Taiwania, **52**(4): 343-351, 2007

Distribution Patterns of Tree Species in the Lanjenchi Lowland Rain Forest

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(Manuscript received 12 July, 2007; accepted 15 October, 2007)

ABSTRACT: Spatial patterns of trees in a lowland rainforest in the 5.88-ha Lanjenchi plot of the southernmost Taiwan were evaluated. Among the 88 species with more than 15 individuals, 87.5% had an aggregated distribution pattern, and 9.1% species were randomly distributed. Rare species tended to be more aggregated than common species at all distance scales. As for different DBH size classes, 35.5% species shifted from highly aggregated patterns to a low level of aggregation or random distribution with an increase in tree size, and 11.3% species had an inverse pattern. When comparing spatial patterns among different habitats within the plot, the aggregation intensity increased along a wind-stress gradient from the sheltered creek to the most exposed slopes. No species displayed a regular pattern in any size class or habitat type. This study revealed that distribution of most species within the Lanjenchi forest was related to habitat heterogeneity. Other factors, such as dispersal limitation, however, may also play a role in determining the distribution patterns.

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

INTRODUCTION

The spatial pattern of species may be able to explain what controls species existence and high species diversity in the tropics (Condit et al., 2000). Lieberman and Lieberman (1994) found that most species in a wet forest were not aggregated, which supports the Janzen-Connell hypothesis that conspecifics are widely distributed to against natural enemies (Janzen, 1970; Connell, 1971). However, Hubbell (1979) found that the spatial patterns of most species in a dry forest in Costa Rica were aggregated. Condit et al. (2000) compared the spatial patterns in six tropical forests (including dry deciduous to wet evergreen forest on two continents) and also found that most species were more aggregated. These spatial patterns may be caused by differences in topography, dispersal limitation, and disturbance regime (Condit et al., 2000; Plotkin et al., 2002). Besides, many factors like predator, pathogen, environment and density-dependence were thought to be the spacing agents that reduce juvenile density near conspecific large tree (Janzen, 1970; Connell, 1971; Condit et al., 1994; Thomson et al., 1996).

The Lanjenchi plot is one of the Forest Dynamic Plots (FDP) in the southernmost part of Taiwan, and all trees larger than 1 cm diameter at breast height (DBH) have been regularly measured and mapped since 1991. Previous studies showed that habitat differentiation significantly influenced species composition and forest structure (Sun, 1993; Sun and Hsieh, 2004; Chao, 2007), soil properties (Chen et al., 1997), leaf structure (Su, 1993), litterfall decomposition (Liu, 1994) and ecophysiological characteristics (Wang, 1995; Yang, 1997).

In this study, the spatial patterns of conspecific trees in the Lanjenchi plot were analyzed and possible controlling factors for these spatial patterns were also investigated. We tested whether spatial distributions of tree species in this lowland rainforest varied by species abundance (from rare to common species), tree size (from small to large), and spatial scales (from plot-level to habitat level).

MATERIALS AND METHODS

Study site

The Lanjenchi plot is located in the Nanjenshan Nature Reserve, southernmost Taiwan (Fig. 1). It was

