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Distribution Patterns of Tree Species in a Lowland Rainforest at Nanjen Lake, Southern Taiwan

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ABSTRACT: Spatial patterns of trees in a lowland rainforest at Nanjen Lake, southern Taiwan were evaluated. Among the 91 species with more than 15 individuals in the 1.61-ha plot, 90.1% species showed an aggregated distribution pattern, and 8.8% species were randomly distributed at the 4 m scale. Along the distance scales, 71.4% species kept aggregated distribution pattern, and only one species remained randomly distributed at all distance scales. Rare species tended to be more aggregated than the common species. As for trees in different size classes, 40.9% highly aggregated species became less aggregated or even randomly distributed with the increase of tree size, while 9.1% species had an inverse pattern. As for trees in the size class ≥ 8 cm diameter, 68.2% species were randomly distributed and only 29.6% species were aggregated. No species displayed a regular pattern in any size class. There were four major habitat types in the study plot, including ridge, mid-slope, valley and streamside types. Our results suggested that the distribution patterns of most species within the Nanjen Lake plot were related to habitat heterogeneity, such that some species were only distributed along the streamside and some species could only be found on the ridge top. Other factors, such as dispersal limitation, might also play a role in determining the distribution patterns of trees.

KEY WORDS: Habitat type, spatial pattern, wind-stress, Nanjenshan, lowland rain forest, tropics, Taiwan.

INTRODUCTION

Spatial pattern of trees can possibly indicate stand history, population dynamics, and species competition (Haase, 1995), and it may be able to explain what controls the co-existence and diversity of species in a forest (Batista and Maguire, 1998; Condit et al., 2000). The Janzen-Connell hypothesis suggests that conspecifics are widely distributed caused by density-dependent mortality by natural enemies (Janzen, 1970; Connell, 1971). Other studies suggested that distribution patterns are also likely to be related to density dependent mortality (e.g., Skarpe, 1991; Condit et al., 1994) and habitat differentiation (e.g., Condit et al., 2000).

In a lowland forest in southern Taiwan, Fan et al. (2005, the Nanjen Lake plot) and Chao et al. (2007a, the Lanjenchi plot) both denoted that species composition and forest structure were correlated with wind exposure. This indicates a pattern related to habitat differentiation. As for the species spatial distribution, Chao et al. (2007b) found that most species in the Lanjenchi plot were aggregated regardless of tree size, and the aggregated degrees were positively correlated to wind strength. In this study, we further analyzed the spatial patterns of conspecific trees in the Nanjen Lake plot and investigated the possible controlling factors for their spatial patterns. We tested whether spatial distributions of tree species in this lowland rainforest varied with species abundance (from rare to common species) and tree size (from small to large). Also, we compared the spatial patterns with those of the Lanjenchi plot (Chao et al., 2007b), where the forest composition and structure are similar to our study plot.

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MATERIALS AND METHODS

Study site

The Nanjen Lake plot is located in the Nanjenshan Nature Reserve, southernmost Taiwan (Fig. 1). It is a 2.21-ha plot and was established in 1998. The

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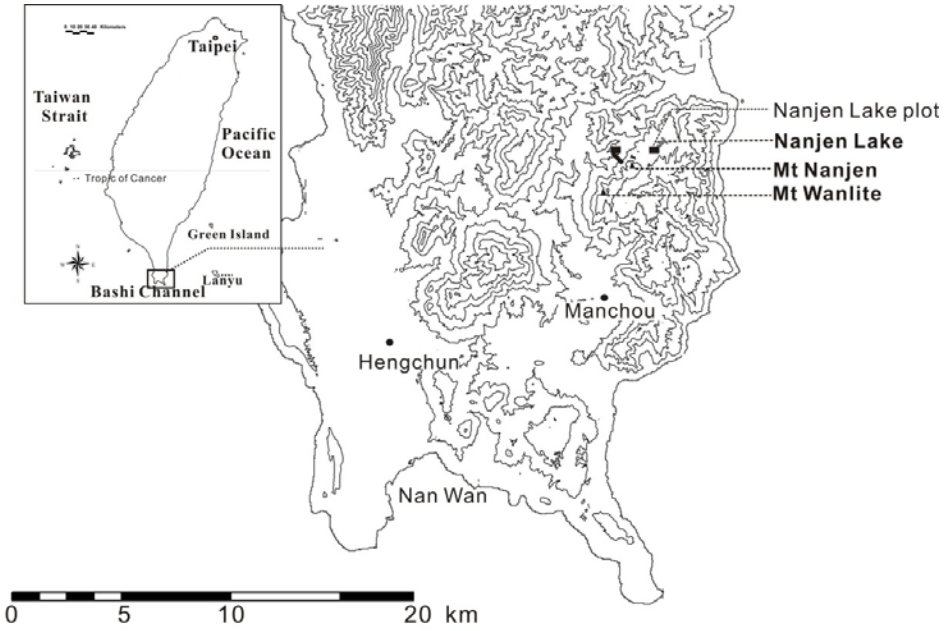


