

Spatial distributions of species in an old-growth temperate forest, northeastern China

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Abstract: Studying spatial distributions of species can provide important insights into processes and mechanisms that maintain species richness. We used the relative neighborhood density Ω based on the average density of conspecific species in circular neighborhoods around each species to quantify spatial distributions of species with ≥ 10 individuals in a fully mapped 25 ha temperate plot at Changbaishan, northeastern China. Our results show that spatial aggregation is a dominant pattern of species in the Changbaishan temperate forests. However, the percentage of significantly aggregated species decreases with spatial scale, especially for rare species. Rare species are more aggregated than intermediate and common species. The aggregation intensity declines with increasing size class (diameter at breast height), i.e., species become more regularly spaced as species grow, which is consistent with the predictions of self-thinning and Janzen–Connell spacing effects. Species functional traits (canopy layer, seed dispersal ability, shade tolerant, etc) also have a significant effect on the spatial distributions of species. Our results partially conform to the prediction that better dispersal reduces aggregation. Consequently, dispersal limitation, self-thinning, Janzen–Connell spacing effects, and habitat heterogeneity may primarily contribute to spatial distributions of species in the temperate forests.

Résumé : L'étude de la distribution spatiale des espèces peut fournir d'importantes informations sur les processus et les mécanismes qui maintiennent la richesse en espèces. Nous avons utilisé la densité relative des voisins Ω basée sur la densité moyenne des individus de la même espèce présents dans un rayon autour de chaque espèce de façon à quantifier la distribution spatiale des espèces comportant plus de 10 individus sur une superficie cartographiée de 25 ha dans une forêt tempérée de Changbaishan, au nord-est de la Chine. Nos résultats montrent que le regroupement spatial est un patron dominant des espèces dans les forêts tempérées de Changbaishan. Cependant, le pourcentage d'espèces significativement regroupées diminue avec l'échelle spatiale, particulièrement pour les espèces rares. Les espèces rares sont davantage regroupées que les espèces communes et intermédiaires. L'intensité de regroupement diminue avec l'augmentation de la classe de diamètre à hauteur de poitrine, de telle sorte que l'espacement entre les individus d'une espèce devient plus régulier à mesure qu'ils grossissent, ce qui est cohérent avec les prédictions de l'autoéclaircie et les effets d'espacement de Janzen–Connell. Les caractéristiques fonctionnelles des espèces (strate de la canopée, capacité de dispersion des graines, tolérance à l'ombre, etc.) ont aussi des effets significatifs sur la distribution spatiale des espèces. Nos résultats supportent partiellement l'hypothèse qu'une meilleure dispersion diminue le regroupement. En conséquence, les contraintes de dispersion, l'autoéclaircie, les effets d'espacement de Janzen–Connell et l'hétérogénéité de l'habitat peuvent contribuer de façon importante à la distribution spatiale des espèces dans les forêts tempérées.

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Introduction

A major objective of ecological research is to infer the underlying processes or mechanisms by analyzing the spatial distributions of species. Although substantial efforts have been made in explaining the observed distributions of species, there are still important challenges, in large part because identical spatial distributions of species may be generated by several different processes. For example, aggregation distributions in species, a widespread pattern observed in nature (He et al. 1997; Condit et al. 2000; Hao et al. 2007), may be broadly attributed to two major, yet contrasting, effects of habitat heterogeneity and dispersal limitation, but the relative contributions of these two effects are difficult to quantify. These two effects represent two major

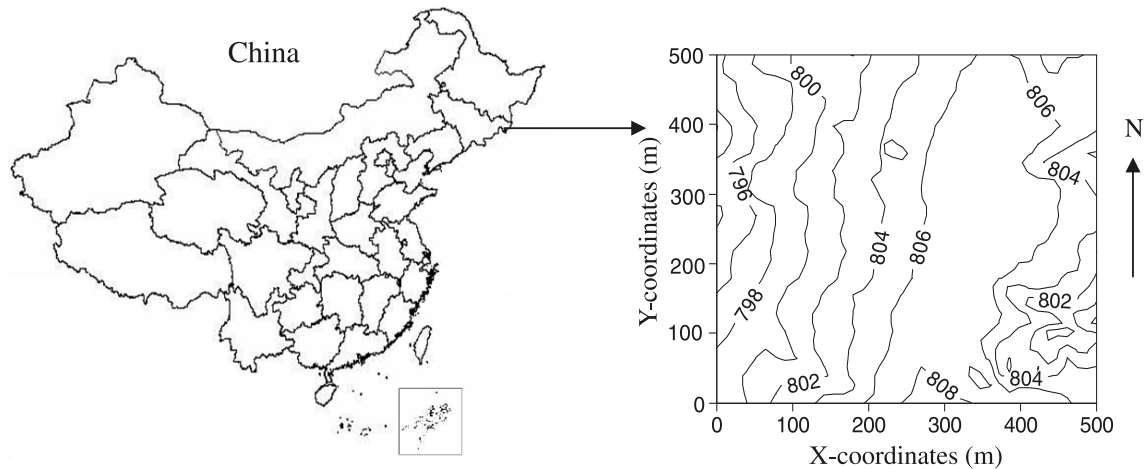
biodiversity theories, niche versus neutral, in biodiversity studies and are fundamental to understanding community assemblages (Hubbell 2001; Chase 2005; Gaston and Chown 2005). Models based on neutral theory assume that species are functionally identical and drift randomly in abundance until they vanish and can form patterns of distribution and abundance similar to those found in nature (Mouquet and Loreau 2003; Chave 2004; Purves and Pacala 2005). However, ample evidence indicates that species are not equivalent; species-specific differences in their functional traits and ecological strategies affect the spatial distributions and dynamics of species (Peters 2003; Lortie et al. 2004; Stoll and Newbery 2005; Condit et al. 2006; Murrell 2009). For example, seed dispersal ability affects distributions of species, with well-dispersed species being less aggregated than

