

# Species spatial distributions in a warm-temperate deciduous broad-leaved forest in China

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**Abstract** Spatial distribution is fundamental for understanding species coexistence mechanisms in forest communities. Here we comprehensively explored fine-scale spatial patterns of tree species in a secondary warm-temperate deciduous broad-leaved forest community in north China. Aggregated distribution patterns were predominant. Species functional traits had no significant effects on their spatial patterns. The aggregation intensity decreased with increasing DBH and abundance. The multivariate linear stepwise regression showed that abundance and maximum DBH were correlated with the aggregation intensity. Our results partially confirm that species attributes (abundance, DBH) and habitat heterogeneity may primarily contribute to spatial patterns and species coexistence in this secondary forest.

**Keywords** Spatial distributions · Aggregation intensity · Species functional trait · Secondary warm-temperate deciduous broad-leaved forest

## Introduction

Species spatial distribution patterns are fundamental for developing a detailed understanding in many branches of ecology, and ecologists study these patterns to infer the existence of underlying processes (Baddeley et al. 2015; Wiegand et al. 2017). The aggregated distribution of species is widespread in nature and may be attributable to two primary factors, habitat heterogeneity and dispersal limitations, which represent niche-based and neutral processes, respectively (Condit et al. 2000; Harms et al. 2001; Hubbell 2001; Wiegand and Moloney 2014). Existing sophisticated statistical tools now permit accurate analyses of spatial patterns to test the hypotheses about underlying mechanisms (Wiegand et al. 2017).

Spatial patterns provide fundamental information for understanding species coexistence mechanisms in forest communities, although spatial patterns alone are insufficient to disentangle underlying mechanisms (Wiegand et al. 2017). The spatial patterns of species have been analyzed in natural old-growth forests in fully mapped tree census plots such as the species-rich tropical forest communities (Condit et al. 2000), a subtropical low-elevation forest community in south China (Li et al. 2009), a mid-subtropical mountain forest community in central China (Guo et al. 2013), and an old-growth temperate forest community in northeastern China (Wang et al. 2010b). These studies have shown that the majority of tree species are spatially aggregated. However, it is still unclear whether general distribution patterns in these natural old-

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growth forests are present in a secondary warm- temperate forest community.

Studies comprehensively exploring fine-scale spatial patterns of tree species are scarce in temperate forest communities (Wang et al. 2010b). In this study, fine-scale spatial patterns of tree species were examined in the 20-ha Donglingshan forest dynamic plot (DLS), representative of a secondary warm- temperate deciduous broad-leaved forest in northern China and a component of the Chinese Forest Biodiversity Monitoring Network (CForBio; <http://www.cfbi.org/>). The objectives were to: (1) analyze conspecific species spatial distributions; and (2) test how species attributes (e.g., abundance, size, canopy layer, shade tolerance, and dispersal mode) affect species spatial distributions. These findings can help elucidate potential mechanisms that are responsible for the formation and maintenance of warm-temperate forest tree assemblages.