Fig. 1. Location of the Nanjen Lake plot in southern Taiwan.

topography of the plot is rugged, with steep slopes, ridges and valleys. A low-lying swamp and a stream pass through the plot (Fig. 2). Annual mean temperature of this lowland rainforest is 23.0°C and annual mean precipitation is 2,809 mm. About 21,592 individuals were recorded in the plot, representing 120 species in 83 genera and 43 families. The most abundant species was *Illicium arborescens* (Illiciaceae) which accounted for 14.2% of all individuals. Fan et al. (2005) classified the plot into four habitat types, including ridge, mid-slope, valley, and streamside types. The four habitats were found to be associated with its distinctive topographic features. These four habitats had significant differences in species composition, number of individuals, and basal area. In this study, we focused on the spatial patterns of woody plants within the forest, so the swamp area of the studied plot was excluded for analyses, and the total area for analyses is 1.61 ha (Fig 2).

Spatial analysis

Among the 120 tree species recorded in the Nanjen Lake forest, 91 species with more than 15 individuals were included in the spatial pattern analysis. The spatial patterns of each species within the plot were compared in two aspects, including two abundance classes (rare vs. common species) and four size classes (1-2 cm, 2-4 cm, 4-8 cm, and ≥ 8 cm diameter at breast height (DBH)). These spatial patterns were analyzed by Ripley's *L(d)* function, where *d* is a distance (radius) scale (m). This function is a transformation of Ripley's *K*-function (Diggle, 1983; Ripley, 1981), which is a second order parameter that measures all inter-plant distances to provide a measure of spatial distribution patterns at various distance scales (Freeman and Ford, 2002). $\hat{L}(d)$ is the estimated value of *L(d)*. $\hat{L}(d) = 0$ indicates a random distribution, $\hat{L}(d) < 0$ indicates a regular distribution, whereas $\hat{L}(d) > 0$ indicates a clumping distribution at the distance *d*. *L(d)* is obtained by calculating relative density *K(d)* of all plants within radius *d*:

$$\hat{K}(d) = A\sum_{i}^{n}\sum_{\neq j}^{n} w_{ij} I_d(i,j) / n^2$$

where *A* is the area of the plot, *n* is number of trees for a species, *d* is the distance (radius) scale and $\sum\sum W_{ij} I_d(i,j)$ is the conspecific numbers within the distance less than *d*, where I_d is the summation of the number of points; *W* is the weighting factor for the edge corrections. Since $\hat{K}(d) = \pi d^2$ when the plants are randomly arranged in a Poisson distributed forest, we plot:

$$\hat{L}(d) = \sqrt{\frac{\hat{K}(d)}{\pi}} - d$$

which is a transformation of $\hat{K}(d)$ as suggested by (Besag, 1977). For an irregular-shaped plot, Goreaud and Pélissier (1999) propose a generalization of the method that computes edge effect correction.

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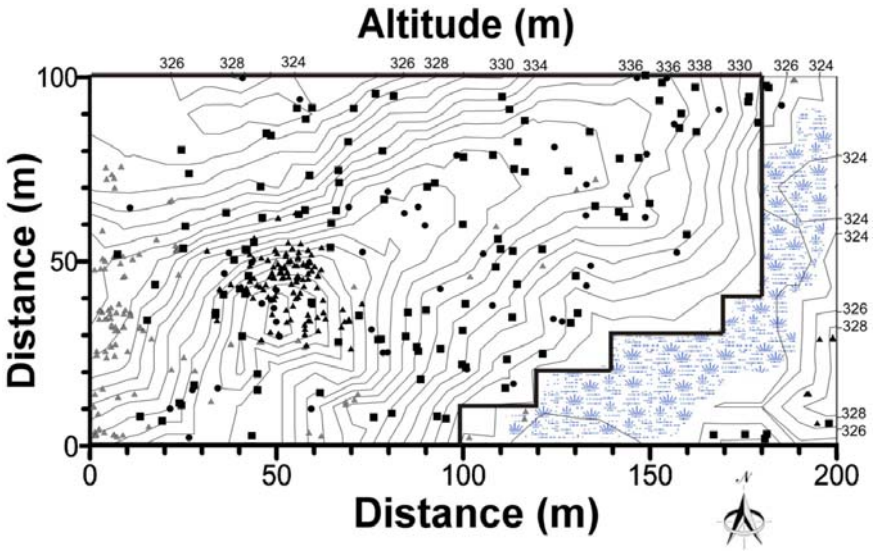


Fig. 2. Topographic map of the Nanjen Lake plot. The area within the boundary was used for analyzing spatial patterns of trees. Species from random distribution pattern (*Elaeocarpus sylvestris* (●) and *Schima superba* var. *kankoensis* (■)), clumped distribution (*Mallotus paniculatus* (grey triangle)), to the strongest clumped distribution (*Rhododendron simsii* (▲)) were also shown on the map.

