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Spatial patterns and habitat associations of Fagaceae in a hill dipterocarp forest in Ulu Gadut, West Sumatra

Sen Nishimura*[1], Tsuyoshi Yoneda†, Shinji Fujii‡, Erizal Mukhtar§ and Mamoru Kanzaki#

* Center for Integrated Area Studies, Kyoto University Yoshida Honmachi, Sakyo-ku, Kyoto, 606-8501, Japan
† Faculty of Agriculture, Kagoshima University, Korimoto, Kagoshima 890-0065, Japan
‡ University of Human Environments, Okazaki, Aichi 444-3505, Japan
§ Faculty of Science, Andalas University, Padang, West Sumatra, Indonesia
\# Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwake, Sakyo, Kyoto, 606-8502, Japan
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Abstract: Spatial distribution patterns and habitat associations of Fagaceae species in a Fagaceae-codominated hill forest in Sumatra were investigated. Ten Fagaceae species believed to be zoochorous (animal-dispersed seed) and five codominant canopy and emergent anemochorous (wind-dispersed seed) species from Anacardiaceae and Dipterocarpaceae were studied. Five Fagaceae species and all codominant anemochorous species were significantly aggregated while the other five Fagaceae species showed a random distribution pattern. The median distance of small saplings from the nearest reproductively mature tree tended to be shorter for aggregated species than spatially random species. This implied that some Fagaceae species dispersed over longer distances than anemochorous species. Relationships between four habitat variables and distribution of the target species were examined with torus-translation tests. Three *Quercus* and one *Lithocarpus* species showed positive habitat associations. Two *Quercus* species aggregated at the preferred habitat, but the others were randomly distributed. Thus tree species with specific habitat preference do not only aggregate at the preferred habitat. The three ridge-specialist *Quercus* species showed gradual changes in habitat association, which could reflect avoidance of competition among the species. Most of the *Lithocarpus* species showed little correlation with habitat variables. Coexistence of the three *Quercus* species partly reflected subtle differences in topographical preferences. Distribution of five of the six *Lithocarpus* species was unrelated to topography, so other mechanisms must be sought to account for the maintenance of coexistence in this species-rich genus.

Key Words: coexistence, Dipterocarpaceae, dispersal constraint, Fagaceae, habitat preference, niche partitioning

INTRODUCTION

The tropical rain forests of South-East Asia are among the most diverse terrestrial ecosystems on Earth (Soepadmo 1995). The species diversity has been explained with regard to coexistence of plant species based on habitat heterogeneity where each species is best suited to a particular habitat (Tilman & Pacala 1993), but whether the habitat heterogeneity maintains the high tree species richness is still controversial. A number of hypotheses have been proposed and these can be categorized into equilibrium and non-equilibrium categories (Connell 1978). The equilibrium category was explained by partitioning of habitat or regeneration niches (Ashton 1969, Grubb 1977). In agreement with these hypotheses, an association of tree species with physical habitats in species-diverse tropical forests and interspecific differences in these habitat associations are commonly observed in tropical rain forests (Clark *et al.* 1998, Comita *et al.* 2007, Davies *et al.* 1998, Debski *et al.* 2002, Harms *et al.* 2001, Itoh *et al.* 2003, Noguchi *et al.* 2007, Sri-Ngernyuang *et al.* 2003, Svenning 1999, Webb & Peart 2000, Yamada *et al.* 2006). On the other hand, non-equilibrium hypotheses were explained by the Janzen–Connell effect (Connell 1971, Janzen 1970) and the unified neutral theory (Hubbell 2001). The Janzen–Connell effect predicts that reduced recruitment near reproductive conspecifics due to host-specific pests will enhance creation of space for other plant species, and whether other plant species can occupy this space depends on chance factors determined by the density of

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[1] Corresponding author. Email: nishimu@cias.kyoto-u.ac.jp

productive trees close to the empty space. Hubbell's model predicts that hyper-diverse communities such as rain forest will principally be determined by neutral factors and successfully explains patterns of relative species abundance in neotropical plant communities.

Although many previous studies found evidence that tree species conform to the equilibrium theory, some studies indicated that limited or habitat-biased distribution patterns may be the ephemeral or transient result of a population's history of seed dispersal and immigration (Losos 1995, Primack & Miao 1992). Harms *et al.* (2001) concluded that the effects of physical factors may contribute little to maintenance of species richness, since so many species exist in the same ecological habitat. In contrast, Noguchi *et al.* (2007) suggested that even among the species which associated with same ecological habitat, the sympatric species slightly differentiate the position of maximum abundance of each population along a habitat gradient to achieve coexistence. Since our knowledge of species-habitat associations in tropical rain forests is inadequate, an integration of information concerning species-habitat associations in many tropical forests is needed (Yamada *et al.* 2006). As a consequence of the above mechanism and biotic interactions (e.g. seed dispersal and host-specific predation), spatial structuring of each species emerges in the tropical rain-forest community. Therefore, studying the spatial organization of such communities should improve our understanding of the mechanisms responsible for the diversity of tropical rain forest (He *et al.* 1996).

Fagaceae, which comprises species of apparently limited dispersal ability (Ashton 1988), are one of the codominant families in montane forest in South-East Asia (Fujii *et al.* 2006, Symington 1943, Wyatt-Smith 1963). Ashton (1988) noted that the altitudinal distribution of Fagaceae and Dipterocarpaceae in Malesia was suggestive of interfamilial competitive exclusion. However, the ecology of Fagaceae in Malesia is poorly investigated (Noguchi *et al.* 2007), although some taxonomic, geological and morphological studies have been undertaken recently (Cannon 2001, Fujii *et al.* 2006, Kamiya *et al.* 2003). In the present study, we investigated the spatial patterns of Fagaceae in association with their ecological habitat in a mid-elevation hill dipterocarp forest in Sumatra.

Fagaceae show greatest dominance and relatively high diversity in Sumatran mid-elevation hill dipterocarp forest (Fujii *et al.* 2006, Nishimura *et al.* 2006a, b). This study aimed to elucidate factors determining the coexistence of species of Fagaceae in a mid-elevation hill dipterocarp forest in Ulu Gadut, Sumatra. To provide a critical test of niche differentiation we studied congeneric species (mainly *Lithocarpus* and *Quercus*), which minimized interspecific differences in dispersal syndrome and the effects such differences would have on spatial patterns (Debski *et al.* 2002). The following hypotheses were addressed: (1) Fagaceae are potentially dispersal-constrained and will thus show an aggregated spatial pattern in the forest compared with that of wind-dispersed codominant species; (2) therefore the distribution of juvenile trees will be associated with same habitat as adult trees; (3) since Ulu Gadut is a topographically complex site, the habitats occupied by Fagaceae will be associated with specific topography; (4) consequently, habitat-associated Fagaceae will aggregate in the preferred habitat; and (5) differences in habitat preference may play an important role in the coexistence of Fagaceae species in the forest.

METHODS

Site description

The study area comprised 3.99 ha within a 6.55-ha plot in a well-developed, mid-elevation hill dipterocarp forest in Ulu Gadut, Padang, West Sumatra (00°53′S, 100°21′E). The site has a humid climate with a remarkable mean annual precipitation of about 6000 mm. The vegetation of the forest stand is essentially hill dipterocarp forest *sensu* Symington (1943) with no species exhibiting dominance. The forest stand has been damaged by small-scale local logging (non-mechanized logging by hand), which is one reason why dipterocarp species did not show dominance. The research plot was divided into 1568 quadrats (5 m × 5 m, horizontal distances) and a PVC post was placed at the corners of each quadrat. The relative elevation at each post was determined by land survey. Detailed description of the vegetation and topography of the site is presented in Nishimura *et al.* (2006a).

Tree census

All trees of 10 cm diameter at breast height (dbh) or greater were mapped, marked with a numbered aluminium tag and the dbh was measured (above any buttresses if present). Each tree was identified to species level at the Herbarium Bogoriense to clarify the species composition of the forest stand. All voucher specimens are lodged in the Kagoshima University, Japan. The heights of 857 trees (25% of the total tree number) of a range of dbh were measured using a measuring pole and Haga altimeter.

Target species

Fagaceae species are one of the major components of this forest stand. The species number, abundance and

Table 1. Status of 23 Fagaceae species within a 6.55-ha plot in a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. The number of individuals and tree density were based on trees with dbh $\geq$ 1 cm. Basal area, mean diameter at breast height (dbh), maximum dbh and maximum height (H) were based on all trees with dbh $\geq$ 10 cm.