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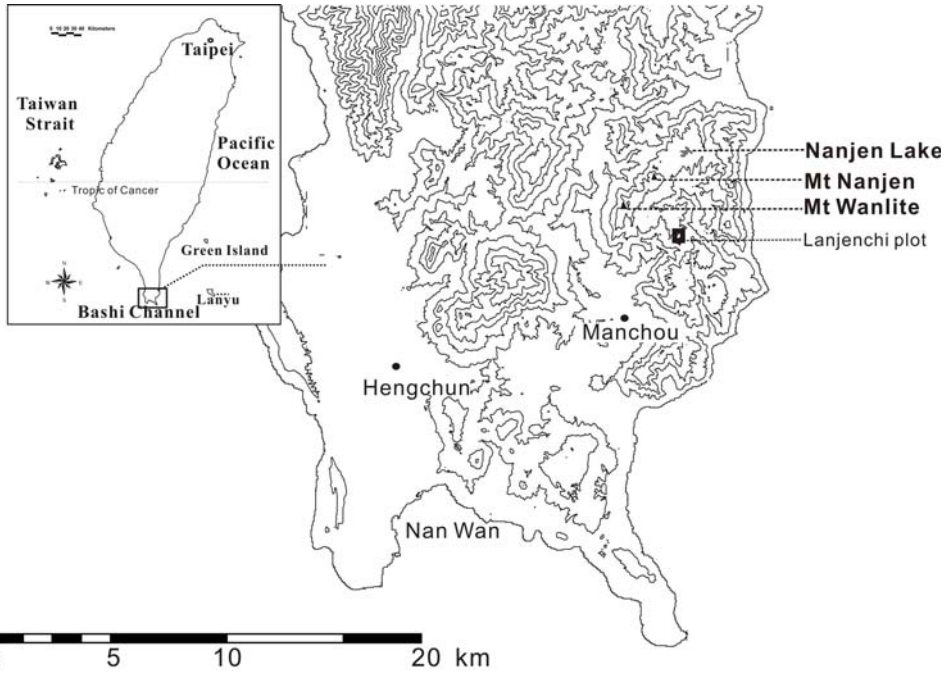


Fig. 1. Location of the Lanjenchi plot in the southernmost part of Taiwan.

originally a 3-ha plot established in 1991 (Sun, 1993; Sun and Hsieh, 2004) and was enlarged to 5.88-ha during 1997-2000 (Fig. 2) (Chao et al., 2007). This lowland rainforest had an annual mean temperature of 22.0 °C and an annual mean precipitation of 3,800 mm. About 60,146 individuals were recorded in the second census, representing 136 species, 83 genera, and 42 families. The most abundant species was *Illicium arborescens* Hayata which accounted for 11.1% of the total number of individuals. Chao et al. (2007) classified the plots into four habitat types, including windward, transition (between windward and leeward), leeward and creek types. The four habitats were found to be associated with distinctive topographic features determining exposure conditions to the prevailing northeasterly winds. Significant differences among these four habitats were found for species composition, number of individuals, and basal area.

Spatial analysis

Among the 136 tree species recorded in the Lanjenchi forest, 88 species each with more than 15 individuals were included in the spatial pattern analysis. The spatial patterns of each species within the Lanjenchi plot were compared in three aspects, including abundance categories (rare vs. common species), growth stages (1-2 cm, 2-4 cm, 4-8 cm, and >8 cm DBH size-classes), and spatial scales (plot-level vs. habitat level). These spatial patterns were analyzed by *L(d)* functions, where d (m) is the distance (radius) scale. This function is a transformation of Ripley's K-function (Ripley, 1981; Diggle, 1983), 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 observed 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 numbers of conspecific within the distance less than *d*, where I_d is the summation of the number of points; W is the weighting factor.

Since $K(d) = \pi d^2$ when the plants are randomly arranged in a Poisson distributed forest, we plot:

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

which is a transformation of $K(d)$ as suggested by Besag (1977).

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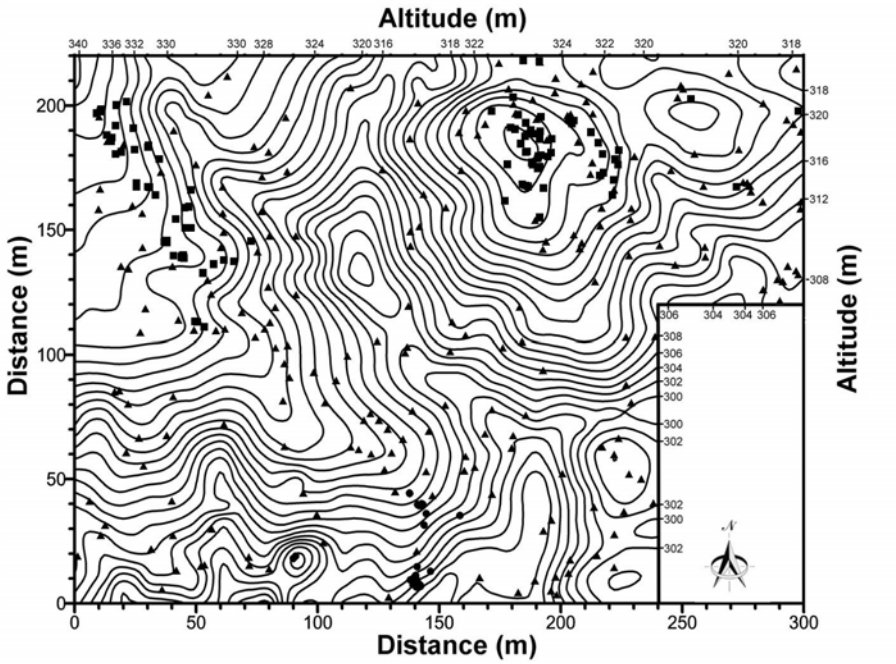


