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Soil-related performance variation and distributions of tree species in a Bornean rain forest

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Summary

1 Spatial distributions of tropical trees often correlate with environmental variation, suggesting that ecological sorting caused by niche differentiation may be important for maintaining species diversity.

2 Four soil types have been identified in a 52-ha forest dynamics plot in Bornean mixed dipterocarp forest (ranked by increasing fertility and moisture: sandy loam, loam, fine loam, and clay). The distributions of 73% of tree species in the plot are significantly aggregated on one of these soil types. We tested the hypothesis that variation in performance (growth and mortality) underlies these edaphically biased species distributions.

3 Annual growth and mortality rates over 5 years were estimated for trees ≥ 1 cm in diameter and compared among soil types, life histories and species-aggregation patterns.

4 Overall, growth and mortality rates were lowest on the poorest soil (sandy loam). Growth rates on each soil type correlated with soil fertility for pioneers, while mortality rates correlated with soil fertility for both pioneers and late-successional species.

5 There was little evidence that soil specialists had a home-soil performance advantage. Soil-specific ranks of growth and mortality rates of each species-aggregation group largely mirrored the ranks of their rates across the plot and did not shift substantially among soil types. On every soil, species aggregated on sandy loam or clay ranked last or next-to-last, and species aggregated on loam ranked the highest.

6 Ecological sorting of species among soils was strong. With increasing diameter, species were lost from the soils on which they were not aggregated more frequently than would be expected based on random mortality. The underlying mechanisms of ecological sorting may involve low mortality rates as a requirement for species to achieve high abundance on the poorest soil, whereas for the richer soils, having high growth rates appears relatively more important for achieving high abundance.

7 Thus, species' demographic responses to resource variation among soil types, especially related to the poorest soil, affects tree species distribution patterns in this forest and thereby influences the structure of tropical forest communities.

Key-words: growth, mixed dipterocarp tropical forest, mortality, niche differentiation, soils

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Introduction

Species composition of tropical rain forest communities is spatially heterogeneous (Aubréville 1938; Richards 1952) as a result of non-random, typically aggregated, distributions of individuals (Condit *et al.* 2000). Spatial distributions of tropical trees often correlate with environments having particular light, soil, moisture and topographic characteristics, suggesting the potential importance of niche differentiation in structuring tropical forest tree communities (Ashton 1964; Baillie *et al.* 1987; Clark *et al.* 1999; Svenning 1999; Webb & Peart 2000; Harms *et al.* 2001). Specialization on narrow niches can increase a community's species richness (Macarthur & Levins 1967) and is one mechanism for

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the maintenance of high species diversity of tropical forest communities (Dobzhansky 1950; Ashton 1969; MacArthur 1969; Tilman 1982).

Observed distribution patterns, however, result from responses of plants to the abiotic environment in combination with biotic interactions, such as those with seed dispersers, natural enemies and competitors (Kneitel & Chase 2004). In addition to niche differentiation, then, spatially aggregated tree distributions can also be established and maintained by dispersal limitation, i.e. the failure of seeds to reach all possible recruitment sites (Hubbell 2001; Dalling *et al.* 2002), as well as intra- and interspecific interactions, such as competition and pathogen-pressure (Janzen 1970; Connell 1971; Louda 1989; Fine *et al.* 2004).

If environmentally biased spatial distributions of tropical trees are primarily the result of niche differentiation or interspecific interactions, as opposed to dispersal limitation, then tree species should show performance differences when growing in different habitats. Such performance variation is the basis for ecological sorting, which is the differential success due to functional characteristics of populations or species in different environments (Weiher & Keddy 1995; Ackerly 2003). When the spatial scale of environmental variation is small relative to that of dispersal, dispersal limitation is negligible. Ecological sorting can then promote variation in species composition among habitats by removing species that may have colonized a habitat from the regional species pool, but that are unsuited to local conditions (Ackerly 2003).

Among plants, growth and mortality of habitat specialists can vary with resource availability (Grime 1979; Chapin 1980). Specialists of stressful or resource-poor environments typically have lower and less variable growth and mortality rates, compared with generalists and specialists of resource-rich environments (Grime 1979; Chapin 1980; Valladares *et al.* 2000). As a result, even when specialists of poor environments experience resource-rich conditions, adaptations to stress tend to restrict their ability to respond with increased growth or re-directed allocation patterns (Grime 1979; Chapin 1980). Thus, if adaptations to stress compromise competitive ability in stress-free environments or, conversely, if species adapted to stress-free environments are less likely to reach maturity under more stressful conditions, then relative performance of specialists should vary significantly among habitats. In contrast, if aggregated species distributions are primarily the result of dispersal limitation, consistent variation in relative performance among habitats would be unlikely.

