

Divergent leaf traits among congeneric tropical trees with contrasting habitat associations on Borneo

Gary David Paoli¹

Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University Ave, Ann Arbor, MI 48109 USA
Indonesian Resource Institute, Bogor, West Java, Indonesia
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Abstract: A prediction of the hypothesis that niche processes control plant species distributions across edaphic gradients is that pairwise comparisons of related species on contrasting soils should show consistent patterns of trait divergence. This hypothesis was tested in lowland Bornean rain forest by combining measurements of leaf traits, soil nutrients and the distribution of tree species in the Dipterocarpaceae across a nutrient gradient. Nine species were studied, comprising four related pairs in *Shorea* (phylogenetic independent contrasts; PICs) and one habitat generalist (*Dipterocarpus sublamellatus*). Lamina area, specific leaf area (SLA), leaf nitrogen (N) and phosphorus (P) were measured for ~10 saplings of each species; habitat associations were defined as a continuous function of soil nutrients and categorically in relation to substrate. Species distributions and traits varied significantly with soil nutrients. When all species were pooled, SLA and leaf P increased significantly with species' distribution across the nutrient gradient; leaf N showed the same trend. Trait shifts with habitat were stronger and more pervasive when habitat was defined categorically – in all four PICs, rich-soil specialists had larger leaves, higher SLA, leaf N and P, and lower N:P ratios. Trait shifts with habitat at least partly reflect intrinsic differences between species. Within *Shorea*, variation in lamina area and N:P ratio were more strongly related to phylogeny than habitat, whereas the reverse held for SLA and leaf P. Phylogeny also influenced the extent of trait divergence between related species on different soils, and patterns of trait correlation within lineages. Results support the hypothesis that niche processes influence the distribution of species and traits in lowland tropical tree communities, and highlight the value of phylogenetic information for increasing the power of comparative studies.

Key Words: Dipterocarpaceae, growth strategy, niche, N:P ratio, phosphorus, phylogeny, saplings, *Shorea*, SLA, trade-offs

INTRODUCTION

A primary goal of ecology is to understand the effects of individual ecological traits on the distribution of species in heterogeneous environments (Chase & Leibold 2003, Tilman 1988, 2004). Studies of trait variation across nutrient gradients in temperate plant communities have documented marked shifts of community averages for numerous traits (Ackerly *et al.* 2002, Aerts & Chapin 2000, Chapin 1980, Fonseca *et al.* 2000), leading to the recognition of trait syndromes characteristic of rich and poor soils. Dominant species on rich soils exhibit high maximum growth and photosynthetic rates, short tissue life spans, high tissue nutrient concentrations

and low plant-level nutrient use efficiency; species on poor soils display opposite trends (Aerts & Chapin 2000, Chapin 1980, Grime 1979). These syndromes, and their attendant ecological trade-offs, are likely to operate in species-rich lowland tropical forests as well. Yet, field studies of trait variation across lowland soil gradients have focused largely on categorical comparisons between markedly different edaphic environments, such as heath versus peat-swamp forests in Asia (Nishimura & Suzuki 2001) or white-sand versus clay forests in Amazonia (Fine *et al.* 2004, Reich *et al.* 1994). These studies document trait shifts with habitat consistent with trait syndromes documented in temperate communities, but it is unclear to what extent these findings apply across continuous gradients at smaller spatial scales. No study has combined quantification of soils, traits and species distributions at one site to relate continuous measures

¹ Email: gary.paoli@gmail.com

of species traits and distribution across a continuous soil gradient (but see Baltzer *et al.* 2005 and Palmiotto *et al.* 2004 for robust categorical comparisons among soil types).

Another factor complicating the interpretation of trait-by-soil correlations in previous comparative studies is the potentially confounding effect of phylogeny on plant traits. If, in the evolutionary history of a lineage, acquisition of a novel trait permitted one ancestral species to invade a new edaphic environment and diversify into multiple sympatric species, then derived taxa will have traits similar to the ancestral species, even though such traits may no longer be what explains co-occurrence in the same habitat. Distinguishing between the potential effects of phylogeny and habitat on trait-by-environment correlations thus requires explicit consideration be given to these factors separately.

Species-rich tropical rain forests provide a model system for applying methods to investigate joint influences of phylogeny and habitat on plant traits. Sympatric shade-tolerant tree species differ markedly in key leaf attributes (Coley 1985, Coomes & Grubb 1998, Thomas & Bazzaz 1999), and distributions covary with soil factors across multiple spatial scales (Hall *et al.* 2004, Potts *et al.* 2002, Valencia *et al.* 2004, Webb & Peart 2000). Species-rich congeneric series are common and often show evidence of habitat partitioning (Fine *et al.* 2004, Rogstad 1990, Schulman *et al.* 2004), making it possible to test for consistent trait associations with habitat across evolutionary lineages.

In this paper, I examine the contributions of phylogeny and habitat to leaf trait variation among nine tropical tree species across a well-defined soil nutrient gradient in lowland Indonesian Borneo. Eight of the species represent four pairs of related taxa in the genus *Shorea* with contrasting distributions. The selection of phylogenetic pairs enabled comparison of phylogenetic and habitat effects on leaf traits and provides a robust test for consistent trait divergences with habitat across lineages. Leaf attributes affecting drought tolerance, herbivory, maximum growth rate and above-ground nutrient use efficiency were studied: lamina size, specific leaf area (SLA), and leaf N and P concentration (Aerts *et al.* 1990, Berendse *et al.* 1987, Coley 1985, Dijkstra 1989, Edwards *et al.* 2000, Givnish & Vermeij 1976, Parkhurst & Loucks 1972, Reich *et al.* 1991, 2003; Wright & Cannon 2001, Wright *et al.* 2004). If above-ground plant traits affect species distributions across the gradient, then I expect to observe correlated trait shifts with habitat for most attributes measured. Three main questions are addressed: (1) How are leaf attributes related to distribution across the nutrient gradient? (2) Are trait shifts with habitat consistent across evolutionary lineages? (3) What are the relative impacts of phylogeny and habitat on species traits?

