

Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical heath forest of Central Kalimantan, Indonesia

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(Accepted 27th December 2001)

Abstract: Small-scale spatial association of the distribution for 55 abundant tree species with two environmental factors (humus depth and surface microtopography) was examined in two 1-ha plots of a heath (kerangas) forest in Central Kalimantan, Indonesia. More than 80% of the 55 species showed a significant habitat preference in humus depth and/or relative elevation in at least one plot. In particular, ten species occurring in both plots showed a consistent significant preference for humus depth or relative elevation in the two plots. Using randomization tests, however, only five species significantly associated with humus depth and no species with relative elevation. These results suggest that edaphic and topographic factors, especially humus depth, contribute to determining local spatial distribution and floristic composition of abundant tree species in the forest.

Key Words: Borneo, humus podzol, kerangas forest, spatial distribution, species diversity

INTRODUCTION

Uncovering associations between the distributions of tree species and edaphic and topographic variation is one of the most important keys to understanding species diversity in tropical forests. Previous studies have demonstrated associations of tree species distribution with several environmental factors at various spatial scales. According to Newbery *et al.* (1986), variation in the spatial distribution of tree species can be recognized at four distinct scales. Geographical distribution of tree species can be recognized as a variation at a very large scale. Differences between forest formations (*sensu* Whitmore 1984) represent a large scale of variation. Variations in forest types are recognized in relation to regional topographic and edaphic factors at a medium scale. Within the forest types, biological traits related to regeneration processes, local environmental differences and stochastic events can promote species variation at a small spatial scale. In addition to these spatial scales, Clark *et al.* (1998) demonstrated the spatial distribution pattern associated with edaphic vari-

ation at a mesoscale landscape level, which is larger than typical plot studies but smaller than regional studies (*c.* 1–100 km²). The environmental factors affecting the variation at these spatial scales include altitude (Lieberman *et al.* 1985), soil-water availability (Becker *et al.* 1988), soil nutrients (Baillie *et al.* 1987, Gartlan *et al.* 1986), soil texture (Davies *et al.* 1998) and topography (Ashton 1976, Austin *et al.* 1972, Hubbell & Foster 1986, Poore 1968). Ashton (1973) pointed out that topography is more important for species distribution at a small spatial scale (more or less uniform lithology) rather than at a large scale (cited in Baillie *et al.* 1987). Tropical forests contain many species even at such a small spatial scale (Webb & Peart 2000). Evaluation of the relative importance of these topographic and edaphic factors for local species distribution and floristic composition is thus needed to explain the mechanism of sustaining species-richness in tropical forest ecosystems. Heath (kerangas) forest is an appropriate subject for the examination of such a local spatial association of tree species with edaphic and topographic factors. The forest is one of the most distinctive vegetation types in lowland Borneo although sporadically distributed. It occurs on silica-derived white sandy substratum which is poor in bases, highly acidic and coarsely textured (Brüning 1974, MacKinnon *et al.* 1996). A rela-

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tively thin layer of humus (< 1 m) covers the surface of the sandy substratum in the forest compared with that in peat-swamp forests (*c.* 7.7 m, Haraguchi *et al.* 2000). Most tree species in the heath forest have several characteristics specialized to their unique environment (e.g. slender trunks and thick leaves) in response to severe nutrient deficiency and periodically limited water availability (Brünig 1974, Richards 1996, Whitmore 1984). Therefore, trees of heath forests appear to be sensitive to the local variation of several environmental factors. We hypothesize that distribution of tree species in heath forest can be closely correlated with the gradient of several environmental factors even at fine spatial scale.

So far, there exist several studies on the relationship between species spatial distribution and environmental factors in heath forests. Brünig (1976) demonstrated that there was no effect of soil variation on tree distribution in a heath forest in Sabal Forest Reserve, Sarawak, Malaysia. In the same site, Newbery *et al.* (1986) ascertained that the moderate edaphic and topographic variation within a 20-ha plot did not account for patterns in the variation of the distributions of tree species. In contrast, Riswan (1982) reported a significant change in floristic composition between 0.5-ha subplots within 2 ha (100 m × 200 m), only 150 m distant from each other (cited in Newbery 1991). Newbery & Proctor (1984) found a strong floristic difference associated with a marked soil difference within a 1-ha plot of heath forest in Gunung Mulu National Park, Sarawak. Newbery (1991) re-analysed 38 plots formerly studied by Brünig (1974) in north-east Sarawak and Brunei, and suggested that a major factor determining the association between vegetation and soil type was clay content, although soil type of each plot was confounded with elevation, rainfall and geographical location. The degree of the association of species distribution with local edaphic and topographic factors in heath forests are thus open to further investigation.

In this study, we evaluated the effect of local spatial variation in depth of humus and that in relative elevation, as one of the indicators of microtopography, on species distribution in a heath forest, using two 1-ha plots in which the two environmental factors are differently correlated.

METHODS

Study site

The study site was located in the area approximately 3–4 km east from Kampung Babugus, Desa Lahei, Kacamatan Metagai, Kabupaten Kapuas, Central Kalimantan, Indonesia (*c.* 40 m asl; 1°55'S, 114°10'E). Palangka Raya, the provincial capital of Central Kalimantan, located *c.* 40 km south-west from the study site had an annual precipitation of *c.* 2800 mm (an average from 1993 to 1999, but *c.* 2970

mm when the data of an El Niño year, 1997, were excluded) and an annual mean temperature of 26–28 °C. Although monthly rainfall was over 100 mm in most months, a few months in the dry season (especially July and August) occasionally had < 100 mm of precipitation recorded. Most of the study area was covered with heath forest, while patches of peat-swamp forest occurred along the Mangkutup River (Sungai Mangkutup), a branch of the Kapuas River (Sungai Kapuas). These different forest types adjoined each other. The heath forests had a lower (*c.* 30 m in height) and relatively smooth upper canopy compared with that of mixed dipterocarp forests, a typical lowland forest vegetation in Borneo (Brünig 1974). Profiles of the two 1-ha plots in the heath forest of this study are compared with those of the other different forest types in Kalimantan in Table 1 (data sources are the same as those of Kohyama *et al.* 2001, Nishimura & Suzuki 2001 and Suzuki 1999). Trees in the heath forests occurred densely on sandy soil and had smaller basal areas compared with the peat-swamp and mixed dipterocarp forests. The number of species and species richness in the heath forests were greater than that in the peat-swamp forests, and much less than that in the mixed dipterocarp forests. By contrast, the number of individuals (≥ 5 cm in trunk diameter at breast height, dbh) was much greater in the heath forests than in the other two forest types. Main dominant species in the heath forests were *Cotylelobium lanceolatum*, *Hopea griffithii*, *Shorea* spp. (Dipterocarpaceae), *Calophyllum* spp. (Guttiferae), *Syzygium* spp. and *Tristaniaopsis* spp. (Myrtaceae) (Appendices 1 and 2).

