

Habitat differentiation of Lauraceae species in a tropical lower montane forest in northern Thailand

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Dependency on topographical habitat was examined for Lauraceae tree species in a lower montane forest using a large-scale research plot established at Doi Inthanon National Park, northern Thailand. Twenty species of 10 genera of Lauraceae were recorded in a 7.5-ha part of the plot; Lauraceae accounted for 18% of the total basal area. Lauraceae was the most species-rich and most abundant family in the plot. In a cluster analysis based on the matrix of spatial associations between species, two clusters were recognized. Members of one cluster seemed to associate with lower-elevation habitats, and members of the other associated with habitats on ridges. By subdividing the study plot into 20 m × 20 m squares, a discriminant analysis could be applied to the presence–absence data for the 17 species that had sufficient population density. The predictor variables used were the relative elevation, slope inclination, slope direction (transformed to deviation from SSW) and slope convexity for each of the squares. The discriminant models were tested statistically by applying the random shift technique. The models were significant for 11 of the species (65% of the species examined) and were associated with the topographical condition of the habitat. Stepwise selection of the predictor variables for these 11 species revealed that relative elevation and slope convexity were the most important factors for predicting the presence or absence of the Lauraceae species. Both these variables were considered to indicate the hydrological condition of the habitat.

Key words: discriminant analysis; Doi Inthanon; large-scale plot; randomization test; topographical habitat.

INTRODUCTION

Fagaceae and Lauraceae are more abundant and more likely to reach the top layer of forest canopies in the tropical montane zone of South-East Asia than in the lowland forests of the same region. The term ‘oak-laurel forest’ has been used for this vegetation type (Kochummern 1989; Tagawa 1995).

Oak-laurel forests are the dominant vegetation type in the mountains of tropical Asia, from the Himalayas to New Guinea, and are closely related to the temperate evergreen oak forests of East Asia (Ohsawa 1991; Tagawa 1995). In South-East Asia, studies of montane forest zonation have been conducted on mountains in the Philippines (Aragones 1996; Buot & Okitsu 1998; Pipoly & Madulid 1998), Indonesia (Yamada 1977; Ohsawa *et al.* 1985; Abdulhadi *et al.* 1998), Malaysia (Proctor *et al.* 1988; Kitayama 1992; Nakashizuka *et al.* 1992), Brunei (Pendry & Proctor 1997) and Thailand (Ogawa *et al.* 1961; Robbins & Smitinand 1966; Santisuk 1988; Maxwell 1995; Maxwell *et al.* 1997). Geographic pattern of montane forests were also conducted for this region

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(Ohsawa 1991, 1995; Tagawa 1995). Studies using large-scale research plots have been carried out in lowland forests since the 1980s (Condit 1995; Ashton 1998). By contrast, there have been few similar intensive studies of the biodiversity, structure, and dynamics of montane forests. We established a large-scale, 15-ha research plot in a well-developed montane forest in northern Thailand, to fill this gap in montane forest studies.

Many factors play important roles in determining the distribution of tree species in a plant community. Grubb (1977) categorized these factors into four component niches: habitat, life-form, phenological and regeneration niches. Large-scale research plots are suitable for studying the association between habitat and plant distribution because such plots usually include various topographical units and the trees can be enumerated throughout the plot, as shown by Hubbell and Foster (1986), Itoh (1995), Yamada *et al.* (1997) and Svenning (1999). In these studies, topographical preference was observed in at least some of the component species. Topographic segregation may contribute to the maintenance of species richness in the communities. In this study, we focused on topographical habitat differentiation among Lauraceae, as one of a series of intensive studies on this family. Lauraceae is the most abundant and species-rich family and includes members ranging from upper-canopy species to under-canopy species in this plot (Hara *et al.* 2002). Therefore, a subsample using Lauraceae trees may represent variation in the whole plant community along topographic gradients.

Many studies on the habitat dependency of trees use subjectively defined habitat types, such as valley-bottom and hilltop habitat (e.g. Hubbell & Foster 1986; Yamada *et al.* 1997; Svenning 1999). The definition of habitat type is always somewhat arbitrary, making comparisons between studies by different authors difficult. For this reason, we used the formula proposed by Yamakura *et al.* (1995) to numerically characterize topography. The use of this method allows unequivocal between-site comparisons. Another advantage is that the method can distinguish the relative importance of elements that characterize microhabitat topography, such as slope inclination and direction. The method also allows a wider choice of statistical methods for studies of habitat dependency.

Recently, a critical problem associated with the statistical test of habitat dependency has been identified. Most statistical tests require that the sampling units be independent. However, many studies have illustrated that most tree species display a patchy distribution pattern (e.g. Hubbell 1979; Condit *et al.* 2000), and the abundances of different tree species in continuously arranged sampling units are spatially autocorrelated (Rossi *et al.* 1992; Roxburgh & Chesson 1998; Webb & Peart 2000). This means that the assumption of randomness is violated, and thus traditional statistical tests cannot be applied (Roxburgh & Chesson 1998; Webb & Peart 2000). To avoid this problem, we applied the 'torus randomization' or 'random shift' technique to test the significance of habitat dependency in this study.

STUDY SITE

A 15-ha research plot was established in a well-developed, well-protected, lower montane rain forest, located at approximately 1700 m altitude in Doi Inthanon National Park (18°31'13" N, 98°29'44" E). Doi Inthanon is the highest mountain in Thailand (2565 m altitude), and lies in the southernmost extension of the Himalayan foothills.

