HABITAT PATTERNS IN TROPICAL RAIN FORESTS: A COMPARISON OF 105 PLOTS IN NORTHWEST BORNEO

MATTHEW D. POTTS,[1,5] PETER S. ASHTON,[2] LES S. KAUFMAN,[3] AND JOSHUA B. PLOTKIN[4]

[1]*Division of Engineering and Applied Sciences, Harvard University, Cambridge, Massachusetts 02138 USA*
[2]*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA*
[3]*Department of Biology, Boston University, Boston, Massachusetts 02215 USA*
[4]*Institute for Advanced Study and Princeton University, Princeton, New Jersey 08540 USA*

Abstract. Understanding the maintenance of high tropical tree species diversity requires disentangling the effects of habitat vs. geographic distance. Using floristic, topographic, and soil nutrient data from 105 0.6-ha plots in mixed dipterocarp forest throughout Sarawak, Malaysian Borneo, we explore the degree to which floristic patterns are habitat-driven from local to landscape scales. We assess how the floristic influence of geographic distance vs. abiotic factors varies from local to regional scales. We employ several multivariate analytical techniques and perform a hierarchical clustering of the research plots using the Steinhaus index of floristic dissimilarity, as well as Mantel analyses on matrices of floristic, habitat, and geographic distance. These analyses indicate that floristic variation is more strongly correlated with habitat than with geographic distance on the regional scale. On the local-landscape to community scale, we find evidence of a resource threshold above which habitat effects weaken; that is, below the resource threshold floristic similarity between sites is dominated by habitat effects, while above the threshold floristic similarity between sites is dominated by geographic-distance effects. We also find evidence that topography and soil nutrients correlate in part independently with floristics. These results, together with previous studies in the Neotropics, emphasize that tree species distribution and community composition are variously influenced by the interplay of both habitat and dispersal-driven effects.

Key words: Borneo, lowland ever-wet rain forest; cluster analysis; deterministic vs. stochastic effects; diversity; habitat effects vs. dispersal-driven effects; Mantel analysis; ordination; Sarawak, Malaysian Borneo; soil nutrients; tropical rain forest.

INTRODUCTION

Most theories of the maintenance of high tropical tree species diversity rely to some degree on habitat and distance effects. Niche-assembly theories (Lieberman et al. 1985, Hubbell and Foster 1986, Denslow 1987, Kohyama 1994, Terborgh et al. 1996, Clark et al. 1998) stress the importance of environmental heterogeneity while dispersal-assembly theories (Tilman and Pacala 1993, Hurtt and Pacala 1995, Hubbell et al. 1999) emphasize the effects of spatial isolation generated by dispersal limitation. Disentangling the effects of habitat vs. geographic distance is essential to understanding the maintenance of high tropical tree species diversity.

The evidence for habitat-driven vs. historically driven floristic patterns in species-rich tropical tree communities is equivocal. A large number of scientists have claimed to show habitat-driven patterns at geographic and landscape scales (Ashton [1964, 1976] and Austin et al. [1972] in Borneo; Gentry [1988], Tuomisto and Ruokolainen [1994], Tuomisto et al. [1995], Duivenvoorden [1995] and Duivenvoorden and Lips [1995], in the Upper Amazon; Clark et al. [1995] in Costa

Rica). But many others have claimed that such patterns are weak and subordinate to the gradual floristic change incurred by limited seed-dispersal distance (Wong and Whitmore 1970, Hubbell 1979, 2001, Hubbell and Foster 1986) and mortality and speciation rates (Hubbell 1997, 2001). To date, only a few studies have investigated the relative influence of habitat factors and geographical distance on floristic composition at a range of spatial scales (Gentry 1988, Terborgh et al. 1996, Pyke et al. 2002).

In this study, we systematically explore the degree to which floristic patterns are habitat driven on the local and landscape scales. We focus our analyses on the lowland ever-wet rainforests of northwest Borneo, a region of uniform climate but extremely rich species diversity and high habitat heterogeneity (Ashton 1964, 1984, Whitmore 1984, Wong 1998).

The floristic and structural diversity of the lowland forests of northwest Borneo have long been documented (Beccari 1902). The zonal forest on lowland red-yellow ultisolic soils is mixed dipterocarp forest (MDF), so called on account of family dominance of the emergent canopy and ectotrophic mycorrhizal Dipterocarpaceae, but absence of species dominance. MDF is distinguished by exceptional albeit variable species richness, and tall stature of 35–75 m Ashton (1964).

Previous studies in Borneo have to some extent doc-

umented relationships between habitat and floristic composition. Austin et al. (1972) showed that tree species composition correlated with topography and/or soil nutrients at two MDFs on contrasting soils >100 km apart in Brunei, each with 50 plots. Newbery and Proctor (1984) compared forests and soils between and within single plots, in Mulu National Park, Sarawak, including MDF, heath forest on podsols, swamp forest, and forest over karst limestone. They found that the relationships among soil nutrients, floristics, and habitat, if any, were complex. This was due in part to the fact that the soils in their samples were derived primarily from organic matter and had higher soil nutrient concentrations than soils derived from rock substrates. Finally, Baillie et al. (1987) analyzed 5000 clustered point samples in MDF throughout a region in Sarawak of ~4000 km² overlying a single sedimentary geological formation; samples from mineral soil were analyzed using similar methods to ours. They found that species' distributions differed in relation to soils' mineral nutrient concentrations, notably phosphorus and magnesium.

In contrast, studies in the Neotropics have reported conflicting results concerning the relationship between habitat and floristic composition. In plots >40 km apart in mature floodplain forests of the Peruvian Amazon, Terborgh et al. (1996) found that mature-forest samples floristically resembled one another more than they did adjacent successional and upland-forest samples. Pitman et al. (1999) compared eight 1-ha plots in 29 sites throughout the Amazon valley, including upland and floodplain forests. They found that forests of the same broad habitat type but in different regions were less similar than forests in different habitats within the same region. Because historical geologic and edaphic variation were apparently correlated at geographical scale, the relative influence of habitat- and history-driven forces could not be disentangled. Terborgh and Andersen (1998) documented the distribution of 825 tree species in plots with an overall area >36 ha in a variety of habitats in 400 km² of the Upper Amazon. There, they found that about 15% were habitat specialists, and concluded that most were generalists; most were also geographically widespread. Pitman et al. (2001) have confirmed that most upland species are widespread in the Peruvian and Ecuadorian Amazon; one third were common to plots 1400 km apart and most generally occurred in very low densities but with nonrandom local abundance. Finally, Pyke et al. (2002) compared samples of mixed lowland semideciduous forest, at known distances apart. They demonstrated that floristic change is strongly correlated with distance between plots, and not, apparently, with abiotic factors. In none of these Neotropical studies were soils samples taken, nor was rainfall seasonality taken into account though the length of the dry season varies by up to four months in the larger scale studies.

Duivenvoorden (1995) and Duivenvoorden and Lips (1995), however, documented similar patterns of species richness to those on low-nutrient soils in northwest Borneo, from the low-nutrient sands of the Guyana Shield rocks of the aseasonal Columbian Amazon. Soils samples were analyzed, but distance relationships were not studied. The main floristic gradient in species-rich mixed forest on red-yellow upland soils over sandstone was correlated with mineral soils nutrients. Species turnover appeared to be lower than reported, for instance by Ashton (1964) in Borneo. Two main species associations were recognized, on soils differing in the form of their surface humus in a manner analogous to temperate mull and mor.

The following questions therefore still remain, and provide the focus of this paper:

1) *How does the relative influence of geographic distance vs. abiotic factors on tree species composition vary from local to regional scales?* This question addresses the fundamental issue, as yet untested by field data, of the relative role of historical factors vs. abiotic factors in structuring rain-forest floristics at landscape and larger scales. The existence of predictable floristic spatial variation is of more than theoretical interest. If species assemblages occur as a mosaic of islands throughout the landscape, then predictions from *The Theory of Island Biogeography* (MacArthur and Wilson 1967) will in part be applicable at this smaller scale. That would imply that plant species extinctions would be substantially delayed if widespread forest fragments are conserved, though this prediction would be invalidated were mobile links lost.

2) *At the local community scale, are the influences of abiotic factors, specifically soils nutrients and topography, stronger in some habitats than others?* (a) Is there a nutrient threshold above which any correlations between nutrient concentrations are relaxed, and overtaken by correlation with between-plot distances? (b) Do the relative strengths of correlations between floristic composition and different abiotic factors vary with habitat? Specifically, do soil nutrient concentrations correlate with floristic composition independently from topography?