STUDY SITE AND SPECIES

The study was conducted at the Cabang Panti Research Station (15 km²) 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 ± SD for 1985–2002), with marked inter-annual variation related to El Niño Southern Oscillation (ENSO) events. In the centre of the park is a pair of interconnected mountain peaks, Mount Palung (1070 m asl) and Mount Panti (1130 m asl), whose western slopes form the watershed of the study area.

Lowland forests on well-drained soils at GPNP (5–280 m asl) are underlain by alluvium, sedimentary and granite parent materials. Alluvium occurs from 5–15 m asl along banks of the Air Putih river bisecting the study area. Sedimentary rock underlies forest on the foothills up to 40–140 m asl, beyond which forest is underlain by granite. Surface mineral soils (0–20 cm) derived from these substrates differ significantly in nutrient content (kg ha⁻¹) but not soil texture, producing steep gradients of extractable P (16-fold); exchangeable K, Ca, Mg (4-, 30-, and 7-fold); and total N and C (4- and 3-fold; Paoli *et al.* 2006). On average, surface soil nutrient content is highest in the alluvium, lowest in granite and intermediate in sedimentary soils. Above-ground net primary productivity varies 3-fold across the gradient and is highest on the alluvium and lowest on the granite (Paoli *et al.* 2005).

The species composition of lowland vegetation at GPNP varies among parent materials, but is dominated by the Dipterocarpaceae throughout the watershed (Cannon & Leighton 2004, Curran & Leighton 2000). Vegetation plots on alluvium and sedimentary soils share on average only 15% of species with plots on granite, and only 22% with each other (Cannon & Leighton 2004). The habitat distribution of approximately half of all species tested show a spatial bias toward nutrient-rich or nutrient-poor substrates (Cannon & Leighton 2004, Paoli *et al.* 2006).

At least 31 *Shorea* species occur in the upland mosaic at GPNP. Distributions of most common *Shorea* are associated with soil factors, and several species pairs in the same section or subsection of *Shorea* have divergent habitat associations (Paoli *et al.* 2006). Eight species among these pairs were chosen for study to contrast traits of related species from different habitats (Table 1). Monophyly of the subgeneric categories relevant to this study (Ashton 1982) have to date been upheld by molecular phylogenetic studies (Kamiya *et al.* 2005), indicating that comparisons among them permit a robust test of consistent trait shifts with habitat across separate lineages (i.e. phylogenetically independent contrasts, PIC; Burt 1989, Westoby *et al.* 1996).

The study species attain maximum size of 80–140 cm diameter at breast height (dbh) and are mature-phase

Table 1. Taxonomic relatedness, geographic range, and habitat associations of tree species in the genus *Shorea* studied along a soil nutrient gradient in lowland rain forest at Gunung Palung National Park, Indonesia.

Subgeneric category and species pair	Geographic range ¹	General habitat association ¹	Soil association at Gunung Palung ²	Taxon code
Section <i>Brachypterae</i> , subsection <i>Brachypterae</i>				
<i>Shorea johorensis</i> Foxw.	Sunda Shelf, widespread	Rich soils on well-drained alluvium and undulating terrain	Alluvium and sedimentary	sjoh
<i>Shorea pauciflora</i> King	Sunda Shelf, widespread	Deep soils on undulating terrain and low hills	Granite	spauc
Section <i>Pachycarpae</i>				
<i>Shorea macrophylla</i> (De Vriese) Ashton	Borneo, widespread	Rich, inundated soils, river banks and well-drained alluvium	Alluvium	smac
<i>Shorea pinanga</i> Scheff.	Borneo, widespread	Clay-rich hillsides, especially ridges	Granite	sping
Section <i>Mutica</i> , subsection <i>Mutica</i>				
<i>Shorea leprosula</i> Miq.	Thailand (S of Kra) and throughout Sunda Shelf	Deep clay soils	Alluvium and sedimentary	slep
<i>Shorea quadrinervis</i> Sloot.	Borneo, widespread	Sandy clay soils on low hills	Granite	squad
Section <i>Richetioides</i> , subsection <i>Richetioides</i>				
<i>Shorea gibbosa</i> Brandis	Patchy distribution within Sunda shelf	Deep, fertile clay-rich soils on low hills	Alluvium and sedimentary	sgib
<i>Shorea faquetiana</i> Heim	Thailand (S of Kra) and throughout Sunda shelf	Well-drained clay soils on low hills and ridges	Granite and sedimentary	sfag

¹Based on Ashton (1982), personal observations of the author and other unpublished sources.²Based on Paoli *et al.* (in press).

canopy or emergent trees with densities > 1 individual ha^{-1} (> 10 cm dbh). All species mast fruit on a 3–7-y cycle corresponding to El Niño Southern Oscillation events (Curran & Leighton 2000, Curran *et al.* 1999). Seeds are dispersed by wind or gyration (Ashton 1982) and at GPNP are consumed by generalist pre- and post-dispersal seed predators (Curran & Leighton 2000, Lyal & Curran 2000, 2003). Species in two PICs are widely distributed across the Sunda Shelf, including Peninsular Malaysia, Sumatra and Borneo (*S. johorensis* and *S. pauciflora* in subsection *Brachypterae*, and *S. gibbosa* and *S. faquetiana* in subsection *Richetioides*); in the third are endemic to Borneo (*S. macrophylla* and *S. pinanga* in section *Pachycarpae*); and in the fourth, one occurs throughout the Sunda Shelf (*S. leprosula*) and the other is endemic to Borneo (*S. quadrinervis* in subsection *Mutica*; Table 1).

