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SPATIAL PATTERNS OF COMMON TREE SPECIES RELATING TO TOPOGRAPHY, CANOPY GAPS AND UNDERSTOREY VEGETATION IN A HILL DIPTEROCARP FOREST AT SEMANGKOK FOREST RESERVE, PENINSULAR MALAYSIA

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NIIYAMA, K., ABD. RAHMAN, K., IIDA, S., KIMURA, K., AZIZI, R. & APPANAH, S. 1999. **Spatial patterns of common tree species relating to topography, canopy gaps and understorey vegetation in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia.** The spatial patterns of the 30 most common tree species and their associations with topography (ridge, slope and valley), canopy gaps, and understorey vegetation (bertam palm, *Eugeissona tristis*, and a common bamboo, *Gigantochloa scortechinii*) were analysed in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia. We enumerated all trees ≥ 5 cm dbh and performed a census on the distribution of gaps, palm and bamboo in a 6-ha

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permanent plot. Most species showed significant aggregated patterns and only two species, *Payena lucida* and *Scaphium macropodum*, were randomly distributed through all quadrat sizes. Thirteen species showed significant positive association with topography; two species were associated with valley, ten species with ridge, and one species with slope. The 30 most common tree species were separated into three groups by a cluster analysis based on the dissimilarity index: $D = (1 - \omega) / 2$, where ω is Iwao's ω-index which reflects the degree of inter-species spatial association. Species group A (7 species) contained two randomly distributed valley species (*Vitex longisepala* and *Crypteronia griffithii*). Group B (11 species) consisted of ridge species. *Shorea curtisii, Lithocarpus wallichianus, Eurycoma longifolia* and others were positively associated with typical ridge sites and/or the distribution of the palm. Group C (12 species) consisted of slope species (*Pimelodendron griffithianum*), gap-associated species, (*Macaranga triloba, Millettia atropurpurea* and *Knema conferta*) and others. Gap species were also associated with bamboo. Distinctive habitat guild was recognised only on the ridge species.

Key words: Canopy gaps - common tree species - hill dipterocarp forest - Peninsular Malaysia - spatial distribution - topography - understorey vegetation

NIIYAMA, K., ABD. RAHMAN, K., IIDA, S., KIMURA, K., AZIZI, R. & APPANAH, S. 1999. Corak taburan spesies pokok utama serta hubungannya dengan topografi, ruang-ruang silara dan tumbuhan bawah di hutan bukit dipterokarpa di Hutan Simpan Semangkok, Semenanjung Malaysia. Analisis terhadap corak taburan 30 spesies pokok utama hutan bukit dipterokarpa serta hubungannya dengan topografi (permatang, cerun dan lembah), ruang-ruang silara, dan tumbuhan bawah (bertam, *Eugeissona tristis*, dan buluh, *Gigantochloa scortechinii*) dijalankan di Hutan Simpan Semangkok, Semenanjung Malaysia. Kami telah mengukur semua pokok ≥ 5 cm ppd dan membanci taburan ruang-ruang, palma dan buluh di dalam petak kekal seluas 6 hektar. Kebanyakan pokok menunjukkan taburan kelompok bererti melainkan *Payena lucida* dan *Scaphium macropodum*, taburannya adalah rawak pada setiap kelas saiz. Tiga belas spesies menunjukkan hubungan positif bererti dengan topografi, dua spesies menunjukkan hubungan dengan lembah, sepuluh spesies dengan permatang dan satu spesies di cerun. Tiga puluh spesies utama ini dibahagikan kepada tiga kumpulan berdasarkan analisis kelompok menggunakan indeks ketidaksamaan: $D = (1 - \omega)/2$, di mana ω ialah indeks Iwao ω yang menggambarkan darjah hubungan taburan antara spesies. Spesies kumpulan A (7 spesies) mengandungi dua spesies taburan rawak dan di lembah (*Vitex longisepala* dan *Crypteronia griffithii*). Kumpulan B (11 spesies) mengandungi spesies di permatang. *Shorea curtisii, Lithocarpus wallichianus, Eurycoma longifolia* dan lain-lain spesies mempunyai hubungan positif dengan permatang dan/atau taburan palma. Kumpulan C (12 spesies) mengandungi spesies cerun (*Pimelodendron griffithianum*), dan spesies yang menunjukkan hubungan dengan ruang, (*Macaranga triloba, Millettia atropurpurea* dan *Knema conferta*) dan lain-lain. Spesies ruang juga ada hubungan dengan buluh. Habitat berkelompok yang ketara hanya dikenal pasti pada spesies permatang.