For correcting the irregular edge effect, (Goreaud and Pelissier, 1999) suggesting for the irregular shape correction:
$W_{ij} = 2\pi / (2\pi - \alpha_{out})$, where α_{out} is the angle which is outside the study area.

A Monte-Carlo simulation was used to test the statistical significance of deviations of $\hat{L}(d)$ from zero, under the null hypothesis of complete random distribution (Besag and Diggle, 1977). Ninety-five percent confidence intervals were generated using high and low values of $\hat{L}(d)$ obtained from 600 simulations of random permutations.

RESULTS

Overall patterns

At a short distance scale (d= 2 m), 12.1% of the 91 species with more than 15 individuals were classified as randomly distributed, and 82.4% showed significantly aggregated patterns (Table 1). The proportion of randomly distributed species decreased with an increase of distance scale (Table 1). For example, at the 10 m scale, only 4.4% species had a random distribution pattern and 95.6% species had an aggregated distribution pattern. There were no species showing a significant regular-distribution at all distance scales (Table 1). Along the distance scale from 1 to 30 m, there were several distribution types (Appendix). Only one species kept a random distribution pattern for all scales (*Sloanea formosana* (Elaeocarpaceae), Fig. 3a), some species showed a clumped distribution for short distance scales and a random distribution for long distances (e.g., *Sapium discolor* (Euphorbiaceae) was clumped until 17.5 m; Fig. 3b), some were randomly distributed for short distances, but clumped for long distances (e.g., *Beilschmiedia erythrophloia* (Lauraceae) was randomly distributed until 6 m, Fig. 3c), and 65 species kept clumped patterns (e.g. *Illicium arborescens* and *Rhododendron simsii* (Ericaceae), Fig. 3d and 3e). Others, such as *Schima superba* var. *kankoensis* (Theaceae), did not have uniform distribution patterns along the distance scales, and were very changeable from random to clumped patterns (Fig. 3f).

The degree of aggregation (values of $\hat{L}(d)$) for trees in the studied forest increased with an increase of distance. The species with maximum values of $\hat{L}(d)$ for each distance scale were *Ormosia hengchuniana* (Fabaceae) for a one meter distance ($\hat{L}(1)$ =8.3), *Rhaphiolepis indica* var. *hiiranensis* (Rosaceae) for a two-meter distance ($\hat{L}(2)$=8.9), and *Rhododendran simsii* for distances larger than three meters ($\hat{L}(3)$ =12.2). These three tree species showed different preferences for habitat types: individuals of *Ormosia hengchuniana* (Fabaceae) were clumped close to the swamp-side or next to the swamp; *Rhaphiolepis indica* var. *hiiranensis* (Rosaceae) were mostly distributed on the ridge; and all individuals of *Rhododendran simsii* occurred on the top of ridge (Fan, 2005; Fig. 2).

