Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees

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Summary

1 The relative importance of niche- and dispersal-mediated processes in structuring diverse tropical plant communities remains poorly understood. Here, we link mesoscale beta diversity to soil variation throughout a lowland Bornean watershed underlain by alluvium, sedimentary and granite parent materials (*c.* 340 ha, 8–200 m a.s.l.). We test the hypothesis that species turnover across the habitat gradient reflects interspecific partitioning of soil resources.

2 Floristic inventories (≥ 1 cm d.b.h.) of the Dipterocarpaceae, the dominant Bornean canopy tree family, were combined with extensive soil analyses in 30 (0.16 ha) plots. Six samples per plot were analysed for total C, N, P, K, Ca and Mg, exchangeable K, Ca and Mg, extractable P, texture, and pH.

3 Extractable P, exchangeable K, and total C, N and P varied significantly among substrates and were highest on alluvium. Thirty-one dipterocarp species (*n* = 2634 individuals, five genera) were recorded. Dipterocarp density was similar across substrates, but richness and diversity were highest on nutrient-poor granite and lowest on nutrient-rich alluvium.

4 Eighteen of 22 species were positively or negatively associated with parent material. In 8 of 16 abundant species, tree distribution (≥ 10 cm d.b.h.) was more strongly non-random than juveniles (1–10 cm d.b.h.), suggesting higher juvenile mortality in unsuitable habitats. The dominant species *Dipterocarpus sublamellatus* (> 50% of stems) was indifferent to substrate, but nine of 11 'subdominant' species (> 8 individuals ha^{-1}) were substrate specialists.

5 Eighteen of 22 species were significantly associated with soil nutrients, especially P, Mg and Ca. Floristic variation was significantly correlated with edaphic and geographical distance for all stems ≥ 1 cm d.b.h. in Mantel analyses. However, juvenile variation (1–10 cm d.b.h.) was more strongly related to geographical distance than edaphic factors, while the converse held for established trees (≥ 10 cm d.b.h.), suggesting increased importance of niche processes with size class.

6 Pervasive dipterocarp associations with soil factors suggest that niche partitioning structures dipterocarp tree communities. Yet, much floristic variation unrelated to soil was correlated with geographical distance between plots, suggesting that dispersal and niche processes jointly determine mesoscale beta diversity in the Bornean Dipterocarpaceae.

Key-words: diversity, dominance, magnesium, mass effects, mesoscale, neutral, niche, phosphorus, *Shorea*

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Introduction

Discontinuities in soil drainage cause major changes in the species composition of lowland tropical tree communities and promote the coexistence of species adapted to contrasting edaphic environments (Lieberman *et al.* 1985; Newbery, Gartlan, McKey & Waterman1986; Clark *et al.* 1999). The effects of discontinuities in geological substrate on community structure (Clark *et al.* 1998, 1999; Phillips *et al.* 2003) are, however, less well understood. Plant-soil surveys across substrate gradients at a regional scale (up to 75 000 km^2) have documented distinct plant communities on contrasting substrates, and linked these differences to variation in soil phosphorus (P) or magnesium (Mg) (Austin *et al.* 1972; Gartlan *et al.* 1986; Baillie *et al.*1987; Swaine 1996; Potts *et al.* 2002). This pattern suggests that substrate-mediated nutrient variation promotes regional beta diversity and, thus, coexistence of tropical trees (Sollins 1998). However, interpreting regional correlations is complex, because regional-scale studies potentially confound the effects of habitat partitioning with dispersal limitation and historical biogeographical processes (but see Phillips *et al.* 2003).

Current understanding of substrate influences on beta diversity of tropical trees is further complicated by field sampling problems, including inadequate attention to the spatial design of soil sampling (e.g. Gartlan *et al.* 1986; Newbery, Renshaw & Brunig, 1986; Ola-Adams & Hall 1987) and insufficient replication of spatially independent floristic plots within substrates (Proctor *et al.* 1983; Newbery & Proctor 1984). Here, we address these limitations by combining intensive soil sampling with replicated tree surveys throughout a lowland Bornean watershed on contrasting geological substrates. We test the hypothesis that canopy tree beta diversity reflects interspecific partition of geological substrates and identify candidate soil nutrients underlying this pattern.

Mesoscale beta diversity (*sensu* Clark *et al.* 1998) measures the extent of species turnover at spatial scales that encompass repeated sampling of landscape units, such as topographic catenas or geological substrates. Mesoscale sampling (1–100 km^2) is broader than local studies (< 100 ha), but smaller than regional studies (10^2 to *c.* 10^5 km^2), and offers three advantages for studying edaphic influences on community structure. First, the mesoscale captures a broader range of soil conditions than local scales and increases power for detecting plant–soil associations. Secondly, because dispersal limitation is less severe across mesoscale landscapes, and biogeographical and climatic histories are similar, plant-soil correlations at the mesoscale more strongly suggest niche partitioning than regional studies. Finally, the mesoscale enables convenient study of the combined influences of deterministic and neutral processes: niche partitioning, for instance, may cause species segregation across substrates, whilst dispersal-mediated

mass effects (Shmida & Wilson 1985) may cause a degree of floristic mixing among them.

Despite advantages of the mesoscale, and continued interest in tropical tree beta diversity (Hubbell 2001; Condit *et al.* 2002; Chave & Leigh 2002), relatively few studies have been conducted at this scale (Ashton 1976; ter Steege *et al.* 1993; Clark *et al.* 1998, 1999; Cannon & Leighton 2004; Hall *et al.* 2004). All of these studies found a significant effect of geological substrate, soil type or topography, but only Hall *et al.* (2004) quantified soil nutrients correlated with floristic change. Whether mesoscale beta diversity reflects niche partitioning, and, if so, the role of specific soil nutrients, thus remains poorly understood.

Here, we combine a floristic inventory of rain forest trees in the Dipterocarpaceae, the dominant family of canopy trees in Borneo (Curran & Leighton 2000; Slik *et al.* 2003), with extensive soil analyses throughout a forested watershed (*c.* 340 ha) underlain by three geological substrates. We quantify soil nutrient variation and its association with species distributions. To evaluate the degree to which species-site correlations reflect niche partitioning vs. dispersal limitation, we conducted Monte-Carlo randomizations and Mantel analyses on specific size classes. Finally, we investigate dominance-distribution relationships throughout the watershed to test for an effect of generalist vs. specialist strategies on rank abundance. Dominant tree species at regional scales in western Amazonia are widespread ecological generalists (Ruokolainen & Vormisto 2000; Pitman *et al.* 2001; Vormisto *et al.* 2004), but dominance-distribution relationships have not been studied at smaller scales across well-defined nutrient gradients.

We focus on the Dipterocarpaceae, a species-rich (*c.* 520 species) monophyletic family of tropical trees, for several reasons. First, Bornean dipterocarps reproduce synchronously every 3–7 years (Curran *et al.* 1999) and share wide-ranging generalist seed predators (Curran & Leighton 2000; Curran & Webb 2000; Lyal & Curran 2000, 2003). This controls for climatic variation during seedling establishment, as well as habitat-specificity in seed predators, two potentially confounding influences on species distributions. Secondly, dipterocarp seed is wind or gravity dispersed, minimizing the effect of divergent dispersal syndromes on species distributions (Ashton 1982). Thirdly, all dipterocarps form ectomycorrhizal associations. Fourthly, 60% of the 267 species in Borneo are endemic (Ashton 1982), implying a shared biogeographical and evolutionary history for much of the flora. Finally, a robust quantification of individual dipterocarp species associations with soil nutrients has been performed only at regional scales (Austin *et al.* 1972; Baillie *et al.* 1987).