3) *Do the geographical and floristic patterns in the Neotropics generalize to other parts of the tropics?*

Materials and Methods

Environmental setting

Northwest Borneo experiences an unusually equable climate with >2500 mm of rain. In general, every month receives on average more rainfall than the expected evapotranspiration. Occasional droughts do occur (Brunig 1969, Baillie 1976). However, the unprecedented El Niño-related drought of 1982–1983 failed to penetrate this region, while the yet more intense 1997–1998 drought only reached the northeast down to Bintulu (Fig. 1), and at relatively low intensities (M. D. Potts, *unpublished manuscript*). Geological evi-
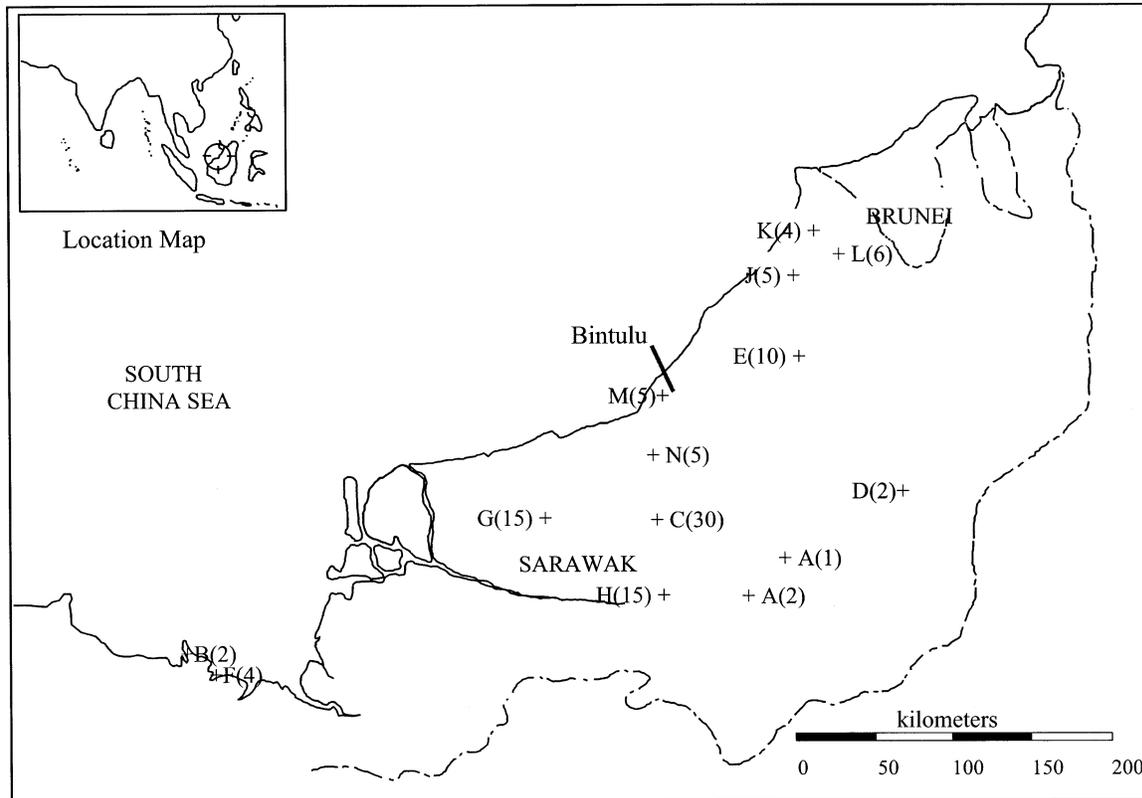
Fig. 1. Map of northwest Borneo, indicating the 12 site locations (see Table 1 for site abbreviations). Numbers in parentheses indicate the number of plots at each site.

dence suggests that northwest Borneo has escaped major changes in rainfall seasonality since the mid-Miocene (Morley and Flenley 1987, Morley 1999).

The lowlands of northwest Borneo are now recognized as an extension of the Riau Pocket (Corner 1960, Ashton 1984, Wong 1998), a floristically distinct and remarkably species-rich plant region (Plotkin et al. 2000*b*) in the center of the Sunda Shelf, also encompassing the Riau Archipelago and eastern peninsular Malaysia. Northwest Borneo consists of late Cretaceous and Tertiary sediments predominated by sandstone, and intercalated with mainly Miocene volcanic intrusions. Intermittent tectonic uplift, which continues, has created a largely rugged landscape but for undulating coastal hills on soft Neogene sediments and extensive peat swamps. Variable susceptibility to erosion of thin sediments and high rainfall characterize the landscape, resulting in generally shallow, often highly leached soils of varying nutrient concentration (Baillie et al. 1987).

Field sampling

Our investigation relies on a set of data collected in the 1960s throughout Sarawak, East Malaysia, the major state in northwest Borneo. One hundred and five 0.6-ha (1.5-acre) plots were laid out throughout apparently mature lowland mixed dipterocarp forest in Sarawak, East Malaysia (see Plate 1), over a distance of 500×150 km at $1.5°–4.5°$ N latitude. The plots were clustered at fourteen localities, here termed "sites" (Fig. 1). The fourteen sites chosen sample the full range of upland yellow/red soils and geological formations found in the region (Table 1). At three sites, judged on existing evidence to be on relatively high-nutrient mineral soils (C), medium-nutrient soils (H), and low-nutrient soils (G), at least 15 plots were established to provide data for independent analysis (Fig. 1, Table 1).

A different number of plots was established at each site (Fig. 1). Plots were placed at least 200 m apart, and were positioned so as to include, as far as possible, a single topographic element: plateaus and convex slopes, concave slopes, and flat alluvium, here termed ridges, slopes, and valley bottoms. Locations with recent or large canopy gaps were avoided. A plot area of 0.6 ha (1.5 acres) was chosen in light of some deficiencies associated with previous 1-acre plot sizes in Brunei (Ashton 1964). As in that study, ridge plots were linear, 300 m long, and slope and valley-bottom plots were rectangular 60×100 m. In each plot, all trees >9.8 cm in diameter at breast height (dbh) (12 inches girth) were measured for girth and identified to species.

In each plot, soils were augered to 30 cm at two random points, and a pit dug to 1 m at a third random

PLATE 1. Canopy of a mixed Dipterocarp forest located in Lambir Hills National Park (see Site L in Fig. 1), Sarawak, Malaysia. Photograph by Matthew D. Potts.

TABLE 1. Summary site descriptions. Soils are listed in order of predominance at each site.

Site	Altitude (m)†	Substrata	Soil
A1) Carapa Pila (Kajang Hill)	870	Tertiary basalt	udult ultisol; red-brown friable loam, thin patchy mor
A2) Ulu Temiai, Mujong Hose Mountains	840	Tertiary dacite	udult ultisol; gray-brown friable loam; thin mor
B) Santubong Mountain	260–340	Paleocene sandstone	humult ultisols; yellow sand; 4–6 cm mor
C) Mount Mersing‡	140–880	Tertiary basalt	udult ultisols, inceptisols; yellow-brown friable clay; thin mor (high ridges)
D) Ulu Dapoi, Tinjar	150–220	Tertiary dacite	humult, (D1) udult (D2) ultisols; yellow clay; thin mor (D1)
E) Bok-Tisam Forest Reserve	30–150	Miocene shale	udult ultisols; yellow brown, friable loam; no mor
F) Bako National Park‡	30–75	Paleocene sandstone	humult ultisols; yellow sand; 6–9 cm mor
G) Iju Hill, Ulu Arip	75–300	Tertiary rhyolite	skeletal humult ultisols, inceptisols; yellow loam; thin patchy mor
H) Raya Hill, Kapit	120–460	Eocene shale, sandstone	skeletal humult ultisols, inceptisols; yellow loam; thin patchy mor
J) Ulu Bakong, Miri	30–90	Miocene shale	udult ultisols; yellow-brown friable loam; no mor
K) Northern Lambir Hills	60–120	Miocene sandstone, clay	humult ultisols; yellow sand, sandy clay; 5–10 cm mor
L) Southern Lambir Hills National Park‡	70–160	Miocene sandstone, shale	humult (L2 udult) ultisols; yellow sand, sandy clay; 5–10 cm mor
M) Nyabau Forest Reserve	45–160	Oligocene sandstone	humult ultisols; yellow-red sandy clay; 5–12 cm mor
N) Segan Forest Reserve	30–210	Oligocene sandstone, shale	humult (udult) ultisols; yellow loam, thin patchy mor

† Above sea level.
‡ Site includes permanent plots (Ashton and Hall 1992).

point. Depths of litter, raw humus free of mineral soil (if present), humus-discolored mineral soil, mineral soil above bedrock, mottling (if present), rooting, substrate fragments, and substrate (when reached) were recorded in the pit. Samples were collected from the mineral soil at two depths (20–30 cm; 70–80 cm) in the deep pit, and at one depth (20–30 cm) at the augered points.

The soil samples were analyzed at the Semongok Research Center of the Sarawak Department of Agriculture, using the methods given by Sim (1965). The samples were separately analyzed for pH (in water). Samples were then air dried. ''Reserve'' contents of phosphorus and the cationic nutrients were extracted with hot concentrated hydrochloric acid (Bailey 1967). The iron and the aluminum contents of this extract were determined by alkaline precipitation and, taken together, are referred to here as ''Group III elements.'' Mechanical analysis was by the pipette method after treatment with hydrogen peroxide and dispersion with sodium hexametaphosphate.