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Fig. 1. Location and contour map of the 25 ha (500 m × 500 m) Changbaishan temperate plot.



poorly dispersed species (Condit et al. 2000; Li et al. 2009). Additionally, as the classical Janzen–Connell spacing effect predicts, spatial distributions of adult trees would become more regular than those of juveniles because of the differential attack rates between adults and juveniles by distance/frequency-responsive pathogens or herbivores (Janzen 1970; Connell 1971). However, lack of effective quantitative methods and high quality data of species distributions at proper spatial and temporal scales has also contributed much confusion and controversy.

Current knowledge on spatial distributions of species and underlying mechanisms is mostly derived from tropical rain forests (but see Li et al. (2009) for subtropical forests). Considering the complexity of these hyperdiverse forests, it may be more realistic to expect these underlying mechanisms to differ among species, just as the resulting spatial distributions of species differ (He et al. 1997). In addition, there are some questions that cannot sufficiently be addressed by studying tropical forests alone. An important question is whether these theories or hypotheses that have been developed to explain the hyperdiverse tropical forests may also be applicable to other forests, such as temperate forests. Although there is a long tradition of analyzing spatial distributions of species in temperate forests (e.g., Kenkel 1988; Duncan 1991), most of these studies have focused on few dominant or overstory species in these forests (e.g., Hao et al. 2007) and have been conducted at small scales (≤ 1 ha) (e.g., Kubota 2006; Gravel et al. 2008; Mori and Komiyama 2008). Consequently, the community-wide analysis of spatial distributions of species, the species–habitat association, diversity pattern, and the underlying mechanisms of species coexistence are not well understood in temperate forests (but see Canham et al. 2006; Papaik and Canham 2006).

Motivated by these challenges and for the ultimate understanding of the mechanisms of species coexistence, the Chinese Academy of Sciences, in collaboration with the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute, has recently initiated an ambitious large-scale, long-term Forest Dynamics and Diversity Plots network. The China network has been designed to establish five 20–25 ha plots along the latitudinal gradient from north to south China. This study reports the spatial distributions of species in the 25 ha Changbaishan (CBS) plot. The CBS

plot is the northernmost plot of the China Forest Biodiversity Monitoring Network (www.cfbiodiv.org), which is also the largest forest plot in a temperate region.

The data from the temperate CBS plot provide a unique opportunity to address how the temperate forest community is spatially structured and the implication of the spatial structure in maintenance of the species assemblage. The specific objectives are (i) to analyze the spatial distributions of conspecific species in the CBS plot and compare spatial distributions in hyperdiverse tropical forests with those in temperate forests, (ii) to investigate the change in spatial distributions of species with spatial scale, (iii) to examine whether the Janzen–Connell spacing effect, i.e., species become more regularly spaced as trees grow, is also in operation in this temperate forest, and (iv) to test whether different functional groups (abundance, canopy, shade tolerance, dispersal mode, etc.) have an effect on the spatial distributions of species. It is expected that this study will provide important insights into the possible mechanisms that structure and maintain the assemblage of the tree species of the temperate forests and also serve as a foundation for subsequent studies.

Materials and methods

Study area

The study site is located in the Changbai Nature Reserve, which was established along the border of China and North Korea extending from $127^{\circ}42'$ to $128^{\circ}17'E$ and from $41^{\circ}43'$ to $42^{\circ}26'N$. The reserve was first established in 1960 and is one of the largest biosphere reserves in China. It has been spared from logging and other severe human disturbances due to its remoteness and inaccessibility to the general public before establishment of the reserve. Changbai Nature Reserve joined the World Biosphere Reserve Network under the UNESCO Man and the Biosphere Programme in 1980. The reserve is about 200 000 ha in size with an elevation ranging from 740 to 2691 m at the summit of Changbai Mountain on the Chinese side. Changbai Mountain is the highest mountain in northeastern China and is the head of three large rivers (the Songhua, Yalu, and Tumen) in the northeastern provinces. Topographic features differ on the four slopes of the mountain, with the northern slope being

Table 1. Functional traits for species with ≥ 10 individuals in the Changbaishan plot.