Fig. 2. Topographic map of the Lanjenchi plot. Species with a random distribution (*Glochidion rubrum*, ▲), clumped distribution (*Pasania formosana*, ■), and the most clumped distribution (*Aucuba chinensis*, ●) patterns are also shown.

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 200 simulations of random permutations. Ripley (1978) suggested another approximate guide that used $1.42n^{-1}\sqrt{A}$ as a 5% significance value. This significance value is used only at the $\hat{L}(d)$ values for each habitat in this study.

For edge effect correction, we used the buffer area around the region of interest, since buffer area mapping has been suggested as the most reliable method (Haase, 1995; Dale, 1999).

RESULTS

Overall patterns

At the 2 m scale, 9.1 % of the 88 species with more than 15 individuals were classified as randomly distributed, and 87.5 % showed significantly clumped patterns (Table 1). The proportion of randomly distributed species decreased with the increase of distance scales (Table 1). For example, at the 8 m scale, only 3.4 % species had a random distribution pattern (Table 1). There were no species showing a significant regular-distribution at all distance scales.

With the exception of few species, most abundant species were aggregated in space. The most abundant species with a random distribution pattern at 2 m distance scale was *Elaeocarpus sylvestris* (n = 364 trees), at 4 m was *Ficus formosana* (n = 21 trees), at 6 m was *Michelia compressa* (n = 198 trees), and at 8 m was *Glochidion rubrum* (n = 225 trees), respectively.

The values of $\hat{L}(d)$ almost increased with the increase in distance. The maximum values of $\hat{L}(d)$ were shown by the species *Aucuba chinensis* (Cornaceae), and ranged from 44.3 ($\hat{L}(2)$) to 71.1 ($\hat{L}(15)$). Most individuals of this species occurred in two clumps in areas of 70 and 270 m^2 (Fig. 2). Six species had $\hat{L}(2)$ -values >10, most of them were habitat-associated species, e.g., *Rhododendron simsii* and *Rhaphiolepis indica* var. *hiiranensis* were mostly distributed in windward and transition habitats (Sun, 1993), and *Alniphyllum pterospermum* occurred mainly in creek habitat, although their $\hat{L}(2)$ -value were only about 10.

Rare versus common species

Rare species were substantially more aggregated than common species at all distance scales (Table 2). The rarest species, *Aucuba chinensis* (n = 21), was also the most aggregated species. The degree of clumping was negatively correlated with the species abundance (Fig. 3).

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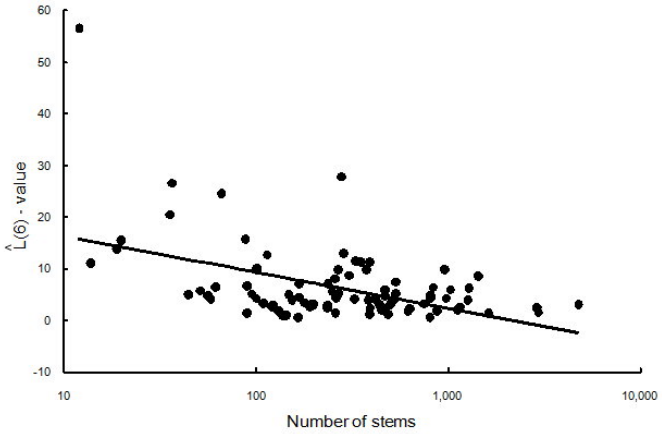


Fig. 3. $\hat{L}(6)$ values for all species with > 15 individuals in the Lanjenchi plot, as a function of the abundance of each species, on a log scale.