Materials and methods

STUDY SITE

The study was conducted at the Cabang Panti Research Station (15 km^2) in Gunung Palung National Park

(GPNP, 90 000 ha) in West Kalimantan, Indonesia (1°00′–1°20′ S, 109°00′ 110°25′ E). Mean annual rainfall is 4125 ± 950 mm (mean $\pm$ SD 1985–2002), with marked interannual variation in dry season intensity corresponding to El Niño Southern Oscillation (ENSO) events. The western slopes of two interconnected peaks in the centre of GPNP, Mt Palung (1070 m) and Mt Panti (1130 m), form the watershed of the research station.

A range of Bornean lowland forest types occurs at GPNP, including peat swamp, freshwater swamp and lowland forests on well-drained mineral soils up to *c.* 300 m a.s.l. Upland forest is underlain by a variety of parent materials. Alluvial deposits occur along banks of the Air Putih River from 5 to 15 m a.s.l., composing a contiguous area of *c.* 100 ha in the study site. Upslope (40–140 m a.s.l.) is a texturally complex zone of sedimentary rock, in which localized patches of quartzite occur. Beyond sedimentary rock, forest is underlain by granite to the summit of both peaks. The Air Putih River separates the sedimentary and alluvium substrates by only 8–15 m. The species composition of woody plants varies among soil types (Cannon & Leighton 2004), but edaphic correlates of floristic variation have not been studied. Throughout Kalimantan, the alluvium, sedimentary and granite substrates present at GPNP underlie 1%, 53% and 7%, respectively, of land area < 500 m a.s.l. (L. M. Curran *et al.*, unpublished data).

FLORISTIC AND EDAPHIC VARIATION

Thirty 40×40 m plots (0.16 ha) were established between 8 and 180 m a.s.l. throughout the watershed (*c.* 340 ha). This plot size was chosen to ensure plots could be treated as 'homogeneous' edaphic units on all substrates. Plots were stratified throughout the watershed on alluvium ($n = 10$), sedimentary ($n = 8$) and granite substrates ($n = 12$). Plot establishment was aided by a network of permanent trails traversing alluvial plain, ridge, valley and slope microhabitats. Plots were positioned at a randomly determined distance (30–150 m) and angle (30–150°) from randomly determined points along trails. Areas with recent gaps (canopy < 5 m) representing > 30% of total plot area were rejected. Distances between plots ranged from 51 to 1747 m; plots were less dispersed on alluvium (median = 362 m) than sedimentary (median = 773 m) or granite habitats (median = 661 m), reflecting the smaller extent of alluvium. Rainfall and maximum-minimum temperature were monitored over 12 months at 10, 40, 60, 180 and 210 m a.s.l. and showed no significant relationship with elevation throughout the study area (G. D. Paoli, unpublished data).

SOIL SAMPLING

We quantified texture and nutrient content of surface soils (0–20 cm) in all 30 plots. Six sampling points were randomly stratified in each plot (5–24 m between points), and five soil cores (2-cm diameter) were collected at each point, one at the centre and four at 2 m in cardinal directions. The five cores per point were combined in the field ($n = 6$ samples per plot), air dried, lightly ground and sieved to remove coarse particles. Mineral fractions ($\leq$ 2 mm) were subsampled (*c.* 150 g) and transported to the USA for analyses.

Total nutrient assays indicate potential long-term nutrient supply, but overestimate short-term availability, whereas labile nutrient assays measure readily available forms that may be poor indicators of long-term availability. Both pools were therefore measured to maximize the power of tests for plant–soil associations. Total C and N were measured by combustion using *c.* 40 mg samples of finely ground soil oxidized at 700 °C (NC2500, CE Instruments, Milan, Italy). Total P, K, Ca and Mg concentrations were determined by digesting 500 mg of finely ground soil in sequential additions of concentrated HF, HCl and H_2O_2 (Bowman 1990). Total P was measured using the orthophosphate procedure on the Alpkem Rapid Flow AutoAnalyser (RFA 3550; OI Analytical, Austin, Texas, USA); cations were measured using ICP Optical Emission Spectrometry (Optima 3000; Perkin Elmer, Shelton, Connecticut, USA). Exchangeable cations were extracted from 10 g samples using 100 mL of M ammonium acetate (without pH adjustment). Extractable P was quantified using the Olsen method (Olsen *et al.* 1954) on 3-g samples.

Texture was quantified for *c.* 50 g samples using the hydrometer method (Sheldrick & Wang 1993) and pH on two 10-g samples, using 20 mL of distilled water or 0.01 M $CaCl_2$ after equilibrating for 1 hour. Soil nutrient content was expressed in kg or Mg (megagram) ha^{-1} by multiplying nutrient concentration (μg g^{-1}) by soil bulk density (g cm^{-3}) and sampling depth (20 cm). Soil bulk density was estimated using Rawl's (1983) regression method. All analyses used nutrient content, not concentration, because the former better describes availability by incorporating bulk density differences. Nutrient concentrations are presented in Table 1 for comparison with other studies.

DIPTEROCARPACEAE SURVEYS

The Dipterocarpaceae were enumerated in all 30 plots. Each plot was separated into 32 quadrats (5×10 m) surveyed for all stems $\geq$ 1 cm d.b.h. Dipterocarp individuals were measured (d.b.h.) and identified to species ($n = 2602$ stems) or morphospecies ($n = 30$ stems). Individuals were identified using published field guides and taxonomic treatments (Ashton 1982; Newman *et al.* 1996, 1998; Webb & Curran 1996), as well as a field guide based on trees previously field-identified by P. S. Ashton.

DATA ANALYSIS

Univariate and multivariate procedures were used to analyse soil variation throughout the watershed.

Table 1 Surface soil nutrients (0–20 cm) in lowland tropical forest on three parent materials at Gunung Palung National Park, Indonesia. Six samples were collected and analysed separately in replicate 0.16-ha plots on each substrate (alluvium $n = 10$, sedimentary $n = 8$, granite $n = 12$). Soil nutrient content (a) is expressed using the following units of mass ha^{-1} to 20 cm depth: Mg ha^{-1} for total C, N, and K; kg ha^{-1} for all others. Soil nutrient concentration (b) is in units of percentage mass for total C and N; cmol kg^{-1} for exchangeable cations; and μg g^{-1} for all others. Data are mean ± 1 SE. Superscripts indicate significant differences between substrates using Scheffe's test following nested two-factor ANOVA. $* P \leq 0.05$, $** P \leq 0.01$, $*** P \leq 0.005$

