

Habitat associations of trees and seedlings in a Bornean rain forest

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Summary

1 In species-rich mixed dipterocarp rain forest in Indonesian Borneo, we evaluated evidence for tree species associations with physical habitat variables (physiography for adults and seedlings, and light for seedlings). A total of 325 species were included in the analysis.

2 A stratified random sample of 28 tree and seedling plots (0.16 ha and 36 m², respectively) was taken from a 150-ha study area on homogeneous parent rock (granite) between 110 and 270 m a.s.l.

3 In a principal component analysis (PCA), based on an abundance index of all tree species, plots segregated into three groups. These corresponded closely with the three physiographically defined habitat types assigned in the field: (i) plateaux with a deep humus layer, (ii) sharp ridges and upper slopes, and (iii) gullies and lower slopes near permanent streams. Segregation of plots by habitat was weaker when seedling (rather than tree) species abundance was used in the PCA.

4 In single species analyses, using Monte Carlo randomization tests, we found significant associations with the three physiographic habitat types in 17 out of 49 abundant species for trees, and in 5 out of 22 abundant species for seedlings. In PCA and single species analyses, weaker associations with habitat for seedlings than for trees suggest higher mortality of seedlings in 'suboptimal' habitats.

5 Seedlings of 8 out of 45 abundant species were also significantly and positively associated with high light availability (measured in 2 × 2 m subplots, using hemispherical photographs).

6 Combining light and physiographic habitat associations, 20 out of the 45 abundant species were associated with at least one habitat factor as either adults or seedlings.

7 Thus, the distributions and abundances of many species are influenced by local heterogeneity in physical habitat variables. However, about half of the abundant species (25 of 45) showed no significant habitat association as adults or seedlings, and in no case did the relative abundance of any species exceed 5% in its 'preferred' habitat.

Key-words: environmental heterogeneity, habitat partitioning, maintenance of species diversity, understorey light level

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Introduction

The association of species with physical habitat variables generates some of the most obvious patterns in the distribution and abundance of organisms, and its study has a long history (Cowles 1899; Whittaker 1956). Differences among species in their habitat

associations with, for example, soil type or elevation clearly contribute to species diversity on a landscape scale. However, the role of habitat heterogeneity in maintaining the high tree species richness of tropical rain forest has been more controversial. Tropical rain forests may contain many tree species even in very small areas (up to 283 species per hectare; Phillips *et al.* 1994).

Theoretical models exist that predict coexistence of plant species based on habitat heterogeneity (summarized in Tilman & Pacala 1993). However, on the scales relevant to adult trees, it has been

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unclear whether actual habitat heterogeneity in rain forests, and the responses of species to that heterogeneity, are sufficient to maintain the local coexistence of so many species. Perhaps the most influential hypothesis for habitat partitioning in rain forest trees relies not on any underlying heterogeneity in the physical environment, but on the endogenous, local heterogeneity generated by canopy openings. The death of canopy trees creates localized patches on the forest floor ('gaps') where seedlings experience modified habitat conditions, including much higher light intensities than in the understorey (Brown & Whitmore 1992). Seedlings of many species do respond to canopy gaps, and some are so dependent on gaps as to be termed 'gap specialists' (Denslow 1987).

It has been proposed that there may be sufficient heterogeneity in light and other physical factors in and around canopy gaps to explain the coexistence of tree species. This is an example of the 'regeneration niche' hypothesis of Grubb (1977, 1996) who proposed that, in many plant communities, habitat partitioning is most plausible at the seedling level, where habitats may be more heterogeneous than those experienced on the scale of adult plants. Other workers, for example Brokaw (1985b) and Denslow (1987), have developed this hypothesis in more detail for the case of canopy gaps in tropical rain forests. However, research on gap habitats and species responses at the seedling level has not yet established a clear basis for the coexistence of so many species in the rain forest canopy.

The lack of conclusive evidence for substantial habitat partitioning has led to increased focus on alternative hypotheses, many of which involve the role of natural enemies in distance and density-dependent mortality of juveniles (Janzen 1970; Connell 1971; Condit *et al.* 1994; Gilbert *et al.* 1994), and the disproportionate mortality of more abundant species ('compensatory mortality', Connell *et al.* 1984; Webb & Peart 1999). In addition, Hubbell (1979) demonstrated that the existence of high tree species richness does not necessarily imply either habitat partitioning or the density-dependent effects of natural enemies: he was able to simulate the long-term coexistence of many species that experience random walk dynamics in an environment without any spatial heterogeneity at all.

Resolving the role of habitat in maintaining tree species diversity in rain forests will depend in part on the analysis of species' habitat associations. Habitat associations alone cannot demonstrate that habitat partitioning is the basis of species coexistence. However, if habitat partitioning is important, we should certainly see evidence in the spatial distributions of species, either as adults, as seedlings, or both.

A comparison between seedlings and adults in the same community can be especially informative in

elucidating the importance of habitat and its interaction with stage of the tree life cycle. We consider the case of physical habitat heterogeneity (as influenced by local topography and soil conditions), on a scale large enough to include and influence adult trees. If we assume that the habitat with which a species is associated (if any) is the same at the seedling and adult stages, the strength of habitat association may follow one of three patterns: (i) seedlings less strongly associated with habitat than adults, (ii) seedlings and adults similarly associated, or (iii) seedlings more strongly associated with habitat than adults.

The first result could occur if seedling survival is best in the habitat with which adults are associated, leading to increasingly strong habitat associations as seedlings grow into adults. However, in each reproductive cycle, seed dispersal out of the optimal habitat should regenerate seedling distributions with weaker habitat associations than those of adults, and the greater the mean seed dispersal distance, the weaker the expected seedling habitat associations. The second result would suggest that seeds are dispersed into the same habitat as their parents, due either to localized dispersal or transport by dispersers with high habitat fidelity. The third result could occur if seedlings established at high densities in their most suited physical habitat, but negative density dependence in seedling survival (e.g. Schupp 1992; Condit *et al.* 1994; Webb & Peart 1999) were so strong there that it outweighed the benefits of optimal seedling habitat, and led to the adults no longer being associated with that habitat. Differences in dispersal and seedling ecology may, therefore, lead to species differing in their observed patterns of seedling vs. adult habitat associations (i–iii, above).

Our knowledge of habitat associations for rain forest tree species is limited, but is more extensive for adult trees than for seedlings. In most cases where spatial variation in the abundances of species of trees has been studied, associations have been found with habitat variables. These include elevation (Lieberman *et al.* 1985), soil nutrients (Gartlan *et al.* 1986; Baillie *et al.* 1987), drainage (Newbery *et al.* 1986; Hubbell & Foster 1986a), soil texture (Davies *et al.* 1998), light availability (Lieberman *et al.* 1995), and topography (Poore 1968; Austin *et al.* 1972; Whitmore 1973; Ashton 1976; Hubbell & Foster 1986a; see reviews by Whitmore 1984; Richards 1996). There are very few studies of seedling species composition in relation to physiographic habitat, but these have shown associations with soil moisture (Russell-Smith 1996) and small-scale soil disturbance (Raich & Christensen 1989; Ellison *et al.* 1993). To our knowledge, there has been no comparative analysis of both adult and seedling habitat associations in a rain forest community.

In this study, we evaluate evidence for habitat association in both trees and seedlings within a local (*c.* 150 ha) area of rain forest in Indonesian Borneo. We examined spatial variation in species' abundances at both life stages, in relation to physiographic habitat (defined here as topographic position, with associated moisture and soil regimes), and (for seedlings) light conditions on the forest floor.