## Materials and methods

### Study site

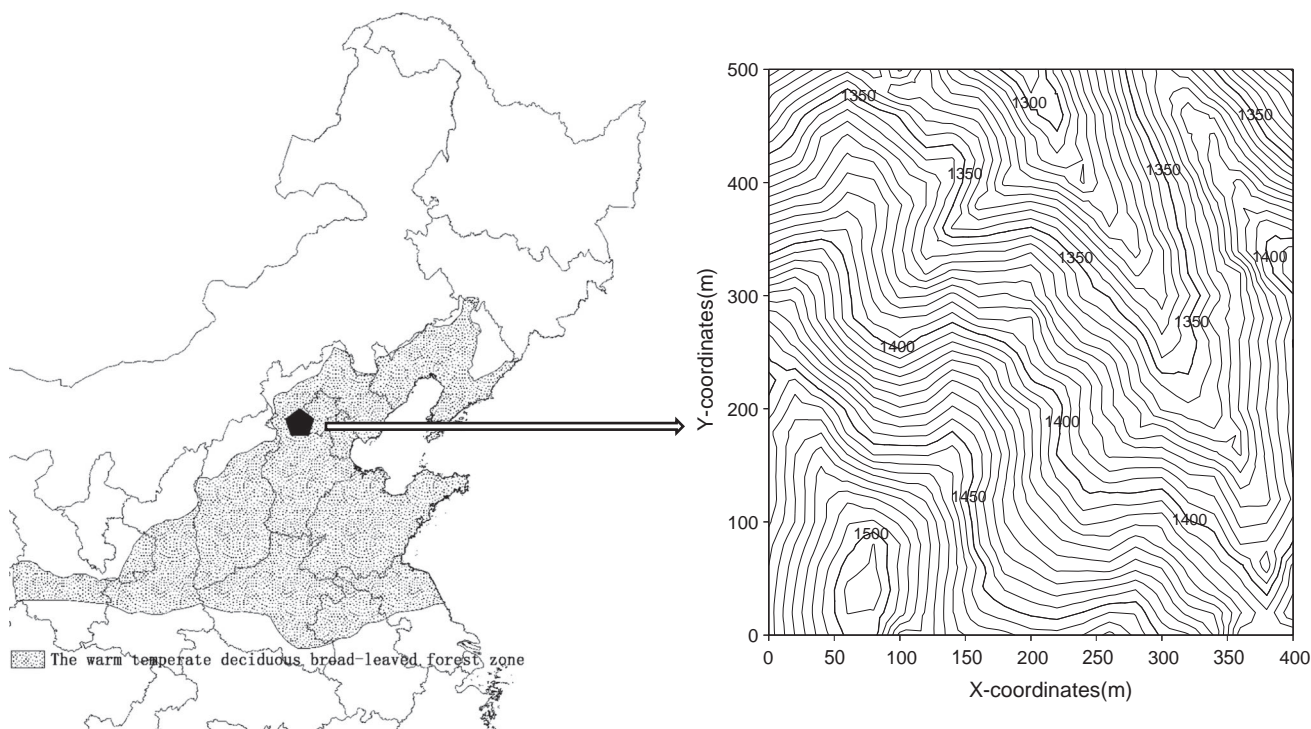
Xiaolongmen National Forest Park is located at the foot of Donglingshan Mountain and typical of the warm-temperate deciduous broad-leaved forest zone (Fig. 1). The original

forests in this area were severely damaged in the 1960s, and large areas have been recolonized by secondary forests (Zou et al. 2015). This region experiences a warm temperate and continental monsoon climate, with an average annual temperature of 4.3 °C and a mean annual precipitation of 589 mm (Su and Li 2012).

The DLS is located in the center of Xiaolongmen National Forest Park and represents a secondary warm-temperate deciduous broad-leaved forest within the middle stages of succession. The forest is approximately 60 years old and mainly consists of *Quercus mongolica* Fisch. ex Ledeb., *Betula dahurica* Pall., *B. platyphylla* Sukaczew, *Populus davidiana* Dode and *Juglans mandshurica* Maxim. (Liu et al. 2014).

### Data collection

The permanent 20-ha (400 m × 500 m) plot was established in 2010 as a node of the CForBio program with the aim to monitor long-term dynamics in a warm-temperate deciduous broad-leaved mixed forest. All woody stems  $\geq 1$  cm at a diameter at breast height (1.3 m; DBH) within the plot were mapped, measured, identified to species, and tagged following standard field procedures (Condit 1998). The plot had 52681 trees belonging to 51 species of 32 genera and 19 families. The most common species were *Quercus mongolica* Fisch. ex Ledeb., *Acer mono* Maxim.,



**Fig. 1** Location and contour map of the 20-ha (400 m × 500 m) Donglingshan temperate plot

*Betula dahurica* Pall., *Syringa pubescens* Turcz., *Abelia biflora* Turcz., and *Corylus mandshurica* Turcz. The terrain is undulate with valleys and ridges, and the elevation ranges from 1290 to 1509 m. To obtain a sufficient sample size for point-pattern analyses, 44 common species were chosen with at least 10 individuals for analysis (Table 1).