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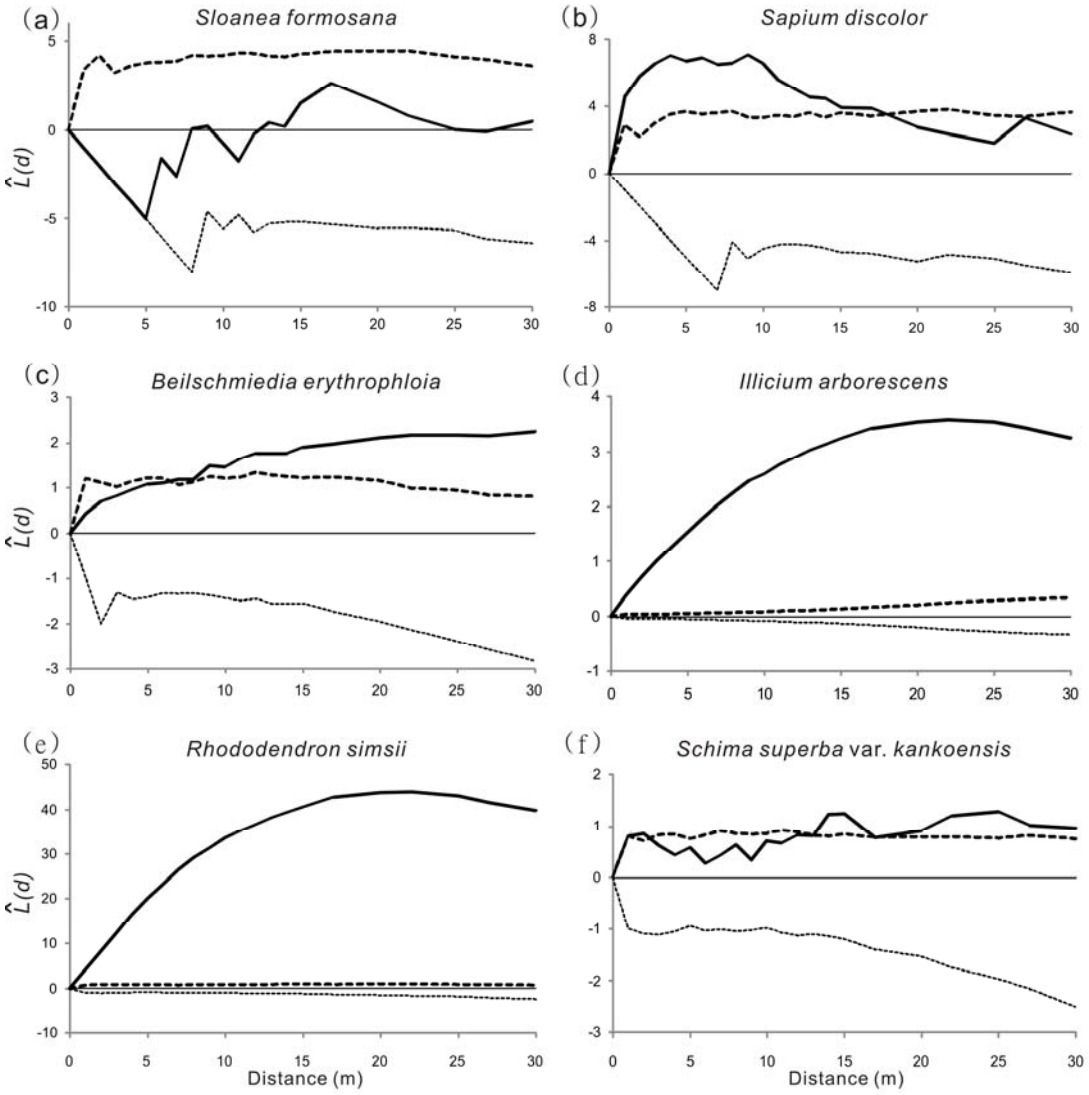


Fig. 3. $\hat{L}(d)$ results for: (a) *Sloanea formosana*, (b) *Sapium discolor*, (c) *Beilschmiedia erythrophloia*, (d) *Illicium arborescens*, (e) *Rhododendran simsii*, and (f) *Schima superba* var. *kankoensis* with DBH ≥ 1 cm. The sample statistic $\hat{L}(d)$ is shown as a solid line, whereas the 95% confidence envelop for Monte-Carlo simulations is given as dotted lines.

Table 1. The proportions (%) of spatial distribution patterns for the 91 tree species with DBH ≥ 1 cm in the Nanjen Lake plot.

Sampling range (m)	Regular distribution	Random distribution	Aggregated distribution	No conspecific individual
2	0.0	12.1	82.4	5.5
4	0.0	8.8	90.1	1.1
6	0.0	7.7	92.3	0.0
8	0.0	7.7	92.3	0.0
10	0.0	4.4	95.6	0.0

Rare versus common species

Rare species were substantially more aggregated than common species at all distance scales (Table 2). The rarest species were not the most aggregated species, the medium values of the two rarest classes (0-35 and 36-70 trees per species) approached each other at larger distance scales. The degree of clumping was negatively correlated with species abundance (Fig. 4).

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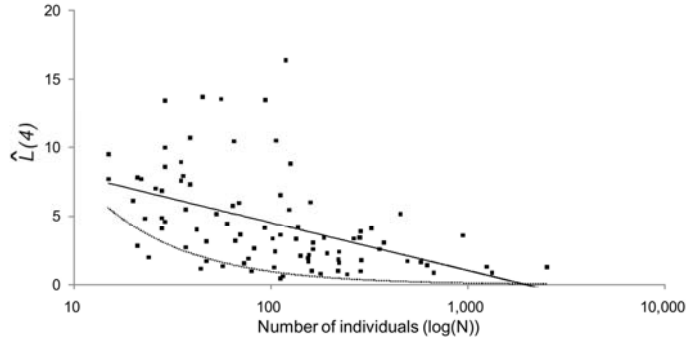


Fig. 4. $\hat{L}(4)$-values, which represented the *L* values at 4 m, for all species with ≥ 15 individuals in the Nanjen Lake plot, as a function of the abundance of each species, on a log scale. The solid line is the regression line and the dotted one is the upper limit of the 95% confidence envelop.