We addressed these questions: (i) are tree and seedling distributions associated with physiographic habitat at the species level, and/or at higher taxonomic levels; (ii) are seedlings associated with light conditions on the forest floor; and (iii) do seedlings and adults differ in the strength of their physiographic habitat associations?

Materials and methods

STUDY AREA

Gunung Palung National Park (West Kalimantan, Indonesia; 1°15' S, 110°10' E) is a 90 000 ha protected area on the south-west coast of the island of Borneo. It contains a wide range of forest types, ranging from mangrove swamp and lowland forest up to montane forest at the summit of the granite mountain, Gunung (Mt.) Palung (1110 m a.s.l.). Since its protection in 1937, the park has been undisturbed by humans, except for some non-mechanized (hand) logging of Bornean ironwood (*Eusideroxylon zwageri* Teijsm. & Binn., Lauraceae) and gaharu (*Aquilaria malaccensis* Lamk., Thymelaeaceae). In particular, vertebrate seed dispersers appear to be at natural densities (M. Leighton, unpublished data).

We studied dipterocarp hill forest (*sensu* Whitmore 1984) on the west slope of Gunung Palung, between 110 and 270 m a.s.l. The general study site was chosen because of its relatively homogeneous parent rock (granite), soil type (tropudult; Indonesian Department of Transmigration & Overseas Development Agency 1987; Soil Survey Staff 1975; Petersen 1991), soil texture (sandy-clay to sandy-clay-loam; Soil Survey Staff 1975), and limited elevational range. However, within the study area there is minor variation in physiography: broad- to narrow-topped ridges, steep slopes, up to *c.* 40°, and narrow valleys with streams. The potential causes of differences among plant species in physiographic distribution include differences in nutrient requirement, drought tolerance, or mechanical tolerance of shifting soil on slopes (Burgess, cited in Whitmore 1984; Whitmore 1984; Bowman & Panton 1993; Burslem 1996).

RESEARCH DESIGN

We sampled the tree community (≥ 10 cm d.b.h.) within 28 tree plots (0.16 ha each) spread over a

total area of *c.* 150 ha in a stratified random pattern. Centred in each tree plot was a 36-m² seedling plot, in which we recorded all tree seedlings (≥ 5 cm tall, but < 1 cm d.b.h.). To assess physical habitat variables at each site, we buried a soil moisture sensor (at 15 cm depth), and collected samples of topsoil (0–5 cm depth) and subsoil (10–15 cm depth) near each seedling plot.

Our approach to analysis was first to explore the vegetation data alone, using principal component analysis (PCA) to examine the variation among tree plots with respect to species composition and abundance. We then compared these results with the physical habitat variables measured at each plot, to determine if ordination-defined vegetation groups could be explained by habitat variation. Ordination can separate groups that have only minor differences in the abundance of species, but with those differences occurring in many species. We also explored whether separate species had significant spatial associations with habitat, using both randomization tests and contingency table, goodness-of-fit analysis.

To examine how seedlings are associated with habitat, we first ordinated the abundance of seedling species in the seedling plots, and then tested for significant species-specific associations of seedlings with habitats. While physiographic habitats are fixed in space (on an ecological time-scale), variation in the light resource occurs in both space and time. As seedlings in a canopy gap grow to adults they change the light environment near the ground, and thus we would not expect trees of light-demanding species to be spatially associated with high light environments on the forest floor. We therefore tested for the association of seedlings, rather than trees, with the light level estimated from hemispherical photographs.

TREE AND SEEDLING INVENTORY

Plot locations (Fig. 1) were stratified by total seedling density (0–10 m⁻², 11–20 m⁻², ≥ 21 m⁻²), to sample seedlings that were experiencing a wider range of local densities than would be obtained by random sampling (Webb 1997; Webb & Peart 1999). Plots were also stratified by elevation (low, medium, high; not related to habitat categories shown in Fig. 1) and ridge system (north vs. south). Within this stratification system, plots were located randomly, by travelling to random points in the forest and accepting or rejecting each site, based on which type of plot was being sought.

To increase the range of seedling light environments, we centred an additional 10 plots in canopy gaps (defined as a 5 × 5 m, or larger, column of empty space, reaching down from the canopy to a height above the ground of no more than 1 m; the column could be inclined up to 20° from the vertical). Despite extensive searches of the *c.* 150 ha area,

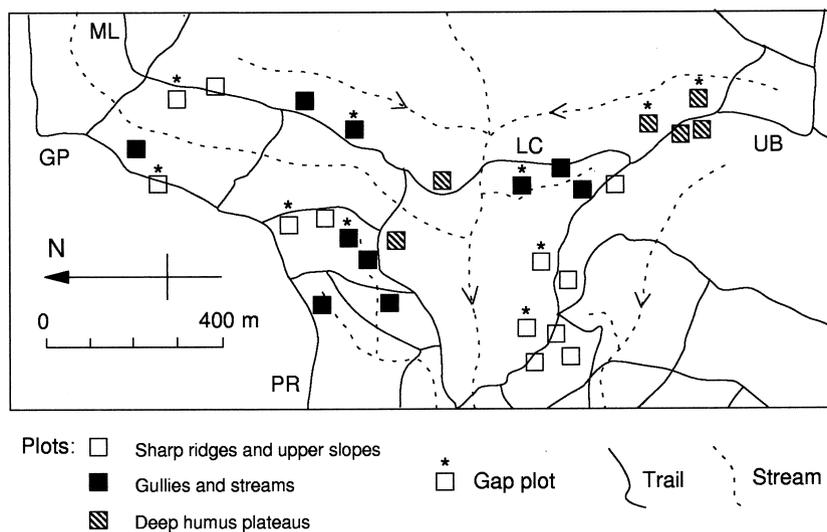


Fig. 1 Study site at Gunung Palung (West Kalimantan, Indonesia), showing 28 plots classified by physiographically defined habitat type. Each tree plot is 40×40 m. The land slopes downwards from east to west, and the GP and UB trails lie on major ridges.

no gaps larger than *c.* 100 m^2 were located (maximum canopy openness: 4.6%, by hemispherical photography). This contrasts with other tropical forests where large gaps are much more common (Brokaw 1985a; Hubbell & Foster 1986b; Brown & Whitmore 1992). The density and species composition of trees in a plot was not affected by the presence of a gap (density: ANOVA, d.f. = 1, $F = 3.18$, $P = 0.086$; composition: ANOVA, no significant effect of gap on PCA axes I, II or III of Fig. 2a, b; see Results). Nor was tree density associated with the density or species composition of seedlings in the centrally located seedling plot (tree density: Pearson correlation, $r^2 = 0.026$, $P = 0.89$; species composition: no significant correlation of seedling density with PCA axes I, II or III of Fig. 2a, b). Plots were therefore pooled over these stratification levels (gap vs. non-gap, and seedling density) for all analyses.

At each plot location, a 6×8 m seedling plot, divided into nine subplots of 4 m^2 (with two 6×1 m unmeasured walkways), was centred within a 40×40 m tree plot. In July 1996, the seedling density (≥ 5 cm tall to ≤ 1 cm d.b.h.) of each of the 28 most abundant seedling species (over all plots) was recorded in three of the subplots (diagonally arranged). Densities of the less abundant species were measured in all nine of the subplots.

All trees (≥ 10 cm d.b.h.) were identified in the 0.16 ha tree plot. For each tree species, we collected fallen leaf specimens from around the base of the tree, and flower and fruit specimens when available. These vouchers were matched with named botanical specimens in the Herbarium Bogoriense and Harvard University Herbaria. We found 325 species

in 4.48 ha, belonging to 50 families, with Dipterocarpaceae the most abundant family in terms of tree density. See Webb (1997) for a full species list.