METHODS

I test the hypothesis that species with contrasting distributions across a nutrient gradient have divergent leaf traits by quantifying leaf attributes in the field and testing for (1) relationships between trait values and a continuous description of species distributions across the nutrient gradient, and (2) evidence for consistent trait shifts with habitat within pairs of related species. Measuring traits on established individuals in the forest permits generalization to the field (Fonseca *et al.* 2000, Wright *et al.* 2002). However, when species are measured in different habitats, phenotypic plasticity may lead to trait correlations with soil, even when distributions are controlled by other factors, such as herbivory or seed dispersal and predation (Fine *et al.* 2004, Goldberg 1985). I address this by conducting within-species comparisons for two species, *Dipterocarpus sublamellatus* and *Shorea faquetiana*, which had populations on both alluvium and granite substrates. The size of within-species trait shifts with habitat provides a preliminary estimate of how much trait divergence within PICs may be explained by phenotypic plasticity.

Measurement of leaf attributes

Lamina area, SLA and mass-based foliar N and P concentrations were measured for saplings of all species. Saplings, rather than seedlings or mature trees, were targeted, because previous research had identified this stage as a potential recruitment bottleneck affecting adult distributions across substrate classes (Paoli *et al.* 2006). Leaves were collected from 10–12 individuals for most species ($N = 8$ for *S. macrophylla*) growing in natural gaps (50 to ~ 200 m^2) that did not vary significantly in size among species. For all species, individuals were

sampled from at least eight different gaps to maximize spatial independence. Sapling height ranged from 2–5 m, and did not differ among species (one-way ANOVA, $F_{8,85} = 1.89$, $P = 0.081$) or between habitats (nested two-factor ANOVA, $F_{1,7} = 0.123$, $P = 0.727$). For each individual, four fully expanded, distal-most leaves were collected from two to four randomly chosen branches. Leaves were traced for lamina area measurement (minus petiole), pressed, dried at 70°C for 2 d, and then weighed individually. Area of leaf tracings ($N = 4$ per individual) was measured on a hand-held LICOR area meter to compute SLA ($\text{cm}^2 \text{g}^{-1}$).

Dried leaves were bulked into one sample per plant to measure mass-based foliar N and P. Leaf tissue was ground in a Tecator mill, and nitrogen content was determined by gas chromatography on ~ 8 -mg samples oxidized at 700°C in an automated C-N analyser (NC2500, CE Instruments, Milan, Italy). Phosphorus content was determined on 500-mg samples combusted at 400°C in a muffle furnace for 5 h and dissolved in a 20-ml solution of 20% HCl and 18% HNO_3 (Allen 1989, Jones *et al.* 1990). The solution was diluted 2:1 and P concentration was determined colorimetrically as in Paoli *et al.* (2005). Two replicate samples from the solution were measured and the mean recorded. If replicates differed by $> 5\%$, a third replicate was measured and all three were averaged.

Vegetation and soil surveys

A floristic inventory of the Dipterocarpaceae (> 1 cm dbh) was performed throughout the watershed in 30 (0.16–ha) plots described in Paoli *et al.* (2006). In each plot, six surface soil samples (0–20 cm) were collected and analysed for exchangeable K, Mg, Ca; extractable P; total C, N, P, K, Mg, Ca; pH; and soil texture. Here, data from Paoli *et al.* (2006) are used to quantify distributions of the nine study taxa across the nutrient gradient using canonical correspondence analysis (CCA) of abundance data (ter Braak & Smilauer 2002). CCA was performed using CANOCO Version 4.5. The species matrix was \ln -transformed as $\ln(x + 0.1)$ due to the predominance of zeros. Soil parameters were entered using a forward-selection procedure, and variables were retained if their contribution to variance explained was significant ($P \leq 0.05$) based on permutation tests. Species scores in CCA ordination represent species' estimated peak abundance across the multivariate gradient. This permitted examination of the relationship between species traits and continuous measures of distribution in the field.

Data analysis

Trait associations with habitat were analysed using bivariate and categorical methods. First, significant

relationships between species traits (including a multivariate index) and distribution across the gradient were tested using least-squares linear regression. Second, effects of habitat and phylogeny on leaf traits were analysed using two-way mixed model ANOVA with habitat (alluvium or granite) as a fixed factor and 'clade' (i.e. section or subsection of *Shorea*) a random factor. If habitat was significant, trait differences between related species were tested using t-tests with Bonferroni adjustment. However, significant differences between related species are less important than consistency of trends across PICs, as the power of this test lies in the generality of trait shifts with habitat across lineages and traits. Pairwise comparisons among PIC (an effect of phylogeny) were made using the post hoc Bonferroni test. Lamina area, leaf P and N:P ratio were ln-transformed to satisfy assumptions of normality and homogeneity of variance. Significant differences between habitat means averaged across species were tested using two-factor nested ANOVA with species nested within habitat. Partitioning of variance between phylogeny and habitat was calculated from factorial ANOVAs as the ratio of sum of squares for each trait to total sum of squares, as in Hoffmann & Franco (2003).