Species	Family	No. of individuals	Canopy layer	Shade tolerance	Dispersal mode
<i>Acer barbinerve</i>	Aceraceae	3910	Understory	Shade tolerant	Wind
<i>Acer ginnala</i>	Aceraceae	108	Understory	Shade tolerant	Wind
<i>Acer mandshuricum</i>	Aceraceae	251	Midstory	Shade tolerant	Wind
<i>Acer mono</i>	Aceraceae	6609	Midstory	Shade tolerant	Wind
<i>Acer pseudo-sieboldianum</i>	Aceraceae	5984	Midstory	Shade tolerant	Wind
<i>Acanthopanax senticosus</i>	Araliaceae	35	Understory	Shade tolerant	Gravity
<i>Acer tegmentosum</i>	Aceraceae	846	Midstory	Shade tolerant	Wind
<i>Acer triflorum</i>	Aceraceae	276	Midstory	Shade tolerant	Wind
<i>Acer tsckonoskii</i>	Aceraceae	39	Understory	Shade tolerant	Wind
<i>Aralia elata</i>	Araliaceae	12	Understory	Shade tolerant	Gravity
<i>Betula costata</i>	Betulaceae	16	Overstory	Light demanding	Wind
<i>Betula platyphylla</i>	Betulaceae	96	Midstory	Light demanding	Wind
<i>Cerasus maximowiczii</i>	Rosaceae	18	Understory	Light demanding	Animal
<i>Corylus mandshurica</i>	Betulaceae	7833	Understory	Shade tolerant	Gravity
<i>Crataegus maximowiczii</i>	Rosaceae	121	Understory	Shade tolerant	Gravity
<i>Euonymus alatus</i>	Celastraceae	38	Understory	Shade tolerant	Gravity
<i>Euonymus macropterus</i>	Celastraceae	10	Understory	Shade tolerant	Gravity
<i>Euonymus pauciflorus</i>	Celastraceae	37	Understory	Shade tolerant	Gravity
<i>Fraxinus mandshurica</i>	Oleaceae	681	Overstory	Midtolerant	Wind
<i>Fraxinus rhynchophylla</i>	Oleaceae	10	Midstory	Shade tolerant	Wind
<i>Lonicera monantha</i>	Caprifoliaceae	27	Understory	Shade tolerant	Gravity
<i>Maackia amurensis</i>	Leguminosae	753	Midstory	Midtolerant	Gravity
<i>Malus baccata</i>	Rosaceae	106	Midstory	Shade tolerant	Gravity
<i>Phellodendron amurense</i>	Rutaceae	60	Midstory	Light demanding	Gravity
<i>Philadelphus schrenkii</i>	Saxifragaceae	470	Understory	Shade tolerant	Gravity
<i>Pinus koraiensis</i>	Pinaceae	2468	Overstory	Midtolerant	Animal
<i>Populus davidiana</i>	Salicaceae	27	Midstory	Light demanding	Wind
<i>Populus ussuriensis</i>	Salicaceae	30	Overstory	Light demanding	Wind
<i>Prunus padus</i>	Rosaceae	515	Midstory	Shade tolerant	Gravity
<i>Pyrus ussuriensis</i>	Rosaceae	74	Midstory	Light demanding	Gravity
<i>Quercus mongolica</i>	Fagaceae	926	Overstory	Light demanding	Animal
<i>Rhamnus davarica</i>	Rhamnaceae	26	Understory	Shade tolerant	Gravity
<i>Rhamnus ussuriensis</i>	Rhamnaceae	118	Midstory	Shade tolerant	Gravity
<i>Sambucus williamsii</i>	Caprifoliaceae	19	Understory	Light demanding	Gravity
<i>Sorbus alnifolia</i>	Rosaceae	19	Understory	Shade tolerant	Gravity
<i>Syringa reticulata</i>	Oleaceae	1598	Midstory	Light demanding	Wind
<i>Tilia amurensis</i>	Tiliaceae	2927	Overstory	Shade tolerant	Gravity
<i>Tilia mandshurica</i>	Tiliaceae	410	Overstory	Shade tolerant	Gravity
<i>Ulmus japonica</i>	Ulmaceae	1109	Overstory	Midtolerant	Wind
<i>Ulmus laciniata</i>	Ulmaceae	192	Midstory	Midtolerant	Wind
<i>Viburnum burejaeticum</i>	Caprifoliaceae	23	Understory	Shade tolerant	Gravity
<i>Viburnum sargentii</i>	Caprifoliaceae	43	Understory	Shade tolerant	Gravity

relatively moderate (average slope $< 3\%$) and other slopes being relatively steep (average 10%). The area has a temperate continental climate with long cold winters and warm summers. Annual mean temperatures vary from $7.3\text{ }^{\circ}\text{C}$ in the lowest reaches of the reserve to $2.8\text{ }^{\circ}\text{C}$ near Sky Lake (the volcanic Crater Lake) on the mountaintop, and annual mean precipitation varies from 750 to 1340 mm.