Several authors have classified the vegetation of Thailand (e.g. Ogawa *et al.* 1961; Smitinand & Nalamphun 1967). Santisuk (1988) summarized those studies and divided the forest vegetation of northern Thailand into two forest zones: a lowland zone (150–1000 m altitude) and a montane zone (over 1000 m altitude). The montane-zone forest is subdivided into lower and upper montane forests. The transition between the lower and upper montane forests lies at approximately 1800 m on Doi Inthanon, and coincides roughly with the lower limit of the cloud zone.

Doi Inthanon is formed by a huge granite mass and three major rock types, gneiss, granite and limestone, are found in the park (Pendleton 1962). Gneiss covers approximately half of the area of the park. The summit area of Doi Inthanon, including the 15-ha research plot, consists of Pre-Cambrian gneissic rock (Faculty of Forestry 1992; TDRI 1997). The substratum rocks on Doi

Inthanon have produced a coarse, sandy loam soil (Pendleton 1962). The soil of the montane forest has a thick, coarse-textured B horizon, exceeding 60 cm in depth (Faculty of Forestry 1992).

The climate of northern Thailand is strongly influenced by the monsoon, and three distinct seasons are recognizable. The rainy season is from June to October. A cool, dry period follows from November to February, and a hot, dry season is from March to May. Data from the Royal Thai Air Force radar base, located at the summit (2565 m), are available from 1982 to 1999. The annual mean daily minimum and maximum temperatures are 7.2°C and 18.6°C, respectively. The annual rainfall is 2279 mm per year. Data collected from 1993 to 1999 at the Royal Project Doi Inthanon Station (at 1300 m) show that the annual mean minimum and maximum temperatures are 16.1°C and 25.7°C, respectively. The mean annual rainfall at 1300 m is 1908 mm, with the highest monthly rainfall in September (371.3 mm) and the lowest in January (3.4 mm). Using temperature data obtained at the two stations from 1993 to 1999, the annual mean minimum and maximum temperatures at a plot were estimated to be 13.2°C and 23.6°C, respectively. Kira's warmth index at the plot was estimated to be 161.3°C months; this meets the criterion for the warm-temperate zone, which ranges from 85°C to 180°C months (Kira 1991).

METHODS

Plot demarcation and tree census

A permanent 15-ha plot was established in the lower montane forest located approximately 7 km south of the summit of Doi Inthanon at an altitude of ~1700 m, from December 1996 to March 1997. The research plot (500 m × 300 m in horizontal distance) was divided into 375 20 m × 20 m squares (horizontal distance) and a post was placed at every corner of each square. The relative elevation at each post was determined by land survey.

The inclination and compass direction of the slope was calculated for each 20 m × 20 m square following the plane regression method of Yamakura *et al.* (1995) with the elevation data for the four corners of each square. The relative eleva-

tion of each square was obtained by averaging the elevations of its four corners. The surface relief of the slope was expressed using the index of slope convexity proposed by Yamakura *et al.* (1995). The index was obtained by subtracting the mean elevation of 12 posts, set at 20-m intervals along the sides of the 60 m × 60 m square surrounding each focal 20 m × 20 m square, from the elevation of the focal square. Therefore, a positive value of the index means that the slope relief is convex. Slope convexity could not be calculated for the marginal squares, because these squares lacked outer squares.

This study was conducted using one half of the 15-ha plot. All woody plants (excluding climbers, bamboos and palms) of at least 1 cm d.b.h. (stem diameter 140 cm above the ground) in the 7.5-ha area (250 m × 300 m) were counted and their d.b.h. measurements were taken. Every tree was mapped and tagged using an aluminum plate with a running number. If a tree had multiple trunks, each trunk was measured and tagged. Leaf specimens were collected from the enumerated trees and sorted by species. Fieldwork was conducted between March 1997 and March 1999. Botanical specimens of flowers and fruits from species recorded in the study plot were collected from the study plot and surrounding area. These botanical specimens were identified by referring to herbarium specimens at the Forest Herbarium of the Royal Forest Department, the Queen Sirikit Botanical Garden and the Herbarium of the Department of Biology, Faculty of Science, Chiang Mai University. The Lauraceae family has not been revised taxonomically for Thailand, so we referred to the floras of surrounding countries to confirm the identifications (Hara *et al.* 2002). The Flora Republicae Popularis Sinicae Tomus 31 (Li 1984), Flora Yunnanica, Tomus 3 (Gan 1983), Flora of British India, vol. 5. (Hooker 1886), and Flora of West Pakistan, vol. 118 (Kostermans 1974a) were consulted. The studies of Kostermans (1970) and Kostermans (1974b) were also consulted. Leaf specimens collected from all enumerated trees were identified by referring to our botanical specimens. Identification was completed in June 2001. All of the voucher specimens are stored in the Herbarium of the Natural History Museum and Institute, Chiba (CBM), Japan.

Spatial analyses of tree distribution patterns

We used the 7.5-ha census data to analyze the spatial distribution pattern, spatial association between species and habitat differentiation of Lauraceae. Species with less than 10 individual trees in the entire 7.5-ha area were excluded from the analysis.