Introduction

The spatial patterns of tropical rain forest are an important key to understanding the coexistence and abundance of tree species. Tree community is an assemblage of tree species which have specific spatial patterns: random, regular, and aggregated patterns in temperate forests (Masaki *et al.* 1992, Yamamoto *et al.* 1995) and also in tropical forests (Ogawa *et al.* 1961, Poore 1968, Armesto *et al.* 1986, Hubbell & Foster 1986b, Manokaran *et al.* 1992). The spatial distributions of tropical trees were usually analysed to test Janzen-Connell model (Janzen 1970, Connell 1971). They predicted that the adult trees were less aggregated than seedlings or saplings. However, many species were aggregated both at sapling and adult stages (Okuda *et al.* 1997, He *et al.* 1997). Although aggregated patterns are dominant, very diverse spatial patterns of tree species were described in a 50-ha plot in Pasoh Forest Reserve in Peninsular Malaysia (Manokaran *et al.* 1992), where distribution of tree species appears to depend on topography, wet soil, the position of large mother trees, and on canopy gaps.

Habitat separation as a result of differentiation in habitat niche is a simple and obvious mechanism that explains species coexistence in plant communities (Grubb 1977). However, the cause of aggregated distribution, the differentiation of habitat niche among tree species, and the intra-community structure such as habitat guild have not been sufficiently studied in tropical forests.

Hill dipterocarp forests, which are well developed on the ridges throughout Peninsular Malaysia and Borneo, are characterised by the distinctive topographic categories, namely ridge, slope and valley. It is expected that habitat separation of tree species that depends on topography and other environmental conditions is more clearly detected in the hill dipterocarp forest than in lowland dipterocarp forest where topography is less undulated.

Canopy gap dynamics also contribute to the spatial patterns of tree species. Armesto *et al.* (1986) reported that large-scale disturbances (such as landslides, fire, volcanic eruption and hurricanes) increase the proportion of random distribution species, whereas canopy gaps due to tree falls act to increase aggregated patterns. In addition to the difference of topography, densities of understorey palm or bamboo colonies differ between lowland and hill dipterocarp forests. Bertam palm (*Eugeissona tristis*) and a common bamboo species (*Gigantochloa scortechinii*) seem to affect the spatial distribution of common tree species in a hill dipterocarp forests (Symington 1943, Wyatt-Smith 1959, 1963, Burgess 1969, 1971, 1975, Whitmore 1984, Wong 1995).

We aimed to study the spatial distribution patterns of the 30 most common tree species according to topography, canopy gaps, and understorey vegetation in a hill dipterocarp forest. The following questions were addressed:

- Do common tree species show aggregated or random distribution?
- Are habitat guilds dependent on topography recognised in the hill dipterocarp forest?
- Does understorey vegetation affect the spatial pattern of common tree species?
- Are there gap-dependent species in the common species?

Materials and methods

Study area

In 1992, we set up a 6-ha plot (200 × 300 m) in a hill dipterocarp forest at the Semangkok Forest Reserve (SFR), which is located beside the road on the way to

Fraser's Hill about 65 km north of Kuala Lumpur, Selangor, Peninsular Malaysia. The study plot is located within compartment 30 of SFR. It is a virgin jungle reserve of about 28 ha surrounded by secondary forests that were selectively logged in the 1980s. A typical hill dipterocarp forest has developed on the narrow ridge and steep slope (Putz 1978), ranging from 340 to 450 m above sea-level. The plot has east and west facing slopes and a ridge (Figure 1). The nearest meteorological station is at Kuala Kubu Bahru, 15 km southwest of the plot; the average annual rainfall is 2414 mm and the average annual minimum and maximum temperatures are 21.9 °C and 33 °C respectively (Saifuddin Sulaiman *et al.* 1991).

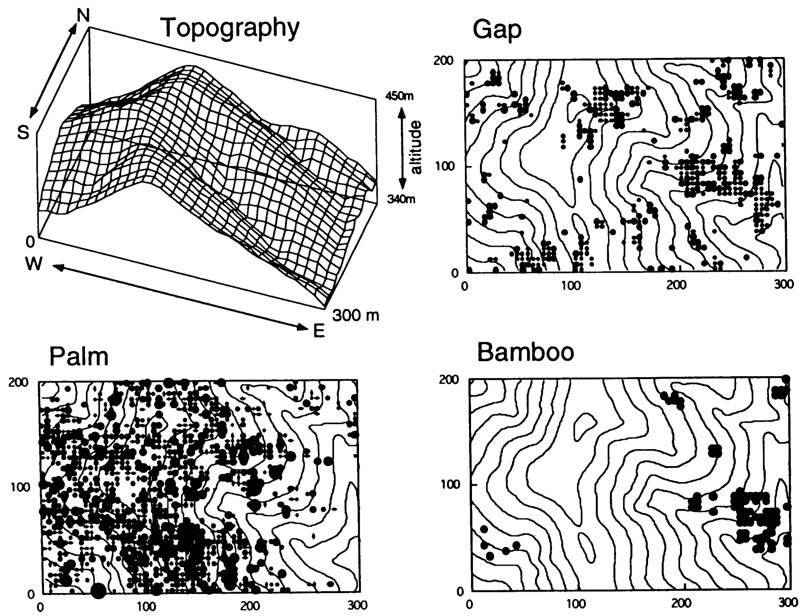

Figure 1. Topography of the 6-ha plot and the distributions of canopy gaps, palm *(Eugeissona tristis)* and bamboo *(Gigantochloa scortechinii)* on the 6-ha plot in Semangkok Forest Reserve, Peninsular Malaysia. In the map of gaps, small and large closed circles show 5-m and 10-m height gaps respectively. In the map of palm, the size of closed circles shows the abundance of palm individuals per 5 x 5 m quadrat. In the map of bamboo, closed circles show the presence of bamboo culm at the 5 x 5 m quadrat.