Table 2. The median value of $\hat{L}(d)$ in each abundance class at six distance scales. The abundance classes are comparable to those of relative to the Lanjenchi 5.88-ha plot (Chao et al., 2007).

Abundance class	Number of species	Medium value of $\hat{L}(d)$					
		2 m	4 m	6 m	8 m	10 m	15 m
0-35	19	5.23	6.93	7.50	8.24	9.09	10.41
36-70	19	3.08	5.15	6.54	6.74	8.16	10.76
71-160	24	2.22	2.87	3.09	3.50	3.99	4.57
>160	29	1.37	1.80	2.51	3.27	3.41	3.55

Table 3. The aggregation patterns from small to large size classes for trees in the Nanjen Lake plot.

Aggregation patterns	2 m	4 m	6 m	8 m
Decreasing pattern	14 (40.0 %)	18 (40.9 %)	16 (34.0 %)	17 (35.4 %)
Increasing pattern	6 (17.1 %)	4 (9.1 %)	4 (8.5 %)	4 (8.3 %)
Convex pattern	7 (20.0 %)	11 (25.0 %)	11 (23.4 %)	14 (29.2 %)
Concave pattern	5 (14.3 %)	2 (4.6 %)	9 (19.2 %)	8 (16.7 %)
Patternless	3 (8.6 %)	9 (20.5 %)	7 (14.9 %)	5 (10.4 %)
Total no. of species	35	44	47	48

Small versus large trees

The relationship between spatial pattern and diameter size were compared for each species with at least three DBH classes and more than 15 individuals at each scale. The patterns varied from species to species. More than one-third of these species (34-41%) showed a decreasing trend in aggregation intensity with increasing diameter size (Table 3), but some of them remained high aggregation intensity at the DBH class ≥ 8 cm, while some became randomly distributed. The second type showed a reverse pattern, *i.e.*, they became more aggregated with increasing diameter size (8.3-17.1% of the species). The third type was that about 20.0 to 29.2% of the species were more aggregated in the medium-diameter trees (DBH from 4 to 8 cm) than smaller (DBH from 1 to 2 cm) and larger trees (DBH > 8 cm).

When the spatial distribution of trees with DBH greater than 8 cm was examined, a great proportion of species were randomly distributed at the 2-4 m distance scale 2 m-4 m distance scales (Table 4). When the radius of the sampling range for spatial analysis was 2 m, there were 45.5% species with random distribution patterns and 18.2% species with significantly aggregated patterns, and 36.4% species with no conspecific individuals. When using the 4 m distance scale ($\hat{L}(4)$), 68.2% of species were randomly distributed, 29.6% of species were significantly aggregated, and remaining 2.3% had no conspecific individual within this range. The percentage of species with random distribution was highest at the sampling scale of 4 m.

Along the 1 to 30 m distance scales, there were five species kept random (e.g. *Ilex uraiensis* (Aquifoliaceae), Fig. 5a) and three species kept clumped patterns. Others appeared to be variable, for example, *Illicium arborescens* (Fig. 5b) was only randomly distributed at ≤ 3 m distance scales, *Elaeocarpus sylvestris* (Elaeocarpaceae, Fig. 5c) and *Schima superba* var. *kankoensis* (Fig. 5d) were mostly randomly distributed but aggregated at some distance scales.

DISCUSSION

Several studies have found that the spatial distribution patterns of tree species tended to be clumped. These include tropical lowland rain forests (Chao et al., 2007b) and temperate forests in Taiwan