To evaluate the spatial distribution pattern of each population, Morisita's I_{δ} index (Morisita 1959) was calculated by dividing the plot into quadrats of various sizes. The smallest quadrat was obtained by dividing the plot into 128×128 rectangular quadrats of 4.58 m^2 area. The largest quadrat was 3.75 ha, obtained by dividing the plot into halves. The clump size of each species was determined using the method proposed by Morisita (1959). In this method, the ratio of I_{δ} for quadrat size s ($I_{\delta(s)}$) to I_{δ} for a doubled quadrat size $2s$ ($I_{\delta(2s)}$), was plotted against the quadrat size using an octave scale. The quadrat size that showed a peak for the $I_{\delta(s)}/I_{\delta(2s)}$ ratio was defined as the mean clump size. When the $I_{\delta(s)}/I_{\delta(2s)}$ curve peaked at more than two quadrat sizes, we recognized all of these sizes as the clump size.

Spatial overlap between species was measured using Iwao's ω index (Iwao 1977). The ω index was obtained for every pairwise combination of Lauraceae species by changing the quadrat size in the same way as in the calculation of I_{δ} .

Species were classified according to the degree of interspecific spatial overlap using a cluster analysis. First, a dissimilarity matrix was obtained by transforming the ω index into dissimilarity coefficients (D , ranging from 0 to 1) using the equation (Masaki *et al.* 1992),

$$D = (-\omega + 1)/2.$$

Then the matrix was subjected to average linkage clustering using SPSS Base 10.0 J (SPSS Inc. 1999).

Discriminant analysis

Discriminant analysis was applied to the presence-absence data of each species using a $20 \text{ m} \times 20 \text{ m}$ square size to test the habitat dependency of species in the 7.5-ha plot. The predictor variables of the analysis were the topographical variables

obtained for every $20 \text{ m} \times 20 \text{ m}$ square. All four topographic variables, relative elevation and slope inclination, direction and convexity, were used as predictor variables in the first step. Before the analysis, however, slope direction was converted to the deviation from south-southwest to reflect the exposure to sunlight of each square. Because the convexity of the slope could not be obtained for the marginal squares in the plot, those squares were excluded from the analysis. We used 143 squares within an inner 5.72-ha area of the plot for the analysis. The best linear model to discriminate between presence and absence was obtained for each species using SPSS Base 10.0 J (SPSS Inc. 1999).

In the second step, the predictor variables were selected using a stepwise method. The method for controlling the entry or removal of predictor variables from the model was based on Wilks' lambda, and the critical value of probability was set to <0.05 for the entry of a new variable and >0.10 for the removal of a variable (SPSS Inc. 1999).

Randomization test

First, the significance of the obtained discriminant model was tested using an ordinary χ^2 test of Wilks' lambda. Second, we applied the randomization test. In our random shift technique, the distribution map of each tree species was randomly shifted along both the x - and y -axes by 20-m increments. When the map was shifted beyond the edge of the plot, it was automatically wrapped around to the opposite side of the plot. In all, 100 iterations were performed. For each of the randomized tree maps, a discriminant model was obtained and the fitness of the model was evaluated using Wilks' lambda, which represents the proportion of the information not explained by the model obtained. The probability distribution of Wilks' lambda was obtained from 100 randomized tree maps. When Wilks' lambda obtained from the actual tree map was smaller than the fifth smallest Wilks' lambda obtained from the randomized iterations, the actual tree distribution pattern was judged to be significantly ($P < 0.05$) dependent on the topography. The test was applied to the discriminant analysis using all four predictor variables.

RESULTS

Abundance and size structure of Lauraceae

In total, 141 species of 85 genera and 49 families were recorded in the study plot. Of these, 20 species in 10 genera were members of the family Lauraceae, which was the most species-rich family in the plot. Lauraceae was also the most abundant family and accounted for 18.0% of the total basal area and 18.8% of the trees in the plot (Table 1).

Of the 10 genera, *Litsea*, which included seven species, was the richest in number of species (Table 1). At the species level, *Cryptocarya densiflora* was the most abundant in terms of basal area (2.16 m² ha⁻¹, including multiple trunks) and *Litsea beusekomii* had the highest density (182

trees ha⁻¹) among the 20 species of Lauraceae. In contrast, three species were represented by less than seven trees in the plot. These three species were excluded from further analysis because of insufficient data.

Four species of Lauraceae had a maximum d.b.h. exceeding 70 cm, indicating that these species reach the upper canopy layer after maturation. The maximum d.b.h. of the other species ranged from 35 to 59 cm, excluding *Litsea cubeba*, which consisted of trees smaller than 16 cm d.b.h. (Table 1).

Spatial distribution pattern

All Lauraceae species were distributed unevenly throughout the plot (Fig. 1) and, except for *Litsea*