Species	No. of trees	Tree density (ha^{-1})	Basal area (m^2 ha^{-1})	dbh$_{\text{mean}}$ (cm)	dbh$_{\text{max}}$ (cm)	H$_{\text{max}}$ (m)
Castanopsis inermis	20	3.1	< 0.01	19.8	19.8	N/A
Castanopsis rhamnifolia	16	2.4	0.33	36.0	65.5	32.4
Lithocarpus daphnoideus	28	4.3	N/A	N/A	N/A	N/A
Lithocarpus elegans	2	0.3	N/A	N/A	N/A	N/A
Lithocarpus encleisocarpa	10	1.5	0.08	40.0	49.3	32.7
Lithocarpus gracilis	6	0.9	0.06	29.0	65.9	30.8
Lithocarpus hystrix	41	6.3	0.15	37.5	62.7	32.1
Lithocarpus indutus	5	0.8	0.10	54.5	81.6	32.0
Lithocarpus javensis	18	2.7	0.33	36.8	80.4	42.0
Lithocarpus lucidus	18	2.7	0.25	40.7	67.9	39.7
Lithocarpus luteus	3	0.5	0.16	21.9	41.5	25.4
Lithocarpus macphailii.	32	4.9	0.12	27.7	66.9	30.2
Lithocarpus meijeri	17	2.6	0.79	71.8	103.4	35.8
Lithocarpus reinwardtii	38	5.8	0.28	47.7	80.2	37.0
Lithocarpus sp. 1 (cf. *ewykii*)	20	3.1	0.17	51.4	69.1	30.3
Lithocarpus sp. 2 (cf. *lampadaria*)	3	0.5	0.26	30.2	47.2	23.5
Lithocarpus sp. 3 (cf. *woodii*)	24	0.6	1.26	63.1	71.4	33.1
Quercus argentata	95	14.5	0.32	41.9	98.1	41.6
Quercus gemelliflora	43	6.6	0.40	42.6	83.2	41.7
Quercus gaharuensis	1	0.2	0.03	47.2	47.2	26.5
Quercus oidocarpa	28	4.3	0.22	39.4	85.7	34.1
Quercus elmeri	N/A	N/A	N/A	N/A	N/A	N/A
Quercus sp. 1 (cf. *subsericea*)	18	2.7	0.06	37.8	63.1	31.1

basal area dominance of this family ranked sixth, sixth and first, respectively, out of 64 families in the 6.55-ha plot (Nishimura *et al.* 2006a). At least 23 Fagaceae species grew in the plot. Most of these are canopy tree species up to 30–40 m in height (Table 1). Among these, 10 target species from the genera *Castanopsis* (one sp.), *Lithocarpus* (six spp.) and *Quercus* (three spp.) were selected for use in this study based on their density in the plot, i.e. those species exceeding 10 individual trees of dbh $\geq$ 1 cm in the inner 3.12-ha area (as the outermost quadrats of 3.99-ha were unavailable for calculations of slope convexity). Scientific names used follow those in the revision by Soepadmo (1972) and the check-list by Govaerts & Frodin (1998). Detailed morphological and ecological descriptions of the species in Malesia are given by Soepadmo (1972).

Five canopy or emergent codominant tree species, comprising one Anacardiaceae and four Dipterocarpaceae species, were selected for comparison. Each species can be a competitor of Fagaceae in terms of sharing the same or an upper stratum. Three of the species currently show high dominance and the other two species formerly exhibited high dominance in the plot. *Swintonia schwenkii* (T. & B.) T. & B. (Anacardiaceae) and *Parashorea lucida* (Miq.) Kurz (Dipterocarpaceae), the main emergent trees in the plot, are among the most common species at present. *Hopea dryobalanoides* Miq. (Dipterocarpaceae) is also one of the most common canopy trees. Some mature trees of *Shorea maxwelliana* King and *Shorea atrinervosa* Sym. were once the target of small-scale local logging (Nishimura *et al.* 2006a). These two species were formerly among the emergent and dominant species in the plot. Kochummen (1989) and Ashton (1982) were used for identification of Anacardiaceae and Dipterocarpaceae, respectively.

All of the target Fagaceae species produce nuts, which are only shed beneath the canopy of the mother tree, whereas the five codominant species have winged fruits dispersed by wind. Fruit morphology suggests that the nuts are zoochorous through caching by small mammals after barochory and that the winged fruits are anemochorous probably with zoochory as a secondary dispersal mechanism.

All individuals, including newly established seedlings, of the 15 target species in the plot were mapped, marked with a numbered plastic tape, and the dbh and tree height were measured. In this study, trees greater than 1-cm dbh were defined as the tree stage and included pole and mature trees. Trees less than 1 cm dbh were categorized into two additional developmental stages, namely the large-sapling stage (dbh < 1 cm and height $\geq$ 50 cm) and small-sapling stage (height < 50 cm).

Seed dispersal of the target species was not observed in this study, therefore it is not possible to specifically discuss seed dispersal of these species. However, as Webb & Peart (2000) noted, seedling distributions are strongly influenced by seed dispersal patterns, so the distribution patterns of plants at early growth stages should reflect seed dispersal patterns. On this basis, we estimated the dispersal constraint of these species using data for the small-sapling stage, which are expected to be less affected by biotic interaction than the tree stage. The median distances between small saplings (height < 50 cm) and the nearest reproductively mature conspecific tree (dbh ≥ 30 cm) were calculated for each species in the 6.55-ha plot to estimate dispersal constraint.

Data analysis

Univariate spatial patterns of the target species were analysed using Ripley's $\hat{K}(t)$ function (Ripley 1977). The function $\lambda\hat{K}(t)$ ($\lambda =$ intensity) is defined as the expected number of target species within distance t of an arbitrary target species. The unbiased estimate of $\hat{K}(t)$ is defined as:

$$\hat{K}(t) = n^{-2}|A| \sum \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij}),$$

where n is the number of target species in a plot; $|A|$ denotes plot area; U_{ij} is the distance between the ith target species and jth target species in A; $I_t(u)$ is equal to 1 if $u \leq t$ and 0 otherwise; w_{ij} is the proportion of the circumference of a circle with its centre at the ith target species and with radius u_{ij} that lies within A; and summation is for all pairs of target species not more than t apart (Diggle 1983, Ripley 1977).

Square-root transformation of $\hat{L}(t)$, as suggested by Besag (1977), was applied in this study to detect spatial patterns for the tree stage. $\hat{L}(t)$ is defined as:

$$\hat{L}(t) = \sqrt{\hat{K}(t)/\pi} - t$$

A value of $\hat{L}(t) = 0$ indicates that the spatial pattern at distance t is random. Values of $\hat{L}(t) > 0$ indicate clumped distributions. Values of $\hat{L}(t) < 0$ indicate regular distributions. Significance of this function was determined with Monte Carlo simulations (Besag 1977, Besag & Diggle 1977, Marriott 1979). For this analysis, the null hypothesis is complete spatial randomness. A total of 10 000 simulations were performed to create 95% confidence intervals. $\hat{L}(t)$ was examined for every 1-m interval from 0–60 m for distance t.

The inclination and compass direction of the slope was calculated for each 10 m × 10-m quadrat following the plane regression method of Yamakura *et al.* (1995) using the elevation data for the four corners of each quadrat. The relative elevation of each quadrat was obtained by averaging the elevation at each corner. The surface relief of the slope was expressed using the index of slope convexity (IC) proposed by Yamakura *et al.* (1995). A positive value of the index means that the slope relief is convex. IC could not be calculated for the marginal quadrats because the elevation outside the target quadrat is needed.

Since the study site was disturbed previously by local logging, we used the canopy height as one of the habitat variables that might explain the distribution of target species. Each 10 m × 10-m quadrat contained nine points in a grid of 5-m quadrats, and the height of the highest crown at each point was recorded. Crowns up to 15-m high were measured with a height-measuring pole. For crowns above 15 m in height, we used the height of the nearest measured tree to estimate relative height visually. The average canopy height of the quadrat was defined as the average value of the height of these nine points.

To detect the significance of habitat association of the target species, a torus-translation procedure was used based on that of Harms *et al.* (2001). This procedure consisted of moving the true habitat map about a two-dimensional torus by 10-m increments in the four cardinal directions (Harms *et al.* 2001). More maps can be generated by each of three translations: 180° rotation, mirror image, and 180° rotation of the mirror image. On this basis a true habitat map and 1247 simulated habitat maps were produced. For the test of association, each of the 1248 habitat maps was overlain by the true distribution of trees and the relative density of each species was calculated for each habitat. Within the 6.55-ha plot, a 3.12-ha area was utilized for analysing the association of target species across the three developmental stages. The tree density of target species in the study site is rather lower than in previous studies (Aiba *et al.* 2004, Harms *et al.* 2001, Yamada *et al.* 2006) that used the same analytic method. However, there are no compelling differences in how this method assesses the degree of habitat association between low-and high-density species (Harms *et al.* 2001), therefore we proceeded to use this method to analyse the data.