Seedlings were identified using field characters (Burger Hzn 1972; de Vogel 1980; Ng 1992; Webb & Curran 1996), and by matching with adults of the same species. Matching criteria (in decreasing order of importance) were: (i) seedlings germinated from seeds collected from an adult, (ii) detailed matching of morphological characters expressed in both seedlings and adults, (iii) concentration of conspecific seedlings around known adult trees. Of the 325 species in the tree plots, 81% were matched to seedlings with high confidence, 9% were matched with low confidence, and 8% of tree species were not encountered as seedlings. Analyses involving both adults and seedlings use only those species that were matched to a high level of confidence.

LIGHT MEASUREMENTS AND SOIL SAMPLES

In April 1996, we took hemispherical photographs of the underside of the canopy, from a height of 90 cm above the centre of each of five seedling subplots (four corner and one central subplots) at each location. We used a Sigma 8 mm f4 fish-eye lens, mounted on an Olympus OM-1 body, with 400 ASA Ektachrome colour slide film. Photographs were under-exposed by three stops, to increase contrast between the sky and foliage. After developing, slides were digitized using a Polaroid SprintScan 35 slide scanner and the blue spectrum was analysed with an image processing program, GLI/C (Canham 1995). This program computes a Gap Light Index

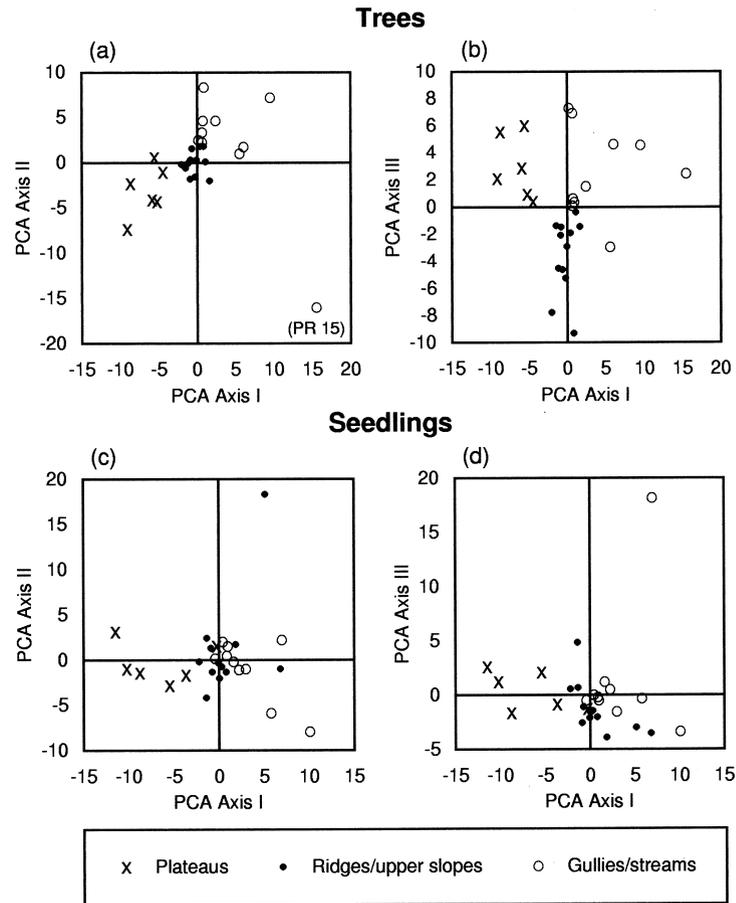


Fig. 2 Principal component analysis of the species abundance index of adults (≥ 10 cm d.b.h.) (parts a and b) and seedlings (≥ 5 cm tall to ≤ 1 cm d.b.h.) (parts c and d) in 28 plots (0.16 ha for adults, 36 m² for seedlings). $\log_{10}(N + 1)$ transformation was used on species abundance indices (see Methods). Variation (%) explained by each axis: trees (a, b), I = 7.88, II = 6.43, III = 5.44, and seedlings (c, d), I = 9.37, II = 7.42, III = 6.48. Correlations of PCA axes with environmental variables are given in Table 1. Symbols indicate independently assigned physiographic habitat.

(GLI; Canham 1988) that estimates the percentage of photosynthetically active radiation reaching the point where the photograph was taken. GLI integrates both direct and diffuse light (Direct and Indirect Site Factors; Mitchell & Whitmore 1993), and is directly comparable to Global Site Factor (Clark *et al.* 1993) and Total Site Factor (Whitmore *et al.* 1993). GLI values for subplots in which photographs were not taken were estimated by the mean measured GLI of the adjacent three subplots.

At each location, soil samples were collected from three points on the perimeter of the seedling plot (at two adjacent corners and the middle of the opposite side). We extracted a 2-cm diameter core of the topsoil (0–5 cm depth) and of the subsoil (10–15 cm depth) at each point, bulked the samples of each layer from the three collection points, and dried them overnight at *c.* 70 °C. Topsoil samples were analysed at the Cornell Nutrient Analysis Laboratories (Cornell Cooperative Extension/Department of Soil, Crop and Atmospheric

Sciences, Ithaca, NY) for available cations (Morgan's solution; procedure 1100), total phosphorus ($\text{Mg}(\text{NO}_3)_2$ ashing; procedure 2601), and organic matter (percentage loss-on-ignition; procedure 1810). Subsoil samples were analysed for soil texture, using a hydrometer method (Day 1965; Sheldrick & Wang 1993; clay/silt settling time boundary: 2 h).

In November 1993, a gypsum conductance block (*c.* 4 × 2 cm), used for soil moisture measurement, was buried to 15 cm depth in the central subplot at each plot location. Conductance readings were taken every 2 weeks at all plots with a hand-held meter (KS-D1, Delmhorst Instrument Company, Towaco, NJ), and converted to soil matric potential (MPa). Mean matric potential for each plot was calculated over November 1993 to January 1995, and the most extreme potential was noted (observed for all plots on 19 September 1994, after a 4-month drought). Matric potential becomes more negative with decreasing soil moisture (Jenny 1980).

Spatial aggregation in either trees or seedlings would lead to non-independence of samples from neighbouring subplots within a plot. We therefore used indices of abundance at the plot level in our analyses. For seedlings, we used the number of 4-m² subplots in each seedling plot (36 m²) in which seedlings of a species occurred (an index ranging from 0 to 9). We scored adult abundance for each plot by the number of 10 × 20 m subplots in which a species occurred within the 40 × 40 m plot (an index ranging from 0 to 8). Principal component analyses of tree and seedling species composition were performed on the correlation matrix of log₁₀(N + 1)-transformed species abundance indices, using JMP software (SAS Institute 1995).

We tested single species habitat association using two methods. In the first, we simply compared the observed abundance indices of a species, summed among plots within a habitat type, with expected values (based on the sum of abundance indices of all species in each habitat), using a maximum likelihood χ^2 test (SAS Institute 1990). We used a second, randomization test of single species habitat associations, to avoid the problem of non-independence (caused by spatial clumping of individuals, Hubbell 1979) that invalidates the standard contingency test. If many individuals of a species occur in one or a few plots of one habitat type, due solely to the proximity of parent trees, a spurious statistical association between the species and the habitat could occur (Clark *et al.* 1998). We therefore shuffled the habitats on which each of the 28 tree plots occurred, and calculated a deviation statistic based on the abundance indices of species in each habitat type: $\Sigma[(\text{Randomized} - \text{Expected})^2 / \text{Expected}]$. We repeated this 1000 times for each species and compared the observed deviation value with this randomized distribution of deviation values. We considered observed values more extreme than 95% of these randomized values to indicate significant habitat association.