Field survey

A total of four plots (P1–P4) were established in the study site from July 1997 to January 1998. In 1997, a large part of the surrounding area of these plots was burnt by forest fire due to extraordinarily dry conditions in the dry season. These plots were set up in the remaining unburnt sites. Two 1-ha plots (P1 and P4) were established in the heath forest. They were located at *c.* 2 km from each other. Another 1-ha plot (P2) was established in the peat-swamp forest covering a riverside area *c.* 1 km east from P1. Plot size of P3 (20 m × 20 m) was smaller than those of the other three plots. It was established in an area of shrubland, where the bog moss *Sphagnum* sp. was found, and was located at *c.* 2 km west from P1. In this study, only the data from P1 and P4 were used for analyses. In P1, there were some stumps of *Agathis borneensis*, one of the most characteristic species in heath forests which had been selectively logged. There were no such traces of disturbance in P4. Topography over the study site was generally flat. P1 had a gentle slope in an east–west direction, while P4 had a slope with undulation in a south–west–north–east direction (Figure 1). Since the range of elevation change in the surrounding area of plots was < 10 m

Table 1. Comparison of basal area, species richness and tree density among 1-ha plots of three different types of forests in Kalimantan, Indonesia.

	Forest type ¹				
	HF		PF	MDF	
	P1	P4	P2	S1	S2
Basal area (m ² ha ⁻¹)	30.1	27.6	45.5	42.2	44.6
No. of species (species ha ⁻¹)	144	122	69	269	320
Tree density (individuals ha ⁻¹)	2016	1982	1475	1280	1353
Species richness (Fisher's α)	35.7	28.6	15.0	103.9	132.2

Data on trees with dbh \geq 5 cm were used.

¹HF, heath forest; PF, peat-swamp forest; MDF, mixed-dipterocarp forest. Location of each plot is as follows: P1 and P4, Central Kalimantan (this study); P2, Central Kalimantan (data source is the same as that in Nishimura & Suzuki 2001); S1 and S2, West Kalimantan (data source is the same as that in Kohyama *et al.* 2001 and Suzuki 1999).

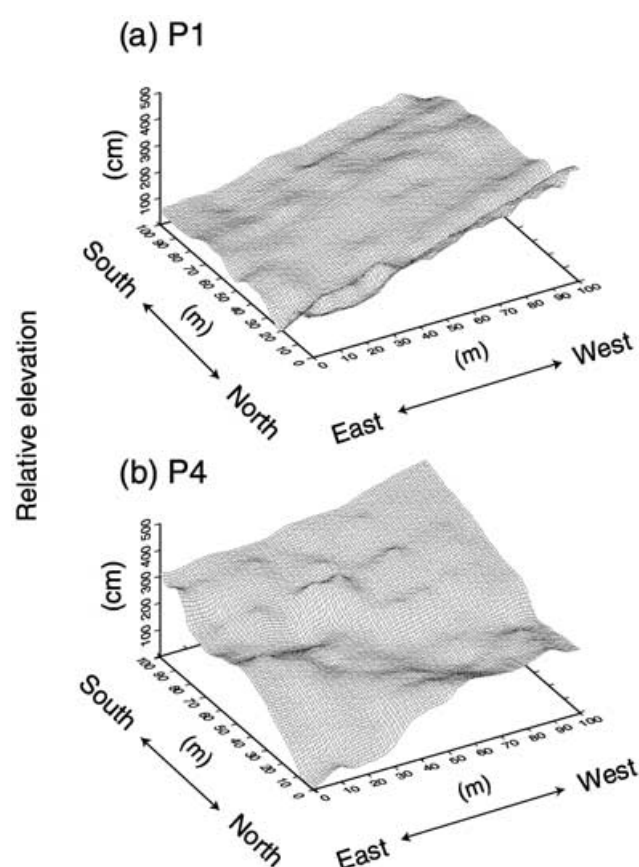


Figure 1. Topography of the two 1-ha research plots (P1 (a) and P4 (b)) in a heath forest of Lahei, Central Kalimantan, Indonesia.

(Haraguchi *et al.* 2000), the elevation range (*c.* 5 m) within each plot represents a large part of the whole range in the surrounding area. The forest floor in each plot was covered with humus layer (< 1 m in depth). Humus deposition > 1 m was found only in a valley near P2 (Haraguchi *et al.* 2000), where peat-swamp forest, not heath forest, occurs. The range of humus depth in P1 and P4 can be considered, therefore, to represent most of the variation in humus depth for the surrounding area of heath forest. Relative elevation was defined as the elevation from the

lowest point of the 10 m \times 10 m grid points within each 1-ha plot. Although the elevation range was small, P1 showed a clear decline of humus depth with increasing relative elevation (Spearman's rank correlation coefficient, $r_s = -0.635$, $P < 0.001$, Figure 2). On the other hand, P4 showed the opposite relationship to that in P1: deep humus deposition was found at middle and high elevation ($r_s = 0.321$, $P < 0.001$). In the two plots, all trees \geq 15 cm in girth at breast height (gbh) were labelled with aluminium tags, and gbh and horizontal location of stem bases in the plots recorded. Measurements of microtopography (relative elevation from the lowest point within each plot) and humus depth were carried out at every corner of each 10 m \times 10-m subplot (total 121 points per plot) in August 1997 (for topography in P1) and November 1999 (for topography in P4 and for humus depth in both plots). No ground disturbance occurred in the plots during the census period. Specimens for identification were collected in triplicate from all species in the plots. Numbered vouchers are deposited in Herbarium Bogoriense, Bogor, Indonesia (BO), the Faculty of Science of Kagoshima University, Kagoshima, Japan (KAGS), and the Graduate School of Environmental Earth Science of Hokkaido University, Sapporo, Japan (Appendices 1 and 2).