Spatial interactions among species that showed the same habitat preference at the tree stage were analysed using the bivariate $\hat{L}_{1,2}(t)$ function, a transformation of function $\hat{K}_{1,2}(t)$ (Besag 1977, Lotwick & Silverman 1982, Ripley 1977):

$$\hat{L}_{1,2}(t) = \sqrt{\hat{K}_{1,2}(t)/\pi} - t$$

The $\hat{L}_{1,2}(t)$ function indicates the spatial independence among two species at distance t. To examine statistical significance, we used simulated $\hat{L}_{1,2}(t)$ values at the limit of the 2.5% tails of 10 000 torus randomizations (mean $\pm$ 1.96 SD) for 95% confidence intervals. If the sample statistic remains within the bounds of the confidence interval at any given t, the null hypothesis of spatial independence is not rejected, but when it exceeds the upper (or lower) boundaries the sampled points are regarded as an attractive (or repulsive) pattern (Diggle 1983).

Fisher's exact test was used to compare the median distance between small saplings and the nearest reproductively mature conspecific tree. False discovery rate (FDR)-corrected alpha (Verhoeven *et al.* 2005) was applied for the multiple comparisons across species.

RESULTS

Spatial pattern

The spatial patterns of ten Fagaceae (Figure 1) and five codominant wind-dispersed species (Figure 2) were investigated. Among Fagaceae, five species (*Castanopsis rhamnifolia*, *Lithocarpus meijeri*, *L. reinwardtii*, *Quercus argentata* and *Q. gemelliflora*) were significantly ($P < 0.05$) aggregated within most of the 60-m interval, whereas the other five species (*L. hystrix*, *L. javensis*, *L. lucidus*, *L. macphailii* and *Q. oidocarpa*) exhibited a rather random pattern (Figure 3). All of the codominant wind-dispersed species showed significantly aggregated distributions (Figure 4).

Habitat association

The results of torus-translation tests of habitat associations are shown in Appendix 1. Six Fagaceae species (*C. rhamnifolia*, *L. hystrix*, *L. reinwardtii*, *Q. argentata*, *Q. gemelliflora* and *Q. oidocarpa*) were significantly associated with one or more of the four habitat types at the small-sapling, large-sapling and/or tree stages. On the other hand, *L. javensis*, *L. lucidus*, *L. macphailii* and *L. meijeri* were considered to be independent of the four habitats tested in this study. Three of the codominant species (*Hopea dryobalanoides*, *Shorea maxwelliana* and *Swintonia schwenkii*) had significantly positive habitat associations.

For most of the species exhibiting significant habitat associations, the associations were not consistent at the three developmental stages. Among four topographic categories, IC was the biggest contributor to the habitat association. Among seven species that were associated positively with habitat at the tree stage, all of them were associated with IC. Although not statistically significant, some of the *Lithocarpus* species showed a tendency to be distributed on convex topography.

The population histograms for the three ridge-specialist *Quercus* species at the tree stage in relation to IC are shown in Figure 5. The histogram for *Q. argentata* is broader and with a less marked peak than for the other two *Quercus* species.

Spatial interaction between species

Spatial interaction between species was tested for each pair of congeneric species that showed the same habitat preference at the tree stage (Figure 6). Among congeneric *Quercus* species, spatial interaction between *Q. argentata* and *Q. gemelliflora* was negative or random throughout the 0–45-m distance interval. On the other hand, the interaction between *Q. oidocarpa* and *Q. argentata* was positive over a distance of 2–45 m. For *Q. gemelliflora* and *Q. oidocarpa* a mostly random interaction between 10 and 45 m and a negative interaction from 0 to 10 m was indicated.

Spatial interaction between *Quercus* and anemochorous species (*Hopea dryobalanoides*, *Shorea maxwelliana* and *Swintonia schwenkii*) that preferred the same habitat was tested. The interaction between *Q. argentata* and *H. dryobalanoides* was negative and that between *Q. oidocarpa* and *S. schwenkii* was random within 45 m, other than that the interactions between three ridge-specialist *Quercus* species and three ridge-specialist anemochorous species overlapped positively within 45 m. Spatial interaction among ridge-specialist anemochorous species was positively overlapping within 45 m in all species combinations.

Distance between small saplings and nearest reproductively mature tree

The median distances between small saplings (height < 50 cm) and the nearest reproductively mature conspecific tree (dbh ≥ 30 cm) are shown in Table 2. Although there were no significant differences among aggregated and random distributed species at the threshold distance (around 20 m), species with an aggregated distribution at the tree stage showed a tendency for small saplings to be closer to reproductively

Table 2. Median distance of small saplings (height < 50 cm) from the nearest reproductively matured conspecific tree (dbh ≥ 30 cm) in a 6.55-ha plot in a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. Median distances with the same letter indicate that values do not differ significantly at the 5% significance level. False discovery rate-corrected alpha (Verhoeven *et al.* 2005) was used. *Shorea atrinervosa* and *Shorea maxwelliana* were omitted from this analysis because of a low sample size (n = 2).

Species	Median distance of small saplings (m)	No. of trees in 6.55 ha (N)	Spatial pattern
Hopea dryobalanoides	6^{a}	134	aggregated
Quercus argentata	10^{b}	214	aggregated
Quercus gemelliflora	12^{c}	267	aggregated
Parashorea lucida	13^{bcd}	24	aggregated
Castanopsis rhamnifolia	$16^{abcdefg}$	8	aggregated
Lithocarpus meijeri	17^{de}	46	aggregated
Swintonia schwenkii	17^{d}	289	aggregated
Lithocarpus javensis	22^{de}	20	random
Quercus oidocarpa	36^{def}	32	random
Lithocarpus lucidus	38^{defg}	20	random
Lithocarpus reinwardtii	38^{efgh}	73	aggregated
Lithocarpus hystrix	45^{g}	109	random
Lithocarpus macphailii	64^{h}	17	random

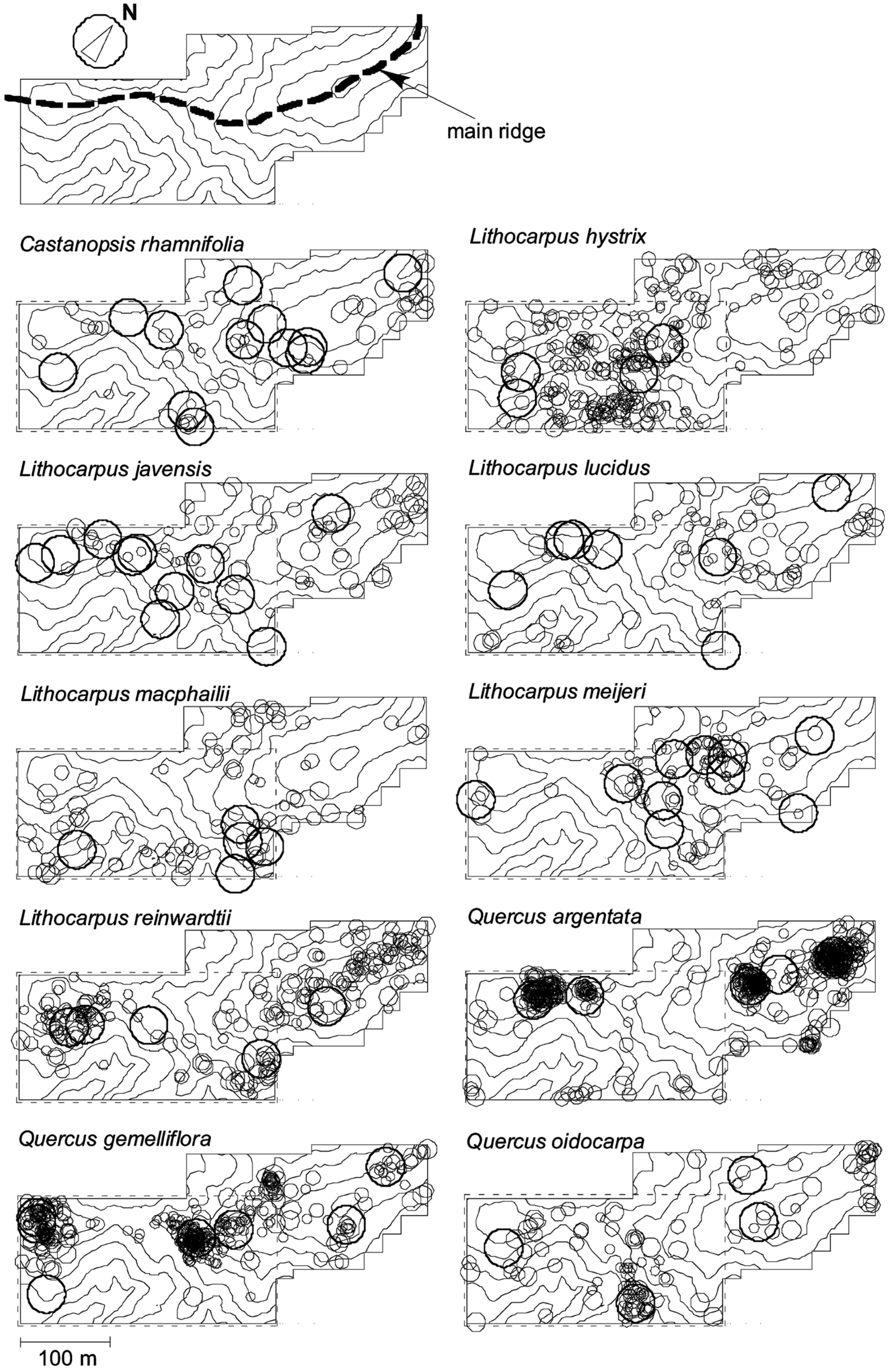

Figure 1. Spatial distribution of ten Fagaceae species in a 6.55-ha plot within a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. Key to symbols: The circles indicate (from smallest to largest circle, respectively) the small sapling stage, large sapling stage, tree stage, and reproductively mature trees (dbh ≥ 30 cm). The dashed line indicates the 3.99-ha area used for the spatial pattern analysis. The contour interval is 10 m.