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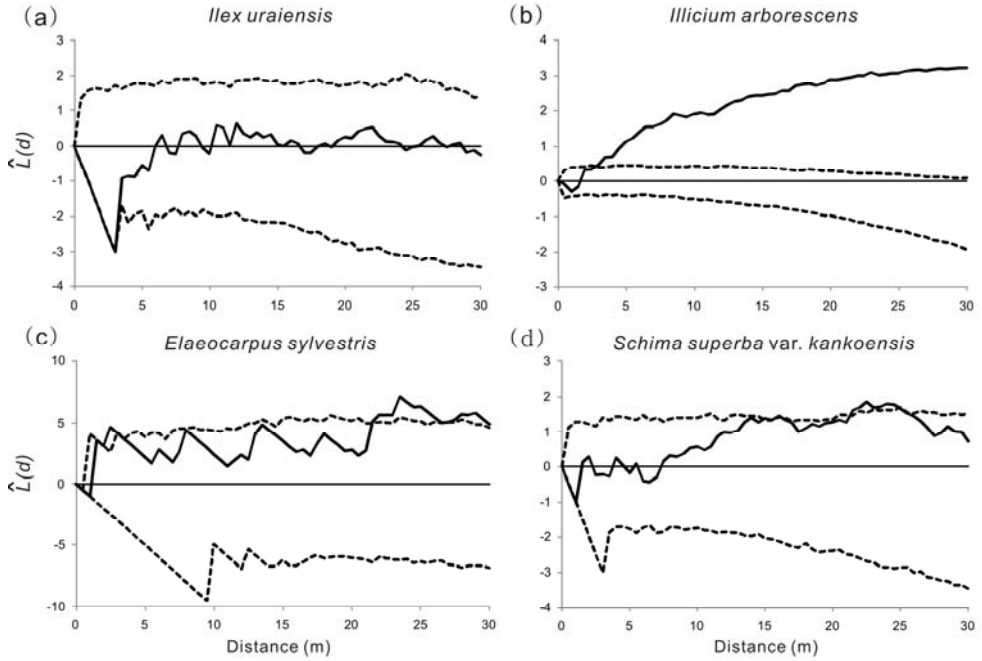


Fig. 5. $\hat{L}(d)$ results for: (a) *Ilex uraiensis*, (b) *Illicium arborescens*, (c) *Elaeocarpus sylvestris*, and (d) *Schima superba* var. *kankoensis* with DBH ≥ 8 cm. The sample statistic $\hat{L}(d)$ is shown as a solid line, whereas the 95% confidence envelop for Monte-Carlo simulations is given as dotted lines.

Table 4. Proportions (%) of tree species exhibiting different spatial distribution patterns at five distance scales in the Nanjen Lake plot. Only 44 species with DBH ≥ 8 cm were included.

Distance scale (m)	Regular distribution	Random distribution	Aggregated distribution	No conspecific individual
2	0.0	45.5	18.2	36.3
4	0.0	68.2	29.6	2.3
6	0.0	52.3	47.7	0.0
8	0.0	45.5	54.6	0.0
10	0.0	36.4	63.6	0.0

(Lin, 2001) in Taiwan, tropical dry and wet forests in Asia and American (He et al., 1997; Condit et al., 2000), temperate forest in northern China (Hou et al., 2004) and America (North et al., 2004). In this study, the major spatial distribution patterns of all species seemed to be aggregated at all distance scales, suggesting a strong environmental differentiation in the plot. Fan et al. (2005) proposed that wind stress and resource availability could influence floristic composition and physiognomic characteristics of the Nanjen Lake forest. Some ecophysiological researches showed that the variation in the habitats might affect the efficiency of water usage for trees and seedling, and also the mortality, productivity, and biomass in the stand (Wang, 1995; Yang, 1997; Hon, 2003; Fan, 2005), resulting in the differences of species distribution.

The species composition and forest structure were similar between the Nanjen Lake and Lanjenchi plots (Chao et al., 2007a; Fan et al., 2005). The present results showed that the spatial patterns were also similar for the two plots, such that most species were aggregated and only a few species were randomly distributed. The most abundance species, *Illicium arborescens*, which was shared among the Nanjen Lake, Lanjenchi (Chao et al., 2007a), and Lopei (Lin, 2002) plots, showed the same pattern in the three plots. It kept clumped at all distance scale regardless of tree size (Chao, 1997; Lin, 2002). *Rhododendran. simsii* was the most clumped species at most distance scales in both Nanjen Lake and Lanjenchi plots. This species was mainly distributed at higher elevation and on northeastern slopes in both plots (Chao, unpublished). However, a shared species, *Sloanea formosana*, showed different patterns in the Nanjen Lake and Lanjenchi plots (Chao et al., 2007b). It was randomly distributed at all distance scales in the study plot (Fig. 4a) but was clumped in the Lanjenchi plot (Fig. 6a, Chao et al., 2007b). This may be due to the present of a higher

