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Spatial Patterns and Associations of Dominant Tree Species in Subtropical Evergreen Broadleaved Forest in Southern China*

中国亚热带常绿阔叶林优势种的空间格局与关联

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Abstract：**【Objective】**It is well known that the spatial pattern in plant communities plays an important role in community assembly and dynamic. **【Methods】**We analyzed the population structure of eight dominant tree species at a 3.2hm^2 subtropical evergreen broadleaved forest plot in Damingshan Nature Reserve in southern China. Based on the O-ring statistic, a technique of spatial point pattern analysis, we analyzed small-scale intraspecific spatial distribution patterns and intra- or inter-specific spatial association patterns among eight dominant species. **【Results】** The results showed that significant aggregated for intraspecific, and for smaller trees within species at small scales. Large trees of *Huodendron biaristatum* and *Diospyros morrisiana* showed significant positive association with their smaller trees at small scales, while large tree of *Acer fabric* showed significant negative association with its smaller trees at all scales of 0～40m. Only 2 of 58 species pairs among these species showed significant small-scale positive association. **【Conclusion】**These results revealed that seed dispersal limitation and microhabitat heterogeneity might contribute to the coexistence of these dominant species at subtropical evergreen broadleaved forest in Damingshan. However, the ecological assembly rules in subtropical evergreen broadleaved forest are required to further explore in southern China.

Key words：point pattern analysis, the O-ring statistic, spatial association, subtropical evergreen broadleaved forest, community assembly

摘要：**【目的】**种群空间格局对阐明植物群落构建与动态具有重要意义。**【方法】**在广西大明山国家级自然保护区建立了一个面积3.2hm^{2}的常绿阔叶林固定样地。运用O-ring空间点格局分析方法对样地8个优势种的空间格局以及种群大小关联和种间关联进行了研究。**【结果】**8个优势树种及其小径级个体在小尺度上均为聚集分布；云贵山茉莉和毛狗骨柴的大径级与其小径级个体在小尺度上呈正相关，而罗浮槭的大径级与小径级在0～40m上为负相关；58个种对中有2个种对在小尺度上表现正相关。**【结论】**种子扩散限制与微生境异质性是大明山常绿阔叶林优势种共存的原因。但是，有关中国亚热带常绿阔叶林的群落构建机制还有待深入研究。

关键词：点格局分析　O-ring统计　空间关联　亚热带常绿阔叶林　群落构建
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The problem of how communities are structured over space and time is a central issue in ecology[1]. Analyzing spatial patterns in plant communities may provide insight into the importance of different processes for community assembly and dynamics[2～4].

Although plant community assembly is driven

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by the spatial segregation hypothesis[5], competition or facilitation[6,7], dispersal limitation[8,9], habitat preference[10,11], and the Janzen-Connell hypothesis[12,13], there are still important challenges, mainly because similar patterns can be explained by different theories[14]. For example, the spatial segregation hypothesis was known from theoretical models to promote species coexistence. The assumeption that intraspecific aggregation and interspecific segregation can decreases the probability of interspecific encounters and competitive exclusion is prevented[15~17]. In contrast, the Janzen-Connell hypothesis suggested that seedlings of tropical trees found close to conspecific adults often suffer higher mortality than seedlings further away and can free up space for heterospecifics to colonize, contributing to species coexistence in a community[18~20].

The important processes structuring plant community are likely to leave strong imprints on the spatial patterns of the location of plants within a community[14,21~23]. In order to detect the underlying ecological processes controlling the observed spatial patterns, the methods of spatial point pattern analysis are commonly used to analyze the intraspecific spatial distribution patterns and interspecific spatial association patterns among species within plant communities[24~28].

In recent years, several attempts have been made to explore spatial structure of all dominant species in forest community of the world, largely in temperate and tropical forest communities [14,29~35], however a relative few studies were implemented in subtropical evergreen broadleaved forests of southern China, an area of the most important world subtropical forests. Therefore, such studies are of prime importance for advancing our understanding of spatial processes and mechanisms in subtropical evergreen broadleaved forest communities.

In this paper, we analyzed population size-class and point pattern data of the eight dominant tree species from a 3.2hm^2 plot of subtropical evergreen broadleaved forest community located in Damingshan Nature Reserve, southern China. The following questions were to be tested: (1) Are there significant difference in population structure among these dominant species? (2) Is the univariate small-scale spatial pattern aggregated or regular? (3) Are smaller individuals from the species 1 attracted or repulsed by larger individuals of the conspecific? and (4) What are the interspecific small-scale relationships among these dominant species in the forest?