mature conspecific trees than for species with a random distribution pattern, except for *L. reinwardtii*. Among these species, the median distances of *H. dryobalanoides*, *Q. argentata* and *Q. gemelliflora*, each of which are habitat-associated and spatially aggregated species, were significantly smaller than the other species

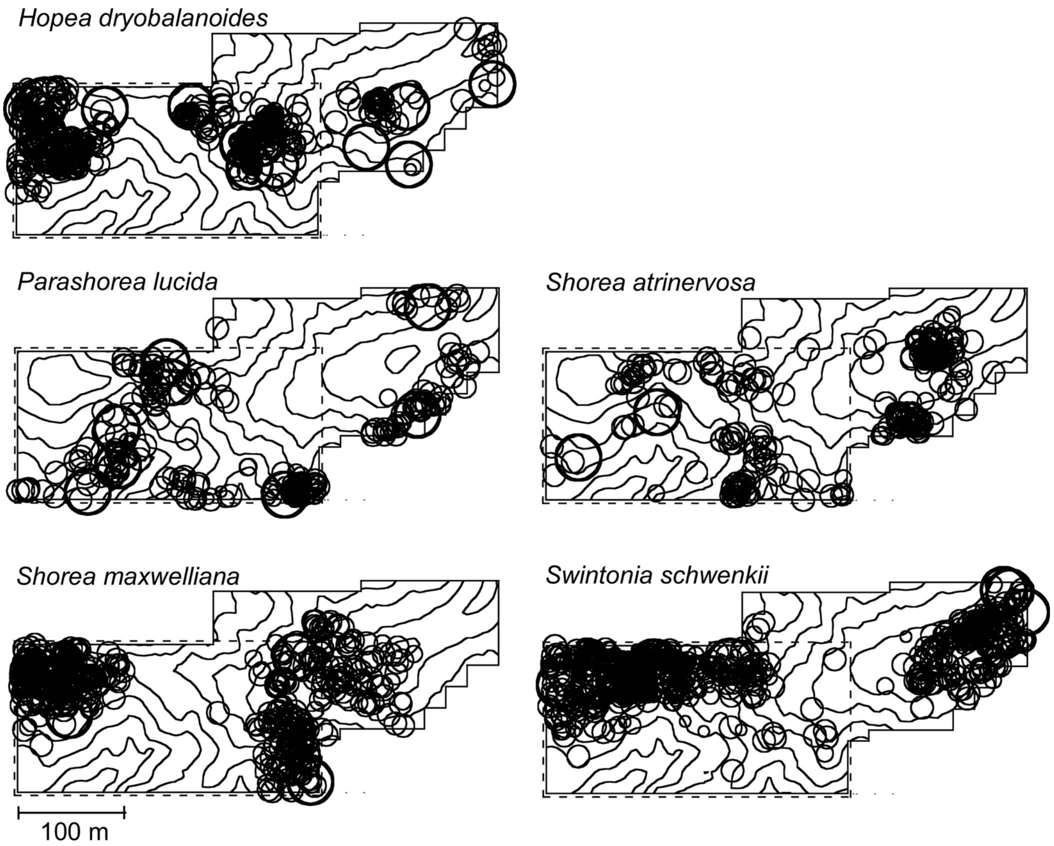

Figure 2. Spatial distribution of five codominant species in a 6.55-ha plot within a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. See Figure 1 for explanation of the symbols.

(except for *S. schwenkii*). On the other hand, the distance to reproductively mature conspecific trees was greater in spatially random species. The average median distance was significantly shorter in the aggregated group than in the spatially random group (Mann–Whitney *U*-test, $n_1 = 8, n_2 = 5, U = 1.0, P < 0.01$). However, comparison of the average median distance among *Lithocarpus* (37 m), *Quercus* (19 m) and anemochorous species (12 m) was not significant (ANOVA, df = 2, $F = 3.5$, $P = 0.07$).

DISCUSSION

Factors influencing spatial pattern

Of the ten Fagaceae species examined in the present study, five species exhibited an aggregated distribution pattern at the tree stage while the other five species showed a rather random spatial pattern. How did these spatial patterns come to arise? These ten species can be categorized into four groups based on their spatial pattern and habitat association (Table 3). It is likely that if a species has a specific habitat preference, the spatial pattern of the species will aggregate at the preferred habitat. For example, a previous study showed that 24 out of 25 bird-dispersed *Aporosa* species showed an aggregated distribution in the preferred habitat at Lambir, Borneo and/or Pasoh, Peninsular Malaysia (Debski *et al.* 2002). The relationship between spatial pattern and habitat association of *Q. argentata* and *Q. gemelliflora* was in accordance with this assumption. However, for other species, this was partly rejected, as *Q. oidocarpa* and *L. hystrix* were distributed randomly but associated with a specific habitat. This implies that these species might exhibit superior survival at the preferred habitat after being widely dispersed. *Castanopsis rhamnifolia*, *L. meijeri* and *L. reinwardtii*, which are considered to be independent of habitat but have aggregated spatial

Table 3. Grouping of ten species of Fagaceae based on spatial pattern and habitat association.

Spatial pattern	Habitat association positive	not positive
aggregated	*Quercus argentata* *Quercus gemelliflora*	*Castanopsis rhamnifolia* *Lithocarpus meijeri* *Lithocarpus reinwardtii*
random	*Lithocarpus hystrix* *Quercus oidocarpa*	*Lithocarpus lucidus* *Lithocarpus javensis* *Lithocarpus macphailii*