The following topographic variables were also recorded at each plot: altitude, ''steepness'' (estimated as the change in altitude averaged over all the 20 × 20 m subplots), and land formation (ridge or slope).

Data analysis

To determine the scale and relative importance of abiotic factors in shaping community structure, we employed four distinct methodological approaches. All methods relied upon the same basic measure of floristic dissimilarity between sites. Alternative floristic metrics (which we also tested) yielded similar results.

Indices of floristic similarity.—Throughout the paper, we utilize the Steinhaus index of floristic dissimilarity. The Steinhaus is equivalent to the Bray-Curtis index of dissimilarity on the number of stems by species (Legendre and Legendre 1998).

The Steinhaus dissimilarity index, D_S, between plots A and B is defined as follows:

$$D_S(A, B) = 1 - \frac{2 \sum \min(n_i^A, n_i^B)}{\sum (n_i^A + n_i^B)}. \tag{1}$$

The sum is taken over all species, and n_i^A denotes the abundance of the ith species at plot A. Therefore, the denominator of D_S is simply the total number of individuals at both sites.

Habitat factors.—The abiotic variables that we analyzed were altitude, steepness, ridge vs. slope, pH,

and percentage clay. Soil chemistry is expressed as concentrated HCl-extractable P, Ca, Mg, K, and Group III elements (Al and Fe) at 20–30 cm. We also analyzed the Group III ratio between the two sample depths (20–30 cm and 70–80 cm) as a measure of leaching (Fig. 2).

Cluster analysis.—We performed a cluster analysis on the floristic composition of our 105 study plots. We used a standard, hierarchical average-linkage clustering algorithm. This algorithm initially assigns each plot to a separate group; at each iteration, the clustering routine unites the two groups that have the smallest mean dissimilarity (i.e., floristic dissimilarity, measured via D_S) between them. The algorithm is complete when all the plots are united into one group. The results of such an analysis are easily visualized in a dendrogram. The average-linkage clustering makes no a priori assumptions about underlying structure in the data.

At each iteration in the cluster analysis, we determined whether any habitat variables were significantly correlated with the clustering. In other words, at each bifurcation, a boot-strapping permutation test (Good 1994) determined whether the mean values of each habitat factor differed significantly between the two cluster groups.

Mantel analyses.—We used a Mantel analysis (Mantel 1967, Legendre and Legendre 1998) to investigate the relative strengths of geographic distance vs. abiotic habitat factors as determinants of floristic composition. A complete Mantel analysis entails computing distance matrices and then computing simple and partial Mantel statistics that are identical to those of simple and partial Pearson correlation coefficients, except the Mantel statistics take into account the natural dependence found in the distance matrices. Significance of results is usually judged (as it was in this case) by empirically deriving a test statistic by bootstrapping the original data. It should be noted that results of a Mantel analysis are correlations between matrices that measure the extent to which the variation in the distances of one matrix corresponds to the variation in the distances of the other matrix.

We performed the Mantel test on the data set as a whole as well as those plots from Mount Mersing (C), Raya Hill (H), and Iju Hill (G) in which at least 15 plots were sited, separately. At the Mersing site we only used the 15 low-altitude plots (<500 m). Owing to concerns of significant floristic dissimilarity between plots in different sites, the Mantel test on the data set

$\rightarrow$

FIG. 2. Box plots of habitat factor data, by site. The height of the box is equal to the interquartile distance (IQD) which is the difference between the third and first quartile of the data. The whiskers extend to the extreme values of the data or $1.5 \times$ IQD from the center, whichever is less. A_1 and A_2 are in different sites (see Fig. 1); E_1, K_1, and L2 are plots that clustered far from the other plots in their respective sites. (see Fig. 3). The ''a'' after the soil habitat factor indicates the sample was taken at 20–30 cm depth; ''ppm'' means parts per million, i.e., micrograms soil residual element per gram universal soil.
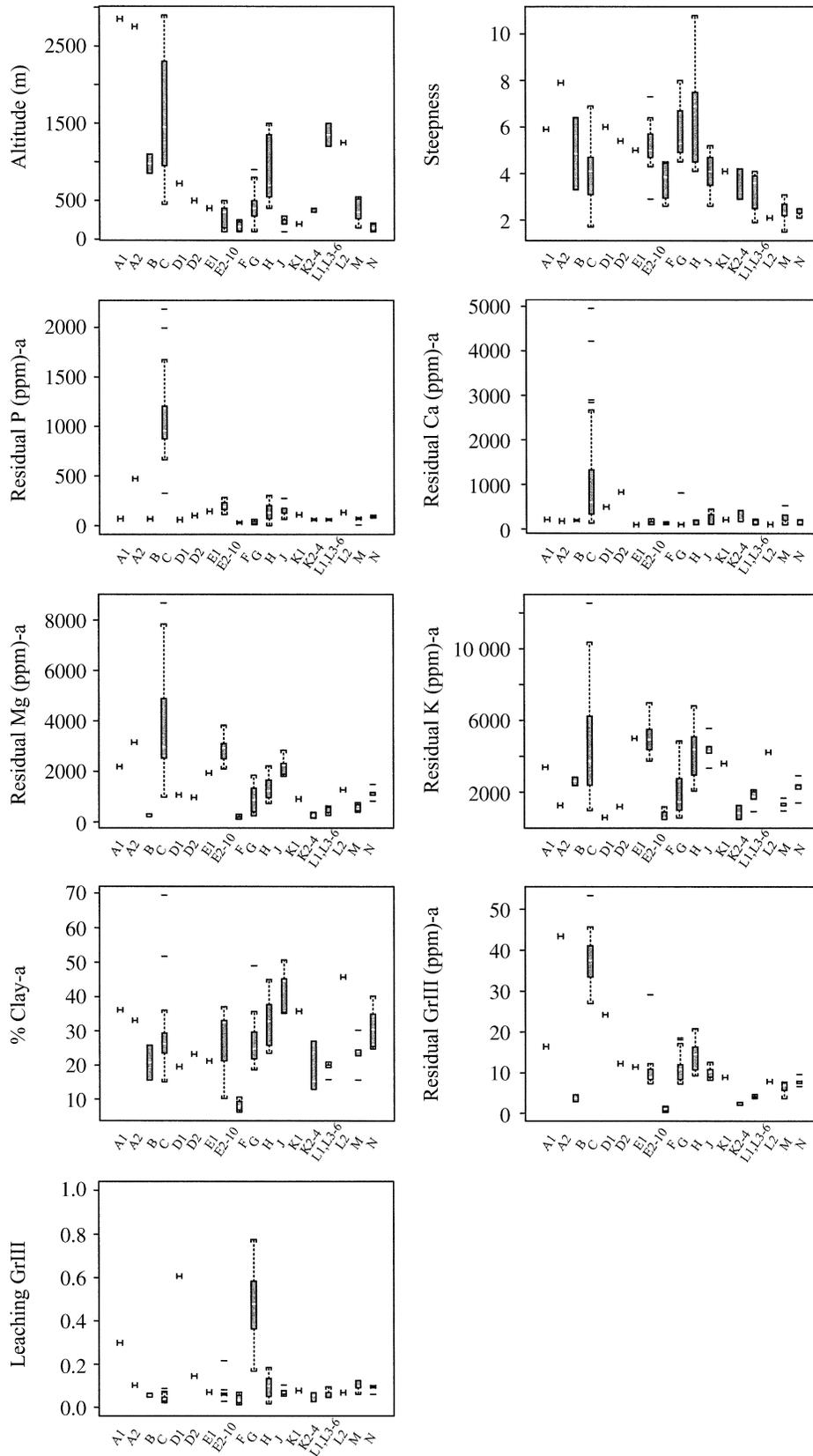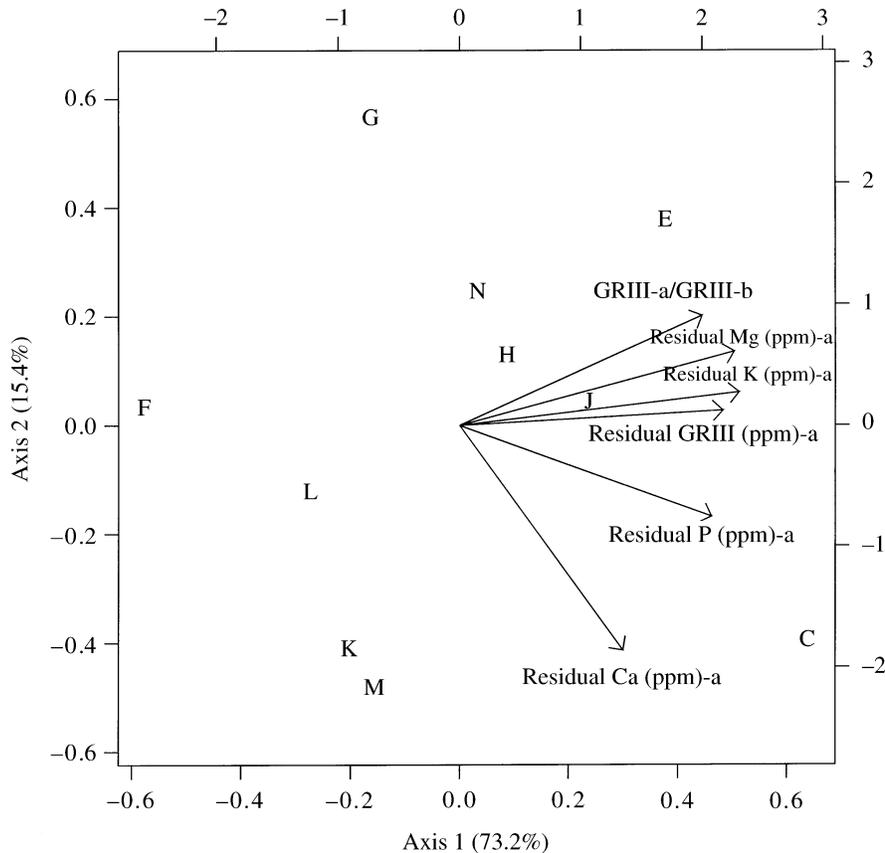
F‍IG. 3. Biplot of results of principal components analysis (PCA) for soil habitat factors across all 105 plots. The *x*-axis represents the scores for the first principal component, the *y*-axis the scores for the second principal component; in the axis label the percentage of variance explained is given in parentheses. The original variables are represented by arrows that graphically indicate the proportion of the original variance explained by the first two principal components. The direction of the arrows indicates the relative loadings on the first and second principal components. After the variable names, ''a'' means samples were taken at a depth of 20–30 cm, while ''b'' means 70–80 cm; ppm = parts per million (i.e., μg element/ g mineral soil).