1 Materials and methods

1.1 Study area

The study site is located in the Damingshan Nature Reserve, southern China (23°10′~23°38′N, 108°18′~108°45′E). It is a typical evergreen broadleaved monsoon forest reserve located on the Northern Tropic of Cancer in China. The highest peak is 1760.4m, and 1563m for maximal elevation differences. The dominant soil type is mountain yellow earth.

A 3.2hm^2 (160m × 200m) plot located in the core zone of the Damingshan Nature Reserve was established in August 2009, and is representative of subtropical evergreen broadleaved forest, an old-growth forest in species composition and community structure for the region. The forest plot is located on a steep North-west-facing slope (average incline is 34°), with altitudes ranging from 1020m to 1180m. Soil conditions are nearly homogeneous, with the thin soil layer and limestone outcrops. Mean annual air temperature is 15.1℃, with a January mean of 5.8℃ and a July mean of 21.9℃. Mean annual precipitation is 2511mm, with mainly occurring from April to September[36].

We recorded stem coordinates (exact to 0.1m), species and diameters at breast height (DBH, 1.3m above the ground) of all live trees with DBH≥1cm within the study plot. The total number of living individuals was 8889, consisting of 241 species, 110 genera, and 54 families. The dominant species were *Huodendron biaristatum*, *Acer fabric*, *Litsea suberosa*, *Machilus pauhoi*, *Stewartia gemmata*, *Diospyros morrisiana*, *Betula utilis*, and *Sloanea chingiana*. The ecological characteristics of these species are shown in Table 1.

Table 1 Properties for the dominant tree species in a subtropical evergreen broadleaved forest community in southern China

Species	Abundance of species	Family	Stand layer	Shade tolerance	Fruit type	Dispersal mode
Huodendron biaristatum	1096	Styracaceae	Canopy	Shade tolerant	Capsule	Gravity
Acer fabric	482	Aceraceae	Canopy	Shade tolerant	Samara	Wind
Litsea suberosa	359	Lauraceae	Canopy	Midtolerant	Berry	Gravity
Machilus pauhoi	476	Lauraceae	Midstorey	Shade tolerant	Berry	Gravity
Stewartia gemmata	96	Theaceae	Midstorey	Shade tolerant	Capsule	Gravity
Diospyros morrisiana	199	Ebenaceae	Canopy	Midtolerant	Berry	Gravity
Betula utilis	72	Betulaceae	Canopy	Light demanding	Samara	Wind
Sloanea chingiana	144	Elaeocarpaceae	Canopy	Midtolerant	Capsule	Gravity

1.2 Statistical analysis

To detect the spatial correlation structure within and between species, we employed the O-ring statistic[24,37] as test statistic. The O-ring statistic O(r) advocated by Wiegand and Moloney (2004)[27] is the analogue of Ripley's K function[24] when replacing the circles of radius *r* by rings with radius *r*, but it presents two advantages over the K function: Especially sensitive to small-scale effects, and be able to isolate scale effects[27,28]. Thus, using the O-ring statistic as complement to Ripley's K function may be particularly useful in situations where possible violation of homogeneity is not obvious from visual inspection of the pattern[27]. Similar to Ripley's K function, the O-ring statistic includes both univariate and bivariate statistics. The univariate O-ring statistic O_{11} (r), which is the average density of points in a ring of radius *r* and width *dr* centred in an arbitrary point in the whole studied area, was used to detect the spatial patterns of the eight tree species and the patterns of these species in two size classes; the bivariate O-ring statistic O_{12}(r), which is the average density of points of pattern 2 in a ring of radius *r* and width *dr* centred in an arbitrary point of pattern 1, was used to detect the intraspecific associations of two size classes and the interspecific associations among all studied species. Two size classes were larger (DBH≥5cm) and smaller (DBH <5cm).