Plot establishment

We divided the 6-ha plot into 150 20 × 20 m quadrats and 2400 5 × 5 m subquadrats. All young and mature trees ≥ 5 cm diameter at breast height (dbh) were tagged, measured, and identified in 1993, 1995 and 1997. The position of each tree was coded to each 5 × 5 m that was the smallest unit of spatial distribution. This method follows that used for a temperate 6-ha plot (Masaki *et al.* 1992).

To examine the distribution of canopy gaps in the 6-ha plot, we checked tree height at the center of 5 × 5 m subquadrats using a 10-m pole and by visual observation in January-February 1994. This is similar to the gap census in the 50-ha plot at Barro Colombo Island (BCI) (Hubbell & Foster 1986a). We defined '5 m gap', '10 m gap' and 'closed canopy' in tree heights of 0–5 m, 5–10 m and >10 m respectively. The number of palm individuals (*Eugeissona tristis*) and the presence or absence of bamboo culm (*Gigantochloa scortechinii*) were checked in each 5 × 5 m subquadrat simultaneously with gap census.

Analysis

The 30 most common tree species among a total of 455 species ≥ 5 cm d.b.h. were analysed using the recensus data set in 1995. Spatial patterns were analysed by Morisita's Iδ-index where the significance of aggregation or randomness was tested by F-value (Morisita 1959). Pairwise interspecific spatial association was estimated by Iwao's ω-index (Iwao 1977) with the unit quadrat of 400 m² (20 × 20 m). Dissimilarity index for cluster analysis was calculated as follows:

$$D = (1 - \omega) / 2 \qquad (1)$$

where D is dissimilarity index ranging from 0 (complete overlap) to 1 (complete separation). See Masaki *et al.* (1992) and Yamamoto *et al.* (1995) for examples of this index used in forest ecology. The ω-index is as follows:

$$\omega_{(+)} = (\gamma - \gamma_{(ind)}) / (1 - \gamma_{(ind)}) \text{ for } \gamma \geq \gamma_{(ind)} \qquad (2)$$

or

$$\omega_{(-)} = (\gamma - \gamma_{(ind)}) / \gamma_{(ind)} \qquad \text{for } \gamma \leq \gamma_{(ind)} \qquad (3)$$

where

$$\gamma = \sqrt{\left[\frac{m^*_{YX}}{m_X} \cdot \frac{m^*_{XY}}{m_Y}\right] \Big/ \left[\frac{m^*_X + 1}{m_X} \cdot \frac{m^*_Y + 1}{m_Y}\right]} \qquad (4)$$

$$\gamma_{(ind)} = \sqrt{\frac{m_X}{m^*_X + 1} \cdot \frac{m_Y}{m^*_Y + 1}} \qquad (5)$$

and m_X, m^*_X, m_Y, and m^*_Y are mean density and mean crowding (Lloyd 1967) of species X and Y respectively. In the equation (4), m^*_{YX} and m^*_{XY} are mean crowding on species Y by species X and that on species X by species Y respectively. More details of equations are shown in Iwao (1977). Species groups were recognised by cluster analysis with the group-average method (Greig-Smith 1983) that is one of common clustering procedure. Cluster analysis was carried out by the statistics program SYSTAT (SYSTAT, Inc. 1992).

The associations among the distribution of 30 most common tree species and topographic categories (ridge, slope and valley), canopy gap, and understorey vegetation types (palm and bamboo) were tested by Fisher's exact probability test using the statistics program StatView (Abacus Concepts Inc. 1992). One hundred and fifty 20 × 20 m quadrats were separated into ridge, slope, and valley. The ridge quadrat was defined as a 20 × 20 m quadrat less than 15 m in undulation and higher than 400 m in mean elevation. Valley quadrats were decided by the counter map and the visual observation at each quadrat. The other quadrats except ridge and valley quadrats were defined as slope quadrats. In the Fisher's test (2 × 2 test) 150 quadrats were always divided into three types; ridge quadrats and the others, slope quadrats and the others, and valley quadrats and the others. The gap quadrat was defined as a 20 × 20 m quadrat containing more than four gap-subquadrats (one subquadrat, 5 × 5 m = 25 m^2). The palm quadrat was defined as a 20 × 20 m quadrat which included more than 20 palm individuals. This stemless palm usually develop to a multi-leaved individual. The bamboo quadrat was a 20 × 20 m quadrat which included a living culm of bamboo. In the Fisher's test 150 quadrats were divided into gap quadrats and the others, palm quadrats and the others, and bamboo quadrats and the others in each calculation. The associations among the topographic categories (ridge, slope, valley) and other three factors (gap, palm, and bamboo) were also analysed by the Fisher's test.