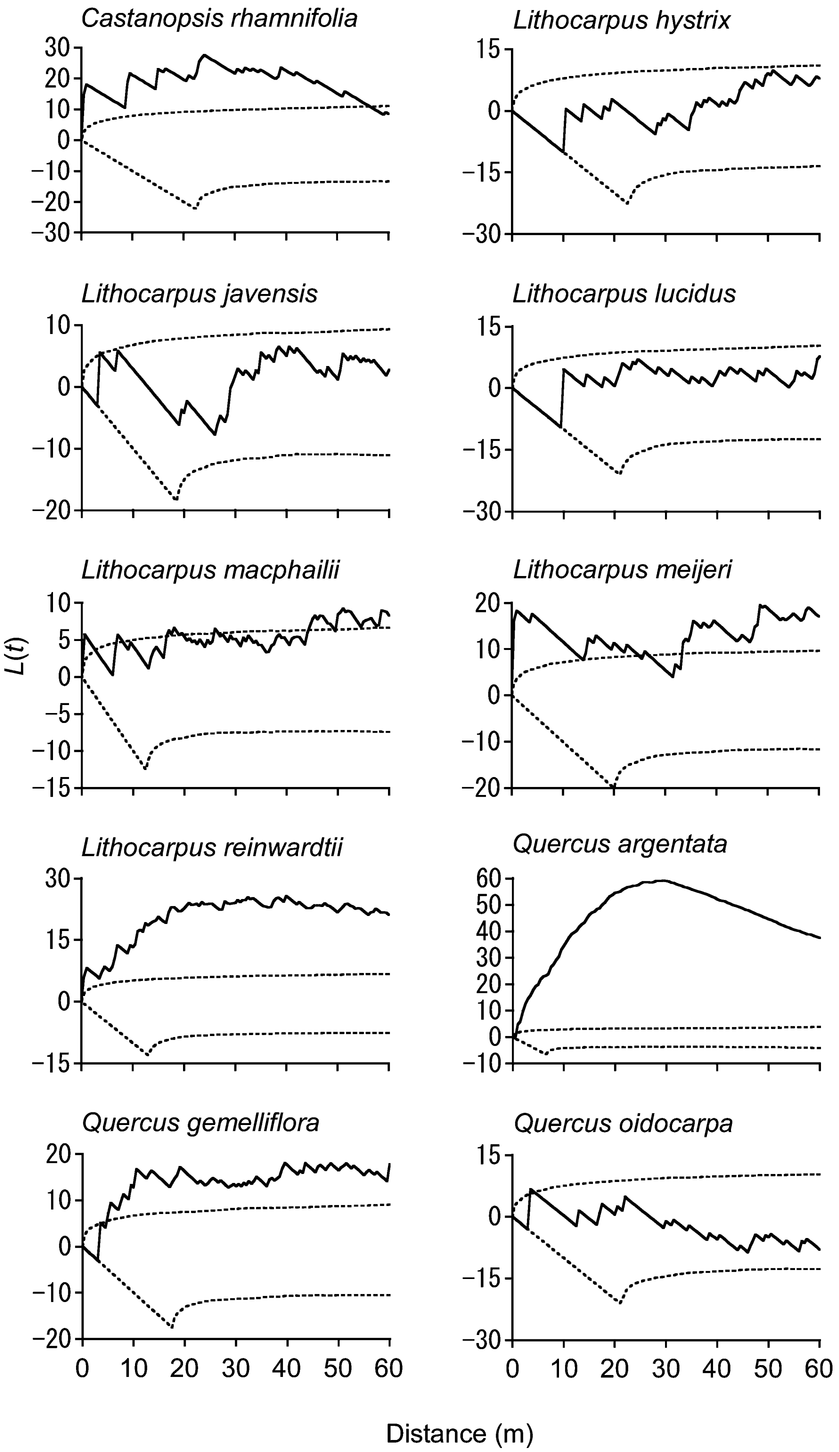

Figure 3. $\hat{L}(t)$ values for the ten species of Fagaceae at the tree stage in a 3.99-ha plot within a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. The solid line represents actual $\hat{L}(t)$ values for extant plants. The dashed lines represent the 95% confidence limits for the pattern expected from a random distribution of plant locations generated by 10 000 simulations. Values outside the limits indicate significant departure from a random distribution.

patterns, might be able to establish irrespective of the specific habitat but their dispersal seems to be limited. The independence of habitat association and the random spatial pattern for three species (*L. lucidus*, *L. javensis* and *L. macphailii*) indicates that chance biotic interactions, such as secondary dispersal and/or post-dispersal survivorship, seem to be more important for determining the spatial pattern for these species. With regard to the wind-dispersed

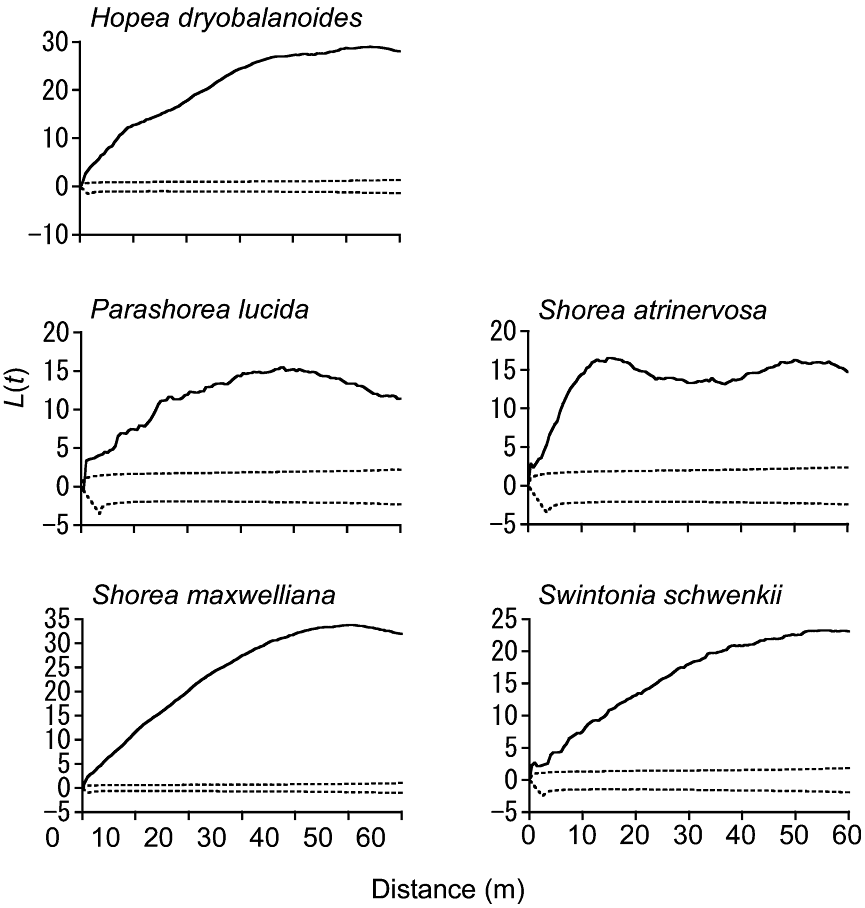

Figure 4. $\hat{L}(t)$ values for the five codominant species at the tree stage in a 3.99-ha plot within a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. See Figure 3 for explanation of the lines.

codominant species, all of the species showed an aggregated distribution pattern. Three of the species had specific habitat preferences while two species did not.

In Fagaceae the nut falls to the ground directly beneath the mother tree and apparently has limited dispersal ability (Ashton 1988) in contrast to the anemochorous species. Our results, however, showed that five Fagaceae species have a random distribution pattern whereas all of the wind-dispersed codominant species were aggregated. Enhanced seed dispersal reduces aggregation (Condit *et al.* 2000), thus an increasingly random spatial pattern is expected with increasing seed dispersal distance. Consequently, species with a random spatial pattern may be dispersed more widely than aggregated species. This implies that limitation of seed dispersal occurs in not only the five Fagaceae species but also in the codominant wind-dispersed species in the study plot. Comparison of the average median distance among *Lithocarpus* (37 m), *Quercus* (19 m) and anemochorous species (12 m) was not significant. However, there was a tendency for the median distance of *Lithocarpus* species to exceed that of either *Quercus* or even codominant anemochorous species. Seed dispersal mechanisms of Fagaceae in South-East Asia are poorly known (Cannon 2001), but it is thought that the nuts are scatter-hoarded by terrestrial squirrels (Corlett 1998, Leighton & Leighton 1983, Vander Wall 2001). We found quite a number of empty nuts with holes of *L. javensis* in a ground hollow that might have been carried and consumed there by a porcupine, which would indicate the existence of an animal disperser for at least some species of Fagaceae (S. Nishimura pers. obs.). Our results indicated that while the primary dispersal of Fagaceae nuts may be restricted to beneath the canopy of the mother tree, secondary dispersal by animals of spatially random species may occur over a longer distance than aggregated species in the study plot. If this is true, spatially random species must attract animals to disperse the nuts over greater distances. Animal preference for certain species might reflect differences in the concentration of polyphenols (condensed or hydrolysable tannin) in the nuts, which are thought to reduce the digestive efficiency of the nut predator (Vander Wall 2001). It is also suggested that the longer seed germination period in *Lithocarpus* species, in particular, compared with that of *Quercus* and wind-dispersed species (Ng 1991; S. Nishimura unpubl. data) may increase the chance of the

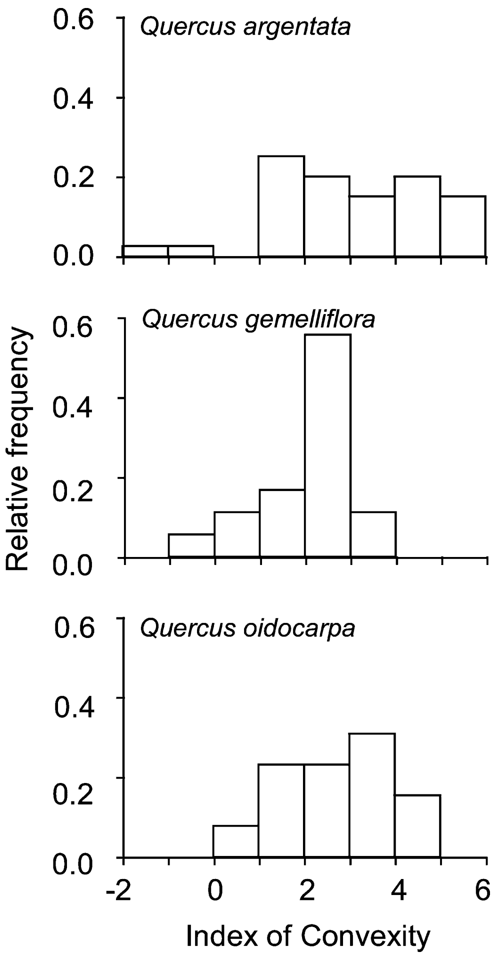

Figure 5. Relative frequency of three ridge-specialist *Quercus* species in relation to the index of slope convexity in a 3.12-ha plot in a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. A positive IC value indicates convex local landforms and a negative value indicates a concave slope.