We used a heterogeneous Poisson (HP) as null model, and a Monte-Carlo approach to quantify the test statistic for significant departure from the null model. The 95% confidence envelopes (i.e. the 5th-lowest and the 5th-highest values of O(r)) for testing spatial randomness were generated from 99 Monte-Carlo simulations of the HP null model[25]. Specifically, when analyzing the intraspecific associations between larger and smaller size classes, we fixed the locations of the larger classes, and distributed the locations of the smaller classes using the HP null model[38], when analyzing the interspecific associations between species, we tested all species pairs, i.e. both species 1 versus species 2 and species 2 versus species 1, because the association may be asymmetric[14].

However, the Monte-Carlo test approach is invalid for inference because it violates the assumptions of Monte-Carlo methods and results in incorrect type I error rate performance[39]. Therefore, we also used the goodness-of-fit test (GoF) to assess significance levels over the full rang of scales. Under the GoF test, the u_0 value was calculated from observed data sets, while the u_i ($i = 1, \cdots, 99$) values were calculated from each of 99 simulations of the null model, and then the rank u_0 among all u_i values was determined. If the rank of u_0 is larger than 95, the data showed a significant departure from the null model with error rate $P < 0.05$. Details on the GoF test can be found in Loosmore and Ford (2006)[39].

In the study, we retained the results for further analysis only when the observed *P* value of the GoF test was smaller than 0.05. All calculations and simulations were performed using the grid-based estimators in the *Programita* software[27]. The ring width used for the estimators was one cell unit, and the cell size was 2m×2m.

2 Results

2.1 Population structure

Diameter size-class distribution of *Huodendron biaristatum* roughly showed the reverse J-shaped pattern. Three species (*Machilus pauhoi*, *Litsea suberosa* and *Diospyros morrisiana*) showed the distinct L-shaped size-class distribution, with more individuals in smaller size classes, and relatively few large individuals. *Acer fabric*, *Stewartia gemmata*, *Betula utilis* and *Sloanea chingiana* had a variability in abundance. They showed a compound size-class distribution, which was descending in the smaller size classes, and had a multiple peak in the larger ones (Figure 1).