Data analyses

Fifty-five species were considered as being abundant species (\geq 15 individuals) in the two plots except for *Neoscortechinia kingii* and *Tetractomia cf. obovata* (Appendices 1 and 2). Although only 14 trees of *N. kingii* were found in P1, sufficient trees (34 individuals) were found in P4. Twelve trees of *T. cf. obovata* were found in P1 but no tree of this species was found in P4. Nevertheless, *T. cf. obovata* was considered in the analyses, because this species was abundant (140 trees ha⁻¹) in the peat-swamp forest near to the two plots and available to an indicator of a peat-swamp-like habitat, namely, wet or humus-rich condition. Twenty-two species were abundant in both plots. Fourteen species were abundant only in P1,

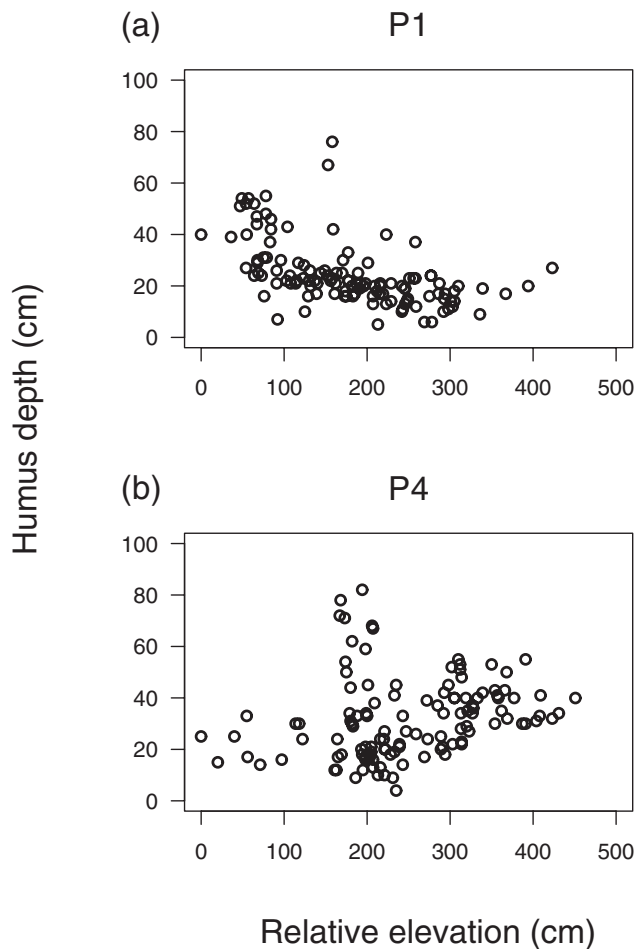


Figure 2. The distribution of humus depth measured at each $10\text{ m} \times 10\text{ m}$ grid point along the gradient of relative elevation in (a) P1 and (b) P4 in Lahei, Central Kalimantan, Indonesia.

while 19 were abundant only in P4. In this study, the former 22 species are called ‘common species’, and the latter 14 and 19 species ‘plot-specific species’.

The assignment of the two environmental variables (i.e. humus depth and relative elevation from the lowest elevation in a plot) to each tree was made for each plot. The environmental variables at each tree location were estimated from the original measurement at each $10\text{ m} \times 10\text{-m}$ grid point using generic mapping tools (GMT). Details of the method of estimation are described in Smith & Wessel (1990). Since the coordinates for each tree location were measured at the resolution of 0.1 m, the original $10\text{ m} \times 10\text{-m}$ grid data of the environmental variables were interpolated and converted to $0.1\text{ m} \times 0.1\text{-m}$ grid data, and then they were assigned to each tree. Moreover, the original data of the environmental variables were converted into $1\text{ m} \times 1\text{-m}$ and $5\text{ m} \times 5\text{-m}$ grid data to calculate expected relative frequencies of these environmental data for goodness-of-fit tests and principal components analysis.

To examine overall relationships between floristic composition and the environmental variables, principal components analysis (PCA) was carried out using both abundance and presence–absence data of $10\text{ m} \times 10\text{ m}$ subplots, and then, the correlation between PCA axes and the environmental variables was evaluated by Spearman’s rank correlation coefficient. The $5\text{ m} \times 5\text{-m}$ grid data calculated for the grid points at the centre of each subplot were used as the environmental variables of PCA analyses.

To detect habitat preference for each species, two different approaches were conducted. First, the habitat preference of each species was analysed using the Kolmogorov–Smirnov goodness-of-fit test for continuous data (hereafter K–S test, Zar 1999). The observed frequency distribution for each species was obtained based on the interpolated data for the environmental variables at $0.1\text{ m} \times 0.1\text{-m}$ grid scale, while the expected cumulative relative frequency was obtained from all grid points of environmental data at $1\text{ m} \times 1\text{-m}$ scale. In this study, the ‘signed’ D value (the test statistic of K–S test) was employed as the indicator of habitat preference. Second, a randomization test on the basis of χ^2 goodness-of-fit test was performed to avoid the problem of non-independence caused by spatial autocorrelation. Spatially autocorrelated data can easily bring about a spurious statistical association between species and habitat, violating the assumption of independence for standard statistical tests (Clark *et al.* 1998, Legendre 1993, Webb & Peart 2000). In other words, new observations cannot be counted for one full degree of freedom (Legendre 1993). In ecological studies, spatial autocorrelation such as clumped distribution pattern of trees due not to habitat preference but to the vicinity of parent trees is widely observed. Using randomization tests, the effect of such spatial autocorrelation on statistical tests can be eliminated by shuffling the habitat types within a plot. The procedure of the randomization test in this study was as follows: (1) Each environmental variable was divided into three levels: A (< 20 cm), B (20–40 cm), C (> 40 cm) for humus depth; A (< 150 cm), B (150–300 cm), C (> 300 cm) for relative elevation. (2) The three levels for each environmental variable were assigned to the $10\text{ m} \times 10\text{-m}$ subplots (a total of 100 subplots) within each 1-ha plot, on the basis of the interpolated environmental data of $5\text{ m} \times 5\text{-m}$ grid scale placed at the centre of each subplot. (3) Observed frequency for a given species was obtained from the sum of presence–absence data of subplots within each level of the environmental variable, while expected frequency was calculated based on the relative frequencies of the subplots within each level and total number of the ‘presence’ subplots of the species. (4) The χ^2 statistic was calculated comparing the observed and expected frequencies. (5) Random assignment of the levels of each environmental variable to the 100 subplots was made, maintaining the original frequency of subplots within each level, then the χ^2 stat-

istic was calculated comparing the randomized frequencies with the expected ones. (6) In this study, this randomization procedure was repeated 2000 times for each species, and the observed χ^2 statistic and the randomized distribution of the statistics were compared. The observed test statistics > 95% of those randomized ones were considered as an indicator of significant association of species with habitat.

RESULTS

In principal components analysis (PCA) using the data on tree abundance in the 100 subplots within each plot, each PCA axis explained variation of scores (%) as follows: I = 15.9, II = 7.3, III = 5.2 for P1 and I = 7.8, II = 6.5, III = 6.1 for P4. The PCA axis I was significantly and most strongly correlated with both humus depth and relative elevation. Axes II and III were not strongly correlated with the two environmental variables. Axis I was strongly correlated with relative elevation in P1 but not in P4, while it was strongly correlated with humus depth in both plots (Table 2). Similar results were obtained using presence-absence data.