Table 1. The spatial patterns for the 88 species at different distance scales in the Lanjenchi plot.

Distance (m)	Number of species			Percentage		
	Regular	Random	Clump	Regular	Random	Clump
2	0	8	77	0.0	9.1	87.5
4	0	6	82	0.0	6.8	93.2
6	0	4	84	0.0	4.5	95.5
8	0	3	85	0.0	3.4	96.6

* At a distance scale of 2 m, 3 species didn't have any individuals.

Table 2. The medium values of $\hat{L}(d)$ in each abundance class at six distance (d) scales.

Abundance class	Number of species	Average $\hat{L}(d)$ value					
		d = 2	d = 4	d = 6	d = 8	d = 10	d = 15
0-100	17	5.6	7.5	6.6	7.4	9.5	11.5
101-250	23	2.1	2.9	3.1	3.6	4.0	5.2
251-500	24	2.6	3.6	4.5	5.3	6.3	8.2
>500	24	1.8	2.7	3.6	4.1	4.6	5.8

Small versus large trees

The relationship between spatial pattern and diameter size was compared for 62 species which had at least three growth stages and with more than 15 individuals at the 4 m scale. About one-third (35.5%) of these species showed a change of aggregation intensity from high to low with the increase of size (Figs. 4 and 5), but some of them remained at high aggregation intensity at the DBH > 8 cm stage (Fig. 4), while some become randomly distributed (Fig. 5). The second type was represented by 11.3% of the species which showed a reverse pattern, i.e., they become more aggregated with increasing diameter size (Fig. 6). The third type was that about 21.0% of the species were more aggregated in medium-diameter trees (DBH from 2 to 4 or DBH from 4 to 8 cm) than smaller (DBH from 1 to 2 cm) and larger trees (DBH > 8 cm) (Fig. 7). Some pioneer species belonged to this type, e.g., *Glochidion rubrum* and *Sapium discolor*. The results of spatial patterns changes with different growth stage were similar at other distance scales.

When diameter classes > 8 cm were considered, most species were aggregated. Among the 45 species with $\hat{L}(2)$ >0, 25 species were significantly aggregated and 22 species were randomly distributed. For the other 18 species, there were no any individuals at the 2 m distance. When using $\hat{L}(4)$, 40 species were significantly aggregated, 19 species were randomly distributed, and the other 6 species had no any individuals at the 4 m distance. For larger trees of most species, there was a tendency towards weaker aggregation intensity at all distance scales.

Plot level versus habitat level

The spatial patterns at 4 m distance scale were also calculated for the whole plot and for each of the four habitats within the plot. For the whole plot, 86.0% of the species had significantly aggregated pattern using the function $1.42n^{-1}\sqrt{A}$ as a 5% significance value as suggested by Ripley (1978). The proportion of species with aggregated pattern was highest in transition habitat, followed by the windward, leeward, and creek habitats. There were no species

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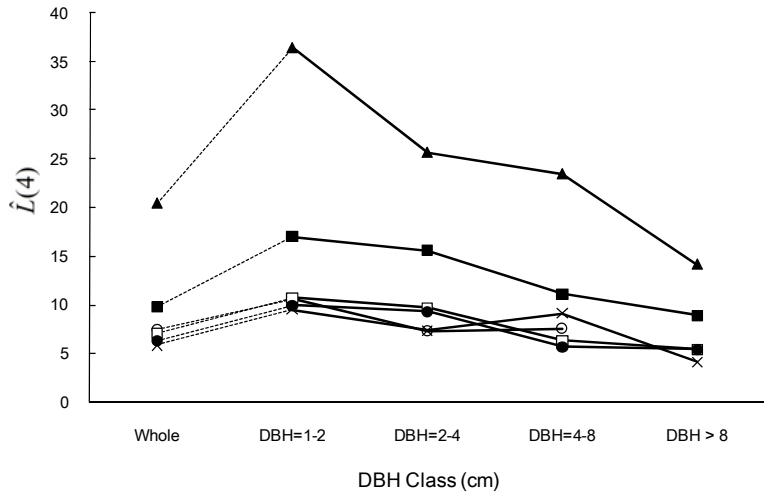