| | Total nutrients | | | | | | Exchangeable nutrients | | | |
| | | | | | | | Olsen | | | |
Parent material	C	N	P	K	Ca	Mg	P	K	Ca	Mg
(a) Nutrient content										
Alluvium	$116.4 \pm 2.8^{a*}$	$5.8 \pm 0.1^{a*}$	$416.8 \pm 15.1^{a***}$	10.8 ± 1.5	814.2 ± 54.7	278.4 ± 23.7	$47.9 \pm 2.9^{a***}$	$158.4 \pm 5.4^{a*}$	243.8 ± 12.2	19.1 ± 3.2
Sedimentary	78.9 ± 5.6^{b}	5.0 ± 0.1^{b}	353.7 ± 33.4^{b}	8.1 ± 1.3	680.6 ± 56.2	444.7 ± 50.9	21.6 ± 3.3^{b}	126.8 ± 6.0^{b}	182.7 ± 13.7	24.8 ± 3.6
Granite	82.2 ± 2.6^{b}	4.7 ± 0.1^{b}	198.1 ± 11.3^{c}	6.1 ± 1.4	625.4 ± 69.3	214.2 ± 25.9	12.1 ± 2.7^{c}	121.0 ± 4.9^{b}	181.9 ± 11.2	8.8 ± 3.0
(b) Nutrient concentration										
Alluvium	$6.9 \pm 0.9^{a*}$	$0.33 \pm 0.03^{a*}$	$232.9 \pm 5.6^{a***}$	5268 ± 260	$429.3 \pm 15.5^{a*}$	$143.8 \pm 10.2^{a*}$	$27.0 \pm 0.9^{a***}$	$0.22 \pm 0.02^{a*}$	$0.33 \pm 0.03^{a*}$	0.047 ± 0.016
Sedimentary	3.8 ± 0.4^{b}	0.24 ± 0.03^{b}	172.5 ± 6.2^{b}	3937 ± 291	325 ± 17.4^{b}	217.1 ± 11.4^{b}	9.9 ± 1.0^{b}	0.15 ± 0.02^{b}	0.22 ± 0.05^{b}	0.052 ± 0.02
Granite	4.1 ± 0.6^{b}	0.23 ± 0.02^{b}	90.6 ± 5.1^{c}	2767 ± 238	274.3 ± 14.2^{cc}	100.7 ± 9.3^{b}	5.3 ± 0.8^{c}	0.14 ± 0.01^{b}	0.20 ± 0.03^{b}	0.016 ± 0.003

Mixed-model nested two-factor ANOVA (sample nested within plot) was used to compare soil parameters among parent materials. Data were log transformed for total C and P, extractable P, and percentage clay, and ln transformed for exchangeable Mg and total K, Ca and Mg. Principal Components Analysis (PCA) was performed on standardized data (z scores) to identify leading dimensions of nutrient variation among substrates. Dipterocarp abundance, richness and diversity (Fisher's α) were compared among substrates using one-way ANOVA or Kruskal–Wallis test if required by the data. Analyses were performed using SPSS (version 11.5).

To test species associations with substrate, we used a Monte-Carlo randomization procedure that accounts for non-independence of individuals within a plot due to restricted seed dispersal (Webb & Peart 2000). We permuted the substrates on which all 30 plots occurred and for each species calculated a chi-square deviation statistic for the simulated data set [$\chi_{sim} = \Sigma(N_{obs} - N_{expec})^2/N_{expec}$], assuming a distribution of individuals across substrates proportional to total stem number (not number of plots) on each substrate. The procedure was repeated 1000 times to produce a simulated distribution of deviation statistics. Species were deemed significantly positively or negatively associated with a substrate if the observed deviation fell within the highest or lowest 5th percentile of the simulated distribution. This procedure was performed for all individuals (> 1 cm d.b.h.) and separately for juveniles (1–10 cm d.b.h.) and trees (> 10 dm d.b.h.). Stronger or more pervasive non-random distribution in larger size classes is a pattern consistent with juveniles experiencing higher mortality in unsuitable edaphic environments, a probable consequence of niche partitioning.

Species associations with soil parameters were tested using Monte-Carlo randomization. First, for all species and soil parameters, the mean *observed value* of a parameter was calculated as the average across all plots in which the species occurred. Observed values were determined on the basis of presence-absence, rather than weighted average, to avoid biases caused by non-independence of individuals in a plot. Then, from the pool of 30 plots, random draws were made equal to the number of plots in which a species was present, and a simulated value for the parameter was computed as the average of these draws. This process was repeated 1000 times to produce a simulated distribution with which to compare observed values of each species. Associations with a parameter were deemed significant if observed values fell with the lowest or highest 5% of the simulated distribution.

Finally, Mantel analyses were performed on distance matrices to compare the strength of correlations between floristic composition and geographical vs. environmental distance among plots (Legendre & Legendre 1998). Floristic dissimilarity was quantified using the Steinhaus dissimilarity index. Canonical correspondence analysis (CCA, ter Braak & Smilauer 2002) was used to identify soil parameters for inclusion in Mantel analyses

based on significant association with floristic patterns. All soil parameters were included in a forward-selection model that retained extractable P, exchangeable Mg and total K and explained 28% of floristic variation ($P < 0.0001$; results available upon request from GDP). We thus computed four matrices to describe edaphic distance: one for each nutrient and a Euclidean combination using standardized values (z scores). We performed full Mantel analyses to quantify overall correlations among matrices and partial Mantel to control for cross-correlation between geographical and edaphic distance. Version 1.0 of zt software was used to compute Mantel correlations and test significance of the *r* statistic using permutation (Bonnet & Van de Peer 2002).

Mantel analyses were first performed on all individuals (≥ 1 cm d.b.h.). If both niche partitioning and dispersal limitation influence dipterocarp community structure, then floristic divergence should be significantly related to both edaphic and geographical distances. We then performed separate analyses for juveniles (1–10 cm d.b.h.) and trees (≥ 10 cm d.b.h.) to test for changes with size class in the relative strength of floristic correlations with geographical and edaphic distance. If seed dispersal influences community structure by restricting local range expansions from one generation to the next, then differences among juveniles should be more strongly related to geographical distance than to edaphic factors. If, consistent with niche theory, juveniles of species poorly adapted to local conditions experience relatively high mortality, then floristic correlations with edaphic factors should be stronger for trees than for juveniles.

Results

SOIL VARIATION

Soil nutrients varied among substrates, and were generally highest in alluvium, intermediate in sedimentary soils and lowest in granitic soils. Total C, N and P, extractable P and exchangeable K were significantly higher in the alluvium than other substrates; total K and Ca, and exchangeable Ca, showed similar trends (Table 1). Averaging across all nutrients, the nutrient content of alluvium soils was nearly twice that of granite soils (Table 1). In contrast to soil nutrients, soil texture was similar across substrates. Only percentage silt varied significantly, and was highest on sedimentary

soils (Table 2). Soil pH was significantly lower in the alluvium than other substrates (Table 2).

In PCA of all data combined, axes 1 and 2 described 47% of variation throughout the watershed (Fig. 1). Alluvium and granite plots segregated along axis 1, representing a gradient of increasing P, N and exchangeable cations, and of decreasing pH; sedimentary plots were widely distributed across this axis (Fig. 1a).

ABUNDANCE AND DIVERSITY OF THE DIPTEROCARPACEAE

A total of 2632 dipterocarp individuals (≥ 1 cm d.b.h.) were enumerated, representing 31 species in five genera: *Shorea*, *Dipterocarpus*, *Hopea*, *Vatica* and *Anisoptera* (see Table S1 in Supplementary Material). Twenty-four taxa were identified to species; seven remain unidentified morphospecies, of which five were singletons. The genus *Shorea* was the most species-rich and dominant numerically, with 23 species and 1389 stems (52.8% of individuals). The genus *Anisoptera* was represented by two individuals of a single species (Table S1).