In 2004, a 25 ha old-growth temperate forest plot of $500\text{ m} \times 500\text{ m}$ was established in Changbai Nature Reserve (Fig. 1). Within the plot, all free-standing trees and shrubs at least 1 cm diameter at breast height (DBH) were identified, tagged, and mapped and their geographic coordinates were recorded following a standard field protocol (Condit 1998). In the study site, the terrain is relatively gentle. The elevation ranges from 791.8 to 809.5 m and mean

elevation is 801.5 m. There were 38 902 stems belonging to 52 species and 18 families (Hao et al. 2008; Wang et al. 2008a, 2008b). Species abundance varied greatly from 1 to 7381 individuals. To obtain a large sample size for the point pattern analyses, we used only 42 species with ≥ 10 trees (Table 1).

Data analyses

Many indices and functions have been widely used to measure spatial distributions of species (e.g., Ripley 1981; He et al. 1997; Wiegand and Moloney 2004; Illian et al. 2008). Here, we used an index called the relative neighborhood density Ω (Condit et al. 2000) to quantify spatial distributions of species. For a given species, Ω equals the average density of conspecifics in the neighborhood of indi-

Table 2. Spatial distributions of species in the Changbaishan plot as measured by Ω .

Annulus (m)	Aggregated				Random			
	Abundant (n = 13)	Intermediate (n = 12)	Rare (n = 17)	Total (n = 42)	Abundant (n = 13)	Intermediate (n = 12)	Rare (n = 17)	Total (n = 42)
0–10	12 (92.3%)	12 (100%)	14 (82.4%)	38 (90.5%)	1 (7.7%)	0 (0%)	3 (17.6%)	4 (9.5%)
10–20	13 (100%)	12 (100%)	7 (41.2%)	32 (76.2%)	0 (0%)	0 (0%)	10 (58.8%)	10 (23.8%)
20–30	13 (100%)	12 (100%)	2 (11.8%)	27 (64.3%)	0 (0%)	0 (0%)	15 (88.2%)	15 (35.7%)
30–40	12 (92.3%)	11 (91.6%)	3 (17.6%)	26 (61.9%)	1 (7.7%)	1 (8.3%)	14 (82.4%)	16 (38.1%)
40–50	11 (84.6%)	11 (91.6%)	4 (23.5%)	26 (61.9%)	2 (15.4%)	1 (8.3%)	13 (76.5%)	16 (38.1%)

Note: Species with <50 individuals were classified as rare, 50–500 individuals as intermediate, and ≥500 individuals as abundant; n indicates the total number of species in each category, and the number in each cell is the significantly aggregated (or random) species in each category.

viduals normalized by the density of individuals of the species in the whole plot as formulated by $\Omega_{x_1,x_2} = D_{x_1,x_2}/\lambda$ (Condit et al. 2000), where $D_{x_1,x_2} = \sum N_{x_1,x_2}/\sum A_{x_1,x_2}$, N_{x_1,x_2} is the number of conspecifics within the annulus defined by the radii x_1 and x_2 , A_{x_1,x_2} is the area of the annulus, and λ is the mean density of the given species in the whole plot. The advantage of Ω over D_{x_1,x_2} is that Ω is normalized and allows direct comparison of patterns that have different intensities (or number of individuals). The index Ω is closely related to Ripley's K function, but K is a cumulative distribution function, whereas Ω is a probability density function, i.e., K_x refers to conspecifics located within distance x centered on the focal individual and Ω_{x_1,x_2} is computed based on the number of individuals within an annulus between x_1 and x_2 metres. Therefore, Ω isolates specific distance classes by using annuli instead of circles, while the K function confounds the effect at larger distances with that at small distances (Condit et al. 2000; Wiegand and Moloney 2004).

For a random distribution, $\Omega_{x_1,x_2} = 1$ within an annulus between x_1 and x_2 metres. If $\Omega_{x_1,x_2} > 1$, the species is considered aggregated, whereas $\Omega_{x_1,x_2} < 1$ indicates regular distribution. We used Monte Carlo simulation to test whether a species is not significantly from random distribution. Four hundred and ninety-nine distributions were simulated by randomly labeling all species in the plot while keeping the abundance of each species the same as the observed. If the observed Ω falls within the 2.5th and 97.5th quartiles, the null hypothesis cannot be rejected. Otherwise, we would conclude that the species in the CBS plot is significantly different from random distribution.