as a whole was performed by pooling four of the plots (<2 km) from each of the sites with at least four plots (C, E, F, G, H, J, K, L, M, N) and using these combined plots to calculate the floristic dissimilarity matrix (a similar procedure was used to calculate the habitat matrix). In this way we hoped to minimize the effects of high species turnover on dissimilarity indices.

The spatial distance matrix was calculated by tabulating the pairwise geographic distances between plots, while the floristic distance matrix was calculated using the Steinhaus index.

The calculation of the abiotic-factor distance matrices was somewhat more complicated. Preliminary analyses of the soil chemistry data indicated a high degree of correlation among the various soil variables. To distill the key edaphic differences between plots, we performed a principal components analysis (PCA) on the correlation matrix of edaphic factors, and used projections onto the first component as a single measure of edaphic distance between two plots (Fig. 3). Before the PCA was performed the soil nutrient data were nor-

malized by the use of the Box-Cox transformation and then standardized. The correlation matrix was used so as to equally weight all soil nutrient factors. For habitat distance matrices involving a single habitat variable (residual Mg and residual P each in parts per million [micrograms of soil residual element per gram of universal soil]), interplot distances were calculated by simply taking the absolute difference in nutrient levels between the sites.

We also computed matrices that summarized the pairwise topographic distances between the plots. The presence of both discrete (ridge vs. slope) and continuous (altitude and steepness) topographic data required the use of Gower's (1971) dissimilarity index. Gower's dissimilarity index, D_G (Legendre and Legendre 1998), between plots A and B with n descriptors is defined as follows:

$$D_G(A, B) = 1 - \frac{1}{n} \sum_{j=1}^{p} s_j. \qquad (2)$$

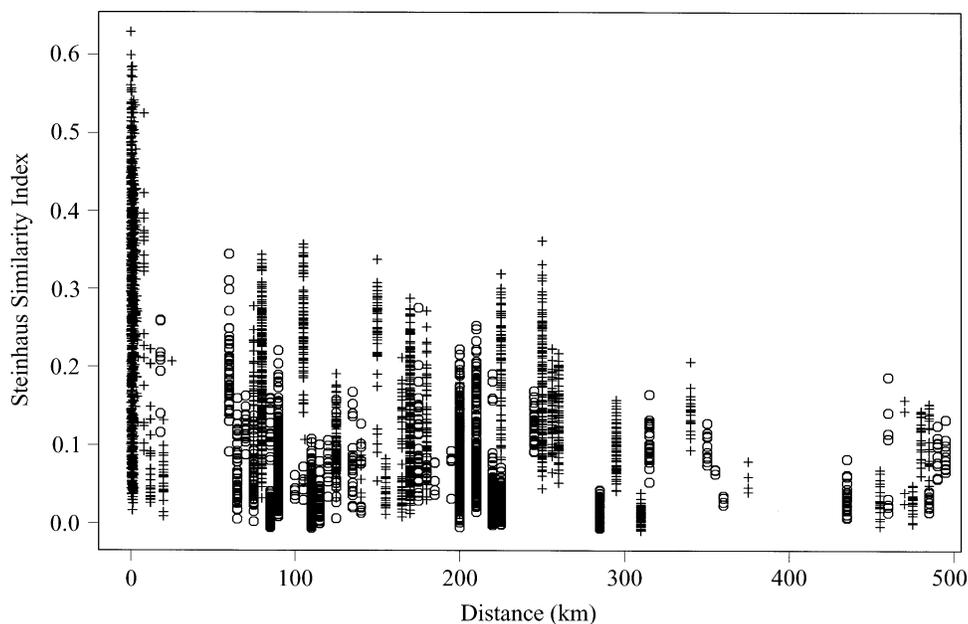In this equation, for a discrete variable j, $s_j = 0$ for

Fig. 4. Plot similarity as a function of distance. An ''○'' indicates pairs of plots differing in soil surface characteristics (humult vs. udult) with different surface lithologies, while a ''+'' indicates pairs of plots with similar soil surface characteristics.

agreement between plots A and B, and $s_j = 1$ for disagreement. For a continuous descriptor j, $s_j = 1 - |A_j - B_j|/R_j$ where R_j is the maximum difference between all plots under consideration. The Gower index conveniently compiles both discrete and continuous topographic variables into a single topographic metric.

The use of a PCA to distill the soil nutrient data and the use of Gower's index to combine continuous and ordinal data have both advantages and disadvantages. Preliminary analysis of the soil nutrient data indicated a high degree of covariation among variables. Using a PCA allowed us to account for this high covariance among soil nutrient variables and create a few combined measures of soil nutrient variability among the plots. We do admit though that PCAs can be noisy and may lead to some loss of information. We believe that its ability to distill the soil nutrient data outweighs any loss of power its use creates. The main advantage of Gower's index was that it allowed us to combine continuous data on altitude and slope with landform data. While the index is sensitive to scale of measurement we have no reason to believe that it drastically altered the results. Analyses using a few plots indicated that the difference between a slope and ridge could be just as significant as a large change in altitude.

Given all the pairwise matrices defined above, the Mantel tests based on Kendall's τ nonparametric rank order statistic were performed. According to Dietz (1983), Kendall's τ has greater power than the standard Z statistic, often used in Mantel analyses. Partial Mantel statistics, whose calculation are identical to first-order Kendall partial correlation statistics, are also reported (Legendre and Legendre 1998). The partial Mantel test measures whether two factors (e.g., floristics and habitat) are correlated across the plots above and beyond cross correlation through a third factor (e.g., distance).

Plot similarity $\times$ distance relationships.—We also plot the relationship between floristic similarity and geographic distance, ignoring all other habitat variables. These results permit comparison with recent work by Pyke et al. (2002) in the Neotropics, where quantitative abiotic data were not available. We have labelled this graph (Fig. 4) according to the surface soil characteristics of the sites, however, to emphasize an abiotic factor-driven trend that explains much of the observed pattern.

RESULTS

Floristic patterns and species habitat preferences

We sampled 47 786 individuals representing 1762 species within the 105 0.6-ha plots. There was significant variation in species diversity, stem density, and Fisher's alpha (Fisher et al. 1943) among the plots (Fig. 5). While 16% of the species sampled only occurred once, <6% of the pairwise comparisons of plots had no species in common (Fig. 5d). Thus, while high, species turnover does not lead to an inordinate number of pairs of plots having floristic dissimilarity of 1.