Fig. 4. The changes in spatial patterns for all individuals and individuals at different growth stages of *Rhaphiolepis indica hiiranensis* (▲), *Syzygium kusukusense* (■), *Syzygium buxifolium* (□), *Gordonia axillaries* (×), *Myrsine seguinii* (○) and *Eurya nitida* var. *nanjenshanensis* (●). Explanation for $\hat{L}(4)$.

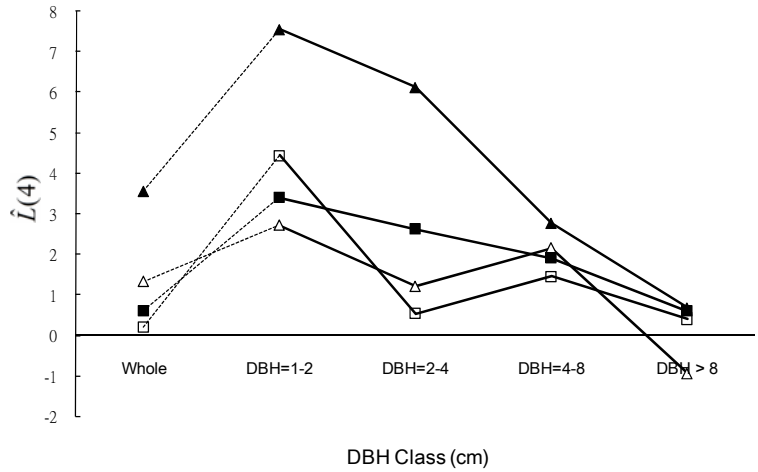


Fig. 5. The changes in spatial patterns for all individuals and individuals at different growth stages of *Adinandra formosana* (▲), *Elaeocarpus sylvestris* (■), *Schefflera octophylla* (□), and *Diospyros eriantha* (Δ). Explanation for $\hat{L}(4)$.

showing regular distribution pattern in all habitats (Table 3). The aggregation intensity of most species(70.0%) increased from a habitat level to a plot level. For other distance scales, a similar trend was observed for all species, but the percentage of aggregation pattern increased with increasing distance.

DISCUSSION

Tree populations at a given distance normally display one of the three distribution patterns: aggregated, random, or regular, depending on underlying ecological processes (He et al., 1997). We found that no species had a regular distribution in the Lanjenchi plot. Most species were clumped, and relatively few were randomly distributed. Similar patterns have been shown in other forests (He et al., 1997; Condit et al., 2000; Lin 2001). However, in a wet forests of Costa Rica, most species were randomly distributed (Lieberman and Lieberman, 1994).

Different factors may influence these distribution patterns. For example, environmental and habitat heterogeneity may result in clumped distribution (Szwagrzyk and Czerwczak, 1993; Duncan, 1993). Other factors include natural and human disturbances (Duncan, 1993; Pelissier, 1998), intra- and

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Table 3. Percentage of species with random, regular and aggregated spatial distributions at the whole plot level and habitat level.

Distribution pattern	Whole plot	Windward habitat	Transition habitat	Leeward habitat	Creek
Regular	0.0	0.0	0.0	0.0	0.0
Random	14.0	32.7	24.6	41.7	70.8
Clump	86.0	67.3	75.4	58.3	29.2