The dipterocarp community (≥ 1 cm d.b.h.) was dominated numerically by *Dipterocarpus sublamellatus* (Fig. 2a), which comprised > 40% of all dipterocarp stems and was present in 20 of 30 plots (Table S1). Dominance by *D. sublamellatus* was pervasive in all size classes (Table S1). In contrast, most other dipterocarp species were rare and sparsely distributed, 15 of 31 species were present in ≤ 3 plots. Across species, occurrence was positively correlated with log mean density throughout the watershed for stems ≥ 1, ≥ 10 or ≥ 30 cm d.b.h. (for all categories Pearson correlation $R \geq 0.88$, $P < 0.001$; Fig. 2b).

Dipterocarp density was similar across substrates, but species richness and diversity were significantly lower in the alluvium (Table 3). Summing across plots within a substrate, only 12 species were present on alluvium, 22 on sedimentary soils and 28 on the granite; lower richness in the alluvium was consistent across size categories (Table 3). Fisher's α index of diversity showed a similar pattern (Table 3).

HABITAT DISTRIBUTION ACROSS SUBSTRATES

Low dipterocarp species richness in the alluvium reflected a nested distribution of species across substrates

Table 2 Texture and pH properties of surface soils (0–20 cm) in lowland rain forest on three parent materials at Gunung Palung National Park, Indonesia. Superscripts indicate significant differences between substrates using Scheffe's test following two-factor nested ANOVA. Data are mean ± 1 SE. *$P \leq 0.05$

Parent material	Soil texture			Soil pH	
	% Sand	% Silt	% Clay	Water pH	CaCl$_2$ pH
Alluvium	65.1 ± 0.8	22.7 ± 0.8[a]*	12.2 ± 0.7	4.20 ± 0.02[a]*	3.54 ± 0.02[a]*
Sedimentary	61.3 ± 0.9	29.6 ± 0.8[b]	9.2 ± 0.8	4.49 ± 0.03[b]	3.70 ± 0.02[b]
Granite	67.7 ± 0.8	19.8 ± 0.7[c]	12.5 ± 0.6	4.51 ± 0.02[b]	3.71 ± 0.02[b]

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(a) Factor scores

(b) Factor loadings
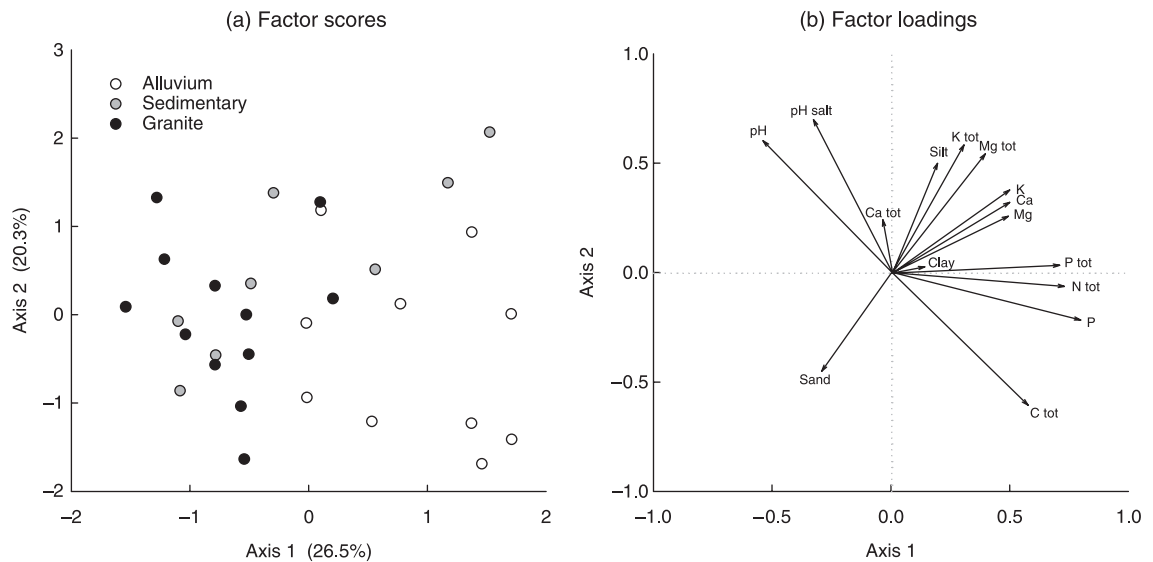
Fig. 1 Principal components analysis of soil nutrients in lowland rain forest on three parent materials at Gunung Palung National Park, Indonesia. PCA was performed on the mean of six surface soil samples (0–20 cm) in each of 30 (0.16 ha) plots analysed separately for 12 parameters including pH, and total and exchangeable nutrients. Factor scores for each plot (a) and axis loadings (b) are presented for PCA axes 1 and 2. Percentage of total variation explained by each axis is shown in parentheses. Total nutrients are denoted by subscript 'tot'.

(a)

(b)

(c)
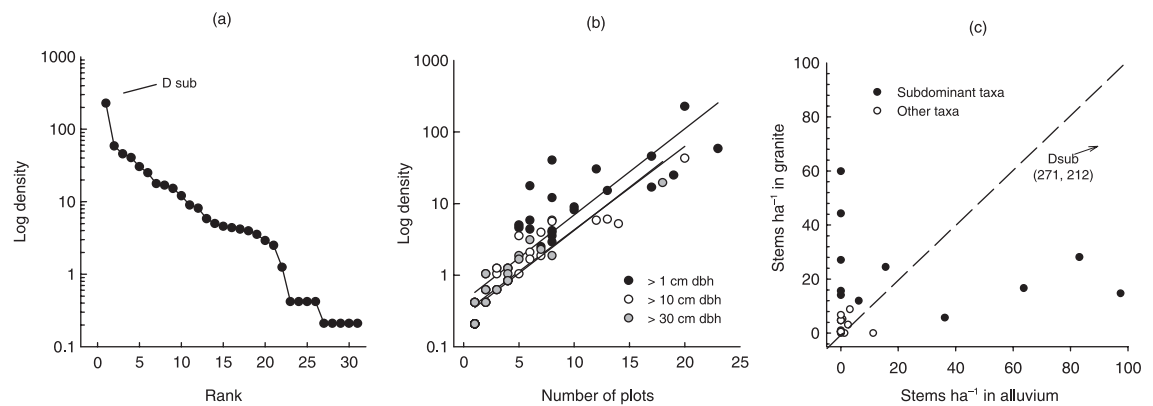
Fig. 2 Demographic attributes of the lowland dipterocarp community at Gunung Palung National Park, Indonesia. (a) Rank vs. log density. (b) Plot occupancy vs. log density plotted separately for nested size classes; curves were fit using least squares linear regression and illustrate the positive correlation between occupanc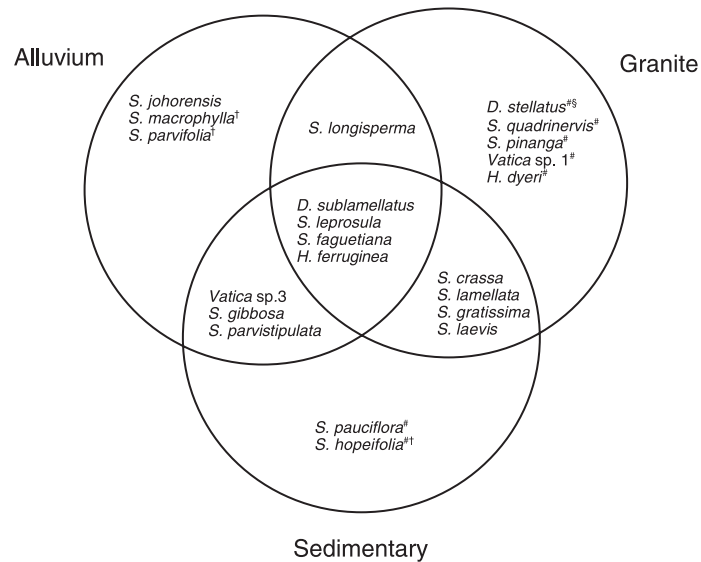y and log density for all size categories ($P < 0.001$ and $R > 0.885$ for all categories). (c) Density on alluvium vs. density on granite substrates (subdominants ≥ 8 individuals ha^{-1} overall); dashed line indicates equal density on both substrates. The widespread dominant *Dipterocarpus sublamellatus* is labelled 'D sub'.