However, species did show a strong geographic affiliation. Of the 436 species that occurred in 10 or more of the plots, 85% of them were geographically associated with a particular site or group of sites (Fisher's

a) Stem Density

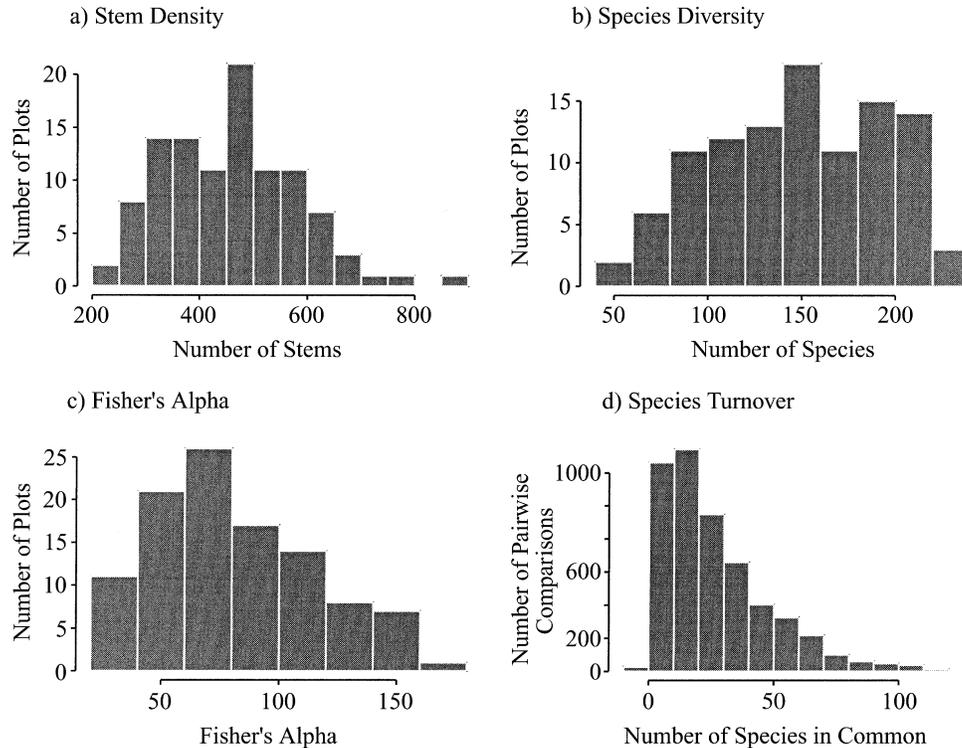b) Species Diversity

c) Fisher's Alpha

d) Species Turnover

FIG. 5. Floristic summary of sample plots: histograms of (a) stem density (median: 459); (b) species diversity (median: 150); (c) Fisher's alpha (median: 74.2); and (d) species turnover as measured by the number of species shared between two plots (median: 21).

exact test [Zar 1984] on species site preference). This high degree of species spatial "clumping" by site precluded us from being able to statistically analyze individual species' habitat preference. However, if we restrict ourselves to the species that were among the 10 most abundant species in at least five of the plots we do find some suggestive evidence for habitat preferences among species (Table 2). Sixty species occurred among the 10 most abundant species in at least 5 plots, 18 species in at least 10 plots, and one in 25 plots. Of these, 51 occurred among the 10 most abundant at more than one site. Of the nine species confined to one site, six were in the Mount Mersing basalt plots (C), and one species each were confined to the G, H, and M plots. Forty-three of the 60 species were confined to one of the two major plot clusters: 23 species to the plot group on siliceous soils and 20 species to the plot group on clay-rich rocks.

Relative importance of geographic distance vs. abiotic habitat factors on the landscape scale

The Mantel test of plots from Sarawak (northwest Borneo) as a whole (Table 3) indicates that the association between floristic composition and edaphic factors (0.651), as measured by the first axis of the soil chemistry variables PCA, is significantly stronger than the correlation between floristics and geographic dis-

tance (0.058). The first axis of the PCA (Fig. 3) is strongly correlated with Mg, K, and Group III elements.

The results of the cluster analysis echo those of the Mantel test. Recall that the cluster dendrogram was calculated from floristic information alone. The first division in the dendrogram (Fig. 6) neatly coincides with two major habitat-related groups: those plots with clay-rich udult soils lacking surface raw humus except >600 m (sites A, C, E, and J) from those plots with sandy or sandy-clay humult soils with a surface raw humus horizon. The two clusters also differ significantly in the majority of the soil mineral variables. The next few bifurcations in the dendrogram are also correlated strongly with habitat characteristics, despite substantial geographic distances between co-clustered sites. For example, the third division breaks off the high-altitude Mount Mersing (C plots) and Carapa Pila (A1) and Ulu Temiai (A2) plots from the rest of udult group; the fourth division breaks off the Raya Hill (H) plots despite their closer geographic proximity to the Iju Hill (G) plots. Nevertheless, the dendrogram does suggest a positive effect of geographic distance on floristics. For example, the second division breaks off the B and F plots, which are the furthest away, spatially, from the rest of the plots, though their soils also have the lowest clay and Group III element content, and represent an extreme on at least one soil gradient (Fig.

TABLE 2. Species rank-order abundance at 14 sites in northwest Borneo. Reported are species occurring among the 10 most abundant species in at least five of the 105 0.6-ha plots.

Genus and species	Type†	No. of plots‡	Plots species occurs in§
Shorea macroptera ssp. *baillonii*	humult	25	G(13) H(10) N(2)
Koilodepas longifolium	generalist	24	C(5) E(2) G(3) H(7) J(4) L(1) N(2)
Vatica micrantha	humult	22	G(9) H(3) K(1) L(3) M(4) N(2)
Allantospermum borneense	humult	22	G(8) K(3) L(3) M(5) N(3)
Shorea balanocarpoides	generalist	19	G(12) H(3) J(2) M(1) N(1)
Dryobalanops aromatica	humult	17	G(9) K(3) L(4) M(1)
Dryobalanops lanceolata	udult	17	C(9) E(8)
Millettia nieuwenhuisii	generalist	16	E(9) H(3) J(4)
Mangifera parvifolia	humult	15	F(1) G(3) H(3) L(6) M(2)
Diospyros curraniopsis	udult	15	C(6) E(7) J(2)
Teijsmanniodendron sarawakanum	udult	15	C(14) D(1)
Dipterocarpus caudiferus	udult	13	C(11) J(2)
Dacryodes expansa	humult	12	G(5) K(3) L(4)
Dryobalanops beccarii	humult	12	B(2) D(1) F(3) H(4) N(2)
Elateriospermum tapos	generalist	12	E(7) G(1) K(2) L(1) N(1)
Mallotus wrayi	generalist	11	C(8) H(3)
Gonocaryum longiracemosum	humult	11	F(2) H(2) K(2) M(3) N(2)
Diospyros sumatrana	udult	10	C(4) D(1) E(5)
Mesua myrtifolia	humult	9	G(6) M(2) N(1)
Hopea andersonii	udult	9	C(9)
Drypetes microphylla	udult	9	C(9)
Eugenia valdevenosa	udult	9	A(2) C(7)
Alangium javanicum	udult	8	C(2) E(6)
Polyalthia cauliflora	udult	8	C(8)
Lophopetalum globrum	generalist	8	C(1) G(4) H(3)
Dipterocarpus globosus	humult	8	K(2) L(5) M(1)
Pimeleodendron griffithianum	generalist	8	E(1) F(2) G(3) H(2)
Gymnacranthera contracta	humult	8	G(2) K(3) M(1) N(2)
Shorea macroptera ssp. *macropteraefolia*	generalist	7	D(1) G(3) J(1) N(2)
Shorea pinanga	generalist	7	H(6) J(1)
Shorea faguetiana	humult	7	G(1) H(5) N(1)
Mallotus leptophyllus	generalist	7	A(1) E(1) H(2) J(2) L(1)
Hydnocarpus polypetala	generalist	7	C(4) E(2) H(1)
Hydnocarpus woodii	udult	7	C(5) E(2)
Eusideroxylon zwageri	generalist	7	C(4) E(2) H(1)
Bouea oppositifolia	humult	6	L(1) M(5)
Hopea dryobalanoides	udult	6	C(4) G(2)
Shorea polyandra	udult	6	E(5) J(1)
Hopea mesuoides	generalist	6	J(2) N(4)
Shorea faguetoides	generalist	6	G(2) H(2) J(2)
Shorea parvifolia	generalist	6	D(1) E(3) J(1) K(1)
Shorea pauciflora	humult	6	G(2) H(3) K(1)
Ptychopyxis arborea	udult	6	C(5) E(1)
Mallotus leucocalyx	udult	6	C(6)
Ganua pierrei	humult	6	B(1) F(1) G(4)
Teijsmanniodendron holophyllum	humult	6	H(4) N(2)
Melanorrhoea wallichii	humult	5	B(2) G(1) H(2)
Gluta laxiflora	humult	5	L(1) M(4)
Orophea sp.	udult	5	A(1) C(3) E(1)
Popowia pisocarpa	udult	5	C(5)
Dipterocarpus rigidus	humult	5	M(5)
Shorea pilosa	humult	5	G(1) H(4)
Shorea rubra	humult	5	H(5)
Shorea xanthophylla	udult	5	C(4) L(1)
Vatica odorata	generalist	5	C(1) H(4)
Vatica vinosa	generalist	5	A(1) C(3) N(1)
Mallotus griffithianus	humult	5	G(3) M(1) N(1)
Cryptocarya densiflora	udult	5	C(5)
Nephelium mutabile	udult	5	C(4) E(1)
Teijsmanniodendron sinclairii	humult	5	G(5)

† Types of occurrence, i.e., whether the species is confined to a particular plot group in the cluster analysis (udult, high nutrient; humult, low nutrient) or whether the species is a generalist.