In north-west Borneo, floristic composition varies significantly across soil types at the regional scale (Ashton 1964; Brunig 1974; Baillie *et al.* 1987; Potts *et al.* 2002). Within a 52-ha forest dynamics plot (hereafter, Lambir) in species-rich mixed dipterocarp rain forest in Borneo, spatial variation in tree species composition was significantly correlated with variation in soil chemistry and topography. Soils in Lambir range from sandy loams, which are sandstone derived, leached, nutrient poor and well drained, to clays, which are shale derived, nutrient rich and less well drained (Lee *et al.* 2002). Of the 764 species tested, 73% had distributions significantly aggregated on at least one of the four soil types identified in Lambir (Davies *et al.* 2005). Variation in soil moisture and fertility may be two important factors underlying this floristic variation among soil types (Palmiotto *et al.* 2004). Mortality induced by periodic El Niño drought is greater on sandy loam than on clay (Potts 2003). Low soil fertility may also limit growth and survival by selecting against species with inefficient nutrient use on sandy loam (Palmiotto *et al.* 2004).

The objective of this research was to test the hypothesis that variation among soils in performance (growth and mortality) underlies the strongly soil-correlated distributions of tree species observed in Lambir. First, we quantified growth and mortality of all trees, of light-demanding pioneer species and of more shade-tolerant late-successional species, to identify whether forest dynamics varied among soil types and with life history. Secondly, we tested whether performance of species on each soil type depended on aggregation pattern (i.e. the soil type on which a species is aggregated). Thirdly, we evaluated the evidence for ecological sorting by quantifying changes in species composition of trees in successive diameter classes on each soil type.

Methods

STUDY SITE

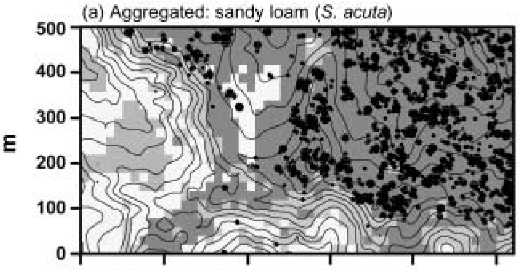
Lambir Hills National Park, Sarawak, Malaysia (4°11′ N, 114°01′ E) encompasses 6800 ha of lowland mixed dipterocarp forest and has the highest tree species diversity recorded in the Palaeotropics (Ashton & Hall 1992; Davies & Becker 1996; Lee *et al.* 2002). Lambir Hills National Park receives *c.* 3000 mm of rainfall annually, with all months averaging > 100 mm (Watson 1985). In 1991, a 52-ha research plot (hereafter Lambir) was established in the Park to monitor all woody plants ≥ 1 cm in diameter at breast height (diameter). The methods for this project followed similar studies coordinated by the Center for Tropical Forest Science (Condit 1998; Ashton *et al.* 1999). All trees ≥ 1 cm in diameter, excluding palms, were tagged, mapped, identified and their diameters measured to the nearest 1 mm. In 1997, all trees from the first (1992) census were recensused to estimate growth and mortality rates. A full description of the floristic composition and stand structure of Lambir is in Lee *et al.* (2002).

The soils and geomorphology of Lambir have been previously described (Lee *et al.* 2002). The soils are Typic and Inceptic Hapludults and related Dystrudepts (Soil Survey Staff 1999). They range from coarse loams that are sandstone derived, leached, nutrient depleted and well drained, with up to 10 cm of raw humus on the surface (referred to in previous publications as humult), to clays that are shale derived, less nutrient depleted and less well drained, with little raw humus (referred to in previous publications as udult; Lee *et al.* 2002). In a previous study (Davies *et al.* 2005), four soil types in Lambir were distinguished based on variation in soil nutrients (total C, N and P and exchangeable K, Ca and Mg) and elevation at a 20 × 20 m scale (Fig. 1, Table 1). Ranked in ascending order of fertility and moisture, these soil types are here referred to as sandy loam, loam, fine loam and clay, which correspond to habitats A, B, C and D, respectively, in Davies *et al.* (2005). Davies *et al.* (2005) identified tree species in Lambir showing spatial distribution patterns biased with respect to these four soil types using a Poisson cluster model (Plotkin *et al.* 2000). This model is a three-parameter stochastic point-process model that replicates small-scale (e.g. dispersal-driven) spatial aggregation while reducing large-scale (e.g. habitat-driven) aggregation, thereby taking into account spatial autocorrelation (Harms *et al.* 2001). The Poisson cluster model was fit to each species with > 50 trees. Soil-type associations of species were judged by comparing the actual percentage of trees found on a soil type to the distribution of the percentages of trees found on a soil type as generated from 1000 random realizations of the best-fit Poisson cluster model. Species were classified as either aggregated on a soil type, if the rank of the actual percentage was in the top 2.5% of the random distribution of percentages, or repelled from a soil type, if its actual percentage was ranked in the bottom 2.5%. Otherwise, a species was classified as neutral with respect to that soil type.

