the abundances of species, life history stages (as measured by different DBH classes) and dispersal modes are important factors affecting spatial patterns of the tree species in our subtropical forest.

Our results show that spatial aggregation generally decreases with DBH (Table 2, 3, Fig. 4). The finding that aggregation is weaker at larger diameter classes (Table 4) is largely due to self thinning. However, herbivores and pest may also partly play a role as spacing mechanism in reducing aggregation. In tropical forests, Harms et al. (2000) and Wills and Condit (1999) show that pests have already substantially weakened aggregation intensity by the time trees enter the census at 1 cm diameter. In Dinghu forest, it has been observed that some species, such as

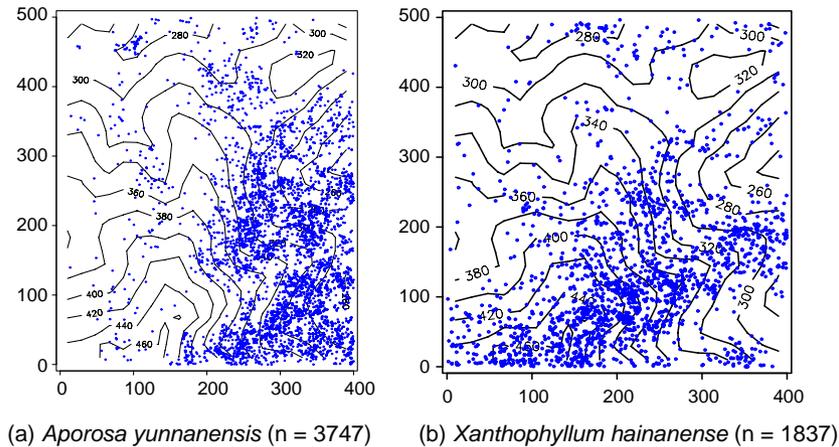


Figure 5. Trees of *Aporosa yunnanensis* and *Xanthophyllum hainanense* distribute in different habitats.

Castanopsis chinensis and *Cryptocarya concinna*, could endure insect infestation at early life stage (Peng and Xu 2005).

Studies of tropical tree species show dispersal limitation is a potential mechanism for separating species in space and reducing competitive exclusion (Seidler and Plotkin 2006). Indeed, tropical forests exhibit extensive aggregation of conspecific trees at scales ranging from a few meters to a few hundred meters (Hubbell 1979, Condit et al. 2000, Plotkin et al. 2000). Seidler and Plotkin (2006) demonstrated that the extent and scale of conspecific spatial aggregation was correlated with the mode of seed dispersal. This relationship holds for saplings as well as for mature trees. Condit et al. (2000) suggested that species whose seeds are dispersed by animals were better dispersed than wind or explosively dispersed species. The results of this study are consistent with that of Condit et al. (2000). We found that in general species dispersed by both modes are less clumped than species dispersed by animal or wind, respectively. Furthermore, we showed that animal borne species are less aggregated than wind or explosively dispersed species. This result is evident by the examples shown in Fig. 2.

Habitat heterogeneity has been considered to be a primary factor controlling the distribution of species (Hutchinson 1957). One study in the tropics suggested that niche differentiation with respect to soil water availability is a direct determinant of both local- and regional-scale distributions (Engelbrecht et al. 2007). Habitat specialization based on niche differentiation of resources can be the reason that different species of trees are best suited to different habitats, showing competitive dominance and relatively higher abundance (Harms et al. 2001). Species aggregate on patches that can provide suitable resources for their regeneration. As a result, habitat conditions can strongly influence species distribution. For example, the two middle canopy species, *Aporosa yunnanensis* favors relatively wet valley habitat, but *Xanthophyllum hainanense* favors dry ridge habitat (Fig. 5). Different species groups can differ in their ability to adapt to different environmental conditions and that may explain the differential patterns of richness in relation to environment (Cody 1991).

As a conclusion, we have found that tree species in the species rich subtropical broad-leaved forest of Dinghu plot

are predominantly aggregated. The aggregation intensity clearly declines with the increase in spatial scale, and rare species are more aggregated than common species. The aggregation is weaker for trees of larger diameter classes. Seed dispersal mode can influence spatial patterns of species, with species dispersed by both modes being less aggregated than species dispersed by animal or wind, respectively. Seed dispersal limitation, self-thinning and habitat heterogeneity are considered to play important roles in the spatial patterns observed in the Dinghu plot, while Janzen–Connell spacing hypothesis may also partly contributes to the present patterns. In order to fully understand the mechanisms generating spatial patterns, we are collecting data on seed dispersal and soil conditions of the plot that affect seed germination, tree growth and survival.

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