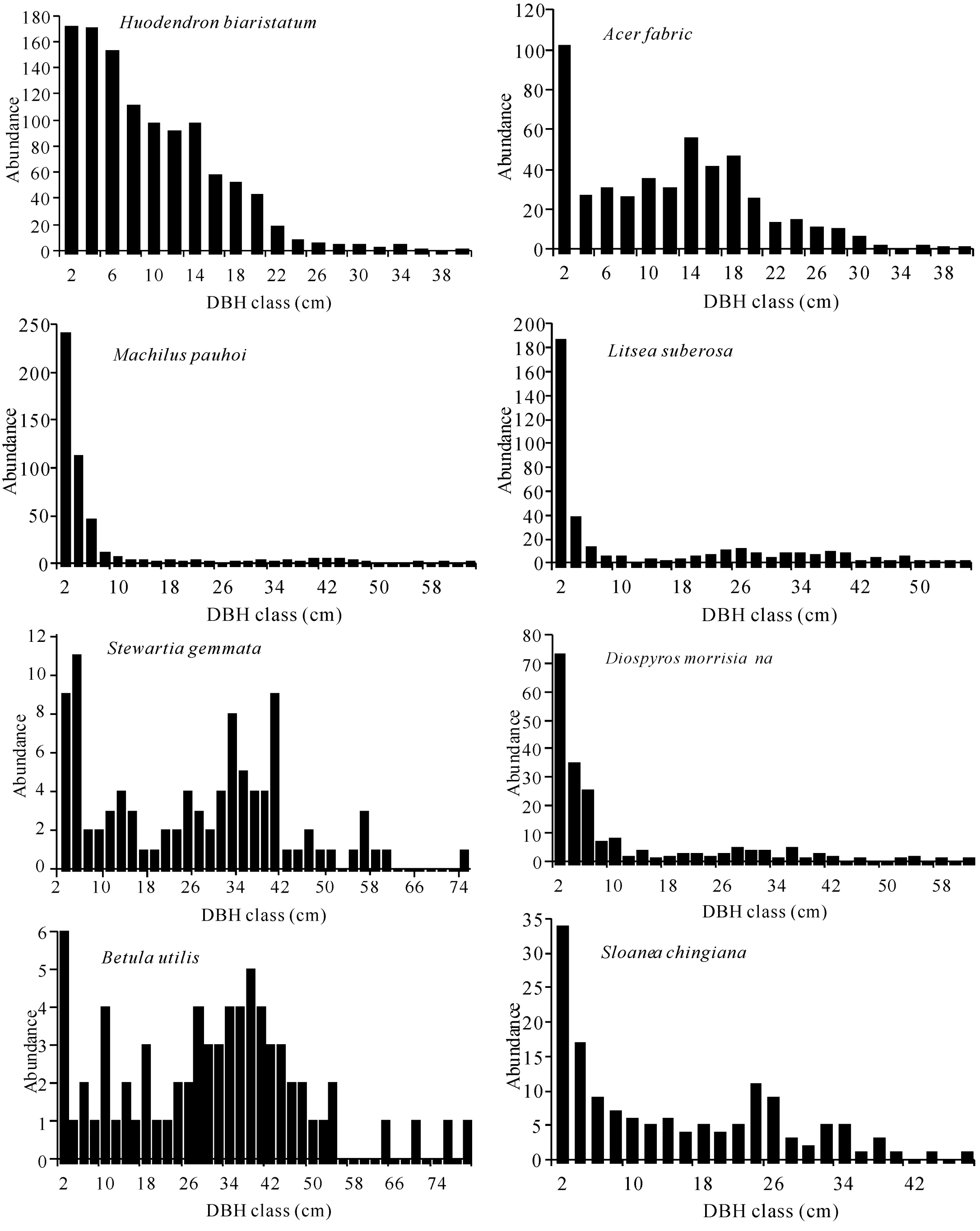

Figure 1 DBH distributions of 2-cm classes for eight dominant species in the study plot

The two lowest abundant species had the biggest diameters, which were ca. 74cm for *Stewartia gemmata* and ca. 80cm for *Betula utilis* (Figure 1). Maximum diameters investigated for the other species were 42.2cm in *Huodendron biaristatum*, 40.5cm in *Acer fabric*, 56.3cm in *Litsea suberosa*, 63.7cm in *Machilus pauhoi*, 61.5cm in *Diospyros morrisiana*, and 48.6cm in *Sloanea chingiana*.

2.2 Spatial patterns

The GoF test revealed for the eight species significant departures from the heterogeneous Poisson null model at small scales (Figure 2). Both four species (*Huodendron biaristatum*, *Acer fabric*, *Litsea suberosa*, and *Machilus pauhoi*) with high