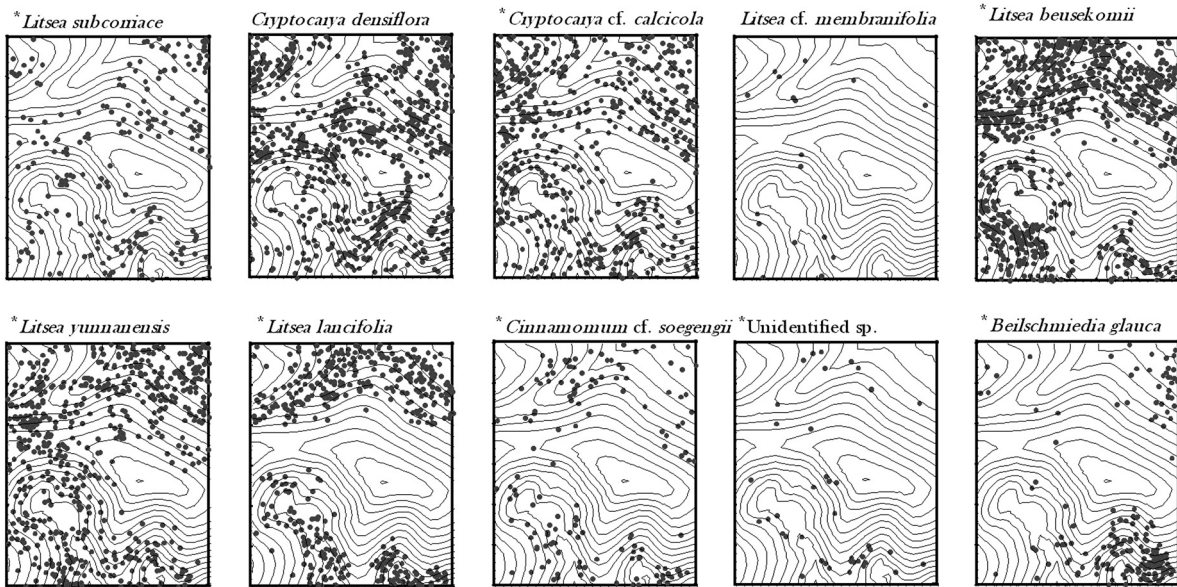
Table 1 Status of 20 Lauraceae species in a 7.5-ha area within a 15-ha plot established at Doi Inthanon National Park

Species [Reference for identification [†]]	No. individuals (plot ⁻¹)	Tree density (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Maximum d.b.h. (cm)	Mean d.b.h. (cm)
<i>Actinodaphne</i> sp.	77	10.3	0.07	35.0	5.8
<i>Beilschmiedia glauca</i> S. Lee et L. Lau var. <i>glaucoides</i> H. W. Li [1,2]	198	26.4	0.07	51.6	3.5
<i>Cinnamomum bejolghota</i> (Ham.) Sweet var. <i>bejolghota</i> [1,2]	171	22.8	0.22	51.7	6.1
<i>Cinnamomum</i> cf. <i>soegengii</i> Kostermans [3]	145	19.3	0.59	95.8	11.1
<i>Cinnamomum</i> sp.	3	0.4	<0.01	–	–
<i>Cryptocarya</i> cf. <i>callicola</i> H. W. Li [1,2]	595	79.3	0.73	59.2	5.8
<i>Cryptocarya densiflora</i> Bl. [1,2]	839	111.9	2.16	55.5	8.7
<i>Lindera metcalfiana</i> Allen [1,2]	960	128.0	0.74	56.5	4.3
<i>Litsea beusekomii</i> Kostermans [4]	991	132.1	0.16	35.2	3.0
<i>Litsea cubeba</i> Pers.	15	2.0	0.01	16.0	5.9
<i>Litsea lancifolia</i> Hook. f. [1,2]	508	67.7	0.26	44.9	5.1
<i>Litsea</i> cf. <i>membranifolia</i> Hook. f. [5]	17	2.3	0.02	40.4	5.7
<i>Litsea pedunculata</i> (Diels) Yang et P. H. Huang [1,2]	177	23.6	0.56	76.9	9.2
<i>Litsea subcorriacea</i> Yang et P. H. Huang [1,2]	234	31.2	0.55	55.7	8.3
<i>Litsea yunnanensis</i> Yang et P. H. Huang [1,2]	660	88.0	0.69	44.4	6.0
<i>Neolitsea zeylanica</i> (Nees) Merr. [5]	101	13.5	0.10	52.2	5.7
<i>Neolitsea</i> sp.	3	0.4	<0.01	–	–
<i>Persea duthiei</i> (King ex Hook. f) Kostermans [6]	6	0.8	0.08	–	–
<i>Phoebe macrocarpa</i> C. Y. Wu [1,2]	149	19.9	0.38	71.7	9.4
Unidentified sp.	43	5.7	0.22	90.1	12.4
Total of Lauraceae	5 892	785.6	7.63		
Total of all species	31 303	4173.7	42.44		

[†][1]: Li (1984). [2]: Gan (1983). [3]: Kostermans (1970). [4]: Kostermans (1974b). [5]: Hooker (1886). [6]: Kostermans (1974a).

Multiple trunks of trees are excluded from the tree density and calculation of the mean d.b.h., but are included in the calculation of basal area. Stems with d.b.h. ≥ 1 cm diameter were enumerated. All the voucher specimens are kept in the Herbarium of the Natural History Museum and Institute, Chiba (CBM), Japan.