‡ Total number of plot occurrences.

§ Numbers in parentheses are the number of plot occurrences by site. See Fig. 1 for site codes and locations.

TABLE 3. Mantel tests of correlation between floristic variation, soils (''habitat''), and topographic and geographic distance in four groups of 0.6-ha plots in Sarawak, East Malaysia.

Data	Floristics	Habitat	Distance	Floristics	Habitat	Distance
a) All log plots						
	Habitat PCA Axis 1			Habitat PCA Axis 2		
Floristics		0.651**	0.058		0.089**	0.058
Habitat	0.651**		0.168	0.083**		−0.127
Distance	−0.068**	0.172		0.0470	−0.123	
b) Low-altitude Mount Mersing (site C) plots, high-nutrient mineral soil						
	Habitat PCA Axis 1			Topography		
Floristics		0.191**	0.269**		0.059**	0.269**
Habitat	0.190*		0.306	0.030**		0.113
Distance	0.269**	−0.022		0.265**	0.101	
	Residual Mg (ppm)			Residual P (ppm)		
Floristics		0.184*	0.269**		0.090*	0.269**
Habitat	0.200*		−0.031**	0.115*		−0.077**
Distance	0.280**	−0.085		0.278**	−0.106**	
c) Iju Hill (site G) plots, medium-nutrient soils						
	Habitat PCA Axis 1			Topography		
Floristics		0.223*	0.271**		0.106**	0.271**
Habitat	0.221*		0.041	0.121**		−0.038
Distance	0.269**	−0.020		0.277**	−0.070	
	Residual Mg (ppm)			Residual P (ppm)		
Floristics		0.420**	0.271**		0.130**	0.271**
Habitat	0.405**		0.121*	0.122**		0.049*
Distance	0.244*	0.009		0.267**	0.014	
d) Raya Hill (site H) plots, low-nutrients soils						
	Habitat PCA Axis 1			Topography		
Floristics		0.041*	0.396**		0.265**	0.396**
Habitat	0.004*		0.096	0.242**		0.111
Distance	0.395**	0.086		0.383**	0.007	
	Residual Mg (ppm)			Residual P (ppm)		
Floristics		0.010**			0.140**	0.396**
Habitat	−0.020**		0.396**	0.014**		0.322**
Distance	0.397**	0.027	0.021*	0.375**	0.294**	

Notes: Mantel statistics are above the diagonal, and partial Mantel statistics are below the diagonal (partial Mantel statistics were calculated with respect to habitat, distance, and floristics). See Fig. 1 for locations of the plots.
* $P < 0.05$; ** $P < 0.01$.

6). In general, the cohesion of the plots at each site in the final clusters notwithstanding within-site habitat variability is also striking (Fig. 2).

The placement of the Bukit Lambir L2 plot and the Ulu Dapoi (D) plots provide the best evidence for the importance of habitat over distance. The L2 plot is on udult clay-loam while the rest of the L plots are on humult sandy soils. The L2 plot is of the same shale geologic formation as the E and J plots and is placed with the rest of the clay plots (sites A, C, E, and J) while the remainder of the humult L plots, which are over an adjacent sandstone geological formation, are placed with the humult cluster. Likewise, D2, which is on a dacite scarp, is placed with the other udults while D1, nearby on the plateau with humult soils, clusters with the remainder of the humult plots.

Finally, the graph of plot similarity by distance (Fig. 4) suggests that sites with the same surface soil characteristics are more similar than sites that do not share the same surface soil characteristics. However, we do not observe any clear relationship between floristic similarity and distance for plots within 200 km of each other. In this range floristic similarity varies from 0 to 0.5.

Resource threshold for habitat effects

Both the results of the Mantel test and the cluster analysis indicate that soil resource levels play an important role in the balance between spatial distance vs. habitat as determinants of floristic similarity—especially for plots within the same local area (site). This conclusion is reached by comparing the differential ef-
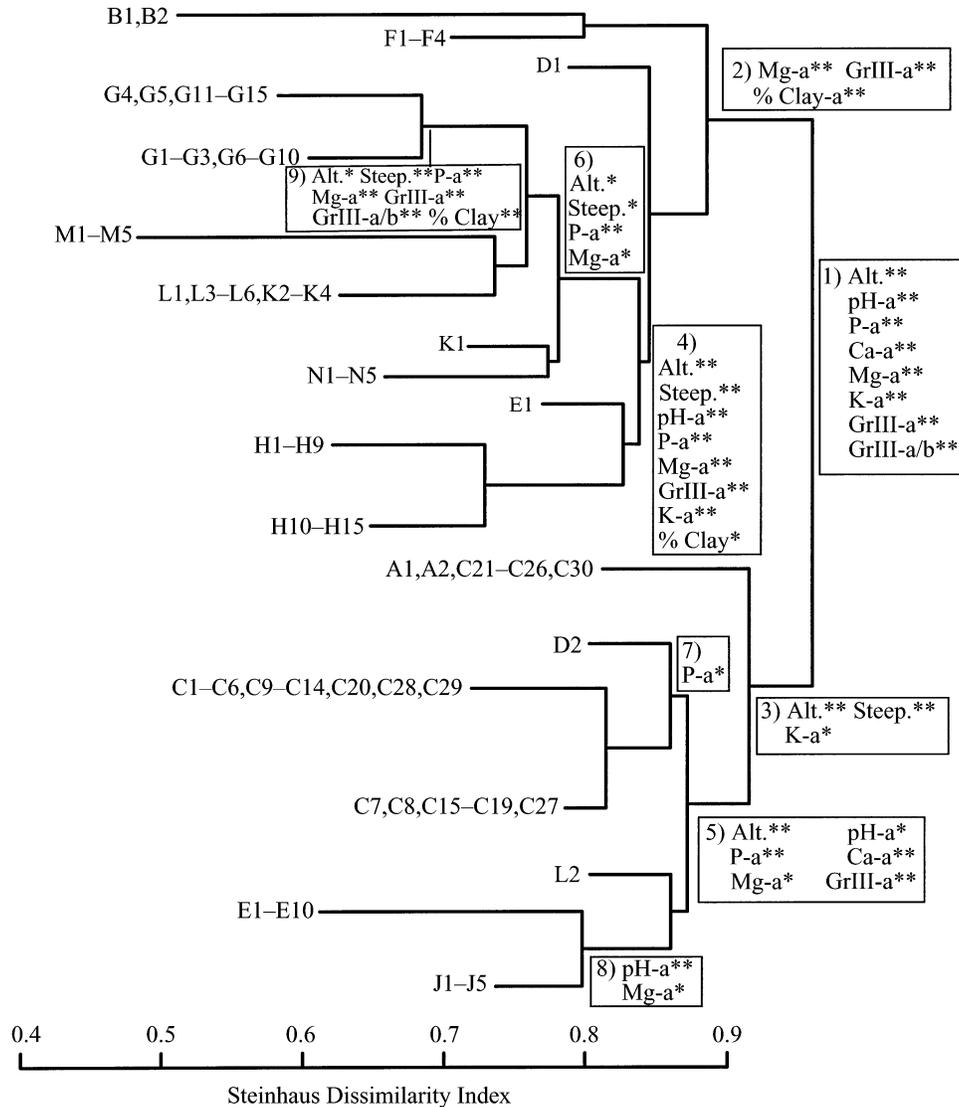
FIG. 6. Cluster analysis, average-linkage clustering, of 105 0.6-ha plots from mixed dipterocarp forests of Sarawak, East Malaysia. Capital letters of plots in dendrogram indicate sites (see Fig. 1, Table 1). Habitat factors significantly ($*P < 0.05$; $**P < 0.01$) related to numbered divisions are listed in boxes. For a full explanation of habitat factors see Fig. 2 and *Materials and methods: Field sampling.*

fects of distance and habitat on floristic similarity in 15 plots at each of sites C (low-altitude plots), G, and H.

The fifteen plots at each of these three sites sample similar ranges of altitude (200–500 m) and topography, although spurs rather than ridges were available at Mount Mersing. Within each site, all plots are a similar distance apart with a maximum of 4 km between plots.