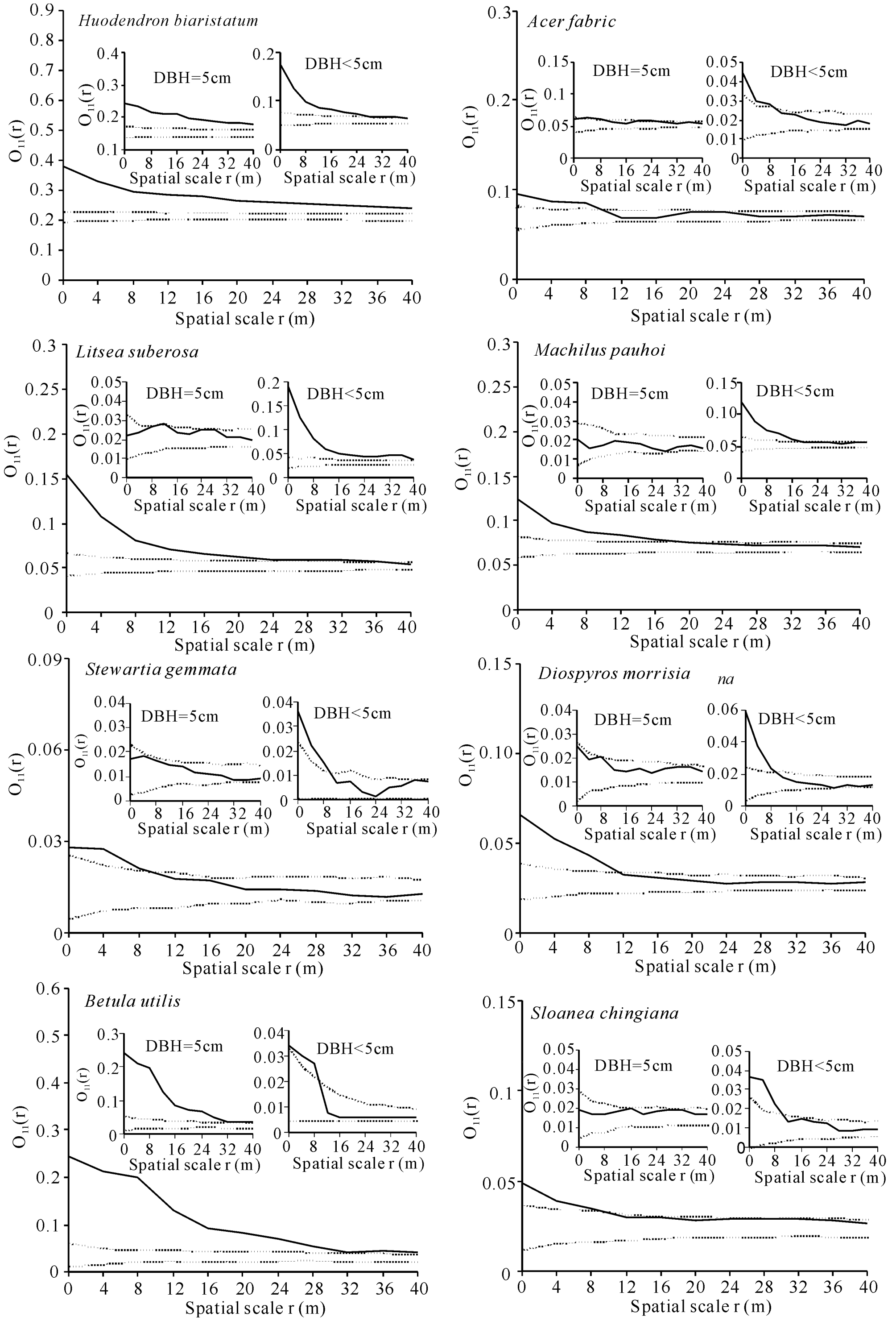

Figure 2 Intraspecific spatial patterns analyses of eight tree species

Note: Insets in each figure show the analyses of the spatial pattern of two different size classes (DBH⩾5cm and DBH<5cm). Black lines stands for the univariate O-ring statistic $O_{11}(r)$; thin dashed lines stands for confidence envelopes using the 5th-highest and 5th-lowest values of $O_{11}(r)$ from 99 simulations of the heterogeneous Poisson (HP) null model. $O_{11}(r)$ values above the upper envelope indicate clustering, within envelope random, and below regularity.

abundance and other four species (*Stewartia gemmata*, *Diospyros morrisiana*, *Betula utilis*, and *Sloanea chingiana*) with low abundance showed significant aggregated pattern at the scale of 0～10m. However, the degree of aggregation of the highest abundant species *Huodendron biaristatum* and the lowest abundant species *Betula utilis* was much higher than that of the other six species.

As for larger trees with DBH≥5cm, the spatial distributions of *Huodendron biaristatum* and *Betula utilis* showed a significant aggregation at all scales, while the other six species were random at scales of 0～40m (Figure 2). For smaller trees with DBH＜5cm, *Huodendron biaristatum* and *Litsea suberosa* showed significant aggregation at scales of 0～40m. Five other species (*Acer fabric*, *Stewartia gemmata*, *Diospyros morrisiana*, *Betula utilis* and *Sloanea chingiana*) showed significant aggregation at scale of 0～10m and random at scales of ＞10m, while the remaining species *Machilus pauhoi* was aggregated at scales of 0～20m and random at scales of ＞20m (Figure 2).

2.3 Spatial associations

The spatial associations among larger trees (DBH≥5cm) and smaller trees (DBH＜5cm) of each species were studied (Figure 3). Large trees of *Huodendron biaristatum* and *Diospyros morrisiana* showed significant positive association with their smaller trees at scales 0～10m, while large tree of *Acer fabric* showed significant negative association with its smaller trees at all scales of 0～40m, and large trees of remaining species did not show significant association with their smaller trees at any scale.