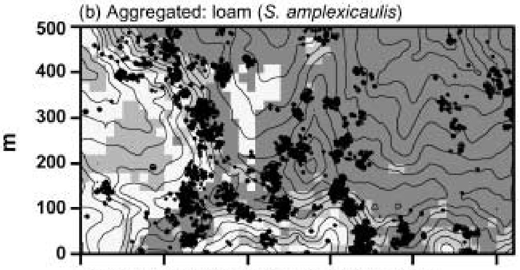
Among the 764 species tested, 73% had distributions significantly aggregated on one or two soil types (Davies *et al.* 2005). Here we focus on these species plus those with a neutral distribution with respect to soil (no aggregation or repulsion, 13% of species). For simplicity, for species that were found to be aggregated on two soil types (11% of all species, Davies *et al.* 2005), we designated the soil type with greater tree density as that of aggregation. Thus, we investigated five possible species-aggregation patterns in this study: species aggregated on sandy loam (285 species), on loam (66 species), on fine loam (152 species) and on clay (57 species), and species showing neutral patterns (100 species). Five species in the genus *Shorea* (Dipterocarpaceae) showing these distribution patterns are illustrated in Fig. 1(a–e).

Lambir is topographically heterogeneous, and disturbance rates vary among the different soil types (Palmiotto 1998). The loam and fine loam have steeper average slopes than do the sandy loam and clay (35.2° and 20.4°, vs. 17.1° and 18.0°, respectively). Consequently, they have more frequent and larger gaps resulting from landslips, as suggested by a map of the locations of the 2% fastest growing stems (Fig. 1f). We therefore quantified the proportions of trees that were in the light-demanding pioneer life-history guild and the growth and mortality rates of trees of pioneer and late-successional species on each soil type. A list of pioneers (140 species)

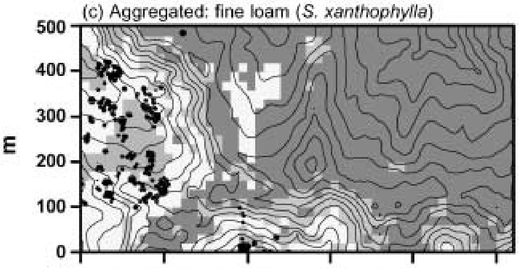
(a) Aggregated: sandy loam (*S. acuta*)



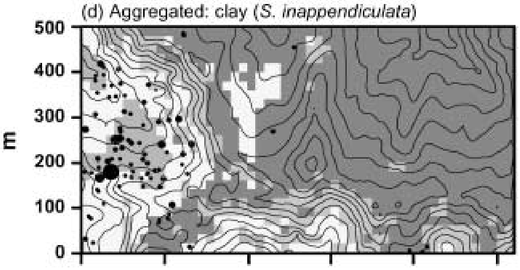
(b) Aggregated: loam (*S. amplexicaulis*)



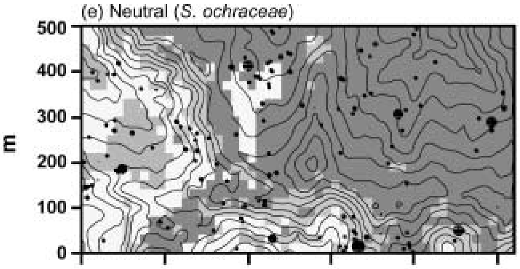
(c) Aggregated: fine loam (*S. xanthophylla*)



(d) Aggregated: clay (*S. inappendiculata*)



(e) Neutral (*S. ochraceae*)



(f) Fastest growing 2% of trees

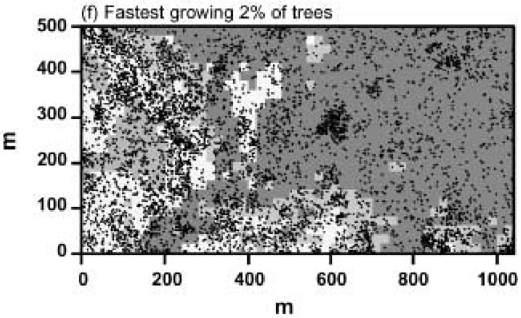


Fig. 1 Distributions of five species of *Shorea* (Dipterocarpaceae) aggregated on sandy loam (a), loam (b), fine loam (c) or clay (d) soils or with a neutral distribution (e) in the Lambir plot. In A–E, circles are scaled according to tree diameter. Locations of the fastest growing 2% of all trees in the Lambir plot (f). Shading indicates soil types: dark grey, sandy loam; light grey, loam; white, fine loam; medium grey, clay.