Particulate organic matter is concentrated in the surface horizons of undisturbed low-altitude upland tropical soils (I. H. Baillie *in* Richards 1996:256–286). By sampling mineral soil below the zone of humic discoloration we minimized the possible influence on nutrient concentration of the litter of individual tree species, whose presence might in turn have been influ-

enced by dispersal and geographic constraints, and thereby increased the validity of cross-site comparisons. The lower mineral ion concentrations are similar at the three sites (Fig. 2), but the highest levels at each of the sites increase from the rhyolite G site through the sedimentary H site to the basic volcanic C site. Maximum concentrations at the C site are sometimes an order of magnitude greater than at the other sites. Variability in mineral ion concentrations was generally lowest at site G and highest at site C.

The results from the Mantel test (Table 3) imply that a threshold exists above which differences in nutrient levels are no longer associated with floristic differences. In the C plots, which have the highest nutrient concentrations but also the highest nutrient variability, the

TABLE 4.　Correlations between topographic variables in three groups of plots in Sarawak, East Malaysia.

Variable	Residual P (ppm)	Residual Ca (ppm)	Residual Mg (ppm)	Residual K (ppm)	Residual GrIII (ppm)	GrIII-a/ GrIII-b
a) Mount Mersing (site C) plots, low altitude						
Slope or ridge	NS	NS	NS	NS	NS	NS
Altitude (m)	−0.352	−0.162	−0.219	0.105	0.257	0.010
Steepness	−0.114	0.019	0.019	0.057	0.019	0.152
b) Iju Hill (site G) plots						
Slope or ridge	NS	NS	**	*	NS	NS
Altitude (m)	−0.486*	0.371*	−0.343	−0.457*	−0.248	−0.095
Steepness	0.314	0.048	−0.010	−0.048	0.295	−0.162
c) Raya Hill (site H) plots						
Slope or ridge	NS	NS	*	NS	NS	NS
Altitude (m)	−0.114	−0.200	0.057	0.171	0.095	0.114
Steepness	−0.190	0.000	0.295	0.086	0.010	0.143

Notes: "GrIII" indicates Group III elements, here iron and aluminum; "a" means soil sample was taken at 20–30 cm depth, "b" at 70–80 cm, and "ppm" means parts per million, i.e., μg element per g soil. For discrete data (landform) results of a permutation test (Good 1994) are reported, while for continuous data (altitude and steepness) the results of a Spearman rank-order correlation are reported.

* $P < 0.05$; ** $P < 0.01$; NS = not statistically significant.

association between floristic similarity and spatial distance (0.269) is much higher than that of edaphic (0.190) or topographic (0.030). Habitat–floristic comparisons using single habitat factors yielded similarly low association levels. Yet in the G plots, with both the lowest levels and lowest variability in nutrient levels, the association between floristic similarity and nutrient levels (0.221) is on par with that of spatial distance (0.269). In addition, among the G plots, when we restrict the habitat variable to the soil mineral Mg, we find that the association between habitat and floristics (0.405) is nearly twice that of association between spatial distance and floristics (0.244). The cluster analysis confirms this trend. The C plots unite quite early in the clustering hierarchy, where divisions correlate with few habitat variables. The G plots, on the other hand, and to a lesser extent the H plots, unite quite late in the cluster analysis and differ in a substantial number of habitat variables.

Edaphic vs. physiographic factors

Few significant correlations exist between edaphic soil mineral variables and physiographic variables (Table 4). However, there is only a consistent but unexplained negative correlation of Mg with ridges vs. slopes. Thus, differences between physiographic and edaphic effects can be compared without concern about autocorrelation.

The results of the Mantel analysis at individual sites (C, G, H) clearly illustrate that edaphic factors are much more important than physiographic factors in explaining floristic similarity between plots. Edaphic factors associate much more strongly with floristic similarity than physiographic effects (0.190 vs. 0.030

across the low-altitude C plots; 0.221 vs. 0.121 at site G).

The exception to this rule is the Raya Hill (H) plots, where the strength of physiographic effects (0.242) are stronger than edaphic effects (−0.011). At the Raya Hill site (H), unlike the Mount Mersing (C plots) and Iju Hills (G plots) that are composed of a uniform volcanic substrate, the sedimentary rocks consist of interbedded sandstones and shales with freely draining erodible sandstones supporting the ridges, while clay-rich landslip-prone soils cover the slopes. These are, in fact, the geomorphological characteristics most often found in the region.

DISCUSSION

Determinism in forest composition

In spite of marked local endemism within these putative northwest Borneo refugium, particularly on the humult ultisols of the coastal hills (Ashton 1992, 1995, Wong 1998), the cluster and Mantel analyses show that habitat is more strongly associated with floristic similarity than is geography on a regional scale. Cluster analysis showed that mixed dipterocarp forest (MDF) is primarily divided into two main groups of species associations, which correlate with the presence of acid surface raw humus analogous to temperate mor, and its absence on soils in which organic matter is relatively sparse. The scale of species spatial patterning on the community level (~50 ha) observed at the Lambir (L) site (Fig. 1) is substantially larger than that which is captured by the sample plot size of 0.6 ha (Plotkin et al. 2000a). Despite the small signal-to-noise ratio in our data, we find significant habitat effects, indicating that habitat effects are strong indeed.

Predictability in composition of the more abundant species on the major soil types provides further evidence that soils mediate the presence of floristically distinct communities, as in temperate forests. Only 17 out of the 60 species that were among the 10 most abundant species in at least five plots were edaphic generalists. All other 43 species were confined to soils with, or without, surface raw humus (humult and udult, respectively, in Table 3). Among these 60 species, the ectotrophically mycorrhizal Dipterocarpaceae were disproportionately represented with 24 species whereas <10% of the species sampled were dipterocarps.

These results are quite surprising when we consider the limitations of both our floristic and soil chemical data. Nevertheless, our nutrient measures correlated with maximum growth rates and the soils range of species with maximum growth rates per plot (Ashton and Hall 1992). We believe the data provide a reliable quantitative measure of edaphic similarity between plots and also an approximation of the long-term nutrient inputs to the forest ecosystem from the substrate.

The observed consistency in composition provides further, albeit circumstantial, evidence that deterministic forces play as strong a role as random forces, drift, and dispersal limitation in shaping forest composition across Northwest Sarawak. In addition, palaeontological evidence suggests that these forests have remained largely unchanged since the mid-Miocene. Thus, using spatial distance as a proxy for time, our results suggest that the landscape is composed of a mosaic of equilibrium forest types. Therefore, for the conservation planner it will be important to ensure adequate conservation of MDF types on the various surface lithologies, but it is also necessary to ensure a geographical spread of conservation areas. In any case, survival of floristic diversity will additionally depend on the survival of pollinators and fruit dispersers.

Resource thresholds in tropical forests

Besides addressing the balance between deterministic and stochastic forces in shaping community structure at local and landscape scales, our data provide evidence of resource thresholds above which the strength of edaphic effects weakens significantly. We have seen that edaphic similarity plays very little or no role in explaining floristic similarity between plots at the high-nutrient C site, while at the low-nutrient G site edaphic similarity overall is as important as distance in explaining floristic similarity between plots. At the G site, similarity in magnesium level between plots is almost twice as correlated with floristic structure than is distance; in fact, at the G site, Mg is as strongly correlated with floristics as any other factor in all the Mantel analyses. The strength of correlation between species composition and Mg in low-nutrient ultisols of northern Borneo has been previously documented (Baillie and Ashton 1983).

Comparison with the Neotropics

Our results amplify but also in part differ from those from the Neotropics. Terborgh et al. (1996), Terborgh and Andersen (1998), and Pitman et al. (1999), Pitman et al. (2001) found that most species in mature forest within a major habitat and geographical region (comparable in nature and extent to our dataset), the uplands of the Upper Amazon, had wide geographic and ecological amplitudes. Local abundance of generally sparsely distributed species does occur, but in the absence of either climate or soils data no habitat-correlated gradients in species composition were demonstrated. The relationships between floristic composition and soils that we have shown in Borneo quite strikingly resemble those recorded by Duivenvoorden (1995) on the Guyana Shield lowlands of the Colombian Amazon, which show apparently similar landscape and soil associations to ours. He too found that the major overall floristic gradient on low-nutrient soils was correlated with mineral soil nutrients. Duivenvoorden provided limited evidence of habitat specificity among tree species on these low-nutrient upland soils. He did not examine the effects of distance on floristic similarity. Pyke et al. (2002) also found little evidence of habitat-related floristic variation, locally or at distances <50 km in Panama, and concluded that pattern was driven by inter-plot distances. Consistency of composition among the most abundant species was markedly lower than in our data sets from Northwest Borneo, and soil analytical data were also unavailable in their case, but their soils were udult clays overlying shale and limestone influenced by basic vulcanicity, and probably contained high relative nutrient concentrations. Our results suggest that geographic distance dominates floristic variation in such habitats in Borneo also.