Group A



Group B

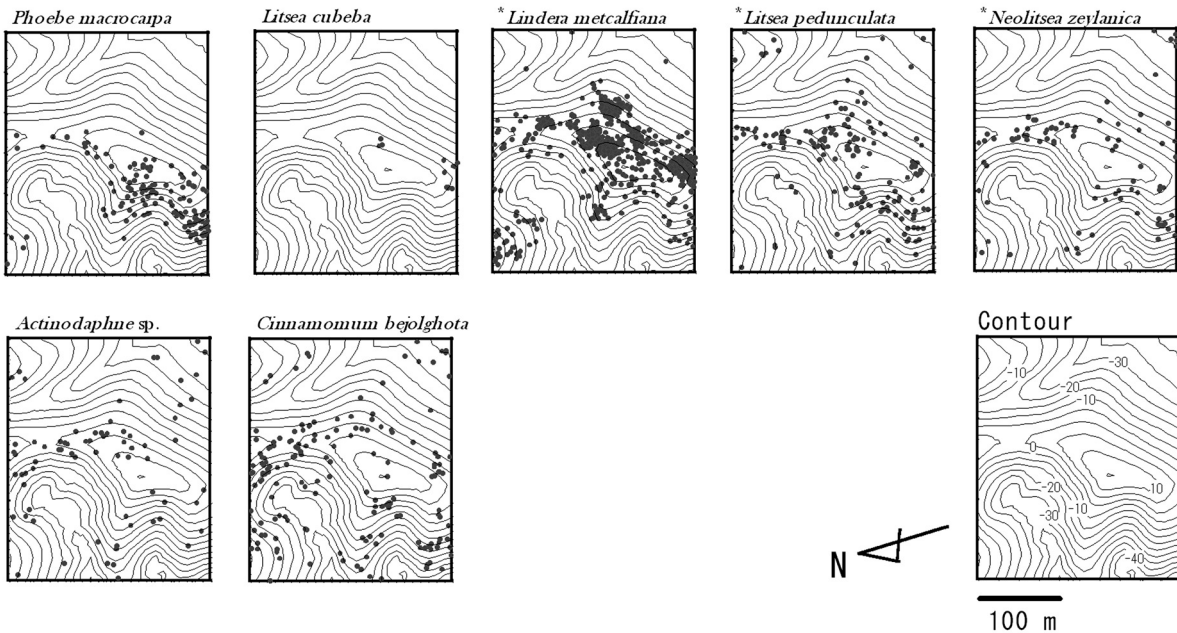


Fig. 1. Spatial distributions of Lauraceae trees with d.b.h. ≥ 1 cm in a 7.5-ha study area established in a tropical lower montane forest at Doi Inthanon National Park, northern Thailand. The species are arranged according to their position in the dendrogram shown in Fig. 3. Groups A and B correspond to the two species clusters in the dendrogram. An asterisk indicates that this species distribution was significantly associated with topography in the randomization test of the discriminant model shown in Table 2.

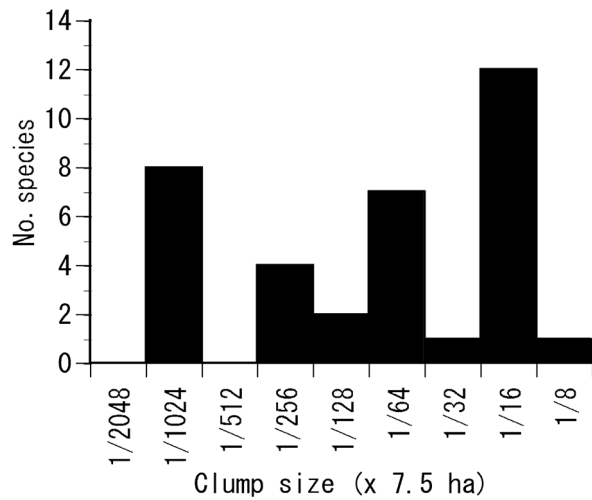


Fig. 2. Clump size distribution of 17 species of Lauraceae determined using Morisita's method. Twelve out of the 17 species examined had a clump size of $1/16 \times 7.5$ ha, which corresponds to a quadrat size of $62.5 \text{ m} \times 75 \text{ m}$. Clumps of trees at this spatial scale appear to be associated with topographical habitat as shown in Fig. 1.

membranifolia, had I_8 values significantly greater than 1.0 for spatial scales of $292\text{--}9375 \text{ m}^2$, revealing the clumping of trees at these spatial scales. Clump sizes, determined by Morisita's method, for each species were pooled and a frequency distribution was determined (Fig. 2). Twelve species out of the 17 species examined clumped at a spatial scale of $1/16 \times 7.5$ ha (4687.5 m^2), which corresponds to a quadrat size of $62.5 \text{ m} \times 75 \text{ m}$. As shown in Fig. 1, most species' distributions appeared to be associated with topography. For example, *Lindera metcalifiana* aggregated on ridges and *Litsea lancifolia* in valley bottoms. The clumping of trees at this spatial scale seems to reflect topographic dependency of the tree species' distributions.

Spatial association between species

Spatial overlap between species was evaluated using the ω index and the $62.5 \text{ m} \times 75 \text{ m}$ quadrat size because most species clumped at this spatial scale. The ω index obtained for 136 pairs of species ranged from -1 to 0.761 . The strongest positive interspecific association occurred between *Lindera metcalifiana* and *Litsea pedunculata* ($\omega = 0.761$) and

between *Litsea yunnanensis* and *Litsea beusekomii* ($\omega = 0.760$). These strong associations between species indicate that they prefer the same habitat. In contrast, *Litsea cubeba* exhibited the strongest negative association with *Litsea membranifolia* and with an unidentified sp. ($\omega = -1$), suggesting that these species preferred different habitats.

The pattern of spatial association between species was summarized using a cluster analysis based on the distance index, D . Two clusters were recognized when the dendrogram was truncated at a dissimilarity level of 0.51 (Fig. 3). Group A in the diagram consisted of 10 species; nine species in this group were distributed at lower elevations and most of them avoided habitat on ridges. In contrast, the seven species in Group B were distributed along ridges in the plot. Thus, the clusters obtained by spatial association appear to reflect habitat guilds among Lauraceae species.