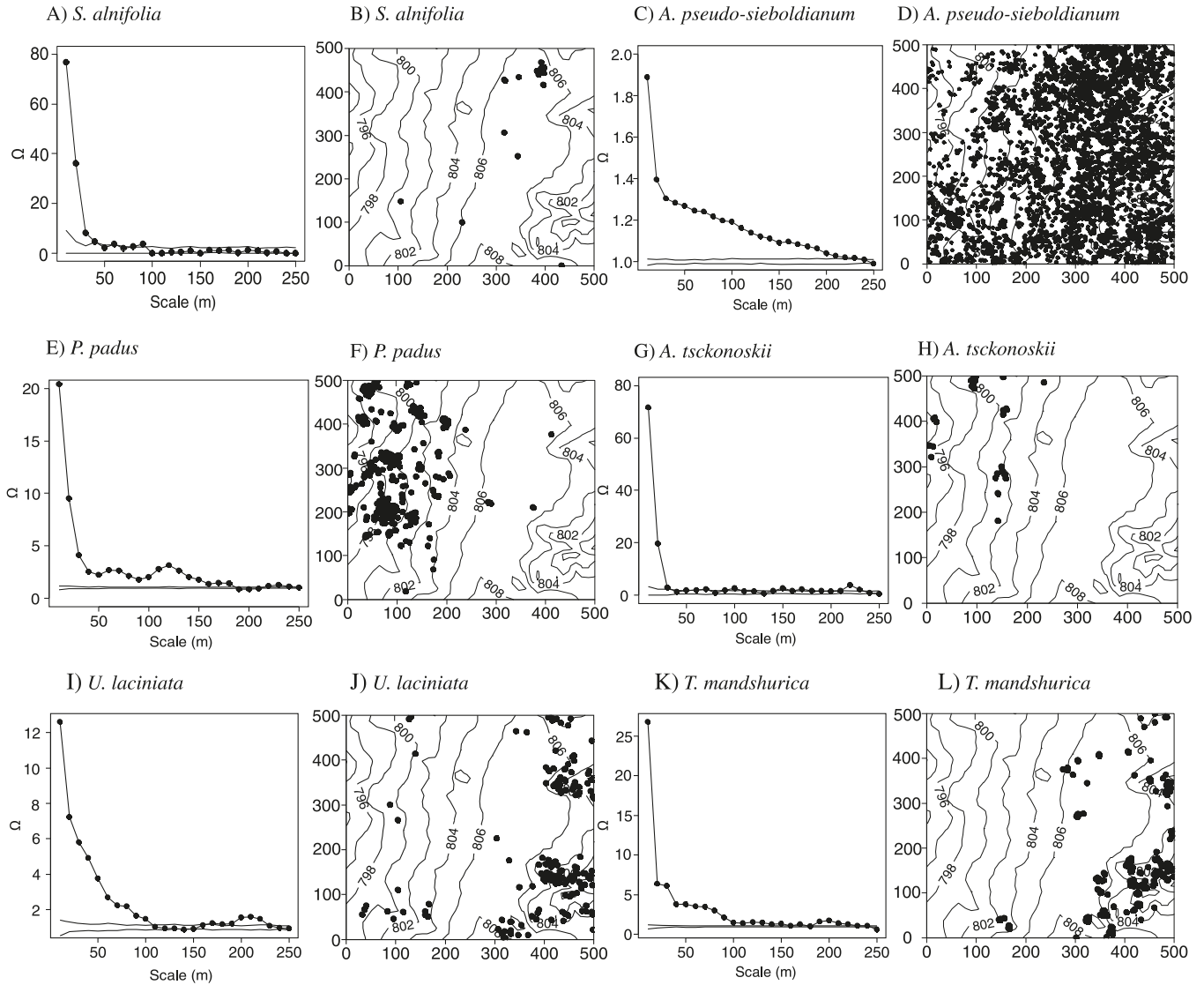
Because Ω values in nearby distance classes were highly correlated with one another, we used Ω_{0-10} , the mean conspecific density within 10 m of an individual, as a simple measure of the intensity of aggregation of a species (Condit et al. 2000) to compare spatial distributions of species in different guilds (Table 1). We chose 10 m because direct interactions among species only occur within a limited distance of 10 m (Wang et al. 2010). First, we divided species into three abundance classes: rare (with abundance <50), intermediate (50–500), and abundant (common) (≥500) species. Second, we used DBH to divide species into seven size classes: (0–5, 5–10, 10–20, 20–30, 30–40, 40–50, and ≥50 cm). Third, species were classified into overstory, mid-story, and understory species. Finally, we compared spatial distributions of species at different seed dispersal mode: wind, gravity, and animal.

In addition, we conducted multiple regression to analyze the effects of different guilds on the spatial distribution pattern of species with >10 individuals using Ω_{0-10} as dependent variables and abundance, maximum DBH, mean DBH, canopy, shade tolerance, and dispersal mode as independent variables.

Results

Of the 42 species studied in the full CBS plot, 17 are classified as rare, 12 as intermediate, and 13 as abundant. At the <50 m scale, most species are aggregated and no species show regular distribution (Table 2). The percentage of aggregated species decreases with distance. For example, 38 species (90.5%) are significantly aggregated at 0–10 m, 32

Fig. 2. Examples of species distribution patterns in the Changbaishan plot. Panels on the left show the relationship between Ω and scale and panels on the right show the corresponding distribution patterns together with contour lines for six species. The lines with points are for Ω ; the other lines are the simulation envelopes generated from 499 Monte Carlo simulations under the null hypothesis of complete spatial randomness.