The bivariate O-ring statistic was used to analyze the spatial association for 56 (＝8×7) species pairs of the eight dominant species under the heterogeneous Poisson null model. The GoF test revealed significant departures from the null model for 21 species pairs (37.5% of all cases), including positive associations for 2 species pairs (*Litsea suberosa* vs. *Machilus pauhoi* and *Machilus pauhoi* vs. *Litsea suberosa*) at scales of 0～6m and negative associations for 19 species pairs at scales of 0～14m (Table 2). Among 19 species pairs with negative associations, six symmetric species pairs were found in *Huodendron biaristatum* and other five species (*Acer fabric*, *Litsea suberosa*, *Machilus pauhoi*, *Betula utilis*, and *Sloanea chingiana*), *Stewartia gemmata* and *Betula utilis*. *Huodendron biaristatum* showed a significant negative association with *Stewartia gemmata* or *Diospyros morrisiana*, and *Betula utilis* showed a significant negative association with five other species (*Acer fabric*, *Litsea suberosa*, *Machilus pauhoi*, *Diospyros morrisiana* and *Sloanea chingiana*).

3 Discussion

In present work, we studied population size structure for the eight dominant tree species at the subtropical evergreen broadleaved forest, which is now at the late-succession stage, located in Damingshan Nature Reserve in southern China. We found that the types of size class distribution of different species were different. The most abundant species *Huodendron biaristatum* showed a reverse J-shaped distribution, the three species (*Machilus pauhoi*, *Litsea suberosa* and *Diospyros morrisiana*) had L-shaped distributions, and the other four species were compound distributions. These results are consistent with the findings of other old-growth forests[30,38].

It has been known that the aggregation pattern is more popular than random and regular patterns at a given spatial scale in nature [40～42]. In our study, the GoF test revealed that all eight species were significant aggregated distributions at small scales. Similar result was found when Luo et al.[43] analyzed the spatial distribution of tree species in Baishanzu plot (evergreen broadleaved forest in eastern China). The result of our study showed that the above-mentioned general rule is also suitable in Damingshan evergreen broadleaved forest, which provides sound evidence for aggregated distribution of species at small scales. On the other hand, the degree of aggregated distribution of species with low abundance was not lower than that for species with high abundance at small scales (even being higher in some case, e. g. *Betula utilis*), which is consistent with the reports of both the species-rich tropical forest communities and the species-poorer temperate forest communities[8,38,44]. The observed result suggests that the degree of aggregated distribution of species is no significant relation with its abundance at small scales.