The reasons we used a 20 × 20 m quadrat as the size to analyse spatial distribution were as follows: 1) smaller quadrats such as 5 × 5 m or 10 × 10 m contain too few individuals to analyse interspecific spatial association, 2) larger quadrats such as 50 × 50 m or 100 × 100 m contain heterogeneous topography, complex canopy layers, and different densities of palm or bamboo patches. These quadrats, therefore, are inadequate to analyse the spatial associations among the distribution of common species, topography, gaps, palm, and bamboo. The size of 20 × 20 m is an arbitrary size to analyse the spatial distribution of common tree species in a hill dipterocarp forest.

Results

A total of 455 tree species were identified in the plot. The total basal area of stems ≥ 5 cm dbh in the plot was 42.9 $m^2\ ha^{-1}$ where *Shorea curtisii* dominated with 29.0% of the total basal area (Table 1). The 30 most common tree species contain emergent, main canopy and understorey tree species (Table 1).

Total gap area was 15.6% of which about half were 5-m gaps and another half were 10-m gaps (Figure 1). About 11% of canopy gaps were overlapped by bamboo colonies, because tree recruitments were sometimes inhibited by bamboo culms, and bamboo invaded into new gaps. Although most of the gaps had originated from tree falls, a small landslip had also made a gap at the upper part of slope in the plot.

Bertam palm, *Eugeissona tristis*, occupied 40% of 5 × 5 m quadrats in the 6-ha plot except in the shallow valley (Figure 1). In particular, palm density was high on the ridge; the maximum density was 55 individuals/400 m^2 and the mean density of palm was 380 individuals ha^{-1}. The distribution area of palm largely overlapped with that of *Shorea curtisii*. The distribution of bamboo was restricted to the lower slope (Figure 1). This bamboo occurred in 3% of the 6-ha plot.

Most species showed significant aggregated patterns and only two species, *Payena lucida* and *Scaphium macropodum*, were randomly distributed through all quadrat sizes (Table 2). However, aggregation depended on the quadrat size; *Crypteronia griffithii*, *Myristica iners* and *Artocarpus lanceifolius* were not aggregated under 20 × 20 m quadrat sizes and *Dacryodes rostrata* was not aggregated over 50 × 50 m quadrat sizes. As a result, 24 species showed significant aggregated pattern in the 20 × 20 m quadrat size.

Table 1. Population parameters and abbreviations of the 30 most common tree species

Species	Density		Basal area		Max. dbh	Abbreviations
	(No. ha^{-1})	(%)	(m^2 ha^{-1})	(%)	(cm)	
Shorea curtisii	53.3	5.7	12.44	29.0	161.1	SHORCU
Lithocarpus wallichianus	30.2	3.2	1.13	2.6	54.5	LITHWA
Teijsmanniodendron coriaceum	24.2	2.6	0.61	1.4	42.5	TEIJCO
Antidesma cuspidatum	20.3	2.2	0.44	1.0	61.9	ANTICU
Scaphium macropodum	19.2	2.0	2.24	5.2	101.7	SCA2MA
Diospyros latisepala	18.8	2.0	0.01	0.0	28.7	DIOSL1
Eurycoma longifolia	18.7	2.0	0.11	0.3	27.1	EURYLO
Pimelodendron griffithianum	13.0	1.4	0.38	0.9	41.9	PIMEGR
Aidia wallichiana	13.0	1.4	0.20	0.5	34.8	AIDIWA
Macaranga triloba	12.7	1.4	0.09	0.2	24.1	MACATR
Canarium patentinervium	12.2	1.3	0.11	0.2	37.8	CANAPA
Artocarpus lanceifolius	10.8	1.2	0.49	1.1	56.0	ARTOLA
Xanthophyllum griffithii	10.5	1.1	0.38	0.9	55.4	XANTGR
Dacryodes rostrata	10.3	1.1	0.21	0.5	45.7	DACRRO
Myristica iners	10.2	1.1	0.48	1.1	61.9	MYRIIN
Vatica odorata	9.7	1.0	0.22	0.5	39.8	VATIOD
Diospyros venosa	9.7	1.0	0.08	0.2	20.0	DIOSVE
Dacryodes rugosa	9.3	1.0	0.21	0.5	35.1	DACRR1
Payena lucida	9.2	1.0	0.55	1.3	*150.2	PAYELU
Archidendron bubalinum	8.7	0.9	0.13	0.3	31.8	ARCHBU
Milletia atropurpurea	8.0	0.9	0.17	0.4	50.8	MILLAT
Vitex longisepala	7.8	0.8	0.07	0.2	25.6	VITELO
Diospyros styraciformis	7.7	0.8	0.07	0.2	22.4	DIOSST
Anisoptera curtisii	7.5	0.8	0.97	2.3	123.8	ANI1CU
Eugenia ridleyi	7.2	0.8	0.26	0.6	60.0	EUGERI
Ochanostachys amentacea	7.0	0.7	0.51	1.2	57.8	OCHAAM
Crypteronia griffithii	6.5	0.7	0.22	0.5	55.8	CRY2GR
Knema conferta	6.3	0.7	0.10	0.2	29.5	KNEMCO
Diosyros sumatrana	6.3	0.7	0.07	0.2	23.5	DIOSSU
Dialium platysepalum	6.0	0.6	0.37	0.9	73.3	DIALPL
Other species	543.2	57.9	19.60	45.7		
Total	937.3	100.0	42.9	100.0		