(76.2%) are significantly aggregated at 10–20 m, and 27 (64.3%) are significantly aggregated at 20–30 m (Table 2). The Ω generally declines with distance (Fig. 2): $\Omega_{10-20} < \Omega_{0-10}$ in 38 of 42 species and $\Omega_{20-30} < \Omega_{10-20}$ in 35 species. In addition, the percentage of significantly aggregated rare species decreases more rapidly with distance than that of intermediate and abundant species (Table 2). For example, the percentage of rare aggregated species decreases from 82.4% at 0–10 m to 41.2% at 10–20 m and to 23.5% at 40–50 m, whereas the percentages of abundant and intermediate species at all distances <50 m are more than 84%.

There is a clear tendency that the aggregation intensity as measured by Ω_{0-10} declines with abundance, i.e., rare species are more aggregated than intermediate and abundant species (Fig. 3). For example, the median Ω_{0-10} is 24.4 for rare species, 9.9 for intermediate species, and 1.9 for abundant species. The highest Ω_{0-10} of all species studied is 76.7

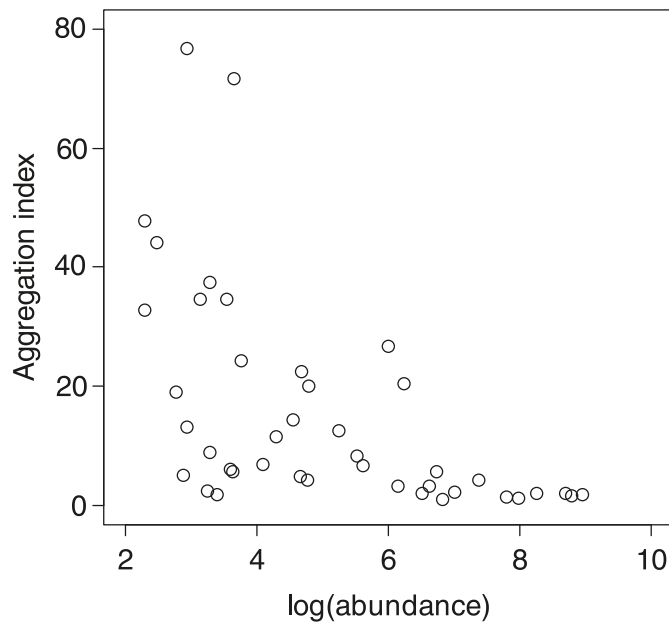
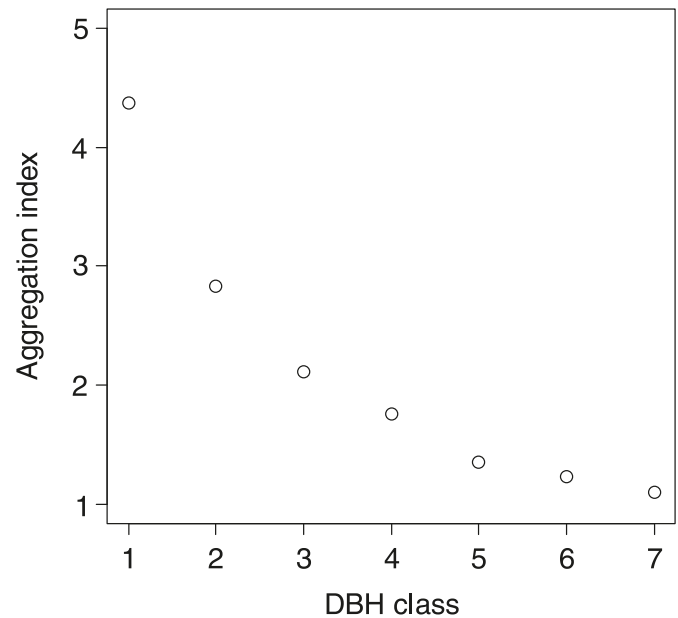
in *Sorbus alnifolia* (Siebold & Zucc.) K.Koch with 19 individuals (Fig. 2A). Most of the abundant species have $\Omega_{0-10} < 5$.

The aggregation intensity varies for different size classes (DBH). The percentage of significantly aggregated species decreases with DBH (Table 3): 90.9% of species at the 1–5 cm DBH size class are aggregated, 71.4% at the 20–30 cm DBH size class, and 16.7% at the >50 cm DBH size class. Also, the median Ω_{0-10} declines with DBH, except for the 20–30 cm DBH size class (Table 3). For example, the aggregation intensity for one of the dominant species, *Tilia amurensis* Rupr., declines with DBH (Fig. 4).

The average Ω_{0-10} of overstory species (6.9, SE = 3.6) is smaller than that of midstory species (13.1, SE = 3.3) and understory species (23, SE = 5.4). Results of a *t* test show significant difference between overstory species and understory species. Overstory species are less aggregated

Table 3. Spatial distributions across DBH classes for species with ≥ 10 individuals in the Changbaishan plot.