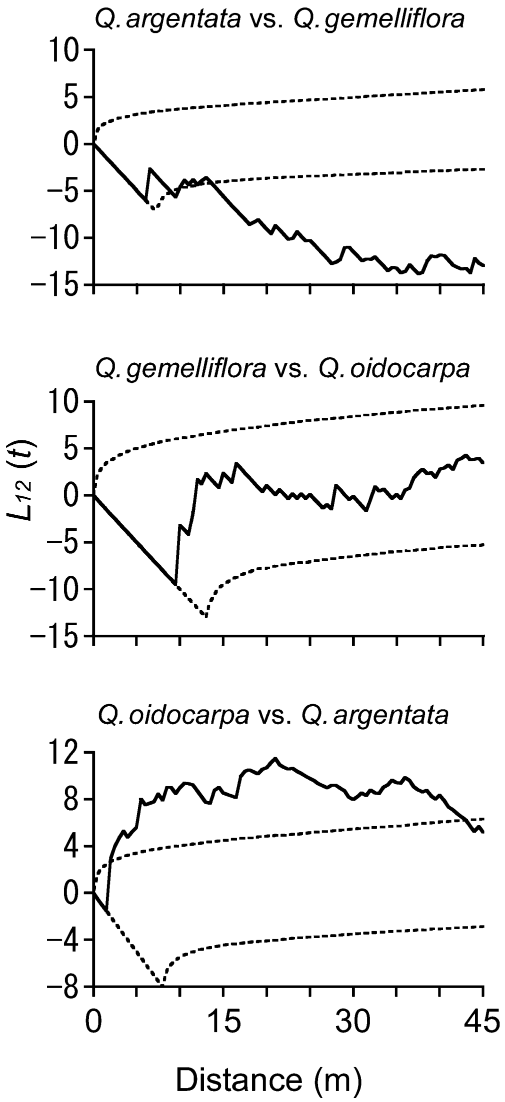

Figure 6. $\hat{L}_{1,2}(t)$ value of bivariate distribution of each pairing between three *Quercus* populations at the tree stage. The solid line shows the actual $\hat{L}_{1,2}(t)$ values for extant plants. Dashed lines show 95% confidence limits for the pattern expected from an independent distribution of plant locations generated by 10 000 simulations.

nuts being found by animals for gathering as a foodstuff for consumption and/or caching.

Species coexistence

Most seeds fall close to parent trees, therefore the density of seeds will tend to be higher in the preferred habitat of adult trees compared with other habitats. Thus seedlings may show associations with the same habitat as adults (Comita *et al.* 2007), especially for potentially dispersal-constrained species such as the aggregated and habitat-associated species in the present study. However, if the associated habitat at the tree stage corresponds with the preferred habitat for the species, most ecological associations of these species will not develop during early growth stages in the study plot, thus the distribution of small saplings does not exactly correspond with the habitat of mature trees even it is an aggregated species with short median distances. A high frequency of seedling establishment beneath the mother tree would result in a high density of small trees in that habitat, but if negative density dependence outweighs the benefits of the habitat, survival in that habitat would be reduced (Comita *et al.* 2007). This may account for the preferred habitat in early growth stages of Fagaceae differing from that of adult trees at Ulu Gadut. However, since those species associating with a specific habitat at the tree stage are retaining an aggregated distribution, seedlings may survive in topographically similar sites a limited distance from the parent tree.

Once the habitat is determined at the tree stage, how important is habitat association for coexistence of congeneric species? Previous studies that suggested the importance of topographical variation at spatial scales of approximately 50-ha showed opposite niche preference of congeneric species along a topographic gradient, e.g. two *Dryobalanops* species (Itoh *et al.* 1997) and three *Scaphium* species (Yamada *et al.* 1997) at Lambir, Borneo. Gunatilleke *et al.* (2006) also showed clear habitat partitioning of two *Mesua* species and three *Shorea* species which are growing sympatrically in a 25-ha plot in Sri Lanka. These results strongly suggest that topographical habitat differentiation determines the coexistence of congeneric species. Our results showed that the spatial distribution patterns of four Fagaceae species were positively associated with topography at the tree stage. Among these species, all *Quercus* species showed a similar dependency on topography and were associated with ridge sites. On the other hand, neutral associations were prominent for most *Lithocarpus* species, although a positive association with ridge sites was detected for *L. hystrix*. Positive association of three *Quercus* species with ridge sites had the effect of reducing confamilial competition from ten to three species, but habitat association alone does not provide sufficient support for the hypothesis that niche differentiation is the primary mechanism maintaining species diversity (Harms *et al.* 2001, Tilman & Pacala 1993, Webb & Peart 2000), since so many species coexist in the same habitat.

Yamada *et al.* (2006) suggested that coexistence of *Heritiera* species preferring the same habitat at Lambir may be related to their occupation of different forest storeys and hence differing regeneration requirements. However, *Quercus* species in the present study seemed to occupy the same stratum (Table 1). Davies *et al.* (1998) demonstrated the distribution of 11 sympatric *Macaranga* species along a light-intensity gradient at Lambir. Our results did not show a significant association between *Quercus* distribution and forest structure (average tree height), so the current distribution of *Quercus* species is likely to be independent of the light environment (but see Aiba *et al.* (2004) that showed significant association with exposed canopy conditions for *Q.* cf. *subsericea*). In addition, the spatial patterns of *Q. argentata* and *Q. oidocarpa* overlapped significantly. Noguchi *et al.* (2007) suggested the importance of habitat divergence in the specialized habitat and showed that sympatric species may offset the position of maximum abundance of each population along a habitat gradient to achieve coexistence, which may contribute to the coexistence of sympatric Fagaceae at Doi Inthanon, Thailand. In the present study, three *Quercus* species showed a different distribution pattern to the slope IC (Figure 5). This subtle difference in their ecological preferences may permit them to coexist even in a similar habitat. It is suggested that positive association of *Q. argentata* with intermediate elevations may be one factor contributing to avoidance of complete overlap with *Q. oidocarpa*, which is monotonically associated with ridge habitats irrespective of elevational range. The reason why *Quercus* species preferred ridge habitats in our study is unknown but this topographic preference may be favourable for their pollination, which is reliant on wind. Therefore evolutionary constraints may at least partially account for the distribution of *Quercus* on the ridge rather than insect-pollinated genera such as *Lithocarpus* and *Castanopsis*. Though the distribution of each of the three *Quercus* species was not associated with forest structure (average tree height), it is likely that their current distribution also reflects the influence of logging. Spatial overlap with *S. maxwelliana*, a previous logging target, indicates that some of the three *Quercus* may have occupied the previous habitat of *S. maxwelliana* following logging. Thus the high dominance of *Q. gemelliflora* (second out of 465 species in the 6.55-ha plot), in particular, may partly reflect logging of the same habitat preferred by competitive species.

Yamada *et al.* (2006) noted that a higher proportion of significantly positive associations between habitats was due to the topographic and edaphic complexity at Lambir. Condit *et al.* (2000) documented that more species are associated with topographic features in rugged topography than in a topographically uniform site. The topography of the present study site was very complex. However, the neutral association with topography for the five *Lithocarpus* species indicated that topographic complexity is not the principal mechanism determining the coexistence of these species. This is in accordance with results for *Lithocarpus* species in Bornean lowland dipterocarp forest at Gunung Palung (Webb & Peart 2000) and partly with Bornean lower montane forest on Mt. Kinabalu (Aiba *et al.* 2004). The latter study reported that two of the four species studied showed a distribution independent of topographic association. However, in lower montane oak-laurel forest at Doi Inthanon, the distribution of all three *Lithocarpus* species studied was associated with habitat (Noguchi *et al.* 2007). Niiyama *et al.* (1999) also reported a significant habitat association for *L. wallichianus* from hill dipterocarp forest in Peninsular Malaysia. Niche partitioning is more likely to explain the coexistence of a high diversity of congeneric or confamilial species distributed in the same forest stand (Davies *et al.* 1998, Yamada *et al.* 2006). However, *Lithocarpus* showed prominent topographic dependency at a site with low diversity at Doi Inthanon (0.2 species ha^{-1}), whereas topographic association was independent of distribution at sites with higher diversity at Ulu Gadut (2.4 species ha^{-1}). Coexistence of a large number of species independent of niche partitioning and coexistence in a non-equilibrium state are remarkable features of *Lithocarpus* in the Ulu Gadut study plot. This implies that, rather than contraction of the distribution over time due to higher survival in the preferred habitat, chance biotic interactions (e.g. the dispersal regime, or density- or frequency-dependent mortality from natural predation) may be important factors determining their distribution. The median distance (Table 3) of these *Lithocarpus* species also indicates that more intense disturbance by animals occurs at an early stage of development or before seed germination, consequently creating an indistinct distribution pattern in the forest stand. For these species, loss of seeds during secondary dispersal may be greater than in habitat-associated species with less widely dispersed seeds, but plants may be able to survive in a wider range of sites and habitats. However, more sophisticated studies, including seed dispersal observations and transplant experiments, are required in the future.