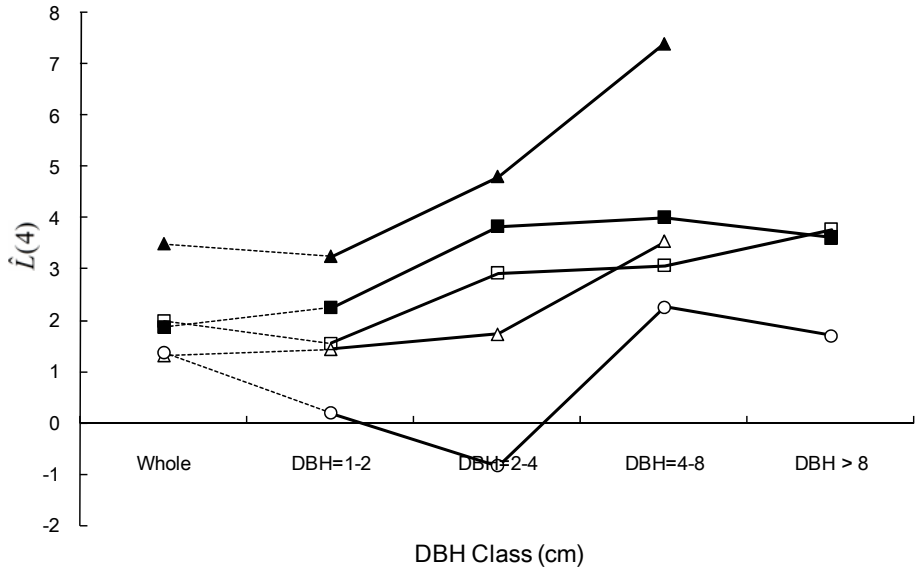


Fig. 6. The changes in spatial patterns for all individuals and individuals at different growth stages. *Ardisia quinquegona* (▲), *Decaspermum gracilentum* (■), *Beilschmiedia erythrophloia* (□), *Psychotria rubra*(Δ), *and Lithocarpus amygdalifolius* (○). Explanation for $\hat{L}(4)$.

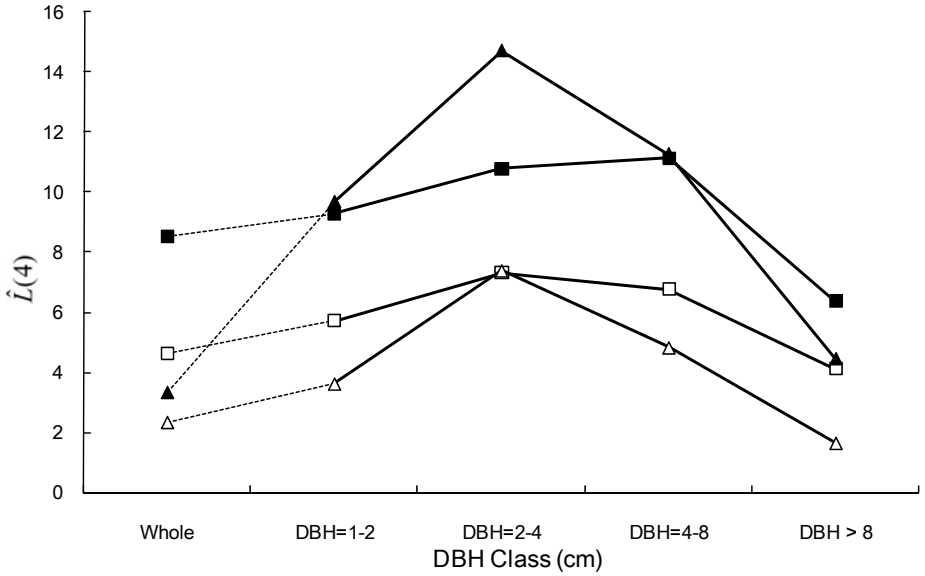


Fig. 7. The changes in spatial patterns for all individuals and individuals at different growth stages of *Sapium discolor* (▲), *Archidendron lucidum* (■), *Podocarpus macrophyllus* (□), and *Castanopsis fabri* (Δ). Explanation for $\hat{L}(4)$.

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inter-specific competition, life history strategies (Skarpe, 1991; Haase et al., 1996, 1997; Kenkel et al., 1997; Takahashi et al., 2001; Rozas, 2003), and regeneration strategies like limited seed dispersal and vegetative recruitment (Houle, 1994; Camarero et al., 2000; Takahashi et al., 2001). On the contrary, some processes can cause a less aggregated to random distribution pattern, such as competition and density-dependent mortality (Kenkel, 1988; Duncan, 1991).