**Table 1** Functional traits for species with  $\geq 10$  individuals in the DLS plot

Species	Family	No. of individuals	Canopy layer	Shade tolerance	Dispersal mode
<i>Abelia biflora</i>	Caprifoliaceae	5190	Understory	Shade-tolerant	Wind
<i>Acanthoanax senticosus</i>	Araliaceae	45	Understory	Shade-tolerant	Animal
<i>Acer mono</i>	Aceraceae	10,547	Overstory	Shade-tolerant	Wind
<i>Betula dahurica</i>	Betulaceae	2542	Overstory	Light-demanding	Wind
<i>Betula platyphylla</i>	Betulaceae	783	Overstory	Light-demanding	Wind
<i>Cornus bretschneideri</i>	Cornaceae	331	Midstory	Mid-tolerant	Animal
<i>Corylus mandshurica</i>	Betulaceae	6185	Understory	Shade-tolerant	Animal
<i>Deutzia grandiflora</i>	Saxifragaceae	60	Understory	Shade-tolerant	Wind
<i>Deutzia parviflora</i>	Saxifragaceae	1526	Understory	Shade-tolerant	Wind
<i>Euonymus alatus</i>	Celastraceae	14	Understory	Shade-tolerant	Animal
<i>Fraxinus bungeana</i>	Oleaceae	111	Midstory	Mid-tolerant	Wind
<i>Fraxinus rhynchophylla</i>	Oleaceae	2286	Midstory	Mid-tolerant	Wind
<i>Hydrangea bretschneideri</i>	Saxifragaceae	333	Overstory	Shade-tolerant	Wind
<i>Juglans mandshurica</i>	Juglandaceae	579	Overstory	Shade-tolerant	Animal
<i>Larix principis-rupprechtii</i>	Pinaceae	156	Overstory	Light-demanding	Animal
<i>Lespedeza bicolor</i>	Leguminosae	130	Understory	Shade-tolerant	Gravity
<i>Lonicera chrysantha</i>	Caprifoliaceae	138	Understory	Shade-tolerant	Animal
<i>Malus baccata</i>	Rosaceae	36	Midstory	Mid-tolerant	Animal
<i>Philadelphus pekinensis</i>	Saxifragaceae	88	Understory	Mid-tolerant	Wind
<i>Populus cathayana</i>	Salicaceae	232	Overstory	Light-demanding	Wind
<i>Populus davidiana</i>	Salicaceae	1740	Overstory	Light-demanding	Wind
<i>Prunus armeniaca</i>	Rosaceae	26	Midstory	Mid-tolerant	Animal
<i>Prunus davidiana</i>	Rosaceae	430	Midstory	Mid-tolerant	Animal
<i>Prunus padus</i>	Rosaceae	79	Midstory	Mid-tolerant	Animal
<i>Quercus mongolica</i>	Fagaceae	5297	Overstory	Light-demanding	Animal
<i>Rhamnus davurica</i>	Rhamnaceae	698	Understory	Shade-tolerant	Animal
<i>Rhamnus globosa</i>	Rhamnaceae	21	Understory	Mid-tolerant	Animal
<i>Rhamnus parvifolia</i>	Rhamnaceae	166	Understory	Mid-tolerant	Animal
<i>Rhododendron micranthum</i>	Ericaceae	1305	Understory	Light-demanding	Wind
<i>Rhododendron mucronulatum</i>	Ericaceae	1410	Understory	Light-demanding	Wind
<i>Ribes pulchellum</i>	Saxifragaceae	81	Understory	Shade-tolerant	Animal
<i>Salix phylicifolia</i>	Salicaceae	22	Midstory	Light-demanding	Wind
<i>Salix viminalis</i>	Salicaceae	148	Midstory	Light-demanding	Wind
<i>Sambucus williamsii</i>	Caprifoliaceae	14	Understory	Mid-tolerant	Animal
<i>Sorbus discolor</i>	Rosaceae	916	Midstory	Mid-tolerant	Animal
<i>Spiraea pubescens</i>	Rosaceae	426	Understory	Mid-tolerant	Wind
<i>Spiraea trilobata</i>	Rosaceae	29	Understory	Mid-tolerant	Wind
<i>Syringa pekinensis</i>	Oleaceae	352	Midstory	Mid-tolerant	Wind
<i>Syringa pubescens</i>	Oleaceae	5979	Midstory	Mid-tolerant	Wind
<i>Tilia mandshurica</i>	Tiliaceae	445	Overstory	Mid-tolerant	Gravity
<i>Tilia mongolica</i>	Tiliaceae	584	Overstory	Mid-tolerant	Gravity
<i>Ulmus laciniata</i>	Ulmaceae	256	Overstory	Light-demanding	Wind
<i>Ulmus macrocarpa</i>	Ulmaceae	499	Overstory	Light-demanding	Wind
<i>Ulmus pumila</i>	Ulmaceae	429	Overstory	Light-demanding	Wind