Discriminant analysis of habitat dependence

The habitat dependence of 17 species was tested using a discriminant analysis. Four topographical variables were used to discriminate between the presence and absence of a given species in $20 \text{ m} \times 20 \text{ m}$ squares. An ordinary statistical test revealed that the distribution of 15 species depended significantly on the topography ($P < 0.05$), although the percentage of correct classification for 10 species was lower than 75%, indicating that the presence-absence of these species was poorly predicted using the model (Table 2).

The randomization test was more conservative. Models for a further four species were rejected and only 11 models remained significant (Table 2). The cluster analysis classified 17 species into two clusters, as mentioned above. Judging from the randomization test, the distribution of eight species in Group A and of three species in Group B depended significantly on topography.

The last five columns in Table 2 show the results of variable selection using a stepwise algorithm. Eleven species whose distributions depended significantly on the topography in the randomization test were subjected to this analysis. One to three predictor variables were selected and the relative

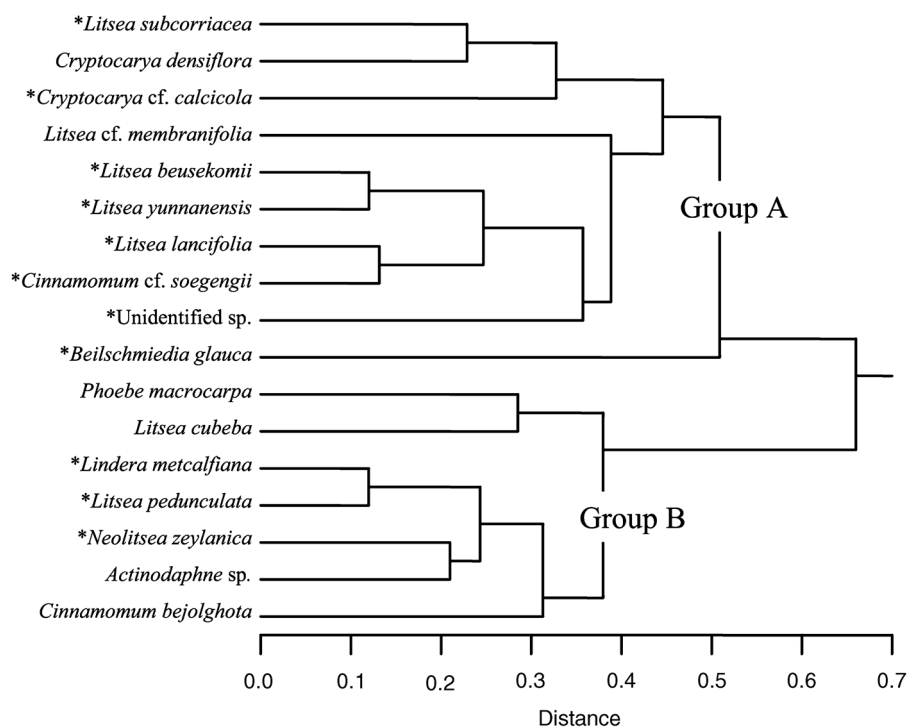


Fig. 3. Dendrogram of 17 Lauraceae species based on the spatial association between species. The analysis was performed using the average linkage method and the distance was based on Iwao's ω index. In this study, we define two clusters, named Groups A and B, corresponding to the species in Fig. 1. An asterisk indicates that a species distribution had a significant association with topography in the randomization test of the discriminant model shown in Table 2.

elevation and convexity were selected for nine and seven species, respectively, while slope inclination and direction were selected in only two and one species, respectively. Thus, the importance of the former two variables in explaining the spatial distribution of Lauraceae species was emphasized.

In the stepwise discriminant analysis, the percentage of correct classification varied from 58.7% to 86.7%. The highest values were obtained for *L. lancifolia* (86.0%) and *L. metcalfiana* (86.7%). Even for these two species, many squares could not be classified correctly using the discriminant model. Locations of the misclassified squares for these two species are shown in Fig. 4. All of the misclassified squares were located along the borders of patches of species examined, or where there were isolated trees. The core area of each species patch was correctly classified using the discriminant models.

DISCUSSION

Abundance and diversity of Lauraceae

Lauraceae was the most abundant and most species-rich family in the study plot. The relative abundance of Lauraceae was 18.0% in basal area and the dominance of the family was shared by 20 species in 10 genera. In the mountains of South-East Asia, Lauraceae species appear over a wide altitudinal range, from lowland forests dominated by dipterocarps to montane habitats dominated by non-dipterocarps (Yamada 1977; Ohsawa *et al.* 1985; Proctor *et al.* 1988; Kitayama 1992; Aragones 1996; Pipoly & Madulid 1998). However, the relative basal area of Lauraceae rarely exceeded 10% of the total area in these studies. At Mt Pangrango, West Java, Indonesia, the highest relative basal area for Lauraceae was recorded at 1600 m altitude; Lauraceae accounted for 10.3%

Table 2 Results of discriminant analyses using a four-variable model applied to the presence-absence data of Lauraceae species