To test for an association of a particular species of seedling with light level, we modelled the presence or absence of a seedling of that species in each 2 × 2 m seedling subplot (a total of 252 subplots) with a logistic regression against log₁₀ GLI (Menard 1995).

Results

We first explored associations among tree plots with PCA, using only the data on tree species composition and abundance in the plots. From this analysis, three groups of plots were apparent (Fig. 2a, b); they were most clearly separated by plotting the first and third PCA axes (Fig. 2b). These groups, defined on the basis of the tree data alone, corresponded closely to the independent physiographic classifica-

tion of habitat that was done for the same plots in the field (see Fig. 1 and symbols in Fig. 2): (i) upper slopes and narrow ridges without humus accumulation, (ii) plateaus and wide ridges with ≥ 3 cm of black humus (peat) accumulation above the mineral soil, and (iii) lower slopes within 10 m of a permanent stream, and plots containing gullies and seasonal streams. The lowest elevation plot (PR15) was an extreme outlier in the PCA (Fig. 2a), probably due to a species composition more characteristic of forest on quartzite- and sandstone-derived soils at lower elevation (C. H. Cannon & M. Leighton, unpublished data).

The first PCA axis was most strongly correlated with elevation, soil organic matter, and soil nutrients; the third axis with soil texture and moisture, while the second axis was not strongly correlated with any of the measured variables (Table 1). The three habitat types that were defined visually, based on physiography, differed in physical factors that were measured in plots in each type (Fig. 3). The plateau plots had the highest mean elevation (Fig. 3a), highest soil organic matter (Fig. 3b), sandiest soil (Fig. 3c), the lowest drought stress (Fig. 3f), and highest levels of plant-available nutrients (K, Mg, Ca; Fig. 3h, i, j). The relatively low total phosphorus in the plateau plots (Fig. 3g), contrasts to the relatively high availability of other nutrients (Fig. 3h, i, j). This difference may be explained by the lower percent mineral soil and lower clay content of plateau soils, and by the fact that phosphates originate in mineral soil (as apatite) and bind strongly to clay particles (Jenny 1980). The plateau plots also had the highest densities of trees (Fig. 3k), and lowest basal area (Fig. 3l). The ridge and gully plots were generally similar in habitat variables, but the ridge plots were drier during the drought (Fig. 3f).

The segregation of plots by habitat in the PCA, on the basis of species composition alone, is reflected in the significant associations between species distributions and the three habitat types (Fig. 4a). Out of 49 species with sufficient numbers of trees for contingency analysis ($\geq 20\%$ of cells must have expected values ≥ 5 ; codes for the species concerned and total numbers of their stems are given in Table 2), 21 species (42%) were significantly associated with habitat type (likelihood χ^2 test, $P \leq 0.05$). Of these 21 species, eight were negatively associated with one habitat and jointly, positively associated with the other two habitats (e.g. PARCOS, CALNOD in Fig. 4a). The remaining 28 of 49 species were not significantly associated with any habitat. Using the alternative randomization method, which is more conservative (see Methods), only 17 out of 49 species (34%) were significantly associated with habitat type(s) (those without asterisks in Fig. 4a). Note that with 49 tests at a significance level of 0.05, we expect only 2–3 false associations of species with habitat, i.e. by chance alone.

Table 1 Pearson product-moment correlation coefficients for physical variables and the first three axes of the principal component analysis of tree species abundance in 28 plots of 0.16 ha (Fig. 1). Bold type indicates the PCA axis most strongly correlated with each physical habitat variable

Physical habitat variable	Correlations with axes of tree abundance PCA		
	Axis I	Axis II	Axis III
Elevation (m a.s.l.)	-0.521	-0.243	0.204
Organic matter (% loss-on-ignition)	-0.674	-0.156	0.152
Organic horizon depth (cm)	-0.370	-0.257	0.222
Sand (%)	-0.158	-0.078	0.311
Clay (%)	0.184	0.030	-0.275
Mean matric potential (MPa)	-0.187	-0.053	0.223
Maximum matric potential (MPa)	-0.021	0.041	0.264
Total P (mg kg ⁻¹)	0.645	-0.094	-0.178
Available K (mg kg ⁻¹)	-0.520	0.111	0.216
Available Mg (mg kg ⁻¹)	-0.567	0.089	0.252
Available Ca (mg kg ⁻¹)	-0.050	0.197	0.389

We also evaluated habitat associations for higher taxonomic levels, by calculating the same per-plot abundance index (0–8) for tree genera and families, and testing with χ^2 and randomization methods (Fig. 4b, c). Using the latter method, 14 out of 48 genera (29%) and 4 out of 28 families (14%) had significant associations with habitat. For those families in Fig. 4c that included one or more species in Fig. 4a, we can compare habitat associations at the family and species level: two families are associated with the same habitat as all their species, six families and all their species were non-associated, three families are associated, but have some non-associated species, and nine families are non-associated, but contained some associated species. Because the same abundance indices were used, the tests have similar power for the different taxonomic levels, despite higher numbers of individuals per taxon at higher taxonomic levels.

Of the 22 species whose physiographic habitat associations were tested at the seedling level (using the randomization method), five species were significantly associated with habitat (compared to 21 out of 49 at the tree level), and only two species had habitat-association patterns similar to conspecific adults (Table 3). Nine species were habitat-associated as adults but not as seedlings, while only three species were not associated with habitat as adults but were habitat-associated as seedlings. Eight species showed no habitat association at either the adult or seedling stage. The segregation of plots into groups in the PCA based on seedling abundances was less strong than for the adult-based PCA (Fig. 2c, d). Together, these comparisons of adults and seedling associations suggest that species of seedlings are less strongly associated with habitat than are adults.

Seedlings of 8 out of 45 species for which their trees were abundant had significant positive associations with light (Fig. 5; the 45 species were those from the 49 in Fig. 4a that were identified as seedlings with high confidence). Of these eight species, only *Chaetocarpus castanocarpus* has very small seeds (C. O. Webb, unpublished data), typical of 'pioneer' species, *sensu* Swaine & Whitmore 1988). True pioneer species, such as *Macaranga* spp. (Euphorbiaceae), are rare in this forest, probably due to the low density of large gaps. No *Macaranga* trees were encountered in the sample of 2862 trees in the tree plots, even though trees of this genus do grow to more than 10 cm d.b.h. (Davies *et al.* 1998).

There was no significant difference in mean GLI of subplots among the three physiographic habitat types (ANOVA, d.f. = 2, $F = 2.18$, $P = 0.114$). We therefore consider the light and physiographic habitat associations to be independent. Comparing the light and physiographic habitat associations (of seedlings and adults, respectively) for 45 species, we found that 25 species (55%) were not habitat-associated for either factor, 4 species were habitat-associated for both factors, and 16 species were associated with only one factor. Thus, 45% of the species showed significant association with at least one habitat factor.