## Data analyses

The relative neighborhood density,  $\Omega$ , is used to quantify spatial distributions and allows direct comparison of patterns with different numbers of individuals or intensities (Condit et al. 2000; Wiegand and Moloney 2004).  $\Omega_{x1,x2}$  is the O-ring scaled by abundance of the species evaluated, as formulated by  $\Omega_{x1,x2} = D_{x1,x2}/\lambda$  where  $D_{x1,x2} = \sum N_{x1,x2}/\sum A_{x1,x2}$ ,  $N_{x1,x2}$  is the number of conspecifics within an annuli between  $x1$  and  $x2$  m,  $A_{x1,x2}$  is the annuli area between  $x1$  and  $x2$  m,  $D_{x1,x2}$  is the species density between  $x1$  and  $x2$  m and  $\lambda$  is the species density in the entire plot. For an aggregated distribution,  $\Omega_{x1,x2} > 1$  within an annuli between  $x1$  and  $x2$  m;  $\Omega_{x1,x2} = 1$  indicates random distribution, whereas  $\Omega_{x1,x2} < 1$  suggests regular distribution. The Monte Carlo simulations are used to determine whether species distribution significantly differed from random. If  $\Omega$  is within the 2.5th and 97.5th quartiles in 499 simulated distributions by randomly labeling all species throughout the plot and retaining the observed species abundance data, the spatial pattern of species is random; otherwise, the species distributions significantly differs from random (Wiegand and Moloney 2004).

The species were separated into three categories based on abundance (rare, abundance < 50; intermediate, 50–500; and abundant,  $\geq 500$ ) and into seven size classes (< 5,  $5 \leq 10$ ,  $10 \leq 20$ ,  $20 \leq 30$ ,  $30 \leq 40$ ,  $40 \leq 50$ , and  $\geq 50$  cm) according to DBH. The species were classified based on canopy location (overstory, midstory, or understory) and shade-tolerance (shade-tolerant, mid-tolerant, or light-demanding). Dispersal modes (wind, gravity, and animal) were also assigned to each species based on fruit morphology, and each species was assigned to one main dispersal mode (Seidler and Plotkin 2006; Guo et al. 2013).  $\Omega_{0,10}$  was used as a simple measure of aggregation intensity of a species (Table 1).

Specific effects of different functional trait guild (canopy location, shade-tolerant ability, dispersal mode) on

$\Omega_{0,10}$  were evaluated by analysis of variance (ANOVA).  $\Omega_{0,10}$  was transformed by  $\log(\Omega_{0,10} + 1)$  to satisfy the assumptions of ANOVA. To sort out the effects of different species attributes on spatial patterns, a multivariate linear stepwise regression was conducted using  $\log(\Omega_{0,10} + 1)$  as the dependent variable, and abundance, maximum and mean DBH, canopy layer, shade tolerance, and dispersal mode as independent variables.

## Results

### Analysis of spatial patterns

Of the 44 species, 16 were classified as abundant, 20 as intermediate, and eight as rare (Table 1). At scales < 50 m, most species had an aggregated pattern and irregular distribution (Table 2). Of all abundant and intermediate species aggregated at scales < 50 m, only *Philadelphus pekinensis* Rupr. was random at a scale of 40–50 m. Most rare species also aggregated at scales < 50 m (Fig. 2). Random distributions were observed at < 10 m and 10–20 m for *Sambucus williamsii* Hance; 30–40 m for *Rhamnus globosa* Bunge and *Spiraea trilobata* L.; 20–30 m for *Euonymus alatus* (Thunb.) Sieber, *R. globosa*, and *S. williamsii*; and 40–50 m for *Malus baccata* (L.) Borkh., *Philadelphus pekinensis* Rupr., *R. globosa*, and *S. williamsii*.

The percentage of aggregated species decreased from 97.7 to 93.2% as the annuli area changed from 0–10 to 40–50 m (Table 2). Of the 44 species,  $\Omega_{10-20} < \Omega_{0-10}$  for 43 species,  $\Omega_{20-30} < \Omega_{10-20}$  for 44 species, and  $\Omega_{30-40} < \Omega_{20-30}$  for 41 species;  $\Omega$  declined with distance.