*Large buttress.

Three species groups, A, B and C were recognised by the cluster analysis (Figure 2). The statistical significance between the distribution of the 30 most common tree species and ridge, slope, valley, gap, palm, and bamboo is shown in Table 3 where species order followed the result of the cluster analysis(Figure 2). The 20 × 20 m quadrats defined as ridge, slope, valley, gap, palm and bamboo quadrats were numbered as 31, 95, 24, 39, 51 and 22 respectively.

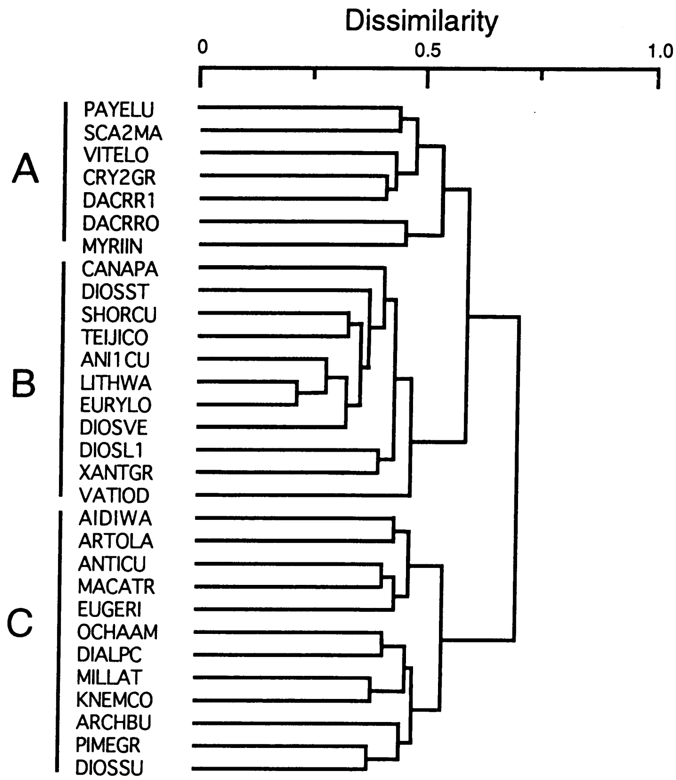

Figure 2. Cluster diagram of spatial association for the 30 most common tree species based on dissimilarity derived from Iwao's ω-index calculated for 20 × 20 m quadrats

Group A (7 species) was randomly distributed or aggregated around valleys (Figure 3). *Vitex longisepala* and *Crypteronia griffithii* showed positive association with valley and negative association with gap or bamboo. These two species are recognised as valley species. *Dacryodes rugosa* showed positive association with palm and negative association with gap. *Myristica iners* showed negative association with slope. *Payena lucida* and *Scaphium macropodum* and *Dacryodes rostrata* were randomly distributed throughout all quadrat sizes or on the sizes over 50 m (Table 2). They did not show significant association with any category. Although *Scaphium macropodum* was widely distributed, large trees were not distributed on the ridge.

Table 2. Analysis of distribution pattern and spatial association based on Morisita's Iδ-index and Iwao's ω-index. Grid sizes are 10 × 10 m to 100 × 100 m. Abbreviations of species name are shown in Table 1. Species order and group follow the result of cluster analysis (Figure 2).