Using a K–S test to detect habitat preference for each abundant species, 45 out of 55 species (82%) showed, at least, one significant biased distribution toward a certain range of humus depth and/or relative elevation in either P1 or P4 (Tables 3 and 4). The sign of D value corresponded well with a tendency of the bias of the observed frequency distribution for each species along each environmental variable. As shown in some examples of Figures 3 and 4, significant positive D values corresponded with the observed distribution biased toward the shallower and lower sites than the expected one, whereas a significant negative D value corresponded with the observed distribution biased toward the deeper and upper sites. Thus, by checking the sign of the D value, a general trend of the species distribution could be detected along each environmental gradient. Based on the habitat preference, each species was classified into the following alternative habitat classes: shallow (S) vs. deep (D) in humus depth, and upper slope (U) vs. lower slope (L) in relative elevation.

Common species

In K–S tests, 10 out of 22 common species (45%) showed a significant and consistent habitat preference in either

humus depth or relative elevation in the two plots: four species (*Cotylelobium lanceolatum*, *Hopea griffithii*, *Shorea retusa* and *Sindora leiocarpa*) were classified into S, three species (*Syzygium* cf. *klossii*, *Neoscortechinia kingii* and *Palaquium leiocarpum*) into D, one species (*Lithocarpus* sp.) into U and two species (*Dipterocarpus borneensis* and *Nephelium* cf. *maingayi*) into L (Table 3). Figures 3 and 4 show the relative frequency distributions along the gradient of humus depth comparing the expected ones for the four species which showed a clear consistent tendency in the two plots. For example, *H. griffithii*, one of the most abundant understorey tree species in the forest, showed a clearly biased distribution toward the areas of shallower humus than the expected distribution (Figure 3a), while *N. kingii* showed a biased distribution toward the deeper humus (Figure 3b). Results using randomization tests on the basis of χ^2 goodness-of-fit test were more conservative, especially in P4 (Table 3). Only five (*C. lanceolatum*, *H. griffithii*, *N. kingii*, *P. leiocarpum* and *S. leiocarpa*) out of 22 species (23%) showed significant and consistent associations with humus depth in both plots, and no species with relative elevation (only *C. lanceolatum* showed a significance at $0.05 < P < 0.1$ in P4). *Syzygium* cf. *klossii* and *Shorea retusa*, which showed a consistent habitat preference in humus depth between the plots using K–S tests, were significant only in one plot. In both K–S and randomization tests, there was no species which showed a significant and consistent association with both environmental variables in the two plots.

Plot-specific species

In plot-specific species, the overall tendency of habitat preference irrespective of species was different between P1 and P4. In K–S tests, 11 out of 14 species (78%) showed a significant habitat preference in humus depth and/or relative elevation in P1, while 12 out of 19 species (63%) did in P4. In randomization tests, 12 out of 14 species (86%) showed a significant habitat preference, whereas only four out of 19 species (21%) did in P4 (Table 4). In P1, eight out of the 14 species were significant in both environmental variables (randomization test). All of the other species, as well as these eight species, were classified into either a combination of ‘S and U’ or that of ‘D and L’, reflecting the gradient of humus depth parallel with relative elevation (Table 4, see

Table 2. Spearman’s rank correlation coefficient between the first three axes of PCA based on species abundance and two environmental variables.

Environmental variables	Rank correlation coefficient with PCA axes											
	I				II				III			
	P1		P4		P1		P4		P1		P4	
Humus depth	0.590	***	–0.581	***	0.206	*	–0.093	ns	0.139	ns	–0.119	ns
Relative elevation	–0.679	***	–0.352	***	–0.203	*	0.397	***	–0.049	ns	–0.275	**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

Table 3. Classification by preferences in humus depth and relative elevation for common species in P1 and P4.

Species	Humus depth						Relative elevation					
	P1			P4			P1			P4		
	D ¹	P(χ^2) ²	Habitat class ³	D ¹	P(χ^2) ²	Habitat class ³	D ¹	P(χ^2) ²	Habitat class ³	D ¹	P(χ^2) ²	Habitat class ³
<i>Baccaurea bracteata</i>	-0.335**	**	D	-0.242		(D)	0.376**	**	L	0.293		(L)
<i>Calophyllum</i> sp.	-0.191***	**	D	-0.071		(D)	0.196***		L	-0.075		(U)
<i>Canarium</i> sp.	-0.379***	*	D	0.118		(S)	0.354**		L	0.117		(L)
<i>Cotylelobium lanceolatum</i>	0.353***	***	S	0.304***	†	S	-0.413***	***	U	0.220*		L
<i>Dipterocarpus borneensis</i>	0.174	*	(S)	0.110		(S)	0.267*	†	L	0.233**		L
<i>Syzygium</i> cf. <i>klossii</i>	-0.221**	**	D	-0.182*		D	0.234**		L	-0.155		(U)
<i>Garcinia</i> sp.	-0.409**	**	D	0.195		(S)	0.406**	*	L	-0.247		(U)
<i>Hopea griffithii</i>	0.318***	***	S	0.454***	**	S	-0.352***	***	U	0.182*		L
<i>Horsfieldia</i> cf. <i>crassifolia</i>	-0.272**	**	D	-0.231		(D)	0.253*	†	L	0.157		(L)
<i>Lithocarpus</i> sp.	0.183		(S)	-0.173	**	(D)	-0.358**		U	-0.306***		U
<i>Neoscortechinia kingii</i>	-0.396*	**	D	-0.319***	***	D	0.373*		L	-0.167	*	(U)
<i>Nephelium</i> cf. <i>maingayi</i>	-0.277		(D)	0.367***		S	0.374**		L	0.354***		L
<i>Palaquium leiocarpum</i>	-0.295*	**	D	-0.179**	*	D	0.407**	**	L	-0.210***	**	U
<i>Palaquium</i> sp.	-0.205	†	(D)	-0.244		(D)	0.363**	*	L	-0.155		(U)
<i>Santiria griffithii</i>	-0.335**	**	D	-0.156		(D)	0.384***	**	L	-0.143		(U)
<i>Shorea retusa</i>	0.248*		S	0.558***	**	S	-0.393***	**	U	0.448***	*	L
<i>Shorea rugosa</i>	-0.215*	**	D	0.237		(S)	0.371***	*	L	0.206		(L)
<i>Shorea teysmanniana</i>	-0.220**	†	D	-0.122		(D)	0.238**		L	0.070		(L)
<i>Sindora leiocarpa</i>	0.173*	**	S	0.401***	*	S	-0.226**	*	U	0.376**	†	L
<i>Stemonurus secundiflorus</i>	-0.309		(D)	-0.224	*	(D)	0.325*		L	-0.220		(U)
<i>Ternstroemia aneura</i>	0.323**	**	S	0.208		(S)	-0.447***	*	U	-0.152		(U)
<i>Tristaniaopsis obovata</i>	0.318***	**	S	0.168		(S)	-0.341***	**	U	0.125	*	(L)

† P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001.