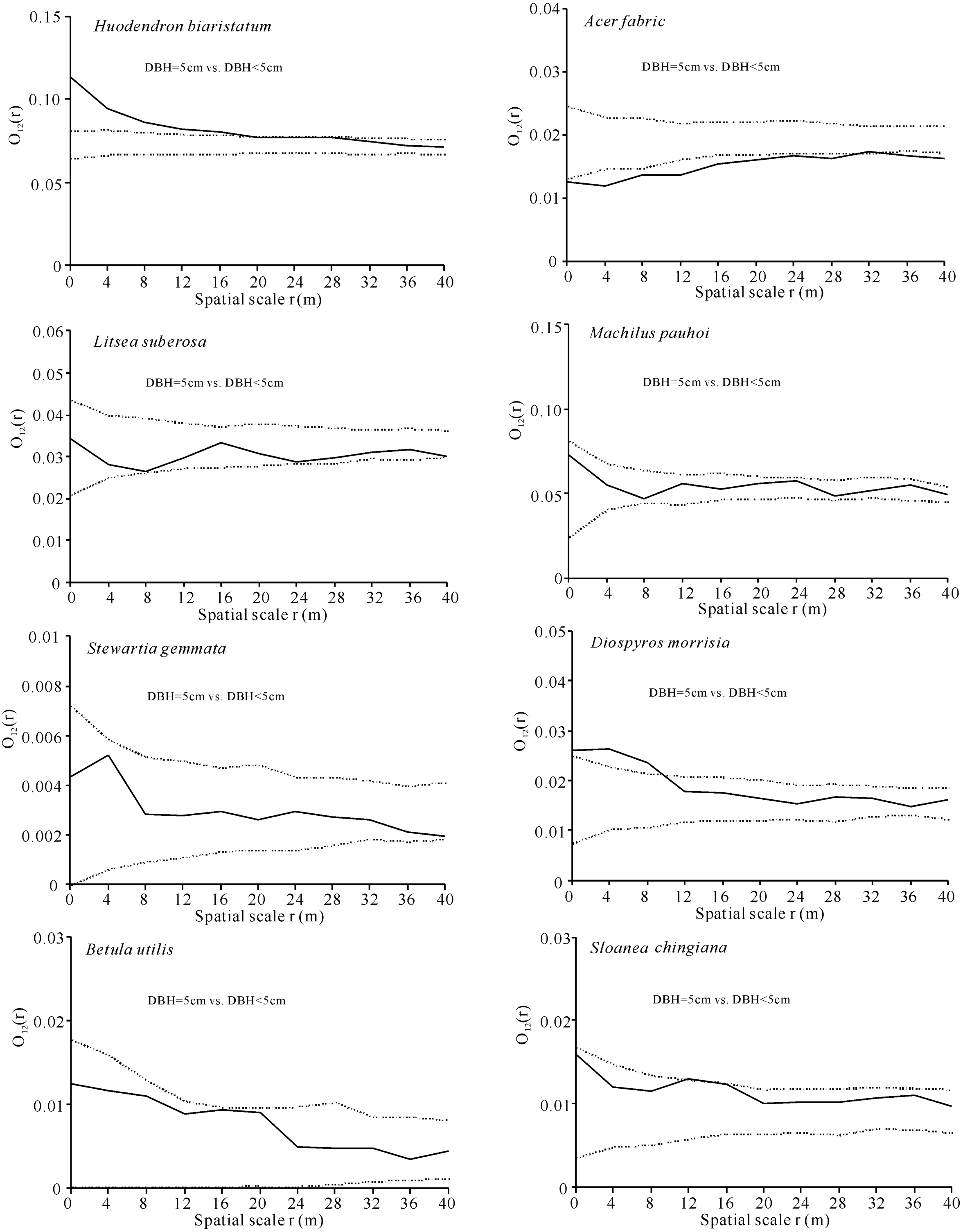

Figure 3 Intraspecific spatial association analyses of eight tree species

Note: Shown are the bivariate O-ring statistic $O_{12}(r)$ of two different size classes (DBH⩾5cm and DBH<5cm) (black lines), and the confidence envelopes (thin dashed lines) being the 5th-highest and 5th-lowest values of $O_{12}(r)$ from 99 replicates of Monte Carlo simulations of the heterogeneous Poisson (HP) null model. $O_{12}(r)$ values above the upper envelope indicate positive association, within envelope indicate no association, and below indicate negative association.

Table 2 Interspecific spatial associations of all studied tree species.

Species pair		Spatial scales r (m)															
Species 1	Species 2	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30
Huodendron biaristatum	*Acer fabric*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Huodendron biaristatum	*Litsea suberosa*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Huodendron biaristatum	*Machilus pauhoi*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Huodendron biaristatum	*Stewartia gemmata*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Huodendron biaristatum	*Diospyros morrisiana*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Huodendron biaristatum	*Betula utilis*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Huodendron biaristatum	*Sloanea chingiana*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Acer fabric	*Huodendron biaristatum*	—	—	—	—	—	—	—	—	—	—	r	r	r	r	r	r
Acer fabric	*Betula utilis*	r	r	r	r	r	—	—	—	—	—	—	—	—	—	—	—
Litsea suberosa	*Huodendron biaristatum*	—	—	—	—	——	—	—	—	—	—	—	—	r	r	r	r
Litsea suberosa	*Machilus pauhoi*	+	+	+	+	r	r	r	—	—	—	r	r	r	r	r	r
Litsea suberosa	*Betula utilis*	r	r	r	—	—	—	—	—	—	—	—	—	—	—	—	—
Machilus pauhoi	*Huodendron biaristatum*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Machilus pauhoi	*Litsea suberosa*	+	+	+	+	r	r	r	—	—	—	—	r	r	r	r	r
Machilus pauhoi	*Stewartia gemmata*	r	r	r	r	—	—	—	—	r	r	r	r	r	r	r	r
Machilus pauhoi	*Diospyros morrisiana*	r	r	r	r	r	r	r	—	—	—	r	r	r	r	r	r
Machilus pauhoi	*Betula utilis*	r	r	r	r	—	—	—	—	—	—	r	r	—	—	—	—
Stewartia gemmata	*Machilus pauhoi*	r	r	r	r	r	—	—	—	r	r	r	r	r	r	r	r
Stewartia gemmata	*Betula utilis*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diospyros morrisiana	*Machilus pauhoi*	r	r	r	r	r	r	r	r	r	—	r	+	r	r	r	r
Diospyros morrisiana	*Sloanea chingiana*	r	r	r	r	r	r	—	r	r	—	r	r	r	r	r	r
Betula utilis	*Huodendron biaristatum*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Betula utilis	*Acer fabric*	—	—	—	—	—	—	—	—	—	—	—	—	—	r	r	r
Betula utilis	*Litsea suberosa*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Betula utilis	*Machilus pauhoi*	—	—	—	—	—	—	—	—	—	—	r	r	r	—	—	r
Betula utilis	*Stewartia gemmata*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Betula utilis	*Diospyros morrisiana*	—	—	—	—	—	—	—	—	—	r	r	r	r	r	r	r
Betula utilis	*Sloanea chingiana*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sloanea chingiana	*Huodendron biaristatum*	—	—	—	—	—	—	—	—	r	r	r	r	r	r	—	—
Sloanea chingiana	*Diospyros morrisiana*	r	r	r	r	r	—	—	—	—	—	—	—	—	r	r	r
Sloanea chingiana	*Betula utilis*	r	r	r	r	r	—	—	—	—	—	r	r	r	r	r	r