Finally, bivariate methods were used to examine the effect of phylogeny on trait correlations, as opposed to trait means. Standardized Major Axis (SMA) regression was used to describe correlations, because SMA is more appropriate than standard linear regression when variables are subject to measurement error (Wright *et al.* 2002). Correlations between all possible trait pairs were quantified for all individuals in each PIC, and comparisons were made among lines describing this relationship to test for differences in slope and intercept across PICs. Slope differences were tested following Warton & Weber (2002). If differences were not significant (test for homogeneity, $P > 0.05$), then a common slope was determined, and intercepts were compared using one-sample ANOVA as in Wright & Cannon (2001) and Wright *et al.* (2002). If significant differences were detected, post-hoc comparisons were made using Tukey–Kramer (equal variance among groups) or Games–Howell (for unequal variance) procedures. These procedures are the SMA analogue of standard ANCOVA and are described fully in Wright & Cannon (2001). Analyses were performed using (S)MATR software Version 1 (Falster, D.S., Warton, D.I. & Wright, I.J. at <http://www.bio.mq.edu.au/ecology/SMATR>).

RESULTS

The CCA model explained 45% ($P < 0.0001$) of variation in species abundance and retained extractable P, and exchangeable Mg, K and Ca as significant factors

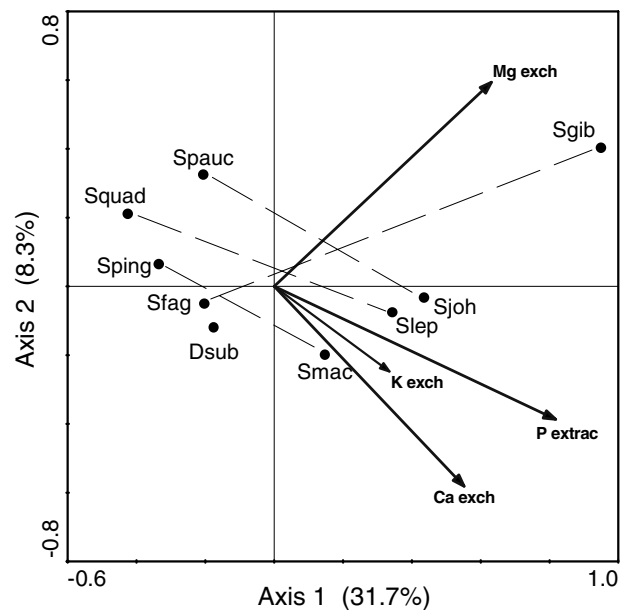


Figure 1. Canonical Correspondence Analysis (CCA) of species distribution in the Dipterocarpaceae (> 1 cm dbh) across a soil nutrient gradient in lowland tropical forest at Gunung Palung National Park, Indonesia. The percentage of total species variance explained by each axis is shown in parentheses. Dotted lines connect *Shorea* species in the same section or subsection of the genus, treated as phylogenetically independent contrasts (Table 1). Arrows indicate regions of CCA ordination space corresponding to high levels of the nutrient specified.

correlated with species distributions (Figure 1). The first canonical axis explained nearly three-quarters of this relationship (31.7 of 45%) and described a gradient of extractable P ($R = 0.818$) and exchangeable Mg ($R = 0.631$) and Ca ($R = 0.598$). Within PICs, species showed opposite patterns of association with nutrients (Figure 1). As a group, granite specialists had significantly lower CCA scores than alluvium specialists (-0.85 to 0.41 vs. 0.3 to 1.91 ; mean \pm SE = -0.59 ± 0.11 vs. 0.94 ± 0.34 , Mann-Whitney test, $U = 0.0$, $P = 0.028$). Species of the same PIC rarely co-occurred in the same plot.

Traits varied markedly across species, ranging 4-fold in lamina area, ~ 3 -fold in leaf P and 1.5-fold in SLA and leaf N (Table 2). Foliar N:P ratios ranged more than 2-fold, from 14.6 in the alluvium specialist *S. gibbosa* to a maximum of 40.4 in the granite specialist *S. pauciflora*. Seven out of eight species had N:P ratios > 16 (Table 2), suggesting widespread P limitation to growth for all species except *S. gibbosa* (Koerselman & Meuleman 1996).

In regression analyses of leaf traits versus distribution across the nutrient gradient, SLA and leaf P were significantly ($P < 0.01$) related to species distribution; leaf N ($P = 0.074$) showed the same trend (Figure 2). Lamina area and N:P ratio were unrelated to distribution. PCA of lamina area, SLA and leaf N and P described 87%

Table 2. Functional leaf traits (mean \pm SE) and distribution along a multivariate soil nutrient gradient for nine species of lowland rain forest trees in the Dipterocarpaceae at Gunung Palung National Park, Indonesia. Species are listed in ascending rank order along a gradient of increasing soil nutrients based on Canonical Correspondence Analysis of soil nutrient and species abundance data.