Table 1 Mean total nitrogen (%), total phosphorus (mg kg^{-1}), pH, exchangeable magnesium (cmol$_c$ kg^{-1}) and calcium (cmol$_c$ kg^{-1}), and elevation (m) for the four soil types in the Lambir plot (Davies *et al.* 2005). Standard errors are in parentheses. Significant differences among soil types are indicated by different lower case letters

Soil type	N	Total N	Total P	pH	Mg	Ca	Elevation
Sandy loam	766	0.093 (0.001)^{a}	43.7 (0.7)^{d}	4.64 (0.00)^{a}	0.12 (0.00)^{d}	0.21 (0.00)^{c}	193.8 (0.7)^{a}
Loam	184	0.099 (0.003)^{a,c}	66.5 (2.3)^{c}	4.41 (0.01)^{b}	0.15 (0.01)^{c}	0.22 (0.00)^{c}	183.1 (1.4)^{b}
Fine loam	270	0.107 (0.002)^{b}	103.3 (2.2)^{b}	4.32 (0.01)^{c}	0.19 (0.01)^{b}	0.30 (0.00)^{b}	152.6 (1.4)^{c}
Clay	80	0.107 (0.003)^{b,c}	133.6 (4.1)^{a}	4.43 (0.04)^{b}	0.70 (0.04)^{a}	0.52 (0.01)^{a}	138.8 (1.7)^{d}

was assembled *a priori* based on previous research in this forest (P. S. Ashton and S. J. Davies, unpublished data). Trees not considered pioneers were classified as late-successionals (1059 species), which thus includes highly shade-tolerant species.

ANALYSES

Annual growth and mortality rates were estimated based on the 1992 and 1997 censuses in Lambir. Diameter growth rate per tree (mm y^{-1}) was calculated as the diameter increment in millimetres divided by the inter-census interval in years, the latter based on exact census dates. Extreme growth rate outliers were excluded because they were likely to be erroneous and only represented 0.04% data points (128 out of 308 494 trees). Trees with annual growth rates either > 75 mm or decreasing in diameter by > 5% per year were considered outliers. Annual mortality rates (% y^{-1}) were calculated as $M = 100 \times (\log(N_0) - \log(S)) / T$, where N_0 is the initial number of live trees, S is the number of surviving trees, and T is the mean interval in years between censuses (Sheil & May 1996). Dead trees were those that were (i) fallen, (ii) missing after a systematic search or (iii) standing dead. Standing dead trees were identified as those lacking leaves and having a dried inner cambium.

Overall variation in performance among soil types was evaluated by quantifying growth and mortality rates on each soil type of trees of all species, of pioneer and late-successional species separately, and within tree diameter classes. For growth, we compared soil types based on 95% confidence intervals (CI) estimated by bootstrapping. For mortality, CIs were calculated based on binomial probabilities by finding the population mean of the number of dead trees (D) for which the binomial probability of observing D would be < 0.025 (for the upper CI) or > 0.975 (for the lower CI) for mortality (Condit *et al.* 1995).

Mean growth and mortality rates of species on each soil type were calculated for species with ≥ 10 individuals on each of at least two soil types. We grouped species according to their aggregation patterns and analysed variation among these groups across the plot and on each soil type individually. Analysis of variance (ANOVA) was used to analyse log-transformed mean growth rates, and Tukey's highly significant difference test (Miller 1981; Chambers & Hastie 1993) was used to evaluate pairwise differences among soil types. Mortality rates were approximately Poisson-distributed and could not be normalized using transformations. We therefore analysed variation in mortality rates using a generalized linear model with a Poisson error distribution and a log link function. Model parameters were maximum likelihood estimates, produced by iteratively re-weighted least-squares (Chambers & Hastie 1993). Differences among soil types in mean mortality rates were evaluated with post-hoc pairwise comparisons (Chambers & Hastie 1993).