According to a previous study at Lambir (Palmiotto et al. 2004), *Swintonia schwenkii* and *Hopea dryobalanoides* showed significant associations with soil type, i.e. low-fertility udult ultisols and moderate-fertility humult ultisols, respectively, and the two species showed a distinct segregation pattern. However, the significantly overlapping distribution of the two species in the present study indicates that edaphic factors are less important for controlling their distribution pattern at Ulu Gadut. The present study, however, did not include edaphic features among the habitat variables. A number of studies have reported a strong association between tree distribution and soil type (Baillie *et al.* 1987, Paoli *et al.* 2006, Phillips *et al.* 2003) or a combination of topography and soil type (Davies *et al.* 1998, Harms *et al.* 2001, Itoh *et al.* 2003, Svenning 1999, Webb & Peart 2000, Yamada *et al.* 2007). Therefore, consideration of edaphic factors should be a component of future investigations. It should also be noted that the limited area of the study site compared with that of other study sites in the tropics might influence the results, since it is unclear whether the distribution patterns of each species at the site are typical.

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LITERATURE CITED

AIBA, S., KITAYAMA, K. & TAKYU, M. 2004. Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. *Plant Ecology* 174:147–161.

ASHTON, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* 1:155–196.

ASHTON, P. S. 1982. Dipterocarpaceae. Pp. 237–552 in van Steenis, C. G. G. J. (ed.). *Flora Malesiana*, series I, vol. 9. Martinus Nijhoff Publishers, The Hague.

ASHTON, P. S. 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. *Annual Review of Ecology and Systematics* 19:347–370.

BAILLIE, I. C., ASHTON, P. S., COURT, M. N., ANDERSON, J. A. R., FITZPATRICK, E. A. & TINSLEY, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on Tertiary sediments in Central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201–220.

BESAG, J. 1977. Contribution to the discussion on Dr Ripley's paper. *Journal of the Royal Statistical Society B* 39:193–195.

BESAG, J. & DIGGLE, P. J. 1977. Simple Monte Carlo tests for spatial pattern. *Applied Statistics* 26:327–333.

CANNON, C. H. 2001. Morphological and molecular diversity in *Lithocarpus* (Fagaceae) of Mount Kinabalu. *Sabah Parks Nature Journal* 4:45–69.

CLARK, D. B., CLARK, D. A. & READ, J. M. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology* 86:101–112.

COMITA, L. S., CONDIT, R. & HUBBELL, S. P. 2007. Developmental changes in habitat associations of tropical trees. *Journal of Ecology* 95:482–492.

CONDIT, R., ASHTON, P. S., BAKER, P., BUNYAVEJCHEWIN, S., GUNATILLEKE, S., GUNATILLEKE, N., HUBBELL, S. P., FOSTER, R. B., ITOH, A., LAFRANKIE, J. V., LEE, H. S., LOSOS, E., MANOKARAN, N., SUKUMAR, R. & YAMAKURA, T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288:1414–1418.

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298–313 in den Boer, P. J. & Gradwell, G. R. (eds.). *Dynamics of populations*. Centre for Agricultural Publication and Documentation, Wageningen.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.

CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews of the Cambridge Philosophical Society* 73:413–448.

DAVIES, S. J., PALMIOTTO, P. A., ASHTON, P. S., LEE, H. S. & LAFRANKIE, J. V. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86:662–673.

DEBSKI, I., BURSLEM, D. F. R. P., PALMIOTTO, P. A., LAFRANKIE, J. V., LEE, H. S. & MANOKARAN, N. 2002. Habitat preferences of *Aporosa* in two Malaysian forests: implication for abundance and coexistence. *Ecology* 83:2005–2018.

DIGGLE, P. J. 1983. *Statistical analysis of spatial point patterns*. Academic Press, London. 148 pp.

FUJII, S., NISHIMURA, S. & YONEDA, T. 2006. Elevational distribution of Fagaceae in West Sumatra. *Tropics* 15:153–163.

GUNATILLEKE, C. V. S., GUNATILLEKE, I. A. U. N., ESUFALI, S., HARMS, K. E., ASHTON, P. M. S., BURSLEM, D. F. R. P., & ASHTON, P. S. 2006. Species-habitat association in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology* 22: 371–384.

GOVAERTS, R & FRODIN, D. G. 1998. *World check list and bibliography of Fagales (Betulaceae, Corylaceae, Fagaceae and Ticodendraceae)*. Royal Botanical Garden, Kew. 407 pp.

GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52:107–145.

HARMS, K. E., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 2001. Habitat association of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89:947–959.

HE, F., LEGENDRE, P. & LAFRANKIE, J. V. 1996. Spatial pattern of diversity in a tropical rain forest in Malaysia. *Journal of Biogeography* 23:57–74.

HUBBELL, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Monographs in Population Biology 32. Princeton University Press, Princeton. 375 pp.

ITOH, A., YAMAKURA, T., OGINO, K., LEE, H. S. & ASHTON, P. S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. *Plant Ecology* 132:121–136.

ITOH, A., YAMAKURA, T., OHKUBO, T., KANZAKI, M., PALMIOTTO, P. A., LAFRANKIE, J. V., ASHTON, P. S. & LEE, H. S. 2003. Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. *Ecological Research* 18:307–320.

JANZEN, D. H. 1970. Herbivores and the numbers of tree species in tropical forests. *American Naturalist* 104:501–528.

KAMIYA, K., HARADA, K., OGINO, K., CLYDE, M. M. & LATIFF, A. M. 2003. Phylogeny and genetic variation of Fagaceae in tropical montane forests. *Tropics* 13:119–125.

KOCHUMMEN, K. M. 1989. Anacardiaceae. Pp. 9–57 in Whitmore, T. C. (ed.). *Tree flora of Malaya*, vol. 4. Malayan Forest Records no. 26. Forest Research Institute Malaysia & Ministry of Primary Industries, Petaling Jaya.

LEIGHTON, M. & LEIGHTON, D. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp. 181–196 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds.). *Tropical rain forests: ecology and management*. Blackwell Science, Oxford.

LOSOS, E. C. 1995. Habitat specificity of two palm species: experimental transplantation in Amazonian successional forest. *Ecology* 76:2595–2606.

LOTWICK, H. W. & SILVERMAN, B. W. 1982. Methods for analyzing spatial processes of several types of points. *Journal of the Royal Statistical Society B* 44:406–413.

MARRIOTT, F. H. C. 1979. Barnard's Monte Carlo tests: how many simulations? *Applied Statistics* 28:75–77.

NG, F. S. P. 1991. *Manual of forest fruits, seeds and seedlings*. Malayan Forest Records no. 34. Forest Research Institute Malaysia, Kepong. 400 pp.

NIIYAMA, K., ABDUL RAHMAN, K., IIDA, S., KIMURA, K., AZIZI, R. & APPANAH, S. 1999. Spatial patterns of common tree species relating to topography, canopy gaps and understory vegetation in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia. *Journal of Tropical Forest Science* 11:731–745.

NISHIMURA, S., YONEDA, T., FUJII, S., MUKHTAR, E., ABE, H. & KANZAKI, M. 2006a. Factors influencing the floristic composition of a hill forest in West Sumatra. *Tropics* 15:165–175.

NISHIMURA, S., YONEDA, T., FUJII, S., MUKHTAR, E., ABE, H., KUBOTA, D., TAMIN, R. & WATANABE, H. 2006b. Altitudinal zonation of vegetation in the Padang region, West Sumatra, Indonesia. *Tropics* 15:138–152.

NOGUCHI, H., ITOH, A., MIZUNO, T., SRI-NGERNYUANG, K., KANZAKI, M., TEEJUNTUK, S., SUNGPALEE, W., HARA, M., OHKUBO, T., SAHUNALU, P., DHANMMANONDA, P. & YAMAKURA, T. 2007. Habitat divergence in sympatric Fagaceae tree species of a tropical montane forest in northern Thailand. *Journal of Tropical Ecology* 23:1–10.

PALMIOTTO, P. A., DAVIES, S. J., VOGT, K. A., ASHTON, M. S., VOGT, D. J. & ASHTON, P. S. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *Journal of Ecology* 92:609–623.

PAOLI, G. D., CURRAN, L. M. & ZAK, D. R. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology* 92:609–623.

PHILLIPS, O. L., VARGAS, P. N., MONTEAGUDO, A. L., CRUZ, A. P., ZANS, M. C., SÁNCHEZ, W. G., YLI-HALLA, M. & ROSE, S. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* 91:757–775.

PRIMACK, R. B. & MIAO, S. L. 1992. Dispersal can limit local plant distribution. *Conservation Biology* 6:513–519.

RIPLEY, B. D. 1977. Modeling spatial patterns. *Journal of the Royal Statistical Society B* 39:172–192.