Species [†]	No. squares present	Canonical correlation	Significance level				Results of stepwise selection of variables				
			Chi-square test of Wilks' lambda	Randomization test	Percentage of correct classification	Standardized canonical discriminant function coefficient					
						Relative elevation	Slope inclination	Slope direction	Slope convexity		
<i>Litsea subcorriacea</i>	83	0.301	0.01	0.03	58.7	1.408	—	—	—	—	-1.075
<i>Cryptocarya densiflora</i>	122	0.197	0.24	0.39	—	—	—	—	—	—	—
<i>Cryptocarya cf. calicicola</i>	118	0.461	<0.01	0.01	71.3	1.000	—	—	—	—	—
<i>Litsea cf. membranifolia</i>	11	0.174	0.37	0.45	—	—	—	—	—	—	—
<i>Litsea beusekomii</i>	101	0.612	<0.01	0.02	81.1	0.509	—	—	0.355	—	0.558
<i>Litsea yunnanensis</i>	115	0.490	<0.01	0.05	74.1	1.000	—	—	—	—	—
<i>Litsea lancifolia</i>	68	0.762	<0.01	<0.01	86.0	0.713	0.347	—	—	—	0.499
<i>Cinnamomum cf. soeengii</i>	57	0.487	<0.01	0.01	72.7	1.000	—	—	—	—	—
Unidentified sp.	24	0.314	0.01	<0.01	62.2	1.000	—	—	—	—	—
<i>Beilschmiedia glauca</i>	39	0.535	<0.01	0.04	73.4	1.202	-0.501	—	—	—	-0.558
<i>Phoebe macrocarpa</i>	37	0.565	<0.01	0.08	—	—	—	—	—	—	—
<i>Litsea cubeba</i>	4	0.270	0.03	0.21	—	—	—	—	—	—	—
<i>Lindera metcalfeana</i>	67	0.730	<0.01	<0.01	86.7	0.691	—	—	—	—	0.476
<i>Litsea pedunculata</i>	58	0.455	<0.01	0.05	70.6	—	—	—	—	—	1.000
<i>Neolitsea zeylanica</i>	33	0.364	<0.01	<0.01	63.6	—	—	—	—	—	1.000
<i>Actinodaphne</i> sp.	42	0.264	0.04	0.17	—	—	—	—	—	—	—
<i>Cinnamomum bejolghota</i>	61	0.266	0.04	0.33	—	—	—	—	—	—	—

[†]Species are arranged according to their position in the dendrogram shown in Fig. 3. Variety name is omitted. For the analysis, a 5.72-ha area was used and the presence-absence of focal species and topographical variables were obtained for every 20 m × 20 m square. In total, 143 squares were used. Significance levels in bold letters indicate values of $P < 0.05$. The last four columns show the standard canonical discriminant function coefficients for the variables adopted by the stepwise selection. The stepwise selection was conducted for the species showing the significance dependency in randomization test.

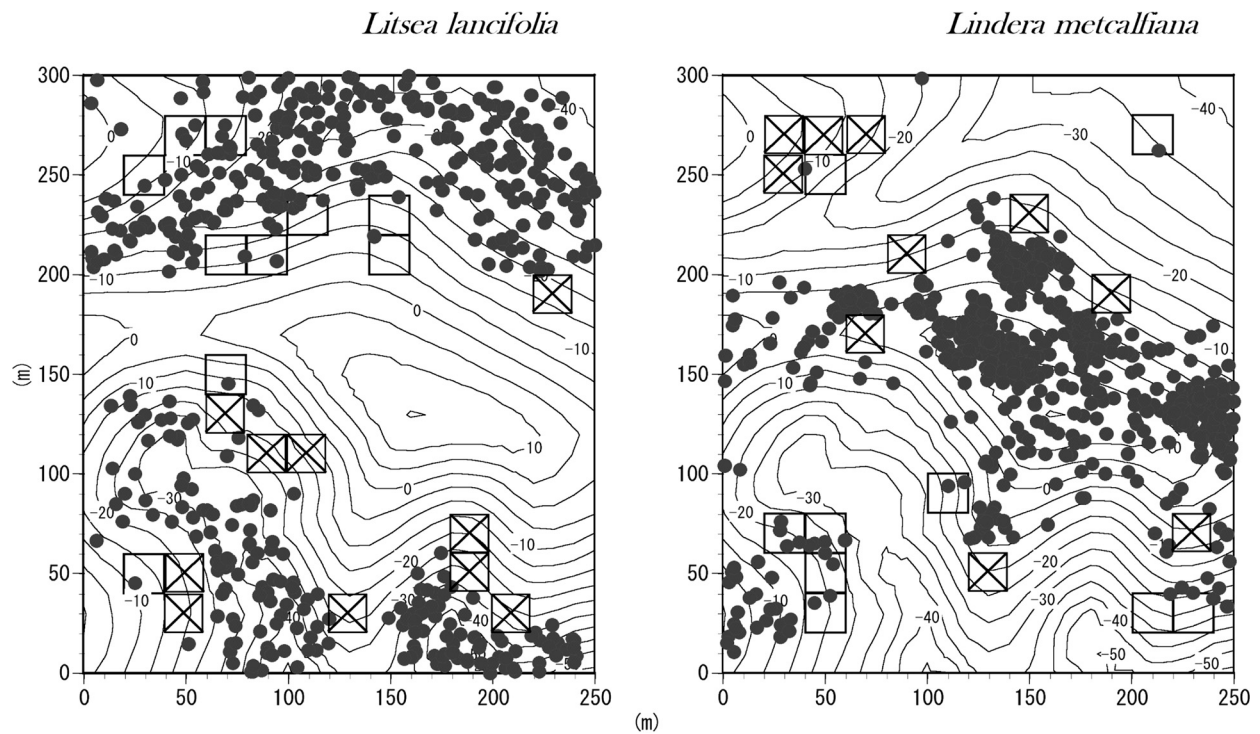


Fig. 4. The locations of squares that were misclassified in the stepwise discriminant analysis of two species. Open boxes in the diagram indicate squares with focal species for which the discriminant model predicted the absence of those species. Boxes filled with a cross indicate the reverse case.