Discussion

TREE HABITAT ASSOCIATIONS

This study demonstrates that there are significant associations of species with variation in physiography, within an area that is homogeneous in parent rock and limited in spatial and elevational range. Similar differences in species composition related to physiography within a locality have been found else-

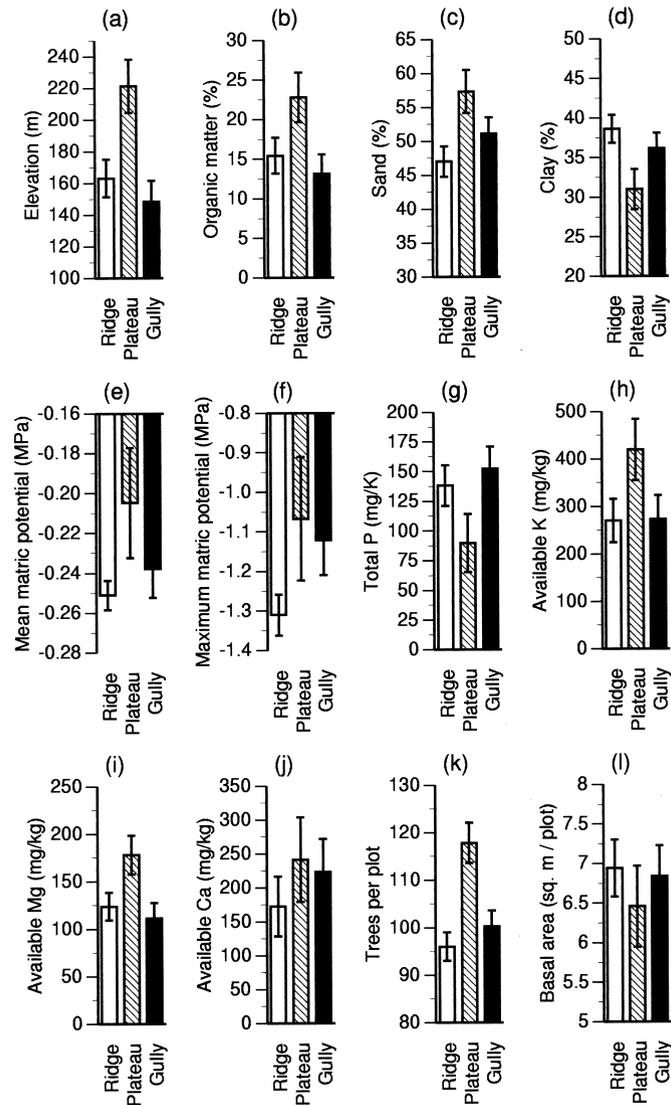


Fig. 3 Mean values of physical factors by physiographically defined habitat type (ridges and upper slopes; plateaux with deep humus layer; gullies, streams and lower slopes), with standard errors: (a) elevation (m a.s.l.); (b) organic matter of topsoil (0–5 cm depth); (c) percentage sand in subsoil (10–15 cm depth); (d) percentage clay in subsoil; (e) mean soil matric potential over 14 months (November 1993 to January 1995) (note that a more negative value indicates drier soil); (f) maximum soil matric potential at the end of a 4-month drought; (g) total extractable P in topsoil; (h) available K in topsoil; (i) available Mg in topsoil; (j) available Ca in topsoil; (k) numbers of stems ≥ 10 cm d.b.h. in 0.16 ha tree plots; and (l) basal area in 0.16 ha, of trees ≥ 10 cm d.b.h.

where in Borneo (Austin *et al.* 1972; Whitmore 1973; Baillie *et al.* 1987), Peninsular Malaysia (Poore 1968; Ashton 1976), Africa (Gartlan *et al.* 1986; Newbery *et al.* 1986), and Central America (Lieberman *et al.* 1985; Hubbell & Foster 1986a; Clark *et al.* 1998). However, Wong & Whitmore (1970) did not find any association between tree species distributions and soil factors at Pasoh, Malaysia, and Whitmore (1984) has suggested that the greater local variation in species composition recorded in northern Borneo, compared to Peninsular Malaysia, may be due to the greater pre-

valence of sharply dissected ridges and valleys in the former.

Of the 49 abundant species we tested, 42% showed significant associations with physiographic habitats (χ^2 test). This was a slightly higher proportion than that of Hubbell & Foster (1986a) who, using similar statistical methods, found habitat associations in 15 (36%) of the most abundant 41 species at Barro Colorado Island (BCI), Panama. However, our site at Gunung Palung encompassed a wider elevation range (157 m) than the BCI plot (39 m), with more extreme slopes and sharper ridges.

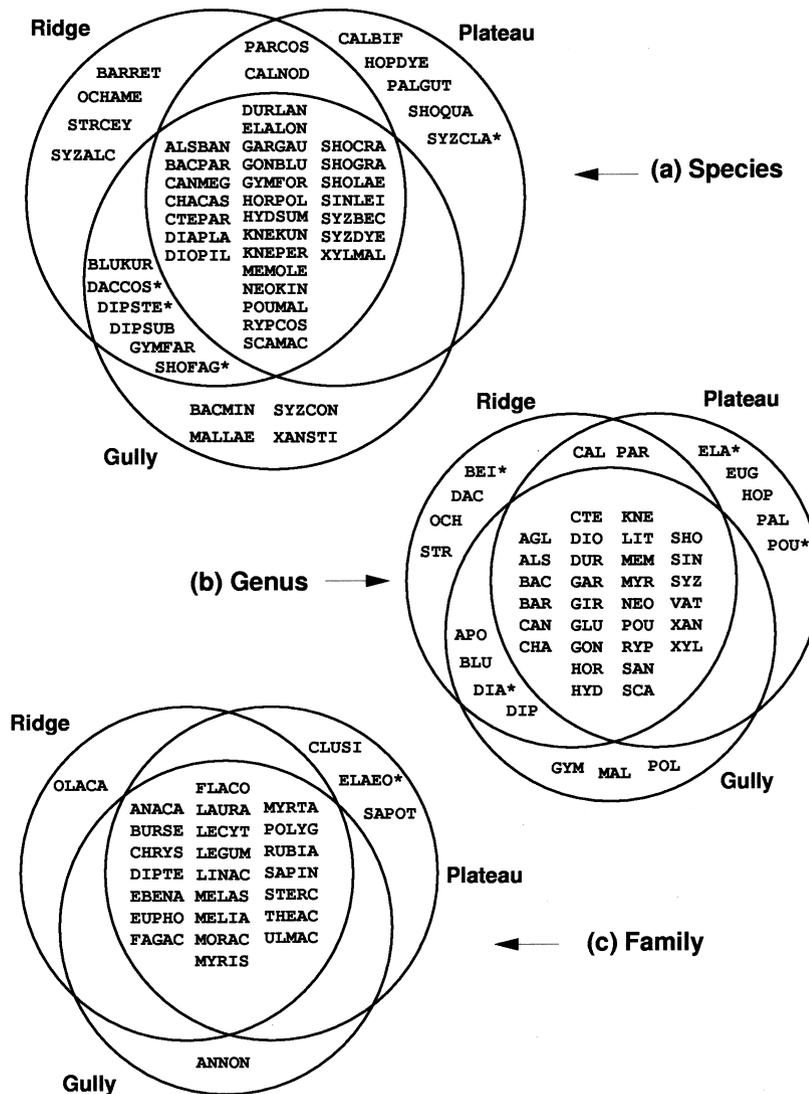


Fig. 4 Venn diagrams showing associations of abundant (a) species, (b) genera and (c) families of trees (≥ 10 cm d.b.h.) with physiographically defined habitats. Habitats are (i) ridges and upper slopes, (ii) plateaux with deep humus layer, and (iii) gullies, streams and lower slopes. Significance of association was determined with χ^2 and randomization tests; an asterisk indicates that the association was significant only with the less stringent χ^2 test. Negative association with a habitat is indicated by taxon code in the intersection of the two other habitats, e.g. PARCOS in (a). Taxon codes are explained in Table 2.

Clark *et al.* (1998) found significant association with particular topographic position, within a soil type in Costa Rica, for 6 out of 9 abundant species (66%), and Svenning (1999) found significant association with microhabitat variables in 20 out of 31 palm and palm-like plants in Amazonian Ecuador (64%).

Our results from the standard contingency table analyses were not greatly different from the more rigorous randomization tests, suggesting that non-independence due to clumping (on the scale of 40×40 m) may be low in trees ≥ 10 cm d.b.h., a conclusion also reached by Clark *et al.* (1998) for trees ≥ 4 cm d.b.h. at La Selva, Costa Rica.