Species	Leaf attributes							
	Frequency ¹	Density ²	Position along CCA gradient	SLA (cm ² g ⁻¹)	Lamina size (cm ²)	%N	%P	N:P
<i>Shorea quadrirervis</i>	8	7.25	-0.850	111 \pm 5	39 \pm 3	1.54 \pm 0.03	0.058 \pm 0.002	26.4 \pm 1.1
<i>Shorea pinanga</i>	10	2.83	-0.670	113 \pm 2	63 \pm 2	1.39 \pm 0.03	0.056 \pm 0.018	25.1 \pm 1.4
<i>Shorea pauciflora</i>	13	12.88	-0.410	122 \pm 4	69 \pm 7	1.71 \pm 0.04	0.042 \pm 0.002	40.4 \pm 3.5
<i>Shorea jaguetiana</i>	19	6.50	-0.410	109 \pm 3	24 \pm 1	1.47 \pm 0.03	0.069 \pm 0.001	21.2 \pm 0.6
<i>Dipterocarpus sublamellatus</i>	19	52.28	-0.350	130 \pm 4	69 \pm 5	1.35 \pm 0.04	0.073 \pm 0.004	18.5 \pm 0.9
<i>Shorea macrophylla</i>	12	9.90	0.300	125 \pm 5	102 \pm 7	1.48 \pm 0.03	0.068 \pm 0.002	21.9 \pm 1.0
<i>Shorea leprostita</i>	10	3.91	0.690	163 \pm 4	47 \pm 3	2.02 \pm 0.03	0.100 \pm 0.004	20.2 \pm 0.9
<i>Shorea johorensis</i>	17	6.29	0.870	136 \pm 4	97 \pm 5	2.05 \pm 0.07	0.075 \pm 0.004	27.4 \pm 1.5
<i>Shorea gibbosa</i>	5	5.25	1.910	152 \pm 4	33 \pm 2	1.74 \pm 0.04	0.120 \pm 0.005	14.6 \pm 0.7

¹Frequency is number of plots (0.16 ha) out of 30 in which the species was encountered.

²Density is mean number of stems per plot where species occurred.

Table 3. Summary of two-way mixed model ANOVA to test for significant effects of phylogeny and habitat on leaf traits of nine tree species in the Dipterocarpaceae at Gunung Palung National Park, Indonesia. The factor 'Clade' refers to species pairs in the same section or subsection of *Shorea*.

Factor	df	MS	MS _{error}	F	P
Lamina area ¹					
Clade	3	5.64	0.057	99.2	0.002
Habitat	1	2.39	0.057	42.1	0.007
Clade \times Habitat	3	0.057	0.046	1.23	0.305
SLA					
Clade	3	1334	2619	0.51	0.703
Habitat	1	19189	2608	7.36	0.073
Clade \times Habitat	3	2618	182	14.3	< 0.001
Leaf N					
Clade	3	0.856	0.172	4.98	0.110
Habitat	1	1.85	0.171	10.8	0.046
Clade \times Habitat	3	0.172	0.019	9.22	< 0.001
Leaf P ¹					
Clade	3	1.14	0.176	6.48	0.080
Habitat	1	4.67	0.176	26.6	0.014
Clade \times Habitat	3	0.176	0.027	6.60	< 0.001
Leaf N:P ¹					
Clade	3	1.63	0.067	24.2	0.013
Habitat	1	1.90	0.067	28.3	0.013
Clade \times Habitat	3	0.067	0.028	2.39	0.074

¹Lamina area, leaf P and N:P ratio were ln-transformed to satisfy assumptions of normality and homogeneity of variance.

of total variation and clearly separated species within PICs along a multivariate gradient of SLA-leaf N-leaf P along the first axis. Species scores on the SLA-leaf N-leaf P axis were significantly related to distribution across the nutrient gradient (Figure 2f). Comparing leaf attributes and distribution within each PIC, the taxon with a higher CCA score (i.e. greater abundance on rich soils) always had larger leaves, higher SLA, and higher leaf N and P (Figure 2).

When habitat distribution was defined categorically as a preference for alluvium or granite soils, consistent trait shifts with habitat were observed for all attributes in all PICs (Figure 3). Alluvium specialists had larger leaves, higher SLA, leaf N and leaf P, and lower N:P ratios than granite specialists (N:P ratio not shown). ANOVA confirmed this pattern, with significant effects of habitat in four of five traits ($P < 0.001$; Table 3), whereas that of clade was significant for lamina area and N:P ratio only (Table 3). The interaction term was significant for SLA and leaf N and P, reflecting the comparatively weak influence of habitat on the species pair *pinanga*-*macrophylla* in *Shorea* section *Pachycarpae* (Figure 3b-d).

Trait shifts with habitat varied in magnitude among pairs and traits. Within *johorensis*-*pauciflora* and *gibbosa*-*jaguetiana*, species differed significantly in lamina area, and leaf N and P, whereas such differences were not significant between *macrophylla*-*pinanga* (Figure 3). Averaging across PICs, trait shifts with habitat were largest for foliar P and SLA (37.8% and 30.1%,