of the total basal area. Ohsawa *et al.* (1985) reported a high relative basal area of 11.9% from a montane forest located at 2100 m altitude on Mt Kerinci, Sumatra. Thus, the dominance of Lauraceae in our plot appeared to be one of the characteristics of the plot.

Numerical characterization of the topography and the randomization test

In this study, the formula proposed by Yamakura *et al.* (1995) was used to numerically characterize topography. This enabled us to apply discriminant analysis to test the habitat dependency of the tree distribution pattern. Thus, numerical characterization of the topography expands the choice of statistical methods in studies of habitat dependency. Another advantage of this method is that it is objective, and allows comparisons of habitat differentiation between different communities.

All the species examined in this study were patchily distributed. Therefore, a randomization test of the significance of the discriminant model

was necessary. Using a χ^2 test of Wilks' lambda, 15 of the 17 species examined were significantly dependent on topography. By applying the randomization test using a random shift technique, however, a further four models were ruled out and only 11 species were concluded to be significantly dependent on topography. The result of the randomization test was not consistent with that of the traditional test: the former test appeared to be more conservative than the latter. Therefore, it is highly recommended that the randomization test is applied to spatial analyses of habitat dependency.

Habitat dependency of Lauraceae species

The spatial distribution of 11 species, which correspond to 65% of the Lauraceae species, was significantly associated with topographical variables, and the species formed two major clusters in our cluster analysis. One cluster included three species, whose presence was significantly associated with convex slopes or higher elevation. The other clus-

ter included eight species and was associated with lower elevation. Thus, topographical habitat differentiation among Lauraceae species is probably important in maintaining the species diversity of this family in the montane forest studied here.

Relative elevation and slope convexity were the most important variables for predicting the presence or absence of a species. The convexity index was adopted as the predictor variable in 7 of the 11 discriminant models obtained using the stepwise algorithm. This index is very simple, but it appears to be sufficient for indicating the hydrological condition and/or factors associated with water availability of the habitat. Relative elevation was adopted as a predictor variable for nine species. The maximum difference in elevation within the plot was only 53 m. Therefore, it is unlikely that species in this study differentiate their niches along a temperature gradient associated with elevation. Because the relative elevation may be correlated with the distance from a stream or ridge, elevation presumably also represents hydrological condition. Microclimate conditions, such as air humidity and wind velocity, may also change with elevation and convexity. In contrast, slope inclination and direction contributed little to the prediction, even though these factors are potentially influential in determining the hydrological conditions of microsites. It is likely that the influence of these factors are important at different spatial scales, and we may have failed to detect the effect of these factors in our analysis. The minor contribution of slope direction, which was likely caused by the difference in incident solar radiation between north and south slopes, is much smaller at low latitudes than at high latitudes. Soil type is another factor that is frequently associated with topography and can control tree distribution (Hirai *et al.* 1995; Clark *et al.* 1998; Webb & Peart 2000; Itoh *et al.* in press), but no data on that variable was available in our study. Many other physical factors and biological interactions may change with topography. Identification of the causal factors that directly control the distributions of tree species is quite difficult and must await future studies.

Studies in other tropical forests have also suggested the importance of topographical variation on spatial scales of approximately 50 ha. Using a 50-ha plot, Hubbell and Foster (1986) found that

half of the 239 tree species in a tropical moist forest in Panama were associated with one of four topographical habitats: slope, plateau, streamside/ravine and swamp. Svenning (1999) demonstrated that the distribution of 20 of 31 palm and palm-like species was significantly related to microhabitat, mainly measured using topography in a 50-ha plot of a tropical rain forest in Amazonian Ecuador. Itoh (1995) and Itoh *et al.* (1997) found the opposite spatial patterns in two *Dryobalanops* species, with both species showing an association with topography and soil texture in a 52-ha plot of tropical rain forest in Sarawak (Itoh *et al.* in press). Yamada *et al.* (1997) reported that three *Scaphium* species were also differentiated by topographical habitat in the same plot. These results strongly suggest that topographical habitat plays an important role in structuring tree species assemblages, even at small spatial scales of less than 52 ha. On a larger spatial scale, Clark *et al.* (1998) demonstrated that soil type significantly controlled the abundance of seven out of nine species examined in a 216-ha study area in Costa Rica. Webb and Peart (2000) also reported significant associations with habitat type in 17 out of 49 abundant species in a 150-ha study area in West Kalimantan.

Thus, edaphic conditions appear to have outstanding effects on various tropical forests, and niche differentiation along the topographical gradient seems to be one of the key factors in understanding the community structure of species-rich tropical forests. Our present study examined only one family and we examined only topographical habitat. Future studies should examine all taxa in the forest and should include other niche components, such as a regeneration niche, in their analyses.

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