Ashton (1988) has suggested that taxa at higher levels than the species may be the natural groups among which selection has led to niche differentiation. If this were true then we should expect to find the strongest evidence for habitat specialization among higher-level taxa, with taxa at lower levels (confamilials, congeners) tending to share the same habitat associations. We found that the proportion of habitat-associated taxa decreased from the species to the family level (with similar power in tests at the different levels). While there are examples of families and genera whose lower-level taxa have the same habitat associations (e.g. Olacaceae, Flacourtiaceae;

Table 2 Families, genera and species of trees analysed for association with habitat factors in Fig. 4, with codes. The number of trees (≥ 10 cm d.b.h.) in 4.48 ha is given for each species. Total tree species in 4.48 ha of tree plots was 325

	Family	Genus	Species	Stems
ANACA	Anacardiaceae	<i>Gluta</i>	GONBLU	17
ANNON	Annonaceae	<i>Goniothalamus</i> <i>Polyalthia</i> <i>Xylophia</i> <i>Durio</i> <i>Canarium</i> <i>Daeryodes</i> <i>Santiria</i> <i>Parinari</i> <i>Calophyllum</i>	<i>G. sp. 'BLU'</i> <i>X. malayana</i> Hk. f. Th. <i>D. lanceolatus</i> Mast. <i>C. megalanthum</i> Merr. <i>D. costata</i> (Benn.) Lam. <i>P. costata</i> (Korth.) Bl. <i>C. biflorum</i> Henderson Wyatt-Smith <i>C. nodosum</i> Vesque <i>G. gaudichaudii</i> Planch. Triana <i>D. stellatus</i> Vesque <i>D. sublamellatus</i> Foxw. <i>H. dyeri</i> Heim <i>S. crassa</i> Ashton <i>S. faguetiana</i> Heim <i>S. grattissima</i> (Wall. ex Kurz) Dyer <i>S. laevis</i> Ridd. <i>S. quadrinervis</i> Sloot.	
BOMBA	Bombacaceae			19
BURSE	Burseraceae			14
				15
				14
CHRY5	Chrysobalanaceae			19
CLUSI	Clusiaceae			70
				81
				15
DIPTE	Dipterocarpaceae	<i>Garcinia</i> <i>Dipterocarpus</i> <i>Hopea</i> <i>Shorea</i>		91
				57
				53
				71
				45
				15
				19
				50
EBENA	Ebenaceae	<i>Vatica</i>		22
ELAEO	Elaeocarpaceae	<i>Diospyros</i> <i>Elaeocarpus</i>	DIOPIL ELALON	18
EUPHO	Euphorbiaceae	<i>Aporosa</i> <i>Baccaurea</i> <i>Blumeodendron</i> <i>Chaetocarpus</i> <i>Mallotus</i> <i>Neoscorthechinia</i> <i>Lithocarpus</i> <i>Hydnocarpus</i> <i>Ryparosa</i> <i>Alseodaphne</i> <i>Beilschmiedia</i> <i>Barringtonia</i>	BACPAR BACMIN BLUKUR CHACAS MALLAE NEOKIN HYDSUM RYPKOS ALSBAN BARRET	40 14 15 25 26 39
FAGAC	Fagaceae			21
FLACO	Flacourtiaceae			22
LAURA	Lauraceae			27
LECYT	Lecythidaceae			69

Family	Genus	Species	Stems
LEGUM	Dialium	<i>D. platysepalum</i> Baker	26
	Sindora	<i>S. leiocarpa</i> Baker ex de Wit	16
LINAC	Ctenolophon	<i>C. parvifolius</i> Oliv.	15
MELAS	Memecylon	<i>M. oleifolium</i> Bl.	18
MELIA	Aglaiia		
MORAC			
MYRIS	Gymnacranthera	<i>G. farquhariana</i> var. <i>eugenifolia</i> (A. DC.) R. Schouten	28
		<i>G. forbesii</i> var. <i>forbesii</i> Sinclair	22
	Horsfieldia	<i>H. polyspherula</i> var. <i>sumatrana</i> (Miq.) de Wilde	19
	Knema	<i>K. kunstleri</i> (King) Warb.	23
		<i>K. percoriacea</i> Sinclair	22
MYRTA	Myristica		
	Eugenia	<i>S. alcine</i> (Merr.) M. P.	22
	Syzigium	<i>S. becarii</i> Ridl.	14
		<i>S. clavatum</i> (Korth.) M. P.	15
		<i>S. confertum</i> (Korth.) M. P.	37
		<i>S. dyeriana</i> King	29
		<i>O. amentacea</i> Mast.	23
OLACA	Ochanostachys	<i>S. ceylanica</i> Gardn.	102
	Strombosia	<i>X. stipitatum</i> A. W. Benntt	15
POLYG	Xanthophyllum		
RUBIA			
SAPIN			
SAPOT			
STERC	Palaquium	<i>P. gutta</i> (Hk. f.) Baillon	53
THEAC	Pouteria	<i>P. malaccensis</i> (Clarke) Baehni	46
ULMAC	Scaphium	<i>S. macropodium</i> (Miq.) Beumee ex Heyne	50
	Girromitera		

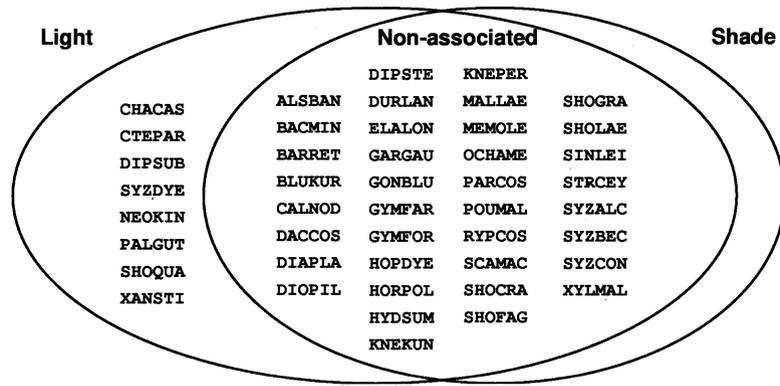


Fig. 5 Venn diagram showing spatial associations of seedlings with light for 45 species (identified with confidence as seedlings) from Fig. 4a. Species with significant ($P \leq 0.05$) positive associations of seedling presence with light are listed in the left-hand ellipse (see text for significance test). No species were negatively associated with light. Species with no significant associations with light are in the intersection of the two ellipses. Species codes are explained in Table 2.

Fig. 2), the majority of taxa show increasing specialization at lower taxonomic levels (e.g. Dipterocarpaceae and Euphorbiaceae). These data therefore do not indicate that physiographic habitat specialization occurs primarily at the genus and family level. It remains possible, however, that analysis of patterns in all species present, rather than just the abundant ones, might reveal such a trend (see Webb, in press).