DBH class (cm)	Median Ω_{0-10}	Total no. of species	No. of significantly aggregated species
1–5	7.79	33	30
5–10	5.45	21	20
10–20	3.83	20	16
20–30	7.54	14	10
30–40	2.81	8	4
40–50	1.28	7	3
>50	1.10	6	1

Fig. 3. Relationship between aggregation index (Ω_{0-10}) and abundance of species with abundances ≥ 10 in the Changbaishan plot.**Fig. 4.** Relationship between aggregation index (Ω_{0-10}) and DBH of *Tilia amurensis*. DBH classes: 1, 1–5 cm; 2, 5–10 cm; 3, 10–20 cm; 4, 20–30 cm; 5, 30–40 cm; 6, 40–50 cm; 7, >50 cm.

than understory species. In contrast, midstory species are not significantly different from overstory species and understory species.

The average Ω_{0-10} of animal-dispersed species (2.5, SE = 1.3) is smaller than that of gravity-dispersed species (17.6, SE = 3.9) and of wind-dispersed species (15.4, SE = 4.8). Results of a *t* test show that the aggregation intensity of animal-dispersed species is significantly different from that of gravity-dispersed and wind-dispersed species. Animal-dispersed species are less aggregated than gravity-dispersed species and wind-dispersed species, whereas gravity-dispersed species are not significantly different from wind-dispersed species.

The average Ω_{0-10} of light-demanding species (11.4, SE = 3.4) is smaller than that of shade-tolerant species (19.3, SE = 4.1), while the average Ω_{0-10} of midtolerant species is the smallest (4.2, SE = 2.1). Results of a *t* test show that the aggregation intensity of midtolerant species is significantly different from that of light-demanding and shade-tolerant species. Midtolerant species are less aggregated than light-demanding species and shade-tolerant species, whereas light-demanding species are not significantly different from shade-tolerant species.

The results of multiple regression for Ω_{0-10} show that the regression model is significant ($P = 0.004$). The standardized coefficients indicate that abundance has the largest effect on spatial aggregation followed by shade tolerance, mean DBH, dispersal mode, maximum DBH, and canopy (Table 4). The effects of mean DBH and canopy on spatial aggregation are negative, i.e., aggregation intensity declines with these factors.

Discussion

The 42 species with ≥ 10 individuals comprised 99.9% of all trees in the fully mapped 25 ha plot at CBS. Most species were aggregated, but the proportion of aggregated species decreased with spatial scale in the temperate forests: aggregation is 90.5% at 0–10 m, 76.2% at 10–20 m and 64.3% at 20–30 m. However, no clear decrease with spatial scale was found in tropical forests and subtropical forests. For example, Condit et al. (2000) found that >97.8% were significantly aggregated at the corresponding scales in tropical forests, and Li et al. (2009) showed that aggregation was >96.1%, slightly lower than that in tropical forests. All of these suggest that the aggregation percentage of species in

Table 4. Multiple regression of aggregation intensity (Ω_{0-10}) with abundance maximum DBH, mean DBH, canopy, shade tolerance, and dispersal mode showing the estimated coefficients, standard errors, and standardized coefficients.

	Unstandardized coefficient		Standardized (beta) coefficient
	Estimate	SE	
Constant	27.727	24.33	
Abundance	-6.084	1.565	-0.644
Maximum DBH	0.036	0.259	0.08
Mean DBH	-0.196	0.388	-0.195
Canopy	-0.551	8.412	-0.022
Shade tolerance	6.125	4.068	0.274
Dispersal mode	4.05	4.908	0.137

Note: The standardized coefficients are partial regression coefficients that indicate the relative effects of each variable on Ω_{0-10} .

natural forest communities may increase with increasing species richness.

Rare species tended to be more aggregated than abundant ones, which was consistent with that found in other forests (Condit et al. 2000; Davis et al. 2005; Li et al. 2009). However, not all species respond in a similar way. For example, *Populus ussuriensis* Komarov, one of the rare species with 30 individuals, is expected to have a high Ω_{0-10} value; however, the Ω_{0-10} only equals 1.8, much less than the median Ω_{0-10} (24.4) of rare species. In contrast, the abundant species *Prunus padus* L. with 515 individuals has a relatively high Ω_{0-10} of 20.4 (Fig. 2E), which is more than the median Ω_{0-10} (1.9) of abundant species. One of the most important reasons is that spatial distributions of species can arise from many ecological processes, such as competition, stochastic recruitment, dispersal limitation, habitat heterogeneity, disturbance, etc. (e.g., Cale et al. 1989; Rees et al. 1996; Tuomisto et al. 2003; Wiegand et al. 2007).