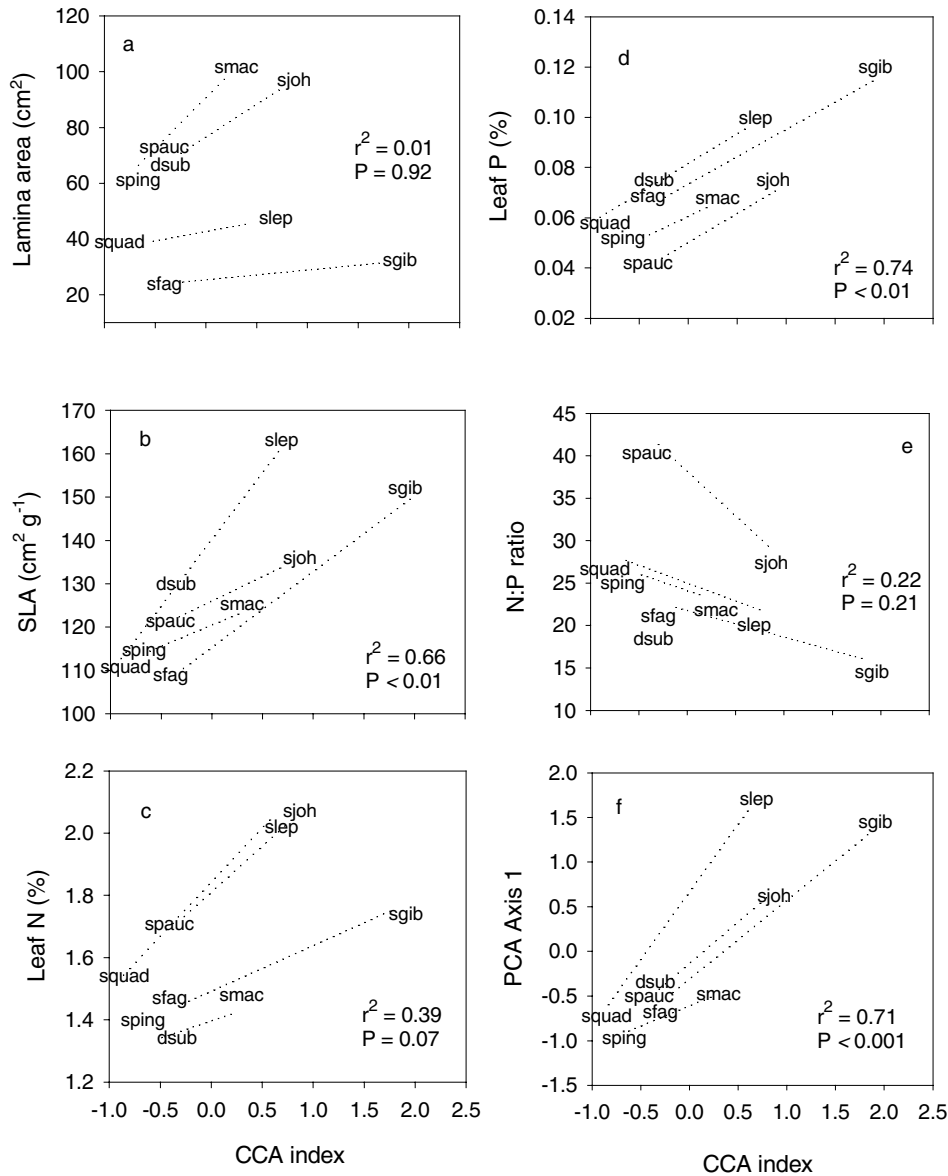


Figure 2. Relationship between leaf attributes and species' mean distribution across a soil nutrient gradient at Gunung Palung National Park, Indonesia. Dotted lines connect related species pairs in the genus *Shorea*. Species codes follow Table 1. Data are species mean for (a) lamina area, (b) SLA, (c) leaf N, (d) leaf P, (e) N:P ratio and (f) a multivariate PCA index of all representing a gradient of increasing SLA and leaf N and P.

respectively) and lowest for foliar N (16.3%). Habitat means differed significantly for SLA and leaf N and P, but not lamina area (Figure 3).

Within-species comparisons showed no evidence for a plastic phenotypic effect of environment on leaf traits. Mean values did not differ significantly between alluvium and granite populations of *D. sublamellatus* or *S. fauetiana* for any traits (data not shown).

Variance partitioning showed that more variation was explained by phylogeny than habitat for lamina area and N:P ratio, whereas the reverse held for SLA and leaf P (Table 4). Leaf N was equally related to both factors. Phylogenetic effects were also apparent in bivariate plots

of all traits. PICs differed significantly in SMA slopes describing relationships between SLA vs. lamina, leaf N vs. lamina, leaf N vs. SLA and leaf P vs. SLA, and also differed significantly in y-intercept for leaf P vs. lamina and leaf N vs. leaf P (Table 5).

DISCUSSION

Two major goals of this study were to (1) quantify functional leaf variation among sympatric *Shorea* species in a watershed with uniform climate but heterogeneous soils, and (2) describe the combined influences of