SEEDLING HABITAT ASSOCIATIONS

Because seedfall tends to be denser near parent trees, we expect seedling and adult distributions to be spatially associated (Hubbell 1979; Ribbens *et al.* 1994). However, some seedlings, especially those of

widely dispersed species, may establish in habitats with which parents are not associated. Nine species were habitat-associated as trees but not as seedlings, a pattern consistent with an expansion and contraction of species' habitat distributions over the stages of the life cycle. Seedlings were apparently dispersing and establishing widely, but suffering higher mortality outside the optimal habitat type, leading to the observed habitat associations of adults. Three species did show the opposite pattern of association, with seedlings habitat-associated and adults not associated, and may be exhibiting the alternate mechanism (iii) suggested in the Introduction, with high survival of rare recruits to suboptimal habitats and high density-dependent mortality of abundant seedlings in optimal habitats. A rigorous test of the

Table 3 Comparison of physiographic habitat associations of adults and seedlings. Significance of associations was tested with Monte Carlo randomizations (see text). The habitats with which species are associated are Ridge (R), Plateau (P) and Gully (G). Adult associations are the same as in Fig. 4a. All species were included (i) that had sufficient numbers of both adults and seedlings to satisfy the sample size condition of contingency analyses (see text), and (ii) for which seedlings had been matched to adults with high confidence

Seedlings	Adults	
	Non-associated	Associated
Non-associated	<i>Alseodaphne bancana</i> <i>Dialium platysepalum</i> <i>Diospyros pilosanthera</i> <i>Dipterocarpus stellatus</i> <i>Garcinia gaudichaudii</i> <i>Shorea crassa</i> <i>Shorea fagueticana</i> <i>Shorea gratissima</i>	<i>Barringtonia reticulata</i> (R) <i>Blumeodendron kurzii</i> (R/G) <i>Hopea dyeri</i> (P) <i>Mallothus laevigatus</i> (G) <i>Parinari costata</i> (R/P) <i>Shorea quadrinervis</i> (P) <i>Stombosia ceylanica</i> (R) <i>Syzigium confertum</i> (G) <i>Xanthophyllum stipitatum</i> (G)
Associated	<i>Elaeocarpus longipetiolatus</i> (P) <i>Neoscortechinia kingii</i> (G) <i>Scaphium macropodum</i> (G)	<i>Calophyllum nodosum</i> (P*) <i>Dipterocarpus sublamellatus</i> (R/G*)

*Seedlings were associated with the same habitat as trees.

mechanisms we propose to explain the difference in adult and seedling associations would require observations of habitat-specific seedling performance, preferably including reciprocal transplant experiments.

SEEDLING LIGHT ASSOCIATIONS

Numerous studies have demonstrated that seedling species differ in their growth and survival response to light (Welden *et al.* 1991; Osunkjoya *et al.* 1993; Kitajima 1994; Press *et al.* 1996), and that seedlings of some species can be found only in gap environments (Ellison *et al.* 1993; Davies *et al.* 1998). Spatial association of juveniles with high light environments could result from seed germination requirements (Garwood 1983; Kennedy & Swaine 1992) or low survival of seedlings in low-light areas (Boot 1996). The brightest site in our sample experienced a GLI, or percentage incident PAR, of only 10.2%, lower than the highest values in other rain forest studies (24%: Clark *et al.* 1993; 58%: Whitmore *et al.* 1993). Thus, our analyses do not include the effects of large gaps, as documented at other sites (e.g. Brokaw 1985a; Brown & Whitmore 1992).

The proportion of abundant species that showed a significant positive or negative association of juveniles with light (8 of 45 species, or 17%) is less than at Barro Colorado Island, Panama (23 of 41 species, or 56%; Hubbell & Foster 1986a). Although comparison must be made cautiously as the methods used to assess the association differ between the two studies, this difference in numbers of species may reflect the lower range of light conditions encountered in our study at Gunung Palung (no gaps larger than 100 m² were found in 150 ha). Hubbell & Foster (1986b) found over 200 gaps of ≥ 25 m² and seven gaps ≥ 100 m² in 50 ha. However, the difference also suggests that, as a result of persistently low rates of gap formation, the community at Gunung Palung does not contain many abundant, light-demanding species, and the gaps that do exist are dominated by the same species that dominate the shaded understorey, as found by Raich & Christensen (1989) at Penang, Malaysia, and by Hubbell *et al.* (1999) on BCI, Panama. Species differences in light association may reflect variation in shade-tolerance among generally shade-tolerant species (Kohyama & Hotta 1990), rather than a continuum from true pioneer species to semi-shade tolerant species, as found, for example, within the genus *Macaranga* by Davies *et al.* (1998).

SPECIES COEXISTENCE

How much then does habitat association contribute to species coexistence? While we did find physiographic or light associations (or both) in 20 of the 45 abundant species tested for both habitat factors, 25 species showed no association with either habitat

factor (Figs 4a & 5), and up to six species shared the same habitat association (e.g. *Blumeodendron kurzii*, *Dacryodes costata* and *Shorea faguettiana* in Fig. 4a). In no case did the relative abundance of a physiographic habitat-associated species exceed 5.4% in its preferred habitat (*Calophyllum nodosum*, in plateau habitat), and all 16 habitat-associated species occurred at least once in a non-preferred habitat. Some degree of habitat association is to be expected when the environment is heterogeneous, unless all species are identical in physiology and ecology. However, this does not necessarily imply competitive superiority of species in the habitats with which they are associated. Habitat association alone does not provide strong support for the hypothesis of niche differentiation (Tilman & Pacala 1993) as a mechanism maintaining species diversity.

Alternative mechanisms of coexistence include density- or frequency-dependent mortality imposed by natural enemies (Janzen 1970; Connell 1971; Clark & Clark 1984; Connell *et al.* 1984). There is evidence for such density and frequency dependence in this forest community (Webb & Peart 1999). Thus, while the clear habitat association (shown for 20 out of 45 abundant species) may contribute to the maintenance of tree species diversity, its importance relative to other mechanisms has yet to be evaluated.

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References

- Ashton, P.S. (1976) Mixed dipterocarp forest and its variation with habitat in the Malayan lowlands: a re-evaluation at Pasoh. *Malayan Forester*, **39**, 56–72.