¹ Signed maximum difference between the observed and expected relative frequencies. Significance was tested by Kolmogorov–Smirnov goodness-of-fit test for continuous data (Zar 1999).

² Significance of randomization test using χ^2 goodness-of-fit test.

³ Abbreviations are as follows: S, shallow; D, deep; U, upper slope; L, lower slope. Abbreviations in parentheses indicate that the classification is based on a non-significant D value.

also Figures 1a and 2a). *Tetractomia* cf. *obovata* showed a clear habitat preference in the deep-humus and lower microsites, and this corresponds to the fact that the species is more abundant in a peat-swamp forest (P2) near the two plots. In P4, only three species significantly associated with relative elevation, while no species significantly associated with humus depth.

DISCUSSION

We found that in 45% of 55 abundant species tested, there were significant and consistent associations of species distribution with the variation in humus depth or relative elevation (K–S test). This proportion is higher than that of Hubbell & Foster (1986) and almost the same as that of Webb & Peart (2000) although we cannot simply compare it with these studies because of the difference in spa-

tial scale and the number of species examined. Hubbell & Foster (1986) found that 15 (36%) of the most abundant 41 species significantly associated with topographic categories on Barro Colorado Island (BCI), Panama. Webb & Peart (2000) reported that 21 (42%) of 49 abundant species showed significant associations with physiographic habitats at Gunung Palung National Park, West Kalimantan. The present result suggests that humus depth and relative elevation contribute to determining the spatial distribution pattern and habitat differentiation in heath forests even at a small spatial scale. The degree of influence on the spatial distribution of species, however, appears to be different between humus depth and relative elevation. Principal components analysis demonstrated a consistent strong correlation of floristic composition (based on abundance or presence–absence data) with humus depth in the plots (Table 2). Randomization tests provided more

Table 4. Classification by preferences in humus depth and relative elevation for plot-specific species in P1 and P4.

Species	Humus depth			Relative elevation		
	D ¹	P(χ^2) ²	Habitat class ³	D ¹	P(χ^2) ²	Habitat class ³
P1						
<i>Agathis borneensis</i>	0.276		(S)	-0.279	†	(U)
<i>Calophyllum pulcherrimum</i>	0.244***	*	S	-0.302***	*	U
<i>Syzygium palembanica</i>	0.376***	***	S	-0.523***	***	U
<i>Syzygium</i> sp. 1	0.571***	**	S	-0.588***	*	U
<i>Syzygium</i> sp. 2	0.414***	**	S	-0.619***	***	U
<i>Garcinia rostrata</i>	0.338***	***	S	-0.414***	***	U
<i>Ilex wallichii</i>	0.156		(S)	-0.157		(U)
<i>Lithocarpus dasystachyus</i>	-0.374*	**	D	0.277		(L)
<i>Pimelodendron griffithianum</i>	-0.320*	†	D	0.400**		L
<i>Polyalthia</i> cf. <i>sumatrana</i>	-0.290	*	(D)	0.454***	*	L
sp. 1 (Rubiaceae)	-0.312*	†	D	0.425**		L
<i>Sageraea elliptica</i>	-0.568***	***	D	0.613***	***	L
<i>Tetractomia</i> cf. <i>obovata</i>	-0.736***	**	D	0.808***	*	L
<i>Timonius flavescens</i>	-0.243	*	(D)	0.269		(L)
P4						
<i>Aglaia</i> sp.	-0.554***		D	0.655***		L
<i>Calophyllum austrocoriaceum</i>	-0.183		(D)	-0.192		(U)
<i>Calophyllum</i> cf. <i>dasypodum</i>	-0.163		(D)	0.122		(L)
<i>Castanopsis</i> sp.	-0.191		(D)	-0.238*		U
<i>Cotylelobium melanoxydon</i>	-0.281		(D)	0.214		(L)
<i>Cratoxylum glaucum</i>	0.165		(D)	0.231	*	(L)
<i>Diospyros hermaphroditica</i>	-0.330*		D	-0.545***	**	U
<i>Diplospora</i> sp.	-0.262**		D	-0.233*		U
<i>Garcinia havilandii</i>	-0.178		(D)	-0.249*	†	U
<i>Goniothalamus malayanus</i>	-0.145		(D)	0.179		(L)
<i>Gymnacranthera eugenifolia</i>	-0.229		(D)	0.310*		L
<i>Macaranga</i> cf. <i>tanarua</i>	-0.255	†	(D)	-0.460**	**	U
<i>Myristica maxima</i>	0.128		(D)	0.317		(L)
<i>Payena endertii</i>	0.336*		S	0.246	*	(L)
sp. 1 (Sapotaceae)	-0.231*		D	-0.318**		U
<i>Shorea</i> cf. <i>parvifolia</i>	0.252		(S)	0.268		(L)
<i>Ternstroemia magnifica</i>	-0.326*		D	-0.358*		U
<i>Xanthophyllum eurhyncum</i>	-0.334**		D	-0.573***	***	U
<i>Xerospermum laevigatum</i>	-0.263*		D	-0.110		(U)

† P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001.

¹ Signed maximum difference between the observed and expected relative frequencies. Significance was tested by Kolmogorov–Smirnov goodness-of-fit test for continuous data (Zar 1999).

² Significance of randomization test using χ^2 goodness-of-fit test.

³ Abbreviations of the habitat classes are the same as those in Table 3.

conservative results on habitat preference for each species than those in K–S tests: five species out of the 22 common species showed significant associations only with humus depth. These results indicate that humus depth has a larger effect in determining local spatial distribution of tree species in heath forests than relative elevation. Our findings support the results of Newbery & Proctor (1984) demonstrating that the distribution of tree species within a 1-ha research plot is associated with soil variables in a heath forest. Their analyses were based on records of only one site (1-ha plot) in each different forest type (alluvial forest, dipterocarp forest, heath forest and forest over limestone). By demonstrating our findings based on records of duplicate 1-ha sites, small-scale habitat association with soil properties in heath forests was ascertained.