(Table S2). Of the 28 species present on granite, 20 also occurred on sedimentary soils, and these represented > 90% of the sedimentary flora (i.e. 20 of 22 species). Ten species were common to sedimentary and alluvial sites, comprising 83% of the alluvium flora (10 of 12 species). Despite the close proximity and spatial contiguity of these habitats, 11 species widespread on sedimentary and granite substrates were absent from the alluvium (Table S2).

Eighteen of 22 dipterocarp species (≥ 1 cm d.b.h.) tested were significantly associated with at least one substrate (Fig. 3). The taxa *Shorea quadrinervis*, *S. pinanga*, *Hopea dyeri*, *Dipterocarpus stellatus* and *Vatica* sp. 1 were consistently encountered on granite soils, but absent from the alluvium, whereas *S. johorensis*,

S. macrophylla and *S. parvifolia* were frequent on alluvium soils, but rare on the granite (Table S2). These associations were confirmed in Monte-Carlo randomization: the former group was associated positively with granite and negatively with alluvium, whereas the latter was associated positively with alluvium and negatively with granite (Fig. 3). The taxa *S. hopeifolia* and *S. pauciflora* were positively associated with sedimentary soils (Fig. 3). A final species group was negatively associated with one substrate, but indifferent to others: *S. gibbosa*, *S. parvistipulata* and *Vatica* sp. 3 were negatively associated with granite, *S. longisperma* was negatively associated with sedimentary soil, and *S. crassa*, *S. laevis*, *S. gratissima* and *S. lamellata* were negatively associated with the alluvium (Fig. 3). In contrast to this

Table 3 Density, species richness and Fisher's α diversity of the Dipterocarpaceae in lowland tropical forest on three parent materials at Gunung Palung National Park, Indonesia. Data are shown separately for three size categories: stems ≥ 1 cm d.b.h., stems ≥ 10 cm d.b.h. and stems ≥ 30 cm d.b.h. Values are mean ± 1 SE among multiple 0.16-ha plots in forest on alluvium ($n = 10$), sedimentary ($n = 8$) and granite ($n = 12$). Superscripts indicate significant differences between substrates using Scheffé's test following one-way ANOVA on untransformed data. $*P = 0.05$, $**P = 0.01$

Parent material	≥ 1 cm d.b.h.				≥ 10 cm d.b.h.				≥ 30 cm d.b.h.			
	Stems ha⁻¹	Species 0.16 ha⁻¹	Total species	α	Stems ha⁻¹	Species 0.16 ha⁻¹	Total species	α	Stems ha⁻¹	Species 0.16 ha⁻¹	Total species	α
Alluvium	599 ± 186	4.9 ± 0.7[a]*	12	1.22 ± 0.09[a]*	119.4 ± 26.2	3.7 ± 0.3[a]*	11	1.52 ± 0.32[a]*	43.1 ± 11.7	1.6 ± 0.2[a]**	9	0.58 ± 0.18[a]**
Sedimentary	528 ± 229	7.8 ± 1.0[b]	22	2.60 ± 0.50[b]	71.9 ± 21.0	4.8 ± 1.0[ab]	19	5.23 ± 1.73[b]	31.3 ± 6.9	1.9 ± 0.5[a]	11	0.94 ± 0.42[b]
Granite	517 ± 84	7.4 ± 0.9[b]	28	2.13 ± 0.31[b]	97.4 ± 8.3	6.2 ± 0.6[b]	25	5.07 ± 1.05[b]	46.4 ± 4.9	3.3 ± 0.4[b]	20	2.73 ± 0.64[b]

general pattern of non-random distribution, the dominant species *D. sublamellatus* was indifferent to substrate.

We tested for stronger patterns of habitat association among larger size classes by comparing habitat associations of juveniles (1–10 cm d.b.h.) and established trees (> 10 cm d.b.h.). Of the 16 taxa sufficiently abundant in both size classes, five were randomly distributed as juveniles, but significantly associated with substrate as established trees ($P \leq 0.05$), and three other taxa displayed the same trend ($P \leq 0.1$, Table 4). Two species were significantly associated with a single substrate at both size classes and five species were randomly distributed at both stages. Only one species (*Shorea macrophylla*) was distributed non-randomly as juveniles but randomly as trees. This finding may reflect reduced power due to smaller sample size of established trees, rather than a broadening of habitat distribution with size class, because, for this species, the proportion of individuals across substrates did not differ between juveniles and trees (proportions on alluvium, sedimentary and granite substrates were 0.92, 0.06 and 0.02 for juveniles and 0.75, 0.07 and 0.18 for trees).

Excluding the widespread dominant *D. sublamellatus*, species with high mesoscale population density (> 8 individuals ha⁻¹) showed a clear bias towards nutrient-poor granite or nutrient-rich alluvium soils (Fig. 2c).

SPECIES DISTRIBUTION IN RELATION TO SOIL NUTRIENTS

Eighteen of 22 species tested were significantly associated with one or more nutrient parameters (Table 5). Thirteen species were either positively (three species) or negatively (10 species) associated with extractable soil P (Table 5). Seven species were significantly associated with extractable Mg, six species with extractable Ca and four species with total K (Table 5).

Most species were jointly associated with soil P and one or more cations. For example, *S. quadrinervis* and *S. pauciflora* were associated with soils low in P, K, Mg and Ca, while *S. johorensis* and *S. gibbosa* were associated with soils high in P, Ca and Mg (Table 5). Exceptions include *Shorea gratissima* and *S. pinanga*, which were negatively associated with P, but indifferent to base cations, and *S. parvistipulata* and *S. longisperma*, which were positively associated with base cations, but indifferent to P (Table 5).

Most species associated with soil nutrients (Table 5) were also associated with one or more substrates (Fig. 3). However, the widespread dominant *D. sublamellatus* and the subdominant *S. faguetiana* were randomly distributed across substrates, but significantly associated with soils low in P, Mg and total C.