Note: Only species pairs (species 1 vs. species 2, and species 2 vs. species 1) with the p value <0.05 according to the goodness-of-fit (GoF) test, are shown. The bivariate O-ring statistic was employed to calculate the spatial associations among eight species under the heterogeneous Poisson (HP) null model. The ring width was one cell unit; cell size was 2m×2m. Monte Carlo confidence was constructed at the 95% confidence level (99 replicates). "+", "r", and "—" indicate positive association, no association and negative association, respectively.

Aggregated distribution pattern can be caused by limited seed dispersal[45] or habitat heterogeneity[10] which may operate at different spatial scales. In our plot, we found that six species (*Acer fabric*, *Litsea suberosa*, *Machilus pauhoi*, *Stewartia gemmata*, *Diospyros morrisiana*, and *Sloanea chingiana*) of the eight dominant species displayed random distribution at larger trees (DBH≥5cm) and aggregation at smaller trees (DBH<5cm). To our knowledge, we inferred that microhabitat heterogeneity was the most likely explanation for patterns of these species at small scales. The microsite conditions that are favorable for initial establishment clearly differ from optimal conditions for sustained sapling growth[46]. Adults might occupy the most suitable sites for the species, while saplings are widely dispersed[44]. The refuge effect usually makes patterns more aggregated distribution[43].

Seed dispersal limitation may also have contributed to the spatial aggregation for these dominant species in Damingshan subtropical evergreen broad-leaved forest. In the present study, we also found that *Huodendron biaristatum* or *Diospyros morrisiana* showed a positive association between smaller and larger trees at scales of 0~10m, implying these two species were short-distanced seed dispersal species. Hubbell[8] and Condit et al.[44] suggested that poor seed dispersal is related to greater aggregated degree of population.

Studies of spatial associations between species are indeed important for species coexistence of plant communities. Positive associations at small scales can be expected when species have similar requirements for establishment sites[47], while negative associations among species established simultaneously can be indicative of the partitioning of establishment sites and/or interspecific competition[48]. In our study, the GoF test revealed that significant positive associations for 2 of 58 species pairs at small scales. Interestingly, the two species pairs with positive associations showed the associations among *Litsea suberosa* and *Machilus pauhoi* at scales of 0～6m. The results indicated that individuals of different dominant species had a tendency to avoid each other, implying interspecific spatial independence in Damingshan plot. The spatial configuration of interspecific segregateion and intraspecific aggregation can contribute to avoid interspecific competition and promote long-term species coexistence[30,38,49]. Thus, our finding is line with the spatial segregation hypothesis.

In conclusion, the comparative analysis of eight dominant species revealed both similarities and differences in population structure as well as spatial patterns and associations, which contribute to their coexistence at the subtropical evergreen broadleaved forest in southern China. Our results clearly showed that multiple factors (e. g. limited seed dispersal, microhabitat heterogeneity, and interspecific segregation) were contributed to the maintenance of the coexistence of the dominant species at this forest. However, we were unable to determine only these factors affecting the coexistence of these species in the forest, because other factors (e. g. seed production and animal-dispersed seeds) may contribute to the spatial patterns. Detailed studies are required to explore the mechanisms of community assembly in Damingshan subtropical evergreen broadleaved forests.

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