Species	Group	Iδ						ω - index		
		10 × 10 m	10 × 20	20 × 20	50 × 50	50 × 100	100 × 100	Total	Max.	Min.
PAYELU	A	0.84	0.84	0.84	1.07	1.12	1.00	-3.14	0.17	-0.56
SCA2MA	A	0.82	0.73	0.96	0.99	1.00	1.03	-1.92	0.14	-0.52
VITELO	A	12.77**	10.55**	8.19**	5.71**	3.33**	1.75**	-6.09	0.19	-1.00
CRY2GR	A	2.43	1.62	1.42	1.55**	1.77**	1.77**	-2.74	0.20	-1.00
DACRR1	A	3.12**	2.73**	1.95**	1.62**	1.67**	1.31**	-4.89	0.20	-1.00
DACRRO	A	2.22*	1.90*	1.82*	1.19	1.07	1.06	-4.69	0.15	-0.75
MYRIIN	A	1.31	1.48	1.31	1.23*	1.05	1.06	-2.08	0.12	-0.61
CANAPA	B	2.97**	2.40**	2.05**	1.63**	1.47**	1.11*	-3.51	0.30	-0.84
DIOSST	B	6.38**	4.06**	4.64**	2.53**	1.86**	1.50**	-5.35	0.35	-1.00
SHORCU	B	1.69**	1.64**	1.49**	1.38**	1.30**	1.24**	-2.09	0.42	-0.88
TEIJCO	B	3.39**	3.10**	2.41**	1.91**	1.74**	1.32**	-4.19	0.37	-0.89
ANI1CU	B	3.03*	3.94**	3.94**	2.50**	1.64**	1.49**	-6.15	0.50	-1.00
LITHWA	B	8.46**	7.27**	3.64**	2.60**	2.31**	1.93**	-5.66	0.59	-1.00
EURYLO	B	3.57**	3.57**	3.09**	2.45**	1.74**	1.53**	-4.70	0.59	-1.00
DIOSVE	B	2.54*	3.27**	2.45**	2.15**	1.65**	1.64**	-4.80	0.51	-1.00
DIOSL1	B	2.09**	2.18**	1.94**	1.75**	1.50**	1.24**	-3.96	0.28	-0.97
XANTGR	B	2.46**	2.00*	1.31	1.36**	1.23**	1.15*	-4.18	0.30	-0.75
VATIOD	B	3.27**	4.72**	4.90**	2.95**	2.14**	2.13**	-7.91	0.33	-1.00
AIDIWA	C	1.60	1.50	1.65**	1.54**	1.49**	1.37**	-2.74	0.17	-0.54
ARTOLA	C	1.44	1.30	1.01	1.38**	1.16**	1.10*	-4.34	0.17	-0.65
ANTICU	C	3.01**	2.36**	1.91**	1.71**	1.58**	1.16**	-2.68	0.20	-0.58
MACATR	C	15.37**	12.74**	7.58**	3.29**	2.07**	1.52**	-9.08	0.20	-0.91
EUGERI	C	5.32**	3.32**	1.99*	1.70**	1.44**	1.14	-3.87	0.20	-0.56
OCHAAM	C	2.09	2.09	2.26**	1.37*	1.42**	1.25**	-6.47	0.19	-0.84
DIALPL	C	2.86	1.90	2.38**	1.56**	1.50**	1.32**	-7.75	0.19	-0.95
MILLAT	C	1.60	1.60	1.73*	1.68**	1.32**	1.33**	-5.76	0.24	-0.81
KNEMCO	C	15.36**	8.53**	7.47**	6.59**	6.69**	4.59**	-15.00	0.24	-1.00
ARCHBU	C	3.17**	2.04*	1.81*	1.25*	1.10	1.17*	-5.63	0.19	-0.82
PIMEGR	C	1.60	1.50	1.80**	1.64**	1.47**	1.38**	-5.44	0.26	-0.77
DIOSSU	C	2.56	5.55**	5.12**	4.40**	2.99**	2.24**	-10.29	0.26	-1.00

**: $p < 0.01$; *: $p < 0.05$.

Group B (11 species) was a very homogeneous group. Most species were associated positively with ridge or palm, and negatively with bamboo. *Lithocarpus wallichianus* and *Eurycoma longifolia* were strongly aggregated to the main ridge. Large trees of *Shorea curtisii* were restricted on the ridge, while small trees were distributed from the middle slope to the ridge. Congeneric species, *Diospyros styraciformis, D. venosa* and *D. latisepala,* showed largely overlapped distribution. *Vatica odorata* was distributed on the southern half of the ridge, which might depend on the position of mother trees and the regeneration site.

Table 3. Significance test of spatial association based on Fisher's exact probability test among the distribution of the 30 most common tree species and ridge, slope, valley, gap, palm and bamboo. Species order and group follow the result of cluster analysis (Figure 2).

Species	Group	Topography			Canopy	Understorey vegetation	
		Ridge (n=31)	Slope (n=95)	Valley (n=24)	Gap (n=39)	Palm (n=51)	Bamboo (n=22)
PAYELU	A						
SCA2MA	A						
VITELO	A		--	++	-		
CRY2GR	A		-	++			-
DACRR1	A				-	++	
DACRRO	A						
MYRIIN	A		--				
CANAPA	B					+	--
DIOSST	B	+				++	-
SHORCU	B	++	-			++	--
TEIJCO	B	++		--	-	++	-
ANI1CU	B	++		--		++	
LITHWA	B	++		-		++	--
EURYLO	B	++		--		++	--
DIOSVE	B	++					--
DIOSL1	B	++		--		++	--
XANTGR	B	+				+	--
VATIOD	B	++				++	-
AIDIWA	C						
ARTOLA	C	--				-	
ANTICU	C						
MACATR	C	--			++	--	+
EUGERI	C					-	
OCHAAM	C	-				--	
DIALPL	C						+
MILLAT	C				+		++
KNEMCO	C	-			+	--	++
ARCHBU	C						
PIMEGR	C	-	+				
DIOSSU	C	-				--	

+, - : $p < 0.05$; ++, -- : $p < 0.01$. +: positive association. -: negative association, n = number of 20 × 20 m quadrats.