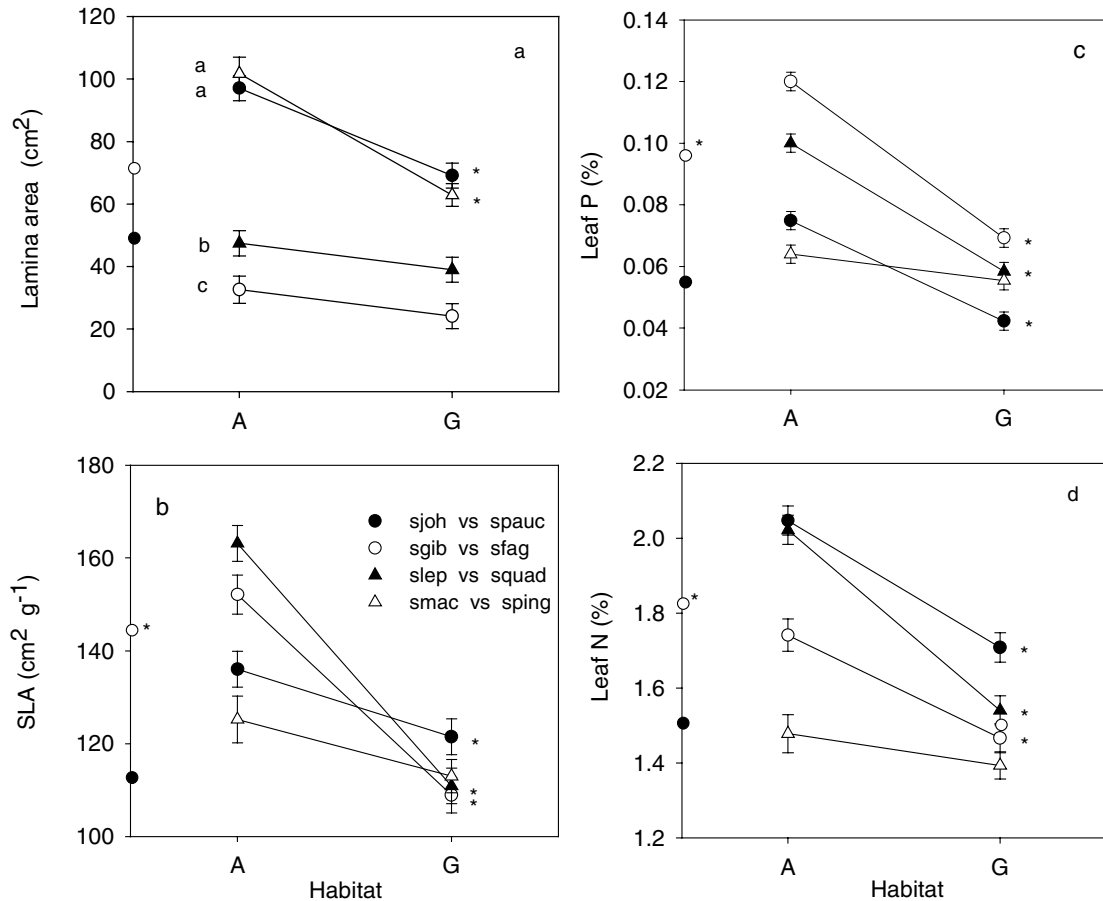


Figure 3. Sapling leaf traits in four pairs of related *Shorea* species associated with rich soils derived from alluvium (denoted A) or poor soils derived from granite (denoted G). Data are species mean \pm 1 SE for (a) lamina area, (b) SLA, (c) leaf P, and (d) leaf N. Lines connect species pairs in each PIC. Averages among four species on each soil type are shown on y-axes as open (alluvium) or closed (granite) circles. Significant differences ($P \leq 0.05$) among PICs are denoted by different letters, and between habitats or species within PICs by asterisks. Species codes follow Table 1.

Table 4. Percentage of total variance explained by phylogeny (section or subsection of *Shorea*) and habitat (alluvium or granite). Partitioning of variance was computed from sums of squares in factorial ANOVAs.

Trait	Phylogeny	Habitat
Lamina area	62.3	10.5
SLA	9.4	45.5
Leaf N	40.4	35.8
Leaf P	30.3	46.3
Leaf N:P	44.0	15.5

phylogeny and habitat on species' traits. Results indicate high levels of functional leaf variation among sympatric *Shorea*; consistent patterns of trait divergence with habitat across lineages; and differences among traits in the relative influences of phylogeny and habitat on quantitative trait values. Species-level findings reported here are broadly consistent with previous community-level studies on adaptive leaf variation across habitat types (Aerts & Chapin 2000, Reich *et al.* 2003), and suggest

a prominent role for niche processes in determining the distributions of sympatric *Shorea* species. Results highlight the potential for combining in situ measurements of quantitative leaf traits with phylogenetic information to elucidate the adaptive significance of plant trait variation across lowland tropical landscapes.

Leaf trait variation

Leaf attributes varied markedly among the nine species studied, with a 4-fold range in lamina area, \sim 3-fold for leaf P and \sim 1.5-fold for leaf N and SLA. Comparable variation among saplings of rain-forest trees has been documented at other lowland sites (Coomes & Grubb 1998, Nishimura & Suzuki 2001, Reich *et al.* 1991, Thomas & Bazzaz 1999). Given the impact of these traits on photosynthesis, respiration and growth rates (Reich *et al.* 2003, Wright *et al.* 2004), it appears that sympatric lowland rain-forest trees at GPNP and elsewhere adopt a wide range of carbon acquisition strategies.

Table 5. Results of SMA regressions between pairs of leaf traits for all individuals in species-pairs from the same section or sub-section of the genus *Shorea*. Superscripts indicate significant differences ($P < 0.05$) among species pairs.

x-y		Regression and homogeneity of slope test													
		johorensis- pauciflora		gibbosa- faquetiana		leprosulata- quadrinervis		macrophylla- pinanga		Common slope		y-intercept with common slope		P	
b ₁	b ₀	b ₁	b ₀	b ₁	b ₀	b ₁	b ₀	b ₁	b ₀	Common slope	johorensis- pauciflora	gibbosa- faquetiana	leprosulata- quadrinervis		macrophylla- pinanga
lamina-SLA	0.37 ^a	1.41	0.82	0.98 ^b	0.53	0.35 ^a	1.42	0.001	-	-	-	-	-	-	-
lamina-leafN	0.41 ^a	-0.51	-0.55	0.65 ^a	-0.80	0.20 ^b	-0.23	0.002	-	-	-	-	-	-	-
lamina-leafP	1.09	-3.33	-2.99	1.29	-3.21	0.70	-2.53	0.063	1.10	-3.35 ^a	-2.64 ^b	-2.91 ^c	-3.28 ^a	-	< 0.001
SLA-leafN	1.13 ^a	-2.11	-1.03	0.66 ^b	-1.15	0.59 ^b	-1.06	0.048	-	-	-	-	-	-	-
SLA-leafP	3.00 ^a	-7.58	-4.24	1.31 ^b	-3.91	2.01 ^b	-5.38	0.006	-	-	-	-	-	-	-
leafN-leafP	2.66	-1.97	-1.57	2.00	-1.611	3.41	-1.75	0.133	2.46	-1.92 ^a	-1.54 ^b	-1.73 ^c	-1.61 ^b	-	< 0.001