Although the association of spatial distribution of species with relative elevation was less obvious than that with humus depth, the possibility of the contribution of relative

elevation to spatial distribution pattern for tree species is not dismissed. As demonstrated in Figure 4, *Dipterocarpus borneensis* and *Lithocarpus* sp. showed a consistent habitat preference to relative elevation in both plots, but not to humus depth. In the plot-specific species, more species showed significant association with relative elevation rather than with humus depth in P4 for randomization tests (Table 4). Becker *et al.* (1988) found that xylem water potentials of tree species paralleled the gradient of increasing soil moisture downslope from the plateau with just 18 m of elevational difference. Nelson & Anderson (1983) reported a relationship between species distribution in a grassland community and a soil moisture gradient along a gentle slope with the range of only 2.1 m in elevation. Relative importance of topographic factors for the distribution of tree species at small spatial scale needs further consideration.

For each species tested, no clear threshold of favourable

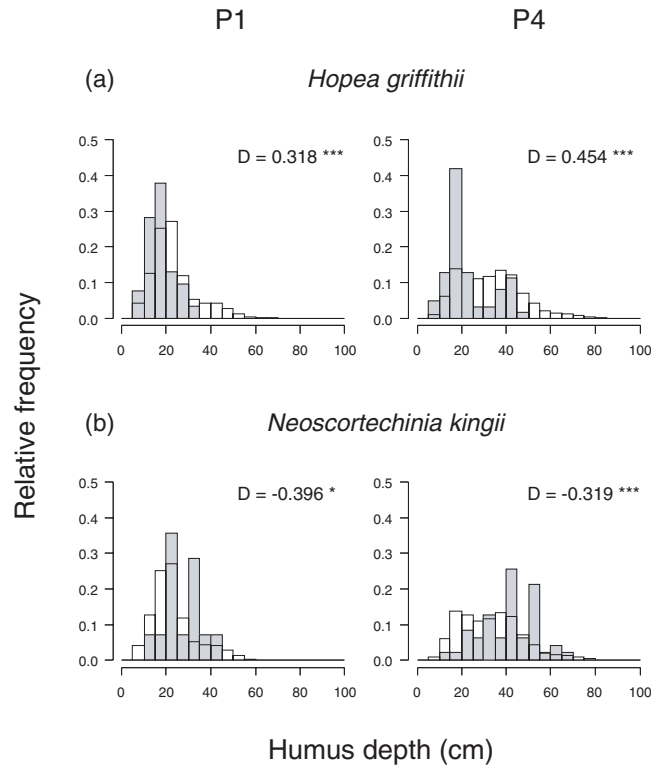


Figure 3. Comparison between observed and expected relative frequencies of humus depth of (a) *Hopea griffithii* and (b) *Neoscortechinia kingii* in P1 and P4. Open bars indicate the expected relative frequency and shaded bars indicate the observed relative frequency. The signed D value was calculated using Kolmogorov–Smirnov goodness-of-fit test for continuous data (Zar 1999). Asterisks show the significance level: *, $P < 0.05$; ***, $P < 0.001$.

habitats was found in humus depth and relative elevation, since most species were distributed even in unfavourable sites (Figures 3 and 4). However, a few species (e.g. *Hopea griffithii* and *Sindora leiocarpa*), which showed a clear preference to the shallow-humus sites, occurred only in the sites < 50 cm in humus depth, suggesting the existence of a favourable ‘range’ of habitats.

Humus depth and relative elevation are not the direct determinants of species distribution in heath forests. They are correlated with other physical and chemical factors to be direct determinants: depth of the ground-water table, and the physical and chemical properties of the soils (Bourgeron 1983). Earlier studies suggest that several edaphic variables are represented by organic carbon, cation exchange capacity and drainage (Lieberman *et al.* 1985, Newbery & Proctor 1984), while microtopographic variation affects water availability, aeration status of soil and again drainage (Baillie *et al.* 1987, Becker *et al.* 1988, Lieberman *et al.* 1985). In particular, Newbery & Proctor (1984) reported that a difference in floristic composition of the abundant species existed between microsites which differ in organic carbon content, total nitrogen and phosphorus and exchangeable calcium and magnesium in heath forest. According to the soil analyses of peat-swamp

forest near P1, large fluctuations with soil depth were found in sodium, magnesium, nitrate and phosphate ion concentrations at 0–100 cm in depth (Haraguchi *et al.* 2000). We consider that humus depth and relative elevation can affect these soil properties, and thereby distribution pattern for each species is determined at a small spatial scale in heath forest.

On the other hand, the possibility that the variation of humus depth is affected by tree distribution, is considered. If a tree species has a large amount of litter input to the forest floor or low decomposition rate (or both), litter accumulation should be larger in the vicinity of the species than in the other sites. Litter-decomposition data on the forest floor in the same plots of this study provides negative results on this possibility (Rahajoe & Kohyama, unpubl. data). *Calophyllum pulcherrimum* (plot-specific species in P1) and *Tristaniopsis* cf. *obovata* (common species) showing a preference to shallower-humus sites in this study (Tables 3 and 4) had a larger amount of litterfall than *Palaquium leiocarpum* (common species) showing a preference to deeper-humus sites. *Tristaniopsis* cf. *obovata* had the highest decomposition rate followed by *P. leiocarpum* and *C. pulcherrimum*. For these three species, there appears to be no relationship between the distribu-

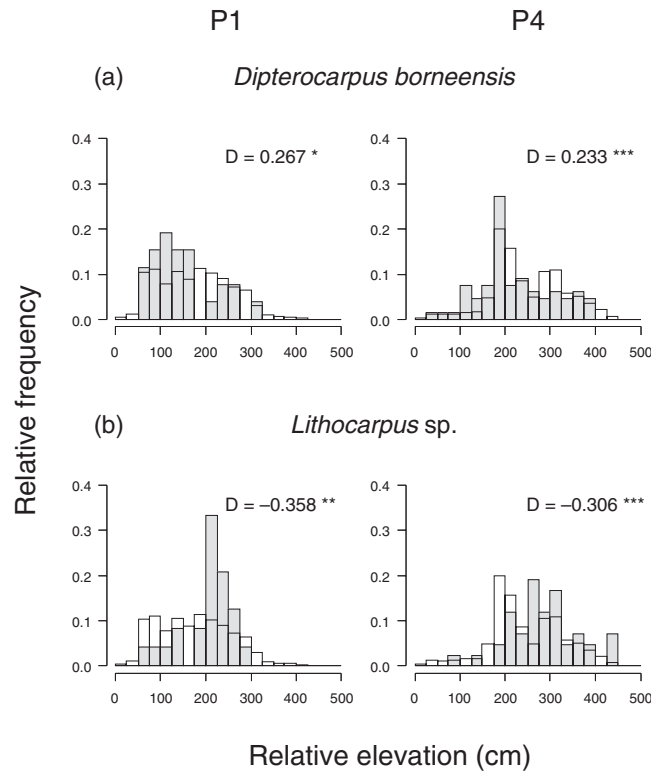


Figure 4. Comparison between observed and expected relative frequencies of relative elevation of (a) *Dipterocarpus borneensis* and (b) *Lithocarpus* sp. in P1 and P4. Open bars indicate the expected relative frequency and shaded bars indicate the observed relative frequency. D values were calculated as in Figure 3. Asterisks show the significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

tion of humus depth and species traits such as the litterfall and decomposition rate. Of course we cannot evaluate the importance of litterfall and decomposition rate to the variation of humus depth from the limited data alone. Further studies examining a number of species are necessary for the evaluation of effects of trees on humus depth.