Group C was the most heterogeneous. *Pimelodendron griffithianum* was the only species that showed positive association with slope. *Artocarpus lanceifolius, Ochanostachys amentacea* and *Diospyros sumatrana* were negatively associated with ridge or palm, which showed slope preference. *Macaranga triloba, Millettia atropurpurea* and *Knema conferta* were positively associated both with gap and bamboo. *Dialium platysepalum* was significantly associated with bamboo (Table 3). *Eugenia ridleyi* showed negative association with palm. The other three species, *Aidia wallichiana, Antidesma cuspidatum* and *Archidendron bubalinum,* had no associations with any other categories.

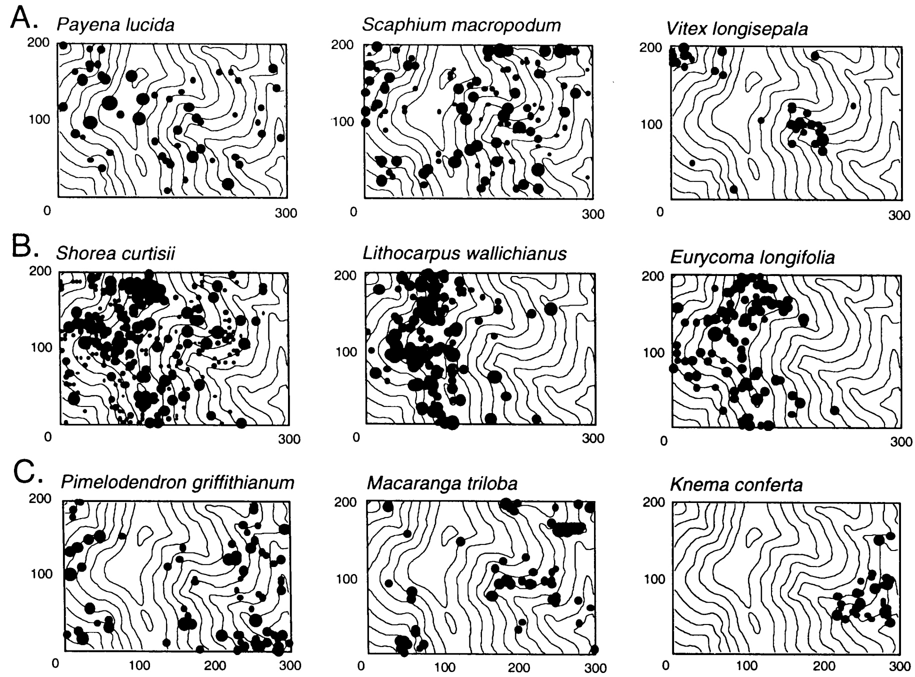

Figure 3. Examples of spatial patterns. Groups A, B and C follow the result of cluster analysis (Figure 2). Closed circles show relative diameter at breast height in each tree species.

As a result, thirteen species showed significant positive association with topographic categories; two species were associated with valley, ten species with ridge, and one species with slope. Six species showed only negative association with topographic categories (Table 3).

Significant association was also detected among the categories. Palm was positively associated with ridge ($p<0.01$) but negatively with valley ($p<0.01$). Bamboo was positively associated with gap ($p<0.05$), and negatively with palm ($p<0.01$) and ridge ($p<0.05$). Gap did not have any significant association with the three topographic categories but had positive association with bamboo ($p<0.05$).

The degree of inter-species overlaps in spatial distribution was well represented by the ω-index (-1:complete separation to 1:complete overlap), and the sum of ω-index with other 29 species ranging from 29 to -29 (Table 2). If a species was completely segregated with other 29 tree species, all inter-species ω-index was -1, and the sum of ω-index became -29. The largest inter-species ω-index of 0.59 was obtained between *Lithocarpus wallichianus* and *Eurycoma longifolia* distributed on the ridge. The means of inter-species ω-index in Groups A, B, and C were 0.17, 0.41, 0.27 respectively. This result shows the largest overlap among Group B of ridge species. *Knema conferta,* which is a typical aggregated distribution species on the lower slope, had the least sum of ω-index of -15.0, because it was completely segregated with many other species. On the other hand, *Scaphium macropodum* had the lowest inter-species ω-index, 0.14 , but showed relatively large sum of ω-index, -1.92.