BETA DIVERSITY AND GEOGRAPHICAL VS. ENVIRONMENTAL DISTANCE

In Mantel analyses of all stems (≥ 1 cm d.b.h.), floristic divergence among plots was significantly related to

Fig. 3 Venn diagram depicting substrate associations for 22 tree species in the Dipterocarpaceae in lowland tropical forest at Gunung Palung National Park, Indonesia. Significance of associations was assessed using Monte-Carlo randomization. Positive associations with a substrate are shown by species name in non-overlapping regions of the diagram, and negative associations at the intersection of the other two substrates. Taxa in the diagram centre were randomly distributed across substrates. Taxa positively associated with one substrate and negatively associated with others are denoted by superscript (alluvium (#), sedimentary (§) or granite (†)).

Table 4 Comparison of substrate association between juveniles (1–10 cm d.b.h.) and established trees (≥ 10 cm d.b.h.) in the lowland Dipterocarpaceae at Gunung Palung National Park, Indonesia. Significant association ($P < 0.05$) was tested using Monte-Carlo randomization. Species present in at least three plots as both juveniles and trees ($n = 16$) were included in the analysis

Juveniles (< 10 cm d.b.h.)	Established trees (> 10 cm d.b.h.)			
	Random		Non-random	
Random	*Dipterocarpus stellatus*	*Shorea crassa*	*Dipterocarpus sublamellatus*	*Shorea quadrinervis*
	Shorea leprosula		*Shorea parvifolia*	*Shorea parvistipulata*†
	Shorea laevis		*Shorea johorensis*	*Shorea pinanga*†
	Shorea gratissima		*Shorea faguetiana*	*Hopea ferruginea*†
Non-random	*Shorea macrophylla*		*Shorea hopeifolia*	*Shorea pauciflora*

†Non-randomly distributed at $\alpha = 0.1$.

geographical distance and to all edaphic parameters except total K (Table 6). However, separate analyses of juveniles (1–10 cm) and trees (> 10 cm d.b.h.) suggested that the effects of geographical and edaphic distance on floristic composition varied with size class (Table 6). In simple Mantel analyses, floristic divergence among juvenile dipterocarps was more strongly related to geographical distance than to edaphic factors, but the opposite was observed for established trees (Table 6). Differences with size class were even more pronounced in partial Mantel. Controlling for cross-correlation between geographical and edaphic distance, floristic differences among juveniles were weakly or unrelated to edaphic factors, but were strongly related to geographical distance. Among established trees, the opposite pattern was observed for the Euclidean index and for exchangeable Mg.

Discussion

High mesoscale beta diversity in the Dipterocarpaceae at GPNP appears to reflect the joint influences of inter-specific edaphic partitioning and, to a lesser degree, dispersal limitation. The majority of common diptero-carp taxa were significantly associated with at least one parent material, species distributions were related to soil nutrients, especially P, and, for many species, habitat associations with substrate were stronger for established trees than juveniles. This suggests that substrate heterogeneity promotes the coexistence of a diverse assemblage of lowland dipterocarp species by allowing spatial partitioning of habitat throughout the water-shed. These findings have important implications for understanding mechanisms underlying dipterocarp community structure in Borneo and highlight the

Table 5 Species associations with surface soil (0–20 cm) nutrient content and soil texture in lowland forest at Gunung Palung National Park, Indonesia. Significance of association was tested using a randomization procedure, wherein species with observed means in the highest or lowest 5th percentile of the simulated distribution were deemed significantly positively (hi) or negatively (lo) associated with that parameter. $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.005$, $****P \leq 0.001$

| Species | Total fraction | | | | | | Olsen P | Exchangeable fraction | | | pH H$_2$O | pH CaCl$_2$ | % Sand | % Silt | % Clay |
	C	N	P	K	Ca	Mg		K	Ca	Mg					
D. sublamellatus	lo***	lo**	lo**	–	–	–	lo*	–	–	lo***	–	hi*	–	–	–
S. crassa	–	lo*	lo****	–	–	–	lo*	–	–	lo*	–	–	–	–	–
S. johorensis	–	–	hi****	–	–	–	hi***	–	hi*	hi*	–	–	–	–	–
S. laevis	–	–	–	–	–	–	l *	–	lo*	–	–	–	–	–	–
S. gibbosa	hi*	hi**	hi*	–	–	–	hi***	–	–	hi***	–	–	–	–	–
H. ferruginea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. faguetiana	lo**	–	–	–	–	–	lo***	–	–	lo***	–	lo****	–	–	–
S. gratissima	–	–	–	–	–	–	lo*	–	–	–	–	–	–	–	–
S. macrophylla	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. parvistipulata	–	–	–	–	lo*	–	–	–	–	–	–	–	–	–	–
S. pauciflora	–	–	–	lo*	–	–	lo****	–	lo**	–	–	–	–	–	–
S. leprosula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. pinanga	lo**	lo***	lo***	–	–	–	lo***	–	–	–	–	–	–	–	–
S. quadrinervis	lo*	lo**	lo***	–	–	–	lo**	–	lo****	lo*	–	–	–	–	–
D. stellatus	–	–	lo*	lo*	–	–	lo****	–	–	–	–	–	–	–	hi*
H. dyeri	–	–	lo*	–	lo *	–	–	–	–	–	–	–	–	–	–
S. hopeifolia	–	–	–	–	–	–	–	–	–	–	–	lo*	–	–	–
S. lamellata	–	–	–	lo*	–	–	lo*	–	lo*	–	–	–	–	–	–
S. longisperma	–	–	–	hi*	–	–	–	–	–	lo*	–	–	–	–	–
S. parvifolia	–	–	–	–	–	lo*	–	–	–	–	–	hi**	–	–	–
Vatica sp. 1	–	–	lo*	–	–	–	lo***	–	lo**	–	–	–	–	–	–
Vatica sp. 3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 6 Mantel tests of correlation between floristic variation, soil nutrients and geographical distance among 30 (0.16 ha) plots in lowland tropical forest at Gunung Palung National Park, Indonesia. Separate analyses were performed on three size categories: ≥ 1 cm d.b.h., 1–10 cm d.b.h. and ≥ 10 cm d.b.h. $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$, $****P \leq 0.0001$

| Soil factor | All stems = 1 cm d.b.h. | | | Stems 1–10 cm d.b.h. | | | Stems = 10 cm d.b.h. | | |
	Floristics	Soil	Distance	Floristics	Soil	Distance	Floristics	Soil	Distance
(a) Euclidean index									
Floristics	–	0.280****	0.348****	–	0.231**	0.365****	–	0.289***	0.264****
Soil	0.175**	–	0.366***	0.113^{ns}	–	0.366****	0.214**	–	0.366****
Distance	0.275****	–	–	0.309*****	–	–	0.178**	–	–
(b) Extractable P									
Floristics	–	0.302***	0.348****	–	0.267***	0.365****	–	0.302***	0.264****
Soil	0.193*	–	0.390****	0.145*	–	0.390****	0.131*	–	0.390****
Distance	0.262***	–	–	0.294****	–	–	0.198**	–	–
(c) Exchangeable Mg									
Floristics	–	0.211*	0.348****	–	0.183*	0.365****	–	0.275**	0.264****
Soil	0.134^{ns}	–	0.260*	0.098^{ns}	–	0.260*	0.221**	–	0.260*
Distance	0.310****	–	–	0.334*****	–	–	0.207*	–	–
(d) Total K									
Floristics	–	0.017^{ns}	0.348****	–	0.014^{ns}	0.365****	–	0.007 ^{ns}	0.264****
Soil	0.004 ^{ns}	–	0.039^{ns}	0.000^{ns}	–	0.039^{ns}	– 0.003^{ns}	–	0.039^{ns}
Distance	0.348****	–	–	0.364****	–	–	0.264***	–	–

Mantel statistics above the diagonal are simple correlations; below the diagonal are partial Mantel statistics after controlling for cross-correlation with the third factor. Euclidean index is the sum of absolute differences in extractable P, and exchangeable Mg and K content between all possible pairs of plots after data were standardized using z scores; these nutrients were retained in canonical correspondence analysis of the association between nutrients and dipterocarp species abundances (available on request from lead author).

effects of substrate heterogeneity on tropical woody plant diversity.