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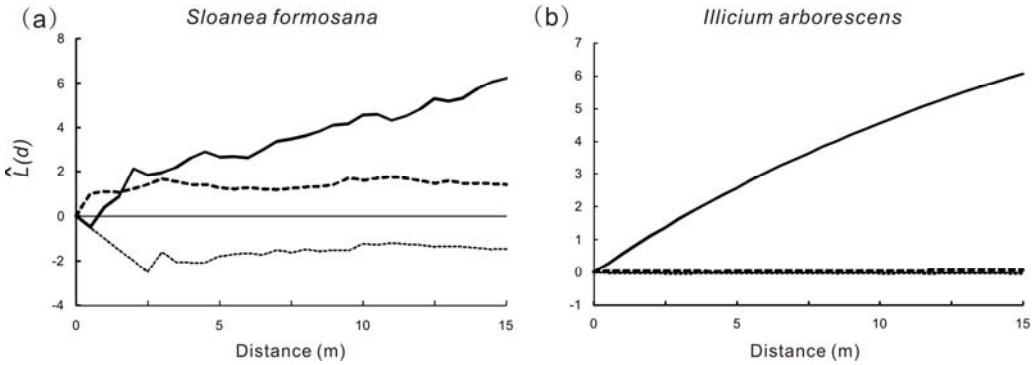


Fig. 6. $\hat{L}(d)$ results for: (a) *Sloanea formosana*, (b) *Illicium arborescens* with DBH ≥ 1 cm in the Lanjenchi plot. The sample statistic $\hat{L}(d)$ is shown as a solid line, whereas the 95% confidence envelop for Monte-Carlo simulations is given as dotted lines.

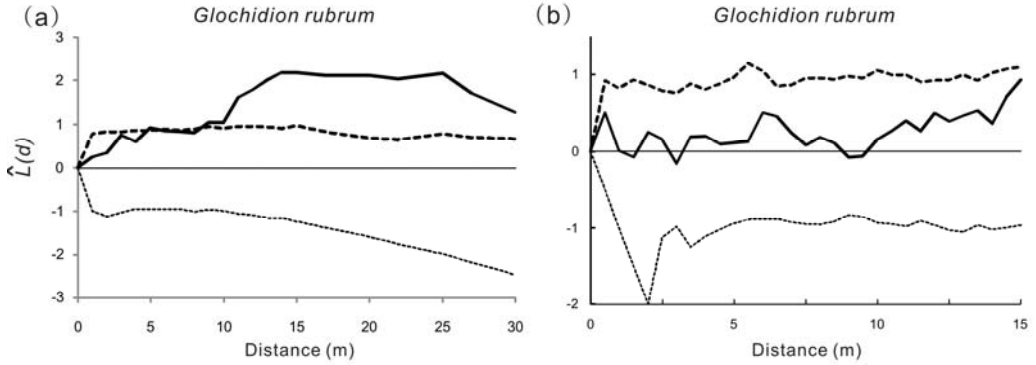


Fig. 7. $\hat{L}(d)$ results for *Glochidion rubrum* with DBH ≥ 1 cm in (a) Nanjen Lake plot and (b) Lanjenchi plot. The sample statistic $\hat{L}(d)$ is shown as a solid line, whereas the 95% confidence envelop for Monte-Carlo simulations is given as dotted lines.

hill on the northern side of the Nanjen lake plot which may reduce the effect of monsoon winds. On the contrary *Glochidion rubrum* (Euphorbiaceae), showing a mostly random distribution in the Lanjenchi plot (Fig. 7b), was only randomly distributed at short distance but significantly clumped at larger distance in the Nanjen Lake plot (Fig. 7a). *Glochidion. rubrum* is a pioneer species and its recruitment depends mostly on gap formation or disturbance (Yeh et al., 2004), indicating that the Lanjenchi plot had a higher spatial frequency of canopy gaps or disturbance.

The clumping intensity decreased as the individual abundance increased (Fig. 4), which is the same with other tropical wet forest studies (He et al., 1997; Condit et al., 2000; Chao et al., 2007b). However, in our study the most aggregated species was not the rarest species (n = 119) indicating a strong habitat preference.

When comparing the median value of $\hat{L}(d)$ in each abundance class, the Lanjenchi plot had higher aggregated indices at most abundance classes (except for the second class, Table 2, and Table 2 in Chao et al., 2007b). Condit et al. (2000) suggested that topographic variation could affect the aggregation intensity. Since elevation difference between the two plots was only 24 m some factors other than elevation (e.g., wind strength) might be more important to determine the spatial pattern of trees in the plots. The Lanjenchi plot was on a sub-ridge of Mt. Wanlite, and its northeastern slopes were directly exposed to strong northeastern monsoon winds. However, partially sheltered by a hill, the Nanjen Lake plot was less exposed.

The spatial patterns of trees at different size classes varied from forest to forest. 40.9% of the tree species were more aggregated in smaller diameter classes at this forest, and only 35.5% of tree species showed this character in the Lanjenchi plot (Chao et al., 2007b). In other tropical forest, there are about two-thirds of tree species showed this character (Condit et al., 2000). A tenth of species were more aggregated when larger in both Nanjen Lake and Lanjenchi plots.