High-nutrient volcanic and other soils are restricted to a small overall area of the humid tropical lowlands (Weischet and Caviedes 1993). Much research in tropical-forest ecology has been focused on habitats such as those in Central America, but it is unclear at present whether most upland rain forest soils carry nutrient concentrations above or below the threshold observed in our results, below which soil resources more influence species composition do than distance effects. Results from the Amazon suggest that soils there may mostly be above the threshold, though more studies are needed from the low-nutrient Guyana and Brazilian Shields. The absence of high species turnover along a nutrient gradient on low-nutrient soils of the aseasonal Colombian Amazon, documented by Duivenvoorden (1995), nevertheless remains unexplained though he suggested that this might be an artefact of the small size of his plots (0.1 ha).

The regions of the Neotropics investigated so far appear to have an almost ubiquitous history of slash-and-burn agriculture. In Borneo, by contrast, traditional slash-and-burn was confined to the most fertile soils

and less steep slopes (M. Dove, *personal communication*). Such land use may increase stochasticity in local floristic composition of communities with limited vegetative regeneration and limited seed dispersal.

Conclusions

Our results, though preliminary, indicate that abiotic factors are more influential in differentiating species associations in primary tropical rainforest than has recently been claimed, particularly in the Neotropics. They suggest important avenues for further research (currently underway in Center for Tropical Science 50-ha plots) to identify and quantify the scale and variation of resource levels in local communities. In the future, we must couple an analytical understanding of such variation to species distributions and performance. In addition, direct experimental studies will be useful to test this hypothesis. Such controlled experiments should further clarify the key functional roles and scales of influence of deterministic and stochastic effects on floristic composition.

Literature Cited

Ashton, P. S. 1964. Ecological studies in the mixed dipterocarp forests of Brunei State. Oxford Forestry Memoirs **25**.

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. 1984. Biosystematics of tropical forest plants: a problem of rare species. Pages 497–518 *in* W. F. Grant, editor. Plant biosystematics. Academic Press, Toronto, Ontario, Canada.

Ashton, P. S. 1992. Plant conservation in the Malaysian region. Pages 86–93 *in* S. K. Yap and S. W. Lee, editors. In harmony with nature: Proceedings of the International Conference on Conservation of Tropical Biodiversity, Kuala Lumpur. Malayan Nature Society, Kuala Lumpur, Malaysia.

Ashton, P. S. 1995. Biogeography and ecology. Pages xliii–li *in* E. Soepadmo and K. M. Wong, editors. Tree flora of Sabah and Sarawak. Volume 1. Forest Research Institute Malaysia, Kepong, Malaysia.

Ashton, P. S., and P. Hall. 1992. Comparisons of structure and dynamics among mixed dipterocarp forests of northwestern Borneo. Journal of Ecology **80**:459–481.

Austin, M. P., P. S. Ashton, and P. Greig-Smith. 1972. The application of quantitative methods to vegetation survey. III: a re-examination of rain forest data from Brunei. Journal of Ecology **60**:309–324.

Bailey, J. M. 1967. Chemical changes in a Sarawak soil after fertilisation and crop growth. Plant and Soil **27**:33–52.

Baillie, I. C. 1976. Further studies on drought in Sarawak, East Malaysia. Journal of Tropical Geography **43**:20–29.

Baillie, I. C., and P. S. Ashton. 1983. Some soil aspects of the nutrient cycle in mixed dipterocarp forests in Sarawak. Pages 347–356 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forest: ecology and management. Number 2 in Special Publication, British Ecological Society special publication number 2. Blackwell, Oxford, UK.

Baillie, I., P. Ashton, M. Court, J. A. R. Anderson, E. A. Fitzpatrick, and J. Tinsley. 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**:201–202.

Beccari, O. 1902. Nelle foresti di Borneo; viaggi e ricerche di un naturalista. S. Landi, Florence, Italy.

Brunig, E. F. 1969. On the seasonality of droughts in the lowlands of Sarawak (Borneo). Erdkunde **23**:127–133.

Clark, D. A., D. B. Clark, R. M. Sandoval, and M. C. Vinicio Castio. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology **76**:2581–2594.

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

Corner, E. J. H. 1960. The Malayan flora. Pages 21–24 *in* R. D. Perchon, editor. Proceedings of the Centenary and Bicentenary Congress of Biology, Singapore. University of Malaya Press, Singapore, Malaysia.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics **18**: 431–451.

Dietz, E. J. 1983. Permutation tests for association between two distance matrices. Systematic Zoology **32**:21–26.

Duivenvoorden, J. F. 1995. Tree species composition and rain forest–environment relationship in the middle Caquetá area, Columbia, NW Amazonia. Vegetatio **120**:91–113.

Duivenvoorden, J. F., and J. M. Lips. 1995. A land-ecological study of soils, vegetation, and plant diversity in Columbian Amazonia. Tropenbos Series **12**.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology **12**:42–58.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden **75**: 1–34.

Good, P. I. 1994. Permutation tests: a practical guide to resampling methods for testing hypotheses. Springer-Verlag, New York, New York, USA.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. Biometrics **23**:623–637.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science **203**:1299–1309.

Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs **16**:S9–S21.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S. P., and R. B. Foster. 1986. Biology, chance and history and the structure of tropical rain forest tree communities. Pages 314–325 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Hubbell, S. P., R. B. Foster, S. T. OBrien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science **283**:554–557.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history, and competitive differences between plants. Journal of Theoretical Biology **176**:1–12.

Kohyama, T. 1994. Size-structure-based models of forest dynamics to interpret population-level and community-level mechanisms. Journal of Plant Research **107**:107–116.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Lieberman, M., D. Lieberman, G. S. Hartshorn, and R. Peralta. 1985. Small-scale altitudinal variation in low-land wet tropical forest vegetation. Journal of Ecology **73**:505–516.

MacArthur, R. H., and E. O. Wilson, editors. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research **27**:209–220.

Morley, R. J. 1999. Origin and evolution of tropical rain forest. John Wiley and Sons, Chichester, UK.

Morley, R. J., and J. R. Flenley. 1987. Late Cenozoic vegetational and environmental changes in the Malay Archipelago. Pages 50–59 *in* T. C. Whitmore, editor. Biogeographical evolution of the Malay Archipelago. Oxford University Press, Oxford, UK.

Newbery, D. M., and J. Proctor. 1984. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. IV. Associations between tree distribution and soil factors. Journal of Ecology **72**:475–493.

Pitman, N., J. Terborgh, M. R. Silman, and P. Nuez. 1999. Tree species distributions in an upper Amazonian forest. Ecology **80**:2651–2661.

Pitman, N., J. Terborgh, M. R. Silman, P. Nuez, D. A. Neill, C. E. Ceron, W. A. Palacios, and M. Aulestia. 2001. Dominance and distributions of tree species in upper Amazonian terra firme forests. Ecology **82**:2101–2117.

Plotkin, J. B., M. D. Potts, N. Leslie, N. Manokaran, J. LaFrankie, and P. S. Ashton. 2000*a*. Species-area curves, spatial aggregation, and habitat specialization in tropical forests. Journal of Theoretical Biology **207**:81–99.

Plotkin, J. B., M. Potts, D. W. Yu, S. Bunyavejchewin, R. Condit, R. Foster, S. Hubbell, J. LaFrankie, N. Manokaran, H. S. Lee, R. Sukumar, M. A. Nowak, and P. S. Ashton. 2000*b*. Predicting species diversity in tropical forests. Proceedings of the National Academy of Science **97**:10850–10854.

Pyke, C. P., R. Condit, S. Aguilar, and A. Hernández. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. Journal of Vegetation Science **12**(4):533–566.

Richards, P. W., editor. 1996. The tropical rain forest. Cambridge University Press, New York, New York, USA.

Sim, E. S. 1965. Methods of analysis for agricultural materials. Department of Agriculture, Kuching, Sarawak, Malaysia.

Terborgh, J., and E. Andersen. 1998. The composition of Amazonian forests—patterns at the local and regional Scales. Journal of Tropical Ecology **14**:645–664.

Terborgh, J., R. B. Foster, and P. V. Nunez. 1996. Tropical tree communities: a test of the nonequilibrium hypothesis. Ecology **77**:561–567.

Tilman, D., and S. W. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Tuomisto, H., and K. Ruokolainen. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rainforest. Journal of Vegetation Science **5**:25–34.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science **269**:63–66.

Weischet, W., and C. N. Caviedes. 1993. The persisting ecological constraints of tropical agriculture. Longmans Scientific and Technical, London, UK.

Whitmore, T. 1984. Tropical rain forests of the Far East. Clarendon: Oxford University Press, Oxford, UK.

Wong, K. M. 1998. Patterns of plant endemism and rarity in Borneo and the Malay peninsula. Pages 139–169 *in* C. I. Peng and P. P. L. II, editors. Rare, threatened and endangered floras of Asia and the Pacific Rim. Institute of Botany Monograph 16. Academia Sinica, Taipei, Taiwan.

Wong, Y. K., and T. C. Whitmore. 1970. On the influence of soil properties on species distributions in a Malayan lowland dipterocarp rain forest. Malayan Forester **33**:42–54.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.