If ecological sorting occurs among saplings ≥ 1 cm in diameter on each soil type, then species with poor relative performance would be lost with increasing tree size as cohorts aged. We used three sets of analyses to assess the evidence for ecological sorting. First, to determine whether some soil types were more restricted in species composition with respect to aggregation patterns, we evaluated whether soil types differed in the proportions of stems that were of species aggregated on each of the four soil types or of neutral species. Secondly, using a subset of tree species that reached a maximum diameter ≥ 20 cm on the Lambir plot, we quantified the change in species composition in successive diameter classes on each soil type, with respect to species-aggregation patterns. We tested whether the number of species lost in successive diameter classes was significantly different from that expected based on random thinning of trees in smaller size classes. Random mortality was simulated by randomly sampling a subset of individual trees to die that was equal to the difference in the number of trees between the 1–5 cm diameter class and either the 10–20 cm or the ≥ 20 cm diameter classes. The expected number of species lost between these diameter classes due to random thinning was then calculated for each soil type and species soil aggregation pattern from the data set that resulted after simulated mortality. Simulated random thinning was repeated 2000 times, and 95% confidence intervals were calculated from the 2.5th and 97.5th quantiles of the distribution of the numbers of species lost from each soil type and species soil aggregation pattern. Thirdly, we tested for differences among soil types in the skewness (Sokal & Rohlf 1995) of the log tree diameter distribution for all trees and for species with ≥ 50 individuals on a soil type. Confidence intervals of the skewness coefficient were estimated by bootstrapping. The tree diameter distribution should be more right-skewed on the soil type on which a species is aggregated compared with that from which it is repelled.

Results

FOREST DYNAMICS AND LIFE-HISTORY VARIATION AMONG SOIL TYPES

Growth and mortality rates of trees of all species (Fig. 2a,d), as well as of pioneer (Fig. 2b,e) and late-successional species (Fig. 2c,f), were lowest on the most resource-poor soil (sandy loam), compared with the three richer soil types. Ranks of mean growth rate on each soil type were largely parallel for trees of all species, pioneers and late-successionals, although differences were not always statistically significant among the three richer soils (Fig. 2a–c). For all tree species, mean growth rate on clay was lower than on either loam or fine loam (Fig. 2a), and for pioneers, growth rate on loam was significantly lower than on the two more fertile soils (fine loam and clay, Fig. 2b), whereas for late-successionals only, these three soil types did not differ significantly in growth (Fig. 2c). In all cases, variation in mortality corresponded to soil resource availability. The most resource-rich soil (clay) had the highest mortality rates, followed by fine loam, loam and sandy loam, although differences were not significant between clay and fine loam (Fig. 2d–f).

The percentage of stems that were pioneer species was lowest on sandy loam and clay (7% for both), whereas it was highest on loam and fine loam (12% and 11%, respectively). When species were grouped according to their aggregation patterns, the percentage of species that were pioneers in each group varied. Species aggregated on either sandy loam or clay consisted of few pioneers (5% for both), whereas species aggregated on either loam or fine loam were more pioneer rich (30% and 17%, respectively). These differences in life-history patterns among soil types and species aggregation patterns reflect the greater disturbance rates, and hence light availability, on loam and fine loam relative to sandy loam and clay.

Mean growth rates increased with increasing diameter, as did the differences between sandy loam and the other three soil types (Fig. 3a). The lowest growth rates occurred on sandy loam, except in the 1–2 cm diameter class (Fig. 3a). In contrast, mortality rates showed little change with tree diameter and were lowest on sandy loam for all size classes (Fig. 3b).

DOES SPECIES-AGGREGATION PATTERN INFLUENCE PERFORMANCE ON SOIL TYPES?

Mean growth rates of species aggregated on sandy loam were significantly lower than those of species aggregated on either loam or fine loam and tended to be lower than those of species aggregated on clay or neutral species (Table 2). Mean per capita mortality rates of species aggregated on sandy loam were significantly lower than those of species aggregated on either loam or fine loam and tended to be lower than those of species aggregated on clay or neutral species (Table 2). The higher growth

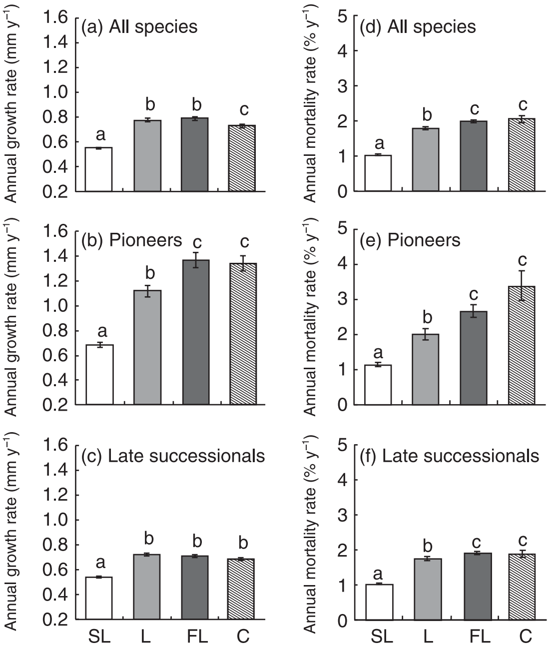


Fig. 2 Mean annual growth (a–c) and annual mortality (d–f) rates of trees of all (a, d), pioneer (b, e) and late-successional (c, f) species on each of the four soil types in the Lambir plot. Soil types are listed from left to right in order of increasing soil fertility and moisture. Error bars are 95% confidence intervals based on bootstrapping (growth) or the binomial distribution (mortality). Lower case letters indicate statistically significant differences among soil types. Abbreviations are as follows: SL, sandy loam; L, loam; FL, fine loam; C, clay.