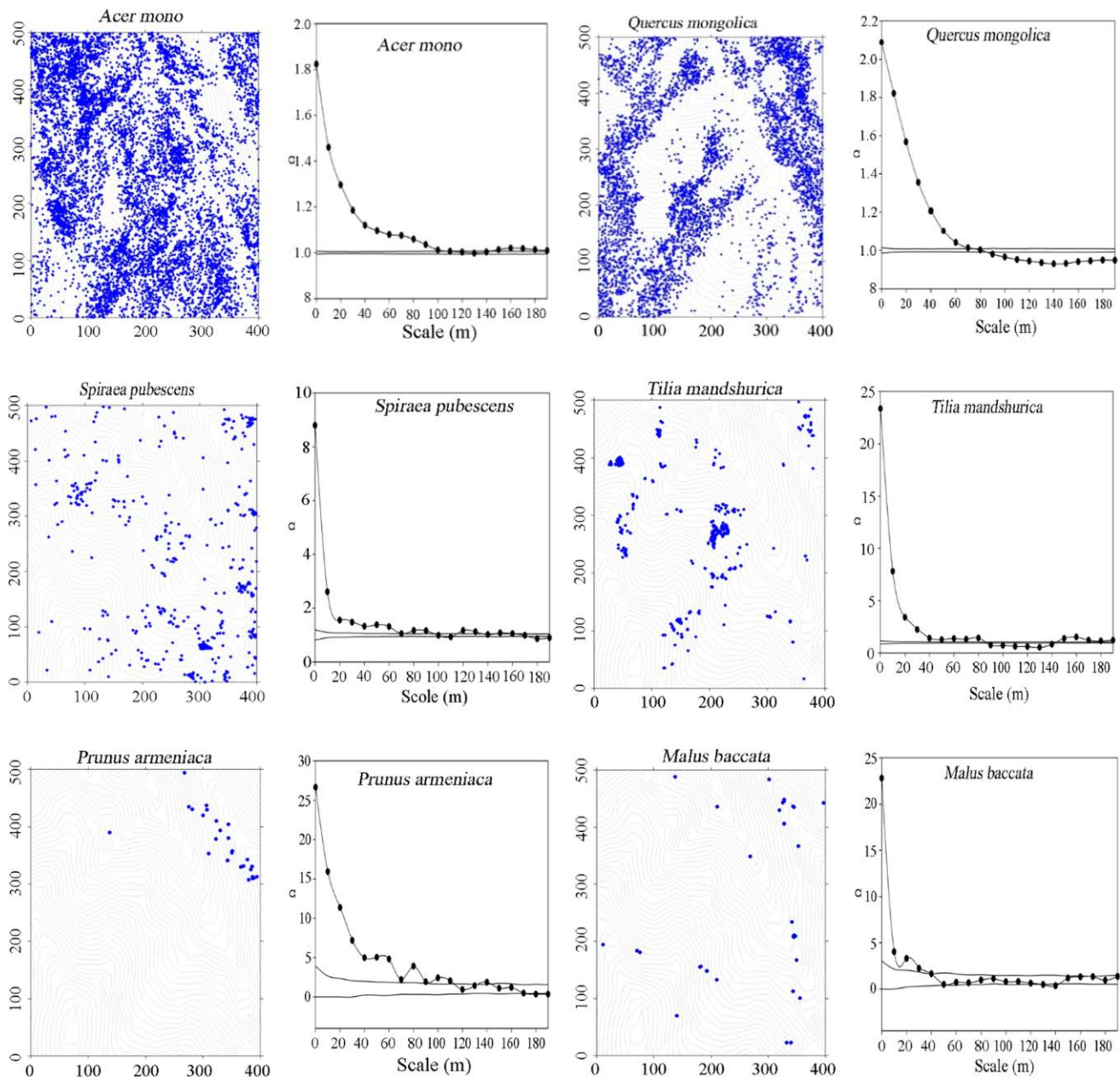
### Aggregation intensity and species attributes

Overstory species (13.2, SE = 3.5) had a smaller average  $\Omega_{0-10}$  than midstory species (20.0, SE = 4.6) and