The functional traits of species (e.g., size class, canopy layer, shade tolerance, and dispersal mode) were important factors in affecting spatial distributions of species in the CBS temperate forests. Species aggregation generally decreased with increasing size class (DBH) in the CBS plot. The finding that smaller individuals of a species were more aggregated than larger individuals may be largely due to self-thinning. However, pathogens or herbivores may also play an important role as spacing mechanisms in reducing aggregation in temperate forests (e.g., Seiwa et al. 2008). In the CBS temperate forests, previous studies showed that the seedlings or saplings near adult trees were often eaten by herbivores (e.g., Zhao and Zhang 2005). There are a number of studies that support the notion of less aggregation with increasing DBH (e.g., He et al. 1997; Condit et al. 2000; Getzin et al. 2008; Seiwa et al. 2008). For example, He et al. (1997) studied the spatial distributions of the 18 most abundant species in the Pasoh Forest, Malaysia, and found a decrease in aggregation with increasing size class (DBH). Similarly, Li et al. (2009) observed a clear trend that aggregation is weaker in larger diameter classes. However, Condit et al. (2000) examined the spatial distributions of species in six different tropical forest plots and found that species at the smaller diameter class were more aggregated at four of the six plots, whereas the pattern was reversed at the other two plots: most species became more aggregated at the large size. According to these contrasting results, Murrell (2009)

pointed out that although there was ample evidence for a reduction in aggregation with an increase in DBH, it was entirely possible for adult trees to be more aggregated than juveniles when adult recruitment rates were low and dispersal was poor even in the absence of any environmental heterogeneity such as slope or elevation.

Dispersal limitation is commonly regarded as one of the important mechanisms to explain species aggregation, especially in hyper-rich tropical forests (Hubbell 1979; Condit et al. 2000; Plotkin et al. 2000). In the CBS temperate forests, the aggregation distributions of species also indicated dispersal limitation. These species occurred in small-scale clumps that did not correspond to topography (Figs. 2F and 2H). They had relatively high Ω_{0-10} values but these decreased rapidly with distance (Figs. 2E and 2G). Some studies indicated that the extent and scale of conspecific spatial aggregation were dependent on the mode of seed dispersal (Condit et al. 2000; Seidler and Plotkin 2006; Li et al. 2009). Species with high dispersal ability were assumed to be better dispersed than species with low dispersal ability, thus causing a less aggregated pattern for these species with high dispersal ability. Our study showed that species dispersed by animals were better dispersed than wind- and gravity-dispersed species. In addition, overstory species usually have well-dispersed seeds relative to understory species and thus are expected to be less clumped than understory species. Here, the prediction that better dispersal reduces aggregation was borne out. Overstory species tended to be less aggregated than understory species in the temperate forests. However, in tropical forests, there was a significant difference in aggregation intensity between overstory and understory species at one plot, but at another plot, there may be not (Condit et al. 2000).

Shade tolerance may also be expected to have a significant effect on species distribution pattern. Previous studies showed that shade-tolerant species tended to have a steeply descending monotonic diameter distribution with a large number of suppressed small trees (Leak 1975; Hett and Loucks 1976; Lorimer 1980; Wang et al. 2009), whereas mid-tolerant species had almost unimodal distributions with few suppressed small trees (Lorimer and Krug 1983; Wang et al. 2009). As we showed above that smaller trees were more aggregated than larger trees, shade-tolerant species were thus expected to be more aggregated than mid-tolerant species. In addition, light-demanding species tended to be

localized in some gaps created by small-scale disturbances (e.g., windthrow), thus causing more aggregation than for midtolerant species. Our studies were consistent with the expectation that midtolerant species were less clumped than shade-tolerant species and light-demanding species.

In addition, spatial heterogeneity, caused by topography, edaphic, or other environmental factors, has been widely considered as an important factor in affecting spatial distributions of species (e.g., Harms et al. 2001; John et al. 2007). Although the terrain of the CBS plot is relatively gentle, J. Ye et al. (unpublished analysis) found that nearly 60% of 35 species studied showed significant habitat association (habitat type was classified based on topography). For example, the two species, *Tilia mandshurica* Rupr. & Maxim. and *Ulmus laciniata* (Trautv.) Mayr favor the slope habitat (Figs. 2G and 2L). Species differ in their ability to adapt to different environmental conditions, which may result in the different distribution pattern of species in relation to environment.

Conclusions

Our study provides unique and comprehensive analyses on the spatial distributions of species in a megaplot of a temperate forest, northeastern China. The results show that most species studied in the CBS temperate forests are aggregated, but the proportion of aggregated species decreases with distance. Analogous analyses in the species-rich tropical or subtropical forests also show that spatial aggregation is the dominant pattern of species but no clear decrease with distance (Condit et al. 2000; Li et al. 2009). In addition, species abundance has significant effects on the spatial aggregation pattern of species in the CBS temperate forests. For example, rare species are more aggregated than intermediate and common species. The aggregation intensity decreases with increasing DBH, i.e., species become more regularly spaced as species grow, which is consistent with the predictions of self-thinning and Janzen–Connell spacing effects. Species functional traits (canopy layer, seed dispersal ability, shade-tolerance, etc.) also have a significant effect on the spatial distributions of species. Consequently, dispersal limitation, self-thinning, Janzen–Connell spacing effects, and habitat heterogeneity may be the primary contributing factors in the spatial distributions of species in the temperate forests.

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