- 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.
- Austin, M.P., Ashton, P.S. & Greig-Smith, P. (1972) The application of quantitative methods to vegetation survey. III. A re-examination of rain forest data from Brunei. *Journal of Ecology*, **60**, 305–324.
- 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.
- Boot, R.G.A. (1996) The significance of seedling size and growth of tropical rain forest tree seedlings for regeneration in canopy openings. *The Ecology of Tropical Forest Seedlings* (ed. M.D. Swaine), pp. 267–83. UNESCO, Paris.
- Bowman, D.M.J.S. & Panton, W.J. (1993) Factors that control monsoon-rain-forest seedling establishment and growth in north Australian eucalyptus savanna. *Journal of Ecology*, **81**, 297–304.
- Brokaw, N.V.L. (1985a) Gap-phase regeneration in a tropical forest. *Ecology*, **66**, 682–687.
- Brokaw, N.V.L. (1985b) Treefalls, regrowth, and community structure in tropical forests. *Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 53–69. Academic Press, New York.
- Brown, N.D. & Whitmore, T.C. (1992) Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society of London, Series B*, **335**, 369–378.
- Burger Hzn, D. (1972). *Seedlings of Some Tropical Trees and Shrubs Mainly of South East Asia*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Burslem, D.F.R.P. (1996) Differential responses to nutrients, shade and drought among tree seedlings of lowland tropical forest in Singapore. *The Ecology of Tropical Forest Seedlings* (ed. M.D. Swaine), pp. 211–244. UNESCO, Paris.
- Canham, C.D. (1988) An index for understorey light levels in and around canopy gaps. *Ecology*, **69**, 1634–1638.
- Canham, C.D. (1995) *GLI/C: Software for Calculation of Light Transmission Through Forest Canopies Using Color Fisheye Photography*. Institute of Ecosystem Studies, Millbrook, USA.
- Clark, D.A. & Clark, D.B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist*, **124**, 769–788.
- Clark, D.B., Clark, D.A. & Rich, P.M. (1993) Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica*, **25**, 397–407.
- 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.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1994) Density dependence in two understorey tree species in a neotropical forest. *Ecology*, **75**, 671–680.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Advanced Study Institute Symposium on Dynamics of Numbers in Populations, Oosterbeek*, pp. 298–312. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Connell, J.H., Tracey, J.G. & Webb, L.J. (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs*, **54**, 141–164.
- Cowles, H.C. (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette*, **27**, 95–391.
- 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.
- Day, P.R. (1965) Particle fractionation and particle-size analysis. *Methods of Soil Analysis* (ed. C.A. Black), pp. 545–67. American Society of Agronomy, Madison.
- Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, **18**, 431–451.
- Ellison, A.M., Denslow, J.S., Loiselle, B.A. & Brenes, D.M. (1993) Seed and seedling ecology of neotropical Melastomataceae. *Ecology*, **74**, 1733–1747.
- Gartlan, J.S., Newbery, D.McC., Thomas, D.W. & Waterman, P.G. (1986) The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroun. *Vegetatio*, **65**, 131–148.
- Garwood, N.C. (1983) Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs*, **53**, 159–181.
- Gilbert, G.S., Hubbell, S.P. & Foster, R.B. (1994) Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia*, **98**, 100–108.
- Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Grubb, P.J. (1996) Rainforest dynamics: the need for new paradigms. *Tropical Rainforest Research – Current Issues* (ed. D.S. Edwards, W.E. Booth, S.C. Choy), pp. 215–33. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Hubbell, S.P. & Foster, R.B. (1986a) Commonness and rarity in a neotropical forest: implications for tropical tree conservation. *Conservation Biology: the Science of Scarcity and Diversity* (ed. M. Soule), pp. 205–231. Sinauer Associates, Sunderland, Massachusetts.
- Hubbell, S.P. & Foster, R.B. (1986b) Canopy gaps and the dynamics of a neotropical forest. *Plant Ecology* (ed. M.J. Crawley), pp. 77–96. Blackwell Scientific Publications, London.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & de Loo Lao, S. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.
- Indonesian Department of Transmigration & UK Overseas Development Agency (1987) *Land status map of West Kalimantan, Indonesia*. RePPPProT series, sheet 1414. Badan Koordinasi Survey dan Pemetaan Nasional, Jakarta.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Jenny, H. (1980). *The Soil Resource*. Springer-Verlag, Berlin.
- Kennedy, D.N. & Swaine, M.D. (1992) Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Philosophical Transactions of the Royal Society of London, Series B*, **335**, 357–368.

- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance in 13 tropical tree species. *Oecologia*, **98**, 419–428.
- Kohyama, T. & Hotta, M. (1990) Significance of allometry in tropical saplings. *Functional Ecology*, **4**, 515–521.
- Lieberman, M., Lieberman, D., Hartshorn, G.S. & Peralta, R. (1985) Small-scale altitudinal variation in lowland wet tropical forest vegetation. *Journal of Ecology*, **73**, 505–516.
- Lieberman, M., Lieberman, D., Peralta, R. & Hartshorn, G.S. (1995) Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology*, **11**, 161–178.
- Menard, S.W. (1995). *Applied Logistic Regression Analysis*. Sage Publications, Thousand Oaks.
- Mitchell, P.L. & Whitmore, T.C. (1993) *Use of Hemispherical Photographs in Forest Ecology*. Oxford Forestry Institute Occasional Papers, 44. Oxford Forestry Institute, University of Oxford, Oxford, UK.
- Newbery, D.McC., Gartlan, J.S., McKey, D.B. & Waterman, P.G. (1986) The influence of drainage and soil phosphorus on the vegetation of Douala-Edea Forest Reserve, Cameroun. *Vegetatio*, **65**, 149–162.
- Ng, F.S.P. (1992) *Manual of Forest Fruits, Seeds and Seedlings*. (2 volumes). Forest Research Institute Malaysia, Kuala Lumpur.
- Osunkjoya, O.O., Ash, J.E., Graham, A.W. & Hopkins, M.S. (1993) Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *Journal of Tropical Ecology*, **9**, 1–18.
- Petersen, L. (1991) Soils of Kalimantan. *Folia Geographica Danica*, **19**, 173–187.
- Phillips, O.L., Hall, P., Gentry, A.H., Sayer, S.A. & Vasquez, R. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences, USA*, **91**, 5–2809.
- Poore, M.E.D. (1968) Studies in Malaysia rain forest. I. The forest on Triassic sediments in Jengka Forest Reserve. *Journal of Ecology*, **56**, 143–196.
- Press, M.C., Brown, N.D., Barker, M.G. & Zipperlen, S.W. (1996) Photosynthetic responses to light in tropical rain forest tree seedlings. *The Ecology of Tropical Forest Seedlings* (ed. M.D. Swaine), pp. 41–58. UNESCO, Paris.
- Raich, J.W. & Christensen, N.L. (1989) Malaysian dipterocarp forest: tree seedling and sapling species composition and small-scale disturbance patterns. *National Geographic Research*, **5**, 346–363.
- Ribbens, E., Silander, J.A.J. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Richards, P.W. (1996). *The Tropical Rain Forest: an Ecological Study*. 2nd edn. Cambridge University Press, Cambridge, UK.
- Russell-Smith, J. (1996) Regeneration of monsoon rain forest in northern Australia: the sapling bank. *Journal of Vegetation Science*, **7**, 889–900.
- SAS Institute (1990). *SAS/STAT, Version 6*. SAS Institute Inc., Cary, USA.
- SAS Institute (1995). *JMP Statistical Discovery Software, Version 3.2.1*. SAS Institute Inc., Cary, USA.
- Schupp, E.W. (1992) The Janzen-Connell model for tropical tree diversity: population implications and the importance of scale. *American Naturalist*, **140**, 526–530.
- Sheldrick, B.H. & Wang, C. (1993) Particle size distribution. *Soil Sampling and Methods of Analysis* (ed. M.R. Carter), pp. 499–511. Lewis Publishers, Boca Raton, USA.
- Soil Survey Staff (1975) *Soil Taxonomy: a Basic System of Soil Classification for Making and Interpreting Soil Surveys*. U.S. Department of Agriculture, Washington, D.C.
- Svenning, J.C. (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, **87**, 55–65.
- Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75**, 81–86.
- Tilman, D. & Pacala, S.W. (1993) The maintenance of species richness in plant communities. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R.E. Ricklefs & D. Schluter), pp. 13–25. University of Chicago Press, Chicago, USA.
- de Vogel, E.F., (1980). *Seedlings of Dicotyledons*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Webb, C.O. (1997) *Seedling Ecology and Tree Diversity in a Bornean Rain Forest*. PhD Thesis, Dartmouth College, New Hampshire, USA.
- Webb, C.O. (in press) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*.
- Webb, C.O. & Curran, L.M. (1996) A field key to dipterocarp seedlings of the Gunung Palung National Park, West Kalimantan, Indonesia. *Tropical Biodiversity*, **3**, 193–225.
- Webb, C.O. & Peart, D.R. (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology*, **80**, 2006–2017.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 35–50.
- Whitmore, T.C. (1973) Frequency and habitat of tree species in the rain forest of Ulu Kelantan. *Gardens Bulletin of Singapore*, **26**, 195–210.
- Whitmore, T.C. (1984). *Tropical Rain Forests of the Far East*. 2nd edn. Oxford University Press, Oxford.
- Whitmore, T.C., Brown, N.D., Swaine, M.D., Kennedy, D., Goodwin-Bailey, C.I. & Gong, W.K. (1993) Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. *Journal of Tropical Ecology*, **9**, 131–151.
- Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs*, **26**, 1–80.
- Wong, Y.K. & Whitmore, T.C. (1970) On the influence of soil properties on species distribution in a Malayan lowland dipterocarp rain forest. *Malaysian Forester*, **33**, 42–54.

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