Based on the present findings, we conclude that a large proportion of tree species in the heath forest is affected by edaphic and topographic factors in terms of their spatial distribution pattern at a small spatial scale. However, more than 50% of the 22 common species did not show any significant and consistent habitat preference in both environmental variables in the two plots (K–S test, Table 1). Furthermore, in plot-specific species in P4, six out of 19 species did not show any significant and consistent habitat preference in both environmental variables for both K–S and randomization tests (Table 4). These results indicate that edaphic and topographic factors alone cannot account for all the small-scale floristic heterogeneity of the heath forest. Several alternatives can be hypothesized such as gap distribution pattern (Denslow 1987, Newbery *et al.* 1986, Svenning 2000) and plant–animal or plant–pathogen interactions (Condit *et al.* 1994, Janzen 1970, Wills *et al.* 1997). Comprehensive evaluation of relative importance of the various environmental factors will be

needed to understand the mechanism of habitat differentiation of tree species in tropical forests.

ACKNOWLEDGEMENTS

We are grateful to the Indonesian Institute of Sciences (LIPI) who sponsored our research, providing helpful suggestions and technical support. Our thanks also go to Mr Suwido H. Limin, Mr Sehat Jaya and Mr Sulmin Gumiri of the University of Palangka Raya for all-round cooperation in our research, Dr Soedarsono Riswan for helpful suggestions, Dr Shiro Tsuyuzaki for valuable advice on statistical analyses, Dr Takashi B. Nishimura and Ms Joeni S. Rahajoe for supporting our field work and helpful suggestions. We wish to thank the staff of Herbarium Bogoriense and students of the University of Palangka Raya for technical support and assistance for field work. Finally, we thank Prof. D. Newbery, Dr Peter Becker and an anonymous reviewer for valuable comments on earlier versions of this paper. This study is a part of the Japan–Indonesia cooperative project, Environmental Management of Wetland Ecosystems in Southeast Asia supported by the Japan Society for the Promotion of Science (JSPS) and Indonesian Institute of Sciences, which is financially supported by the Grant-in-Aid of Sci-

entific Research of the Ministry of Education, Sports and Culture of Japan (No. 10041152).

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Appendix 1. Number of individuals, maximum dbh and basal area of target tree species in P1 in a heath forest of Central Kalimantan, Indonesia.

Species	Family	No.	Max. dbh (cm)	Basal area (m ²)	% of basal area
<i>Cotylelobium lanceolatum</i> Craib	Dipterocarpaceae	107	53.9	4.45	14.8
<i>Shorea teysmanniana</i> Dyer ex Brandis	Dipterocarpaceae	55	63.9	1.89	6.3
<i>Calophyllum</i> sp. (K11869)	Guttiferae	170	30.1	1.87	6.2
<i>Shorea rugosa</i> Heim	Dipterocarpaceae	41	38.7	1.26	4.2
<i>Syzygium</i> cf. <i>klossii</i> Ridl. (K11676)	Myrtaceae	68	32.5	0.88	2.9
<i>Sindora leiocarpa</i> Backer ex K. Heyne	Leguminosae	72	29.3	0.86	2.8
<i>Tristaniopsis</i> cf. <i>obovata</i> (Benn.) Peter G. Wilson & Waterh.	Myrtaceae	52	35.0	0.86	2.9
<i>Hopea griffithii</i> Kurz	Dipterocarpaceae	145	17.3	0.80	2.7
<i>Garcinia rostrata</i> (Hassk.) Miq.	Guttiferae	84	37.4	0.74	2.4
<i>Calophyllum pulcherrimum</i> Wall. ex Choisy	Guttiferae	86	31.9	0.71	2.4
<i>Palaquium leiocarpum</i> Boerl.	Sapotaceae	22	27.6	0.42	1.4
<i>Agathis borneensis</i> Warb.	Araucariaceae	17	30.1	0.40	1.3
<i>Ternstroemia aneura</i> Miq.	Theaceae	34	20.9	0.37	1.2
<i>Palaquium</i> sp. (K11482)	Sapotaceae	21	35.5	0.37	1.2
<i>Syzygium</i> sp. 2 (K11377)	Myrtaceae	53	18.7	0.34	1.1
<i>Dipterocarpus borneensis</i> Sloot.	Dipterocarpaceae	26	29.4	0.34	1.1
<i>Shorea retusa</i> Meijer sp. 1 (K11459)	Dipterocarpaceae	32	34.1	0.33	1.1
<i>Stemonurus secundiflorus</i> Bl.	Rubiaceae	20	26.8	0.28	0.9
<i>Horsfieldia</i> cf. <i>crassifolia</i> (Hk.f. & Thoms.) Warb. (K11485)	Icacinaceae	17	20.1	0.27	0.9
<i>Syzygium palembanica</i> (Miq.) Merr.	Myristicaceae	38	20.3	0.26	0.9
<i>Canarium</i> sp. (K11290)	Burseraceae	30	25.8	0.26	0.9
<i>Garcinia</i> sp. (K11402)	Burseraceae	22	26.2	0.26	0.9
<i>Lithocarpus dasystachys</i> (Miq.) Rehd.	Guttiferae	20	18.3	0.20	0.7
<i>Santiria griffithii</i> (Hk.f.) Engl.	Fagaceae	16	23.8	0.20	0.7
<i>Sageraea elliptica</i> (A.DC.) Hk.f. & Thoms.	Burseraceae	27	17.1	0.19	0.6
<i>Baccaurea bracteata</i> M.A.	Annonaceae	30	18.4	0.17	0.6
<i>Pimelodendron griffithianum</i> (M.A.) Benth.	Euphorbiaceae	23	15.9	0.15	0.5
<i>Polyalthia</i> cf. <i>sumatrana</i> (Miq.) Kurz (K11823)	Euphorbiaceae	21	19.1	0.14	0.5
<i>Ilex wallichii</i> Hk.f.	Annonaceae	18	16.1	0.14	0.5
<i>Lithocarpus</i> sp. (K11472)	Aquifoliaceae	16	17.2	0.14	0.5
<i>Nephelium</i> cf. <i>maingayi</i> Hiern (K11918)	Fagaceae	24	17.8	0.12	0.4
<i>Timonius flavescens</i> (Jack) Baker	Sapindaceae	22	15.6	0.11	0.4
<i>Syzygium</i> sp. 1 (K11351)	Rubiaceae	18	13.0	0.09	0.3
<i>Neoscortechinia kingii</i> (Hk.f.) P. & H.	Myrtaceae	15	11.0	0.07	0.2
<i>Tetractomia</i> cf. <i>obovata</i> Merr. (K11574)	Euphorbiaceae	14	18.4	0.07	0.2
Others (108 spp.)	Rutaceae	12	12.2	0.06	0.2
Total		492		10.03	33.4
Total		1982		30.10	100.0