SPECIES DISTRIBUTIONS IN RELATION TO SOIL FACTORS

Across size classes and substrates, the dipterocarp community was dominated by the emergent tree *Dipterocarpus sublamellatus*, which was indifferent to substrate. The broad habitat distribution of this species, however, was exceptional. Ten of the 22 dipterocarp species tested were both positively associated with at least one parent material and negatively associated with another. Eight additional taxa were negatively associated with one substrate, but indifferent to others, increasing the number of non-randomly distributed species to 82% of those tested. Substrate heterogeneity thus influences the distribution and abundance of most common dipterocarp species in upland soils at GPNP.

Plant associations with parent material have been documented at spatial scales ranging from *c.* 50 ha to > 40 000 km^2 in tropical palms, ferns, understorey and overstorey trees (Gartlan *et al.* 1986; Clark *et al.* 1999; Svenning 1999; Debski *et al.* 2002; Duque *et al.* 2002; Potts *et al.* 2002; Phillips *et al.* 2003; Tuomisto *et al.* 2003). However, the inability to infer process from pattern remains a limitation of the correlative approach. We addressed this problem by testing for indirect evidence of differential juvenile mortality in unsuitable habitats by comparing patterns of habitat association between juveniles and established trees > 10 cm d.b.h. Five of 14 species tested were randomly distributed as juveniles, but were non-random as established trees ($P \leq 0.05$), and three additional taxa displayed the same trend ($P < 0.1$), despite limited power resulting from small sample sizes for trees. It is possible for such a pattern to result from ecological processes unrelated to edaphic specialization: generalist herbivores distributed across a resource gradient could, for example, confer advantage to well-defended species on poor soils, but fast-growing species on rich soils, if a growth-defence trade-off exists (Fine *et al.* 2004). Nevertheless, we believe that stronger patterns of habitat association for established trees than juveniles suggest that dipterocarp beta diversity at our site is driven, at least in part, by interspecific edaphic partitioning. Webb & Peart (2000) reached a similar conclusion at a smaller spatial scale, based on stronger associations with topographic position for adult trees than for seedlings on the granite substrate at GPNP.

Dipterocarp species distributions were unrelated to soil texture or pH, but strongly related to soil nutrients. Seventeen of 22 species tested were significantly associated with one or more nutrients, in particular extractable P (13 species), total P (nine species), and total or exchangeable forms of Mg and Ca (eight species each; Table 5). If such correlation reflects causation, then a hierarchy of control appears to operate, with soil P having the strongest, most pervasive influence (14 species). A

similar conclusion was reached by Hall *et al.* (2004) in Cameroon, but unlike in their study, we found little evidence for finer-scale nutrient partitioning within high or low P soils; most dipterocarp species were associated with soils high or low in *both* P and cations. Dipterocarp associations with nutrients at GPNP thus imply a generalized adaptation to rich or poor soils, consistent with findings across northern Borneo by Potts *et al.* (2002). Future work will focus on mechanisms of interspecific P partitioning (Palmiotto *et al.* 2004) that potentially explain this pattern, as well as the possibility that substrate associations may, for some species, reflect adaptation to periodic variation in drought stress (G. D. Paoli and L. M. Curran, unpublished data).

Baillie *et al.* (1987) studied nutrient correlates of regional beta diversity in northern Borneo and found that tree species distributions were more frequently related to total nutrient pools ('reserve contents', Baillie *et al.* 1987, p. 206) than to labile nutrient forms. They concluded that total nutrients were a better indicator of relative long-term nutrient availability to plants. Our findings suggest a more complicated scenario. We measured labile and total forms of P, K, Ca and Mg, and found that, for three out of four elements, labile forms were more frequently, and often more strongly, associated with species distributions than total forms. Thirteen species were associated with extractable P vs. nine for total P; six vs. two species with exchangeable and total Ca; seven vs. one species for exchangeable and total Mg; and zero vs. four species for exchangeable and total K (Table 5). Most importantly, in 28 of 34 significant associations with P, K, Mg or Ca, species were associated with total *or* labile forms, not both; only P showed concordance between forms (Table 5). Our results demonstrate the utility of well-replicated labile nutrient assays for detecting plant–soil associations, and the need to quantify both nutrient pools, because they provide complementary information.

Plant–soil associations in this study also reveal a striking relationship between phylogeny and habitat distribution. The distributions of several species pairs within the same section or subsection of *Shorea* (i.e. putative close relatives) showed opposite relationships to soil factors. Thus (i) *S. macrophylla* and *S. pinanga* (section Pachycarpae), (ii) *S. leprosula* and *S. quadrinervis* (subsection Mutica), (iii) *S. johorensis* and *S. pauciflora* (subsection Brachypterae) and (iv) *S. gibbosa* and *S. faguetiana* (subsection Richetioides) occupied different edaphic niches (Fig. 3, Table 5). Congeneric rain forest pairs have been shown to partition gradients of climate (Hoffman & Franco 2003), inundation (Rogstad 1990), elevation (Gunatilleke *et al.* 1997; Yamada *et al.* 2000) and white-sand vs. clay soils in western Amazonia (Fine *et al.* 2004), but to our knowledge have not been documented in such large numbers within a single lineage of plants across a well-defined nutrient gradient in a single watershed. This suite of related dipterocarp species with divergent habitat associations offers a unique opportunity to study ecological

correlates of edaphic specialization and to assess its potential role in the evolution of a species-rich series of sympatric rain forest trees (Paoli 2004).

DISPERSAL VS. NICHE ASSEMBLY

The neutral model of Hubbell (2001) posits that beta diversity arises from random, spatially restricted seed dispersal and the local dynamics of extinction and speciation. Dipterocarp beta diversity at GPNP is not explained by local speciation, because most species present are widespread throughout Borneo (Ashton 1982), but dispersal limitation across substrates may be important, given that upland forests at GPNP may be recent post- or late-Pleistocene assemblages (Gathorne-Hardy *et al.* 2002).