When comparing large trees (DBH ≥ 8 cm), most tree species were randomly distributed in the Nanjen Lake plot, but most tree species were aggregated in the Lanjenchi plot. A strong factor like density-dependent mortality or self-thinning process could reduce the aggregation intensity from juvenile

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to adult trees (Condit et al., 1994). However, in a plot with a distinct habitat differentiation (like Lanjenchi forest) species would tend to be more aggregated as tree size increased because of habitat-preference.

Species in Fagaceae, a family with large nuts, were mostly aggregated in the Nanjen Lake and Lanjenchi plots, but some species were randomly distributed at short distance but aggregated at long distance (e.g., *Lithocarpus amygdalifolius* and *Pasania harlandii*). For larger trees (DBH > 8 cm), only two species displayed random distribution patterns, *i.e. Pasania harlandii* in the Lanjenchi plot and *Castanopsis fabri* in the Nanjen Lake plot, others were mostly aggregated. This is more likely to be due to limited seed dispersal. However, other forest revealed a different pattern. In south-central Chile the *Nothofagus oblqua* showed a random distribution in an old-growth forest (Salas et al., 2006).

Overall, not only species composition and forest structure but also the spatial distribution patterns of tree species were similar between the Nanjen Lake and Lanjenchi plots. At the plot level, only a few species showed different patterns between the two plots, which may be caused by the slightly differences in topography features or due to the species's own characteristics. At different DBH classes, more than a third of species trended to have low aggregation intensity, which might have been ascribed to the process of self-thinning. Only a tenth of the species had a reverse pattern, such that they were more aggregated at larger tree size, indicating a habitat-preference. At the diameter size class ≥ 8 cm, species in the Nanjen Lake plot were more randomly distributed than in the Lanjenchi plot, which might be due to a better topographic shelter in the Lanjenchi plot.

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Appendix: List of surveyed species and their spatial distribution patterns.

Species	Patterns
Randomly distributed at all distance scales	
Sloanea formosana	
Aggregated at short distance scales and randomly distributed at long distance scales	
Sapium discolor	Aggregated from 1-17.5 m
Meliosma rigida	Aggregated from 1-22.5 m
Randomly distributed at short distance scales and aggregated at long distance scales	
Anneslea lanceolata	Random at 1 m distance scale, aggregated when > 2 m
Eurya natida	
Garcinia multiflora	
Lithocarpus amygdalifolius	
Symplocos shilanensis	
Drypetes karapinensis	Random at 1-2 m distance scale, aggregated when > 3 m
Dysoxylum hongkongense	
Syzygium buxifolium	
Lasianthus wallichii	Random at 1-3 m distance scale, aggregated when > 4 m
Symplocos theophrastaefolia	
Machilus zuihoensis	Random at 1-5 m distance scale, aggregated when > 6 m
Beilschmiedia erythrophloia	Random at 1-6 m distance scale, aggregated when > 7 m
Ficus formosana	Random at 1-9 m distance scale, aggregated when > 10 m
Changeable	
Elaeocarpus sylvestris	
Bridelia balansae	
Michelia compressa	
Callicarpa remotiflora	
Glochidion rubrum	
Pasania harlandii	
Schima superba var. *kankoensis*	
Tetradium glabrifolium	
Prunus phaeosticta	
Glochidion zeylanicum	

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南仁湖低地雨林動態樣區之樹種分佈類型

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摘　　要

本研究利用 Ripley's *K* 指數來探討臺灣南端的南仁湖低地雨林 1.61 公頃樣區之樹種分佈類型。在整個樣區中，植株數量多於 15 株的植物種類有 91 種，以四公尺的尺度來看，有 90.1%的種類呈現聚集分佈，8.8%呈現隨機分布；以 1-30 公尺的距離尺度來看，有 71.4%的種類在這尺度範圍下維持群聚分佈類型，只有一種保持隨機分佈。以植株數量而言，株數較少的較株數多的種類更為聚集。至於不同徑級大小，40.9%的種類隨著徑級增加而由高度群聚的分佈類型逐漸偏向較低強度的群聚分佈或是隨機分佈，但有 9.1%的物種呈現相反的結果。單純考慮胸徑大於等於 8 公分的大樹時，68.2%的種類為隨機分佈，只有 29.6%的種類仍呈現群聚分佈。在整個樣區中沒有規則分佈的種類。本研究顯示南仁湖樣區的植物分佈和生育地的異質性有關，某些植物僅分佈於山頂或是南仁湖邊。另外大樹隨機比例偏高，顯示樣區中可能有種內競爭導致天然疏伐作用的現象。

關鍵詞：分佈類型、風力、南仁山、低地雨林、熱帶、臺灣。

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