Data for trees ≥ 5 cm in dbh measured in July 1997 are shown. Species are listed in decreasing order of basal area. For unidentified species, voucher numbers are shown in parentheses. The sum of per cent of BA for all species exceeds 100.0 due to rounding.

Appendix 2. Number of individuals, maximum dbh and basal area of target tree species in P4 in a heath forest of Central Kalimantan, Indonesia.

Species	Family	No.	Max. dbh (cm)	Basal area (m ²)	% of basal area
<i>Calophyllum</i> sp. (K11869)	Guttiferae	198	27.2	2.43	8.8
<i>Dipterocarpus borneensis</i> Sloot.	Dipterocarpaceae	66	43.8	2.06	7.5
<i>Cotylelobium lanceolatum</i> Craib	Dipterocarpaceae	40	43.7	2.02	7.3
<i>Palaquium leiocarpum</i> Boerl.	Sapotaceae	96	44.5	1.62	5.9
<i>Syzygium</i> cf. <i>klossii</i> Ridl. (K11676)	Myrtaceae	72	40.0	1.19	4.3
<i>Shorea teysmanniana</i> Dyer ex Brandis	Dipterocarpaceae	105	47.1	1.05	3.8
<i>Diplospora</i> sp. (K5011)	Rubiaceae	44	38.7	0.99	3.6
<i>Shorea rugosa</i> Heim	Dipterocarpaceae	29	43.2	0.96	3.5
<i>Garcinia havilandii</i> Stapf	Guttiferae	36	29.1	0.90	3.3
<i>Tristaniaopsis</i> cf. <i>obovata</i> (Benn.) Peter G. Wilson & Waterh.	Myrtaceae	45	31.7	0.78	2.8
<i>Goniothalamus malayanus</i> Hk.f. & Thoms. sp. 1 (K11425)	Annonaceae	40	28.8	0.61	2.2
<i>Calophyllum lanigerum</i> var. <i>austroriciaceum</i> Whitm.	Sapotaceae	33	36.6	0.58	2.1
<i>Cotylelobium melanoxylon</i> (Hk.f.) Pierre	Guttiferae	26	41.9	0.48	1.7
<i>Cotylelobium melanoxylon</i> (Hk.f.) Pierre	Dipterocarpaceae	17	39.4	0.47	1.7
<i>Ternstroemia aneura</i> Miq.	Theaceae	36	28.5	0.45	1.6
<i>Xanthophyllum eurhynchum</i> Miq.	Polygalaceae	29	29.5	0.43	1.6
<i>Myristica maxima</i> Warb.	Myristicaceae	15	32.8	0.42	1.5
<i>Neoscortechinia kingii</i> (Hk.f.) P. & H.	Euphorbiaceae	47	20.4	0.37	1.4
<i>Sindora leiocarpa</i> Backer ex K.Heyne	Leguminosae	26	34.3	0.37	1.3
<i>Hopea griffithii</i> Kurz	Dipterocarpaceae	62	16.7	0.37	1.3
<i>Diospyros hermaphroditica</i> (Zoll.) Bakh.	Ebenaceae	22	36.9	0.35	1.3
<i>Nephelium</i> cf. <i>maingayi</i> Hiern (K11918)	Sapindaceae	32	29.3	0.35	1.3
<i>Calophyllum</i> cf. <i>dasypodum</i> Miq. (K11870)	Guttiferae	34	32.5	0.33	1.2
<i>Canarium</i> sp. (K11290)	Burseraceae	48	21.2	0.32	1.1
<i>Payena endertii</i> H. J. Lam	Sapotaceae	21	31.4	0.29	1.0
<i>Shorea retusa</i> Meijer	Dipterocarpaceae	24	27.6	0.28	1.0
<i>Stemonurus secundiflorus</i> Bl.	Icacinaceae	29	20.5	0.27	1.0
<i>Aglaiia</i> sp. (K11441)	Meliaceae	18	26.8	0.26	0.9
<i>Lithocarpus</i> sp. (K11472)	Fagaceae	42	13.9	0.23	0.8
<i>Santiria griffithii</i> (Hk.f.) Engl.	Burseraceae	20	20.0	0.23	0.8
<i>Castanopsis</i> sp. (K4899)	Fagaceae	34	14.7	0.17	0.6
<i>Gymnacranthera farquhariana</i> (Hk.f. & Thoms.) Warb. var. <i>eugeniifolia</i> (A.DC.) R.Schouten	Myristicaceae	21	21.1	0.16	0.6
<i>Horsfieldia</i> cf. <i>crassifolia</i> (Hk.f. & Thoms.) Warb. (K11485)	Myristicaceae	30	17.0	0.16	0.6
<i>Garcinia</i> sp. (K11402)	Guttiferae	17	16.5	0.15	0.6
<i>Cratoxylum glaucum</i> Korth.	Guttiferae	16	24.5	0.15	0.5
<i>Ternstroemia magnifica</i> Stapf	Theaceae	17	21.2	0.15	0.5
<i>Xerospermum laevigatum</i> Radlk.	Sapindaceae	29	11.5	0.12	0.4
<i>Shorea</i> cf. <i>parvifolia</i> Dyer (K11848)	Dipterocarpaceae	21	11.4	0.09	0.3
<i>Baccaurea bracteata</i> M.A.	Euphorbiaceae	18	12.9	0.08	0.3
<i>Palaquium</i> sp. (K11482)	Sapotaceae	19	19.3	0.08	0.3
<i>Macaranga</i> cf. <i>tanarius</i> (L.) M. A. (K11856)	Euphorbiaceae	15	9.9	0.05	0.2
Others (81 spp.)		427		4.78	17.3
Total		2016		27.59	100.0

Data for trees ≥ 5 cm in dbh measured in January 1998 are shown. Species are listed in decreasing order of basal area. For unidentified species, voucher numbers are shown in parentheses. The sum of per cent of BA for all species is less than 100.0 due to rounding.