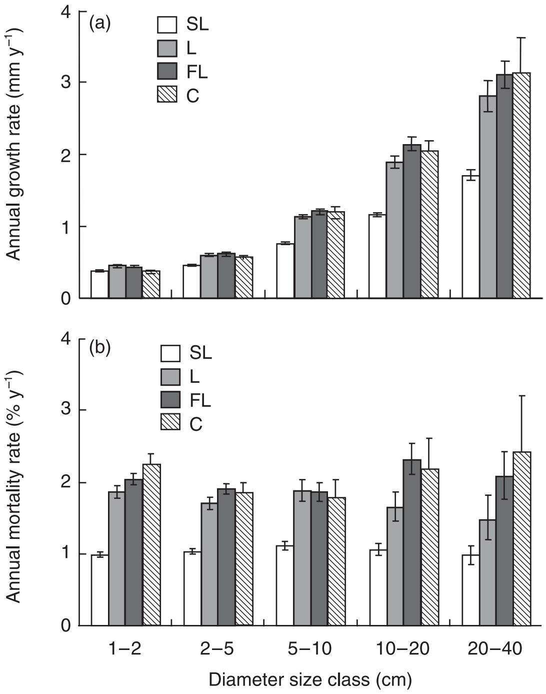


Fig. 3 Mean annual growth (a) and annual mortality (b) rates of trees in five diameter size classes on each of the four soil types in the Lambir plot. Soil types are listed from left to right in order of increasing soil fertility and moisture. Error bars are 95% confidence intervals based on bootstrapping (growth) or the binomial distribution (mortality).

Table 2 Mean growth (mm $year^{-1}$) and annual mortality rate (percentage $year^{-1}$) of species aggregated on each soil type and neutral species in the Lambir plot. Ninety-five percent confidence intervals are in parentheses

	Species-aggregation pattern				
	Sandy loam species	Loam species	Fine loam species	Clay species	Neutral species
Growth	0.61 (0.58–0.66)	1.07 (0.87–1.31)	0.94 (0.81–1.07)	0.75 (0.62–0.88)	0.72 (0.63–0.84)
Mortality	0.81 (0.74–0.88)	1.71 (1.25–2.27)	1.38 (1.16–1.64)	1.11 (0.88–1.38)	1.16 (0.78–1.75)

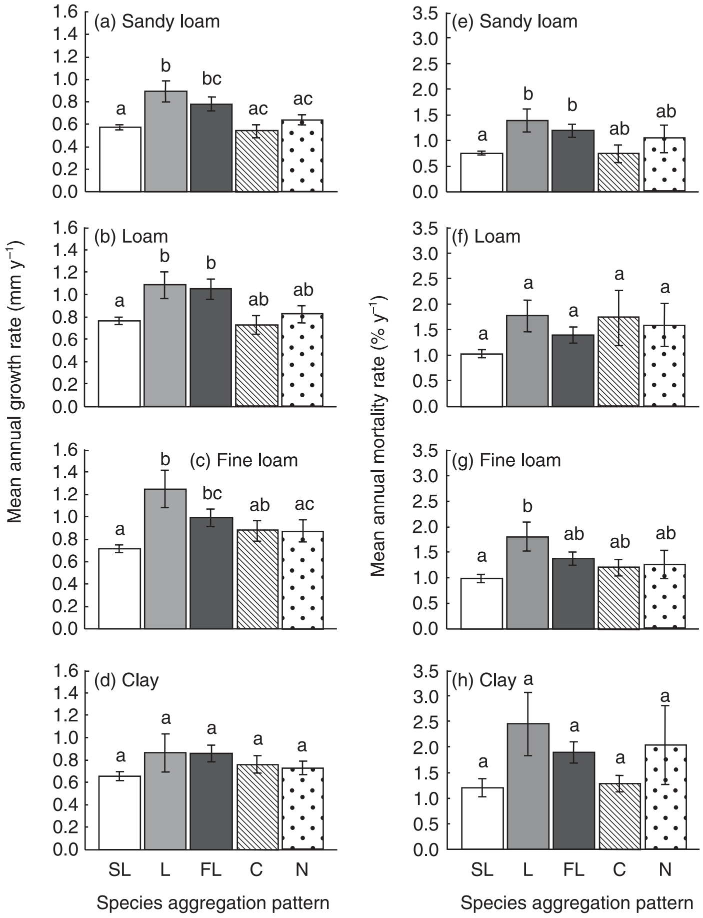


Fig. 4 Mean growth (a–d) and mortality (e–h) of species in each soil-aggregation group and neutral species on each of the four soil types in the Lambir plot: (a, e) sandy loam, (b, f) loam, (c, g) fine loam, (d, h) clay. Error bars are one standard error. Lower case letters indicate statistically significant ($P < 0.05$) differences among soil types.