**Table 2** Spatial distributions of species in the Donglingshan plot as measured by  $\Omega$

Annulus (m)	Aggregated				Random			
	Abundant (n = 16)	Intermediate (n = 20)	Rare (n = 8)	Total (n = 44)	Abundant (n = 16)	Intermediate (n = 20)	Rare (n = 8)	Total (n = 44)
0–10	16 (100%)	20 (100%)	7 (87.5%)	43 (97.7%)	0 (0%)	0 (0%)	1 (12.5%)	1 (2.3%)
10–20	16 (100%)	20 (100%)	7 (87.5%)	43 (97.7%)	0 (0%)	0 (0%)	1 (12.5%)	1 (2.3%)
20–30	16 (100%)	20 (100%)	5 (62.5%)	41 (93.2%)	0 (0%)	0 (0%)	3 (37.5%)	3 (6.8%)
30–40	16 (100%)	20 (100%)	6 (75%)	42 (95.5)	0 (0%)	0 (0%)	2 (25%)	2 (4.5%)
40–50	16 (100%)	19 (95%)	5 (62.5%)	41 (93.2%)	0 (0%)	1 (5%)	3 (37.5%)	3 (6.8%)

Species with < 50 individuals were considered rare, 50–500 individuals were intermediate, and  $\geq 500$  individuals were abundant; n indicates the total number of species in each category, and the number in each cell represents the number of significantly aggregated (or randomly dispersed) species in each category



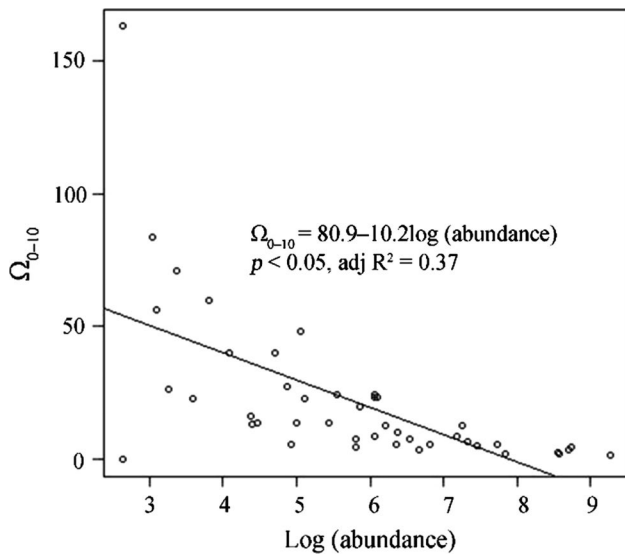
**Fig. 2** Examples of species distribution patterns in the DLS plot. Panels on the left show the distribution patterns and contour lines for six species including two abundant, intermediate and rare species, and panels on the right show the corresponding relationship between  $\Omega$

and scale. The lines with points represent  $\Omega$ ; the other lines represent the simulation envelopes generated from 499 Monte Carlo simulations under the null hypothesis of complete spatial randomness

understory species (30.7, SE = 9.7). For animal-dispersed species, average  $\Omega_{0-10}$  (28.7, SE = 9.5) was larger than that of gravity- (20.3, SE = 5.1) and wind-dispersed species (17.4, SE = 3.8). Average  $\Omega_{0-10}$  for mid-tolerant species (22.4, SE = 5.3) was less than average  $\Omega_{0-10}$  of shade-tolerant species (26.6, SE = 12.3); however, light-demanding species had the smallest average  $\Omega_{0-10}$  (17.5, SE = 4.7). ANOVA showed that  $\Omega_{0-10}$  is not significantly different among the functional groups.

$\Omega_{0-10}$  clearly declined as abundance increased (Fig. 3). For rare, intermediate, and abundant species, the median  $\Omega_{0-10}$  values were 57.3, 18.1, and 5.3, respectively. The highest  $\Omega_{0-10}$  among all species was 162.8 for *Euonymus alatus*, of which there were 14 individuals.

The median  $\Omega_{0-10}$  values were 13.54, 13.17, 12.47, 9.69, 3.04 and 2.39 at < 5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm and 40–50 cm for DBH, respectively (Table 3). The median  $\Omega_{0-10}$  decreased with increasing DBH. In each



**Fig. 3** Relationship between aggregation index ( $\Omega_{0-10}$ ) and abundance of species with abundance  $\geq 10$  in the DLS plot

DBH class except 40–50 cm, the percent of the aggregated species is larger than 80% (Table 3).

The multivariate linear stepwise regression for  $\log(\Omega_{0-10} + 1)$  showed that abundance and maximum DBH were significant factors; the associated regression model was  $\log(\Omega_{0-10} + 1) = 3.3 - 0.0002(\text{abundance}) - 0.017(\text{maximum DBH})$  ( $p < 0.05$ ,  $\text{adj } R^2 = 0.32$ ).