SOEPADMO, E. 1972. Fagaceae. Pp. 265–403 in van Steenis, C. G. G. J. (ed.). *Flora Malesiana*, series I, vol. 7. Martinus Nijhoff Publishers, The Hague.

SOEPADMO, E. 1995. Plant diversity of the Malesian tropical rainforest and its phytogeographical and economic significance. Pp. 19–40 in Primack, R. B. & Lovejoy, T. E. (eds.). *Conservation and* *management of Southeast Asian rain forests*. Yale University Press, New Haven.

SRI-NGERNYUANG, K., KANZAKI, M., MIZUNO, T., NOGUCHI, H., TEEJUNTUK, S., SUNGPALEE, C., HARA, M., YAMAKURA, T., SAHUNALU, P., DHANMMANONDA, P. & BUNYAVEJCHEWIN, S. 2003. Habitat differentiation of Lauraceae species in a tropical lower montane forest in northern Thailand. *Ecological Research* 18:1–14.

SVENNING, J-C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* 87:55–65.

SYMINGTON, D. F. 1943. *Foresters' manual of dipterocarps*. Malayan Forest Records no. 16 (reprinted in 1974). University of Malaya Press, Kuala Lumpur. 519 pp.

TILMAN, D. & PACALA, S. W. 1993. The maintenance of species richness in plant communities. Pp. 13–25 in Ricklefs, R. E. & Schluter, D (eds.). *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.

VANDER WALL, S. B. 2001. The evolutionary ecology of nut dispersal. *Botanical Review* 67:74–117.

VERHOEVEN, K. J. F., SIMONSEN, K. L. & MCINTYRE, L. M. 2005. Implementing false discovery rate control: increasing your power. *Oikos* 108:643–647.

WEBB, C. O. & PEART, D. R. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88:464–478.

WYATT-SMITH, J. 1963. *Manual of Malayan silviculture for inland forests*. Malayan Forest Records no. 23 (reprinted in 1995). Forest Research Institute Malaysia, Kepong.

YAMADA, T., YAMAKURA, T., KANZAKI, M., ITOH, A., OHKUBO, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1997. Topography-dependent spatial pattern and habitat segregation of sympatric *Scaphium* species in a tropical rain forest at Lambir. Sarawak. *Tropics* 7:57–66.

YAMADA, T., TOMITA, A., ITOH, A., YAMAKURA, T., OHKUBO, T., KANZAKI, M., TAN, S. & ASHTON, P. S. 2006. Habitat associations of Sterculiaceae trees in a Bornean rain forest plot. *Journal of Vegetation Science* 17:559–566.

YAMADA, T., ZUIDEMA, P. A., ITOH, A., YAMAKURA, T., OHKUBO, T., KANZAKI, M., TAN, S. & ASHTON, P. S. 2007. Strong habitat preference of a tropical rain forest tree does not imply large difference in population dynamics across habitat. *Journal of Ecology* 95:332–342.

YAMAKURA, T., KANZAKI, M., ITOH, A., OHKUBO, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1995. Topography of a large-scale research plot established within a tropical rain forest at Lambir, Sarawak. *Tropics* 5:41–56.

Appendix 1. Results of torus-translation tests for habitat association of 15 species across three developmental stages in the 3.12-ha plot in a mid-elevation hill dipterocarp forest in Ulu Gadut, West Sumatra. Four habitats were tested independently. Values represent the actual tree number observed in the field. Significant positive associations are denoted by '+' and '++' at significance levels of 5% and 1%, respectively. Significant negative associations are denoted by '-' and '−' at significance levels of 5% and 1%, respectively. The three developmental stages are: small sapling (SS), height < 50 cm; large sapling (LS), height ≥ 50 cm and dbh < 1 cm; and tree, dbh ≥ 1 cm. The small-sapling stages of *Shorea atrinervosa* and *Shorea maxwelliana* were not examined because of low numbers.

			Torus-translation tests for habitat associations											
			Quadrat number			Inclination (°)			Relative elevation (m)			Average canopy height (m)		
Species	Stage	N	IC Convex 1≤IC 141	Flat −1≤IC<1 92	Concave IC<−1 79	Gentle 0–15 24	Steep 15–30 130	Very steep 30≤ 158	Low 0–25 104	Middle 25–50 158	High 50≤ 58	Low 0–15 32	Middle 15–30 236	High 30 44
Castanopsis rhamnifolia (Fagaceae)	SS	6	4	2	0	2	2	2	3	2	1	1	5	0
	LS	11	9	2	0	2	9	0	4	7	0	4	7	0
	Tree	10	7	1	2	5	4	1	3	7	0	1	9	0
Lithocarpus hystrix (Fagaceae)	SS	81	42	18	21	45	33	3	20	41	20	7	68	6
	LS	81	35	25	21	49	26	6	5	44	32	12	58	11
	Tree	14	3	9 +	2	8	4	2	1	4	9 ++	2	9	3
Lithocarpus javensis (Fagaceae)	SS	12	10	2	0	5	5	2	2	10	0	4	8	0
	LS	4	3	1	0	2	2	0	2	2	0	0	3	1
	Tree	16	7	4	5	8	6	2	5	9	2	2	14	0
Lithocarpus lucidus (Fagaceae)	SS	6	2	3	1	2	4	0	4	2	0	0	6	0
	LS	8	6	1	1	3	4	1	4	2	2	0	8	0
	Tree	14	10	1	3	4	9	1	1	8	5	4	10	0
Lithocarpus macphailii (Fagaceae)	SS	10	5	5	0	6	4	0	4	3	3	0	8	2
	LS	17	8	6	3	6	9	2	3	7	7	0	15	2
	Tree	17	7	6	4	12	5	0	2	5	10	1	14	2
Lithocarpus meijeri (Fagaceae)	SS	17	13	4	0	9	5	3	10	7	0	1	15	1
	LS	8	5	3	0	3	4	1	4	4	0	1	6	1
	Tree	15	11	4	0	8	7	0	6	8	1	2	11	2
Lithocarpus reinwardtii (Fagaceae)	SS	38	15	18	5	24	14	0	1	32 +	5	6	0	8
	LS	40	26	11	3 -	22	18	0	6	29	5	7	30	3
	Tree	18	12	2	4	7	10	1	5	11	2	4	12	2
Quercus argentata (Fagaceae)	SS	22	20	2	0	11	3	8	0	22	0	3	19	0
	LS	77	66	11	0	37	34	6	0	76 +	1	29	48	0
	Tree	40	38 +	1 -	1	7	20	1	1	39 +	0	18	22	0

Appendix 1. Continued.

			Torus-translation tests for habitat associations									Average canopy height (m)		
			Quadrat number			Inclination (°)			Relative elevation (m)					
			IC Convex 1≤IC	Flat −1≤IC<1	Concave IC<−1	Gentle 0–15	Steep 15–30	Very steep 30≤	Low 0–25	Middle 25–50	High 50≤	Low 0–15	Middle 15–30	High 30
Species	Stage	N	141	92	79	24	130	158	104	158	58	32	236	44
Quercus gemelliflora (Fagaceae)	SS	233	184	47	2 –	57	150	26	103	130	0	79	153	1 -
	LS	46	44 ++	2 –	0 -	8 -	33 +	5	4	42 +	0	8	34	4
	Tree	18	15 +	3	0	2 -	13	3	6	9	3	3	15	0
Quercus oidocarpa (Fagaceae)	SS	27	10	9	8	18	7	2	0	25 ++	2	4	19	4
	LS	36	18	14	4	19	17	0	1	30 +	5	7	24	5
	Tree	13	12 ++	1	0	6	6	1	2	9	2	3	9	1
Hopea dryobalanoides (Dipterocarpaceae)	SS	129	100	27	2	29	86	14	79	50	0 -	35	94	0
	LS	132	76	44	12	28 -	99	5	45	75	12	8	123 +	1
	Tree	143	105 +	34	4 -	39 -	89	15	43	92	8	21	121	1 -
Parashorea lucida (Dipterocarpaceae)	SS	10	4	2	4	4	6	0	0	4	6	2	6	2
	LS	42	18	14	10	21	15	6	0	20	22	10	25	7
	Tree	67	32	21	14	35	24	8	1	37	29	13	46	8
Shorea atrinervosa (Dipterocarpaceae)	SS	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	LS	13	9	2	2	6	7	0	0	12	1	5	8	0
	Tree	68	46	12	10	36	30	2	7	47	14	18	49	1
Shorea maxwelliana (Dipterocarpaceae)	SS	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	LS	90	72 ++	14 -	4 -	29	51	10	25	64	1	12	65	13
	Tree	192	154 ++	27 -	11	69	89	34	51	138	3	42	127	23
Swintonia schwenkii (Anacardiaceae)	SS	228	128	87	13	141	74	13	2	214 ++	12	49	175	4
	LS	184	133 +	45	6 -	93	75	16	6	171 ++	7	38	140	6
	Tree	89	65 ++	17	7 -	33	45	11	13	69 +	7	18	67	4