and mortality rates of species aggregated on loam and fine loam, relative to those on clay, may partly result from the greater proportion of pioneers in these groups.

IS THERE A HOME-SOIL PERFORMANCE ADVANTAGE?

As a group, home-soil species (those aggregated on a particular soil type) did not in all cases perform better than the non-home-soil species groups on each soil type (Fig. 4). Ranks of soil-specific growth rates of species in each aggregation group (Fig. 4a–d) largely mirrored the ranks of their overall rates across the plot (Table 2). Where there were significant differences in growth rates among species-aggregation groups on a soil type, species aggregated on sandy loam and on clay consistently ranked the lowest on every soil. On the other hand, on all soil types, species aggregated on loam ranked highest and those on fine loam second to highest in growth, but differences among soil types were not always significant. Neutral species ranked intermediate in growth.

As was the case for growth, ranks of soil-specific mortality rates of species in each aggregation group (Fig. 4e–h) largely reflected the ranks of their overall rates across the plot (Table 2), except on loam. Where there were significant differences, species aggregated on sandy loam or clay ranked lowest in mortality on all soils. Species aggregated on loam ranked highest in mortality on all soil types, but differences were not

Table 3 Percentage of trees on each soil type in the Lambir plot that are members of each species-aggregation pattern. Percentages do not sum to 100 because not all trees on a soil type are members of these five soil aggregation categories; some have other distribution patterns and others could not be categorized because of low sample sizes

	Species-aggregation pattern				
Soil type	Sandy loam	Loam	Fine loam	Clay	Neutral
Sandy loam	57	10	6	1	9
Loam	33	22	14	1	9
Fine loam	17	10	30	6	11
Clay	12	6	24	25	8

always significant. On clay and loam, differences between which were not significant, the intermediate rankings switched among soil-aggregation groups. Congruent patterns were found when these analyses were done on pioneer and late-successional species separately (results not shown). Thus, ranks of soil-aggregation groups did not shift substantially among soil types for either growth or mortality. There was therefore little evidence of a home-soil performance advantage in terms of either home-soil species performing better than non-home-soil species (within-panel comparisons, Fig. 4) or home-soil species performing best on their home soil relative to other soils (among-panel comparisons, Fig. 4).

DOES ECOLOGICAL SORTING AFFECT SPECIES COMPOSITION ON EACH SOIL TYPE?

Sandy loam was the most restricted in its species composition with respect to species-aggregation patterns, with 57% of all trees representing species aggregated on that soil type, whereas trees of species aggregated on each of the other three soil types contributed no more than 10% of trees (Table 3). In contrast, on loam, fine loam and clay, trees were more equitably distributed among the different species-aggregation categories.

If ecological sorting occurs as saplings age, then species with poor relative performance would be lost with increasing tree size. On each soil type, there was a steady decline in species richness with increasing diameter that was greatest on clay and least on sandy loam (Fig. 5). These declines are expected based on random thinning and species-area relationships, as the clay and sandy loam soils comprise the smallest and largest areas of the Lambir plot, respectively. However, species were lost more frequently from soil types on which they were not aggregated (Fig. 5), indicating that declines in species richness result from ecological sorting. The observed numbers of species lost from soil types on which they were not aggregated were almost always significantly greater than would be expected based on random thinning.

If this ecological sorting was largely the result of poor performance of only very young saplings on unsuitable soil types, then the proportion of trees in larger diameter classes would be greater on the home-soil type, resulting in a more right-skewed diameter distribution on soils other than the species' home type. However, when species were grouped according to their aggregation patterns, neither the mean skewness of their diameter distributions nor the deviation from the average skewness on a soil type differed significantly among soil types (ANOVA, $P > 0.05$ in all tests). Therefore, ecological sorting appears to affect trees of all size classes without inducing a shift in the diameter distribution.