Discussion

Aggregated spatial patterns were predominant among the 30 most common tree species. However, the degree of aggregation was continuous and the degree of significance depended on the quadrat sizes. This hill dipterocarp forest allows the presence of diverse aggregation patterns and less number of randomly distributed tree species. These spatial patterns are not specific to tropical forests; the forest communities in tropical dry, warm temperate and cool temperate forests also consist of many aggregated species and small numbers of randomly distributed species (Hubbell 1979, Masaki *et al.* 1992, Tanouchi & Yamamoto 1995, Yamamoto *et al.* 1995). Patterns of aggregation or randomness, therefore, do not directly explain the higher tree species diversity in the tropical forest and the abundance of each tree species.

The cause of aggregation patterns depends on the spatial scale. At large scales > 2500 m^2, topography, edaphic factors (Pemadasa & Gunatilleke 1981, LaFrankie 1996), and large historical disturbances contribute to the aggregated patterns. Although there was a distinctive topographic gradient, evidence for large-scale disturbances was not detected in the plot. Variation of species composition among mixed dipterocarp forests has been explained by the soil chemistry such as contents of potassium or magnesium (Baillie *et al.* 1987, Ashton & Hall 1992). On the other hand, variation of species composition or spatial patterns of tree species within a forest community was not well explained by soil chemistry (Newbery *et al.* 1996). Topogrəphy and soil water condition were emphasised to explain the distribution pattern of tree species in a tropical forest (Newbery *et al.* 1996, Walsh 1996). Rare drought events restrict the tree species dominating on the ridge where soil is shallower and becomes much drier than the slope or valley sites. However, soil nutrients were dependent on topography in this plot (Tange *et al.* 1998); total amounts of nitrogen and phosphorus were rich on the ridge. Tree species distributed on the ridge probably depend on both water availability and soil chemistry.

At the micro scale < 2500 m^2, tree gaps (Richards & Williamson 1975, Armesto *et al.* 1986), seed dispersal mode, regeneration around the mother trees and stress factors may cause aggregated patterns. Small- or medium-sized gaps were predominant in the plot. Most of the 30 most common tree species were significantly aggregated at the scale of 10 × 10 m to 20 × 20 m quadrat sizes similar to the size of gaps. Particularly, *Macaranga triloba* and *Knema conferta* showed strong aggregation in the quadrat of size less than 20 × 20 m. Although new recruits of most tree species probably depend on the canopy gaps, a distinctive association with current gaps was detected for *Macaranga triloba, Millettia atropurpurea* and *Knema conferta*. *Macaranga triloba* is a well-known light-demanding pioneer species, but characteristics of other two species have not been studied.

Aggregation patterns also depend on the seed dispersal ability (Poore 1968). The tree species having lower seed dispersal ability will make a clump around the mother trees. This is in contrast with the spatial pattern of *Scaphium macropodum,* which has an effective organ for wind dispersal and was distributed at random throughout the plot. This random distribution pattern occurs for trees larger than 5 cm dbh in the plot. On the other site, seedlings and saplings of *Scaphium macropodum* showed aggregated patterns around mother trees (Yamada & Suzuki 1997).

Vitex longisepala and *Crypteronia griffithii* were restricted to the valley and valley head where shade and wet conditions were predominant. This is an example of the aggregated patterns dependent on specific stressed conditions similar to swamp species (Poore 1968, Hubbell & Foster 1986b).

Habitat guild was recognised in ridge species. Species group B was the most distinctive and homogeneous species group. Most species of the group showed significant positive associations with ridge and palm, and negative association with bamboo. The distribution of tree species largely overlapped within the group B but not with other groups. This group, therefore, is recognised as habitat guild dominated on the ridge. Other species groups were mixtures of species whose spatial patterns and associations with the categories were different from each other. In lowland dipterocarp forest, only swamp species were distinctively distributed with other tree species, because topography was homogeneous (Poore 1968). Habitat guilds were also found in a neotropical forest (Hubbell & Foster 1986b) where five habitat guilds, "Slope", "Indifferent", "Plateau", "Streamside/Ravine" and "Swamp" were recognised.

Among the six site categories, ridge and palm were positively associated. The effects of ridge and palm on tree distribution were not completely separated. It has been pointed out that this stemless palm prevents regeneration of canopy trees (Chong 1970, Burgess & Lowe 1971). The large area of foliage interrupts dispersed seeds and shades the seedlings around the palm, and the thick leaf litter of the palm prevents establishment of tree seedlings. However, it was reported that *Shorea curtisii,* which is the most abundant and largest tree species in the ridge, can survive for several years under these conditions (Whitmore 1984). This species was dominant through most size classes on the ridge. Consequently, water availability and soil chemistry related to ridge topography, regeneration condition related to dense palm cover, and a large stocking of *S. curtisii* make a fundamental set of environmental conditions on the ridge. Tree species of the ridge guild probably depend on or tolerate these characteristic conditions on the ridge.

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