Our study revealed that rare species were substantially more aggregated than other species. This pattern has been shown in most tropical forests (He et al., 1997; Condit et al., 2000), but not in dry forests in India (the Mudumalai site, Condit et al., 2000). However, our surveys do not support Janzen-Connell's hypothesis that conspecifics are often widely distributed to against natural enemies.

The spatial patterns of trees at different size classes varied from forest to forest. About two-thirds of the species were more aggregated in smaller diameter classes in the forests of Barao Colorado Island (BCI, Panama), Huai Kha Khaeng (HKK, Thaliand), Lambir (Malaysia), and Pasoh (Malaysia), but not in the forests of Mudumalai (India) and Sinharaja (Sri Lanka), where most species become more aggregated at larger size. In this study, we found that about a third of the species were more aggregated when smaller, a tenth of species were more aggregated when larger, and others were more aggregated for the medium sized trees or irregular. For species showing more aggregated pattern at smaller size indicates that herbivores and plant diseases may play a role in reducing the aggregation intensity (Condit et al., 2000). For species showing more aggregated when large assumes that there is no dispersal limitation for the small trees, but large trees were subjected to habitat selection (Condit et al., 2000). Our study also found that some species were more aggregated in the medium sized classes, this may suggest a past disturbance or gap formation event.

In Lanjenchi forest, species aggregation was more evident at the habitat level than at the whole plot level. At the habitat level, species were more aggregated in the windward and transition habitats, followed by the leeward and creek habitats. Similar results were obtained in the Lopei plot in northern Taiwan (Lin, 2001) where species were relatively more aggregated in the whole plot than in each habitat type, and the species in the creek habitat was the least aggregated among four habitats. Pelissier et al. (2001) suggested that the partitioning of heterogeneous plots into homogeneous subplots could reduce aggregated patterns. Therefore, habitat differentiation is likely to be one of the factors that control species distributions in the lowland rainforests in Taiwan.

Second-order analysis based on Ripley's K-function has been increasingly used in ecology to characterize spatial patterns and to develop hypothesis on underlying processes. However, the nearest neighbor distance analysis applied to the same data set (a kind of first-order analysis) produce very similar results (Chao, 1997). At the whole plot, most species were aggregated, and 11 species had a random distribution pattern. At the habitat level, species were more aggregated based on the nearest neighbor distance approach than the Ripley's K-function. The same result obtained from both approaches was that each habitat was more homogeneous than the whole plot.

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欖仁溪樣區低地雨林之樹種分佈類型

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(收稿日期：2007 年 7 月 12 日；接受日期：2007 年 10 月 15 日)

摘　　要

本研究探討臺灣南端的欖仁溪低地雨林 5.88 公頃樣區之樹種分佈類型。研究中將樹木依胸高直徑分成四個生長階段，並比較整個樣區及各生育地及不同徑級大小植物分佈類型之差異。在整個樣區中植株數量超過 15 株的種類有 88 種，以兩公尺的範圍來看，有 87.5% 的種類呈現聚集分佈，9.1% 呈現隨機分佈，3.6% 的種類在此範圍內不具任何同種植株。若以植株數量而言，株數較少的種類較數量多的種類更加聚集。至於不同徑級大小，35.5% 的物種隨著徑級增加而由高度聚集的分佈類型逐漸轉移到較低強度的聚集或呈現隨機分佈，但有 11.3% 的物種呈現相反的結果。當比較樣區中各生育地之分佈類型時，則聚集強度隨著風力梯度的增加（即溪谷到迎風坡）而增強。在所有的分析中沒有任何物種表現出規則分佈。本研究顯示欖仁溪樣區之物種分佈類型與各生育地的異質性有關，但其他如種子傳播的限制也可能是影響植物分佈的因子之一。

關鍵詞：生育地類型、分佈類型、風力、南仁山、低地雨林、臺灣。

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