We used Mantel correlation analysis to test for evidence that seed dispersal limitation influences dipterocarp beta diversity by comparing floristic associations with edaphic vs. geographical distance for all stems ≥ 1 cm d.b.h. and at different size stages. For all stems ≥ 1 cm, floristic variation among plots was related more to geographical distance than to edaphic factors, even when cross-correlation between them was controlled (Table 6). However, interpreting this pattern is complex, because the relative strength of edaphic vs. geographical influences on floristic patterns appears to vary with size class. Floristic similarity of juveniles (1–10 cm d.b.h.) was more strongly related to geographical distance than to edaphic factors, whereas the reverse held for established trees (≥ 10 cm d.b.h.). This implies that the composition of juvenile dipterocarp assemblages is strongly affected by dispersal processes, but that the effects of edaphic partitioning increase through subsequent size classes. This pattern is consistent with the results of habitat association tests on different size classes (Table 4), and would be expected if spatial patterns of dipterocarp establishment were determined largely by seed dispersal and escape from predation (Curran & Webb 2000), but then juveniles experienced higher mortality in suboptimal habitats due to trade-offs related to edaphic specialization. In this scenario, seed dispersal limits the spatial distribution and thus range of edaphic conditions encountered by new individuals, after which niche partitioning determines the subset of conditions suitable for long-term growth and survival. Future comparisons of intraspecific growth rate and mortality across the substrate gradient will provide a direct test of this hypothesis.

PATTERNS OF SPECIES RICHNESS

Dipterocarp stem densities were similar across substrates, but species richness and diversity were highest on the nutrient-poor granite (28 species), intermediate on sedimentary soils (20 species) and lowest on nutrient-rich alluvium (12 species). Lower dipterocarp richness on alluvium reflects a general pattern of low woody plant diversity on this substrate (Cannon & Leighton 2004). Low dipterocarp richness on alluvium reflected the local absence of species common on sedimentary and granite soils (hereafter 'hill substrates'). Only 11 of 30 species present on hill substrates (36.3%) occurred in the alluvium, whereas 11 of 12 species present on the alluvium (93.5%) were found on hill substrates (Table S2). The absence of hill species in the alluvium is more striking when just habitat specialists are compared. Of the 11 dipterocarp species positively associated with hill substrates, only one *Hopea ferruginea* individual (d.b.h. = 17 cm) was present on the alluvium, whereas all three species positively associated with alluvium were common on hill substrates (Table S2). The asymmetric distribution of habitat specialists across the gradient is surprising, given the close proximity of alluvium and hill substrates and the expectation that, because dipterocarps are dispersed by gravity or wind, seed dispersal downslope to the alluvium should be more frequent than the converse.

The absence of hill dipterocarps from the alluvium is unlikely to be explained by disproportionate seed predation of hill species in the alluvium, because the most important dipterocarp seed predators at GPNP are mobile generalists that prey on seeds of all dipterocarp species, including the bearded pig *Sus barbatus* (Curran & Leighton 2000) and weevils in the Curculionidae (Lyal & Curran 2000, 2003). Nor does it seem likely to result from lower understorey light in the alluvium, because biomass, basal area and leaf area index are similar across substrates (Paoli *et al.* 2005) and rates of gap formation are higher in the alluvium than the granite (L. M. Curran, unpublished data). Rather, it may be explained by competitive exclusion of hill species from the alluvium, where tree growth is twofold higher than in the granite (Paoli *et al.* 2005), and dominant species have leaf traits that confer higher intrinsic growth potential (Paoli 2004). More rapid competitive exclusion in the alluvium would lead to faster elimination of hill species and, thus, lower dipterocarp richness. This pattern is consistent with ecological theory (Huston 1979; Tilman 1982) and empirical studies documenting declines in species richness on productive sites (Huston 1993; Rajaniemi 2003), further suggesting a deterministic explanation.

DOMINANCE-DISTRIBUTION RELATIONSHIPS THROUGHOUT THE WATERSHED

Nearly 50% of all dipterocarp stems at GPNP are from a single species (*Dipterocarpus sublamellatus*). Yet, an assemblage of 11 subdominant dipterocarp species also attained high mesoscale densities throughout the watershed (> 8 individuals ha^{-1}). Nine of these taxa were positively associated with one substrate and negatively associated with others, indicating that high mesoscale densities were attained through high local densities on one substrate (Figs 2 and 3). This suggests that subdominant dipterocarp species sacrifice broad habitat distribution for high local densities under

restricted edaphic conditions. That dominant rain forest trees are habitat generalists, whereas subdominant taxa are habitat specialists, has been documented at local scales within communities (Valencia *et al*. 2004) and among communities at meso- and regional scales (see data in ter Steege *et al*. 1993; Pitman *et al*. 2001; Phillips *et al*. 2003). Such a dominance-distribution relationship may be a general property of lowland tropical communities, but more data are required.

Dominance of the dipterocarp community by the habitat generalist *Dipterocarpus sublamellatus* is consistent with regional findings from western Amazonia, where separate communities are often dominated by a shared set of so-called 'oligarchs' (Pitman *et al*. 2001). In the present study, we identified only one dominant tree species, *Dipterocarpus sublamellatus*, but the non-dipterocarp *Strombosia ceylanica* (Olacaceae) is also locally abundant and widespread across the gradient (Cannon & Leighton 2004), suggesting dominance by an oligarchy of generalists throughout the watershed. The mechanisms that permit broad habitat distribution and high local densities are not well understood. Regeneration of *D. sublamellatus* is common throughout all gap phases, suggesting that light availability is not a prominent factor. It has been observed in Amazonia that dominant taxa, especially palms, tend to be tall trees with broad geographical ranges (Ruokolainen & Vormisto 2000; Pitman *et al*. 2001). Consistent with this pattern, *Dipterocarpus sublamellatus* is an emergent canopy tree with a broad geographical range spanning Peninsular Malaysia, Sumatra and Borneo (Ashton 1982), but many rare dipterocarps at GPNP (e.g. *S. lamellata*) reach larger maximum size and have broader geographical ranges in Asia. Thus, tree size and geographical range alone do not predict mesoscale distribution or abundance. *Dipterocarpus sublamellatus* may achieve widespread, locally dense populations through exceptional phenotypic plasticity, drought resistance, protection from herbivores and seedling pathogens, or some combination of these factors. Comparative studies of *D. sublamellatus* and edaphic specialists at GPNP will help identify plant traits underlying changes in relative abundance across local habitat gradients.

Pervasive dipterocarp associations with soil nutrients, especially P, in this study support the hypothesis that niche processes structure upland tropical tree communities. Expanding the spatial scale of our study to include other watersheds within the park, or nearby mountain systems with similar substrates, will provide a robust test of generality for the habitat associations documented here. Substantial floristic variations unrelated to soil factors measured in this study, however, were significantly correlated with geographical distance between plots, suggesting a role for dispersal limitation as well. We hypothesize that effects of dispersal limitation are likely to operate more strongly within substrate types than between them; greater plot replication within each substrate will be required to test this. Under this scenario, interspecific trait differences cause habitat

partitioning by dipterocarp species adapted to rich or poor soils, whereas seed dispersal influences the distribution and relative abundance of species within substrates, and promotes a degree of floristic mixing among them. Understanding the interaction between dispersal and niche processes, and their dependency on spatial scale and ecological conditions, represents an area of important future research at GPNP and other tropical sites.

Acknowledgements

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com:

Table S1 Population attributes of the Dipterocarpaceae.

Table S2 Habitat associations of the Dipterocarpaceae.