**Table 3** Spatial distribution across DBH classes for all species with  $\geq 10$  individuals in the DLS plot

DBH class (cm)	Median $\Omega_{0-10}$	Total no. of species	No. of significantly aggregated species (%)
1–5	13.54	42	40 (95.2%)
5–10	13.17	29	29 (100%)
10–20	12.47	21	21 (100%)
20–30	9.69	14	14 (100%)
30–40	3.04	6	5 (83.3%)
40–50	2.39	2	1 (50.0%)

The last column shows the number and percent of species that significantly aggregated

**Table 4** Aggregation rates in different forest types

Forest type	Species richness	No. species analyzed	Abundance	Aggregation rate at spatial scale (m)			References
				< 10	10–20	20–30	
Tropical rain forests	72–1174	1768	$\geq 1^a$	99.2	99.4	97.8	Condit et al. (2000)
Subtropical forest	210	124	$\geq 10$	98	98	96.1	Li et al. (2009)
Warm temperate forest	51	44	$\geq 10$	97.7	97.7	93.2	This report
Temperate forests	52	42	$\geq 10$	90.5	76.2	64.3	Wang et al. (2010b)

<sup>a</sup>Per hectare

### Discussion

Aggregation is common in nature (Condit et al. 2000; Li et al. 2009; Wang et al. 2010b; Guo et al. 2013). This study showed that the dominant distribution pattern of species in a warm- temperate forest was aggregation. Clear decreases in aggregation percentage at the same spatial scale were found from tropical to temperate forests (Table 4). For example, aggregation percentages were 99.2%, 98.0%, 97.7%, and 90.5% at a scale of < 10 m in tropical, subtropical, warm temperate, and temperate forests, respectively. The species richness values for these forests were 72–1174, 210, 51, and 52, respectively, which indicates that species aggregation rates increase in natural forest communities when there is increasing species richness. The relation between aggregation rates and richness should be further analyzed in future.

Species aggregation is affected by species functional traits, including dispersal and degree of shade-tolerance. Species with animal-dispersed seeds are better distributed than those with wind- or gravity-dispersed seeds (Condit et al. 2000; Wang et al. 2010b). The mid-shade tolerant species were predicted to be less aggregated than shade-tolerant species because they tend to have numerous suppressed small trees (Leak 1975; Hett and Loucks 1976; Lorimer 1980; Wang et al. 2010a). Mid-shade tolerant species had few suppressed small trees (Lorimer and Krug 1983; Wang et al. 2010b). Light-



demanding species may be the most dispersed when the first to enter a forest site (Wang et al. 2010b). Our findings did not support these hypothesis according to the ANOVA and may be the result of the forest successional stage. Functional traits may not begin to play important roles in shaping species patterns.

Overall, abundant species were less aggregated than rare species and spatial aggregation decreased with increasing DBH. This was consistent with those of other forests (Condit et al. 2000; Li et al. 2009; Wang et al. 2010b). Aggregation may have been weaker for larger diameter classes because of self-thinning from competition (Zhu et al. 2015, 2018; Pu and Jin 2018). Moreover, herbivores and pests may also contribute to reducing aggregation (Wills and Condit 1999; Harms et al. 2000; Peng and Xu 2005; Zhao and Zhang 2005). The damage of insects to the leaves of *Quercus mongolica* Fisch. ex Ledeb. is very common. The frequency of leaf feeding is about 90%, and the area eaten is about 5% in similar forest type at Dongling Mountain (Yu et al. 2001), which possibly causes increased mortality of seedlings and saplings, and substantially weakens aggregation intensity (Yu et al. 2002). The maximum DBH is significantly negative correlated with aggregation intensity. The maximum DBH characterizes the time the tree begins to grow in the plot while DBH is often correlated with the tree age (Meng 1989; Gu et al. 2013). Species became less aggregated as individuals experienced long-term competition.

Habitat conditions can strongly influence species distribution, even in gentle terrain (Harms et al. 2001; Lai et al. 2009). For example, two middle canopy species had different habitat preferences: *Aporosa yunnanensis* (Pax & K. Hoffm.) F.P. Metcalf favored relatively wet valley habitats, whereas *Xanthophyllum hainanense* Hu. favored dry ridge habitats in the subtropical forest (Li et al. 2009). The DLS plot was divided into six habitats based on topography and 18 of the 19 species studied were significantly associated with habitat (unpublished data).

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