For most traits at GPNP, the range of species means within forests on a single substrate were greater than or equal to the differences between mean values of forests on different substrates. However, trait variation was much higher among species in the nutrient-rich alluvium than nutrient-poor granite (Figure 3). Lower variation in the granite reflected large declines in maximum observed values for most traits, especially SLA and leaf P. Assuming leaf attributes are adaptive, loss from the granite of trait combinations that were viable on alluvium suggests selection for a narrower range of optimal traits on poor soils. This may reflect intensified multiple environmental stresses, including P limitation (Paoli & Curran in review) and more intense periodic drought (L. Curran, unpubl. data). A sample size of four species per substrate permits limited generalization beyond study taxa, but the narrow range of leaf attributes among *Shorea* on granite is noteworthy, given that topographic and nutrient heterogeneity are highest on this substrate (Paoli, unpubl. data).

Trait shifts with habitat

Trait correlations with habitat in *Shorea* strongly suggest functional adaptation to local soil conditions, and a causal effect of allocation-based trade-offs on species distributions. When distributions were defined as a continuous function of soil nutrients, SLA, leaf P and a multivariate PCA index of leaf traits increased significantly with mean position across the gradient; leaf N also showed the same trend. Only lamina area and N:P ratio were unrelated to distribution. Such ‘environmental tracking’ of underlying soil gradients implies a deterministic influence of plant traits on distribution, and suggests that, in some settings, field assays of quantitative leaf traits may be a useful tool for inferring species rank distribution across nutrient gradients where direct quantification of soil parameters is not possible.

Coordinated trait shifts with habitat were even stronger when habitat was defined categorically. Across PICs, granite specialists had smaller leaves with lower SLA, and foliar N and P and higher N:P ratios, indicating a similar, coordinated functional response to soil variation in all four lineages. Common *Shorea* species in the granite, with smaller leaves and lower SLA and nutrient concentrations, likely produce relatively long-lived tissues with higher nutrient retention and plant-level nutrient use efficiency. This coordinated leaf strategy may be a common functional response to increased P limitation in the granite, as suggested by uniformly higher N:P ratios among granite specialists (Figure 3), and recent community-level studies across the nutrient gradient, which documented slower canopy P turnover and higher

stand-level P uptake and use efficiency in the granite (Paoli *et al.* 2005). In contrast, leaf traits of alluvium specialists imply that dominant *Shorea* species on rich soils possess a coordinated leaf strategy that confers higher intrinsic growth capacity in a habitat where nutrient limitation is less severe. A trait screening trial in which seedlings of nine *Shorea* species, including seven of those studied here, were grown in uniform conditions supports this hypothesis (Paoli 2004). Covariation between species traits and distribution across the nutrient gradient at GPNP, combined with evidence from intra-specific comparisons that species traits are at least partially intrinsic, strongly suggests that interspecific leaf trait variation affects the composition of tree communities at GPNP.

Phylogeny and leaf attributes in *Shorea*

Phylogeny is often viewed as a factor that imposes evolutionary constraint on trait divergence among related species, and hence the variety of ecological niches they occupy (Prinzing *et al.* 2001). Such constraints have been documented for many quantitative plant traits, including seed size (Kelly 1995, Kelly & Purvis 1993), fruit morphology (Hererra 1992), and leaf form (Ackerly & Reich 1999). Significant phylogenetic influences on leaf traits were observed in *Shorea* at GPNP, but the relative importance of phylogeny compared to habitat in determining leaf traits differed among traits. Phylogenetic effects were stronger than those of habitat for lamina area and N:P ratio, weaker than those of habitat for SLA and leaf P, and similar to that of habitat for leaf N (Table 4). This suggests that leaf P and SLA may be stronger determinants of species distributions than lamina size or leaf N. Phylogeny also influenced patterns of trait correlation among lineages (Table 5). This suggests evolutionary constraints on quantitative features of the coordinated leaf functional response to soil variation in *Shorea*.

While phylogenetic effects on leaf attributes were apparent in *Shorea*, and may constrain observed values for some traits, closely related species nevertheless occupied very different habitats (Tables 1 and 2). This highlights the importance of distinguishing between effects of phylogeny on *trait similarity* versus *ecological similarity* among species. If habitat use in *Shorea* is a metric for net ecological similarity, then at least some distantly related species at GPNP are more similar ecologically than closely related species in different habitats. Divergent habitat use by closely related species occurs in oak assemblages of southern Florida (Cavender-Bares *et al.* 2004), congeneric trees of the savanna-forest continuum in central Brazil (Hoffmann & Franco 2003), and rain-forest trees of Malesia (Rogstad 1990)

and Amazonia (Fine *et al.* 2005), suggesting that within-clade ecological amplitude may be a common feature of subtropical and tropical communities. Further research on trait divergence within a phylogenetic framework (Cavender-Bares *et al.* 2004) and its consequences for species distribution will improve our understanding of how phylogeny influences community structure and the distribution of traits across environmental gradients in diverse communities (Webb *et al.* 2002).

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