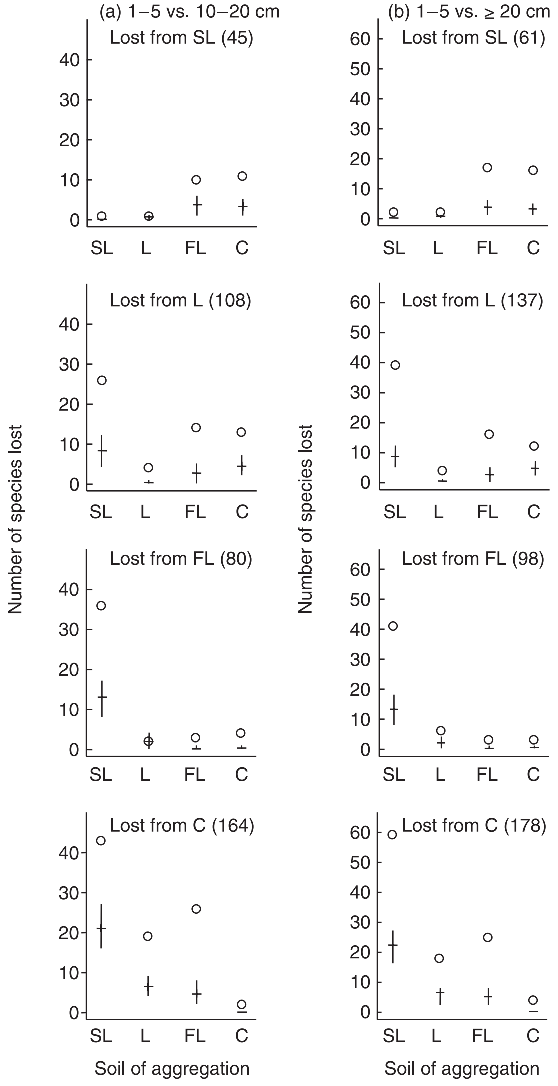


Fig. 5 Numbers of species lost from each soil type in the Lambir plot in the transition between successive diameter classes for each soil-aggregation category. (a) 1–5 vs. 10–20 cm diameter class transition; (b) 1–5 vs. ≥ 20 cm diameter class transition. Open circles are the observed numbers of species lost from a soil type according to their aggregation pattern. Horizontal dashes and vertical bars show the mean and 95% confidence interval of the expected number of species lost based on a random thinning model. Numbers in parentheses are the observed total numbers of species lost from each soil type. Analyses were for only those species reaching ≥ 20 cm in maximum diameter on the plot.

Discussion

We found evidence that variation in performance among soil types, especially that linked to the most resource-poor soil type, promotes strong ecological sorting of species among soil types and underlies distribution patterns in this Bornean rain forest. Growth and mortality varied among soil types and among groups of species aggregated on the different soil types, but there was little evidence of a home-soil performance advantage for soil specialists. Instead, our results are consistent with predictions based on stress physiology of plants (Grime 1979; Chapin 1980) and on life-history trade-offs (Bazzaz 1979), in that species-aggregation patterns in Lambir may be mediated by variation among soils in the relative importance of a species' ability to tolerate low-resource conditions by having a conservative demographic response vs. the ability to respond to increases in resource availability (Bazzaz 1979; Grime 1979).

As a group, species aggregated on sandy loam consistently maintained conservative demographies (slow growth and low mortality rates), even when growing on the more resource-rich soil types, as is frequently observed in stress-adapted plant species (Grime 1979; Chapin 1980; Latham 1992). Because these species had the lowest growth response along a gradient increasing in either below- or above-ground resources, they may be poorer competitors for canopy openings, compared with species aggregated on loam and fine loam. However, their low mortality rates nonetheless allow them to persist on these soil types. In contrast, neutral species and species repelled from sandy loam had both high growth and high mortality rates on this soil type. Taken together, these results suggest that adaptations for rapid growth, such as thin, short-lived leaves with high nutrient concentrations, high photosynthetic rates and reduced allocation to antiherbivore defence, may incur particularly high survival costs on this resource-poor soil type (Chabot & Hicks 1982; Coley 1988; Poorter & Garnier 1999). Indeed, most individuals growing on sandy loam were of species aggregated on this soil type.

In contrast to the conservative demographies of species aggregated on sandy loam, the species with the highest and most variable growth and mortality rates were those aggregated on loam and fine loam and neutral species. Furthermore, the proportion of species that were pioneers, which have high growth and mortality rates (Bazzaz & Pickett 1980; Swaine & Whitmore 1984), was higher for the loam and fine loam species groups, whereas it was lower for the sandy loam and clay species groups. The existence of more gaps (Palmiotto 1998), steeper slopes and higher frequencies of fast-growing trees on the loam and fine loam suggests that trees receive more light on these soil types than on sandy loam and clay. Therefore, the occurrence of the highest and most variable growth rates among species aggregated on loam and fine loam appears to be associated with both higher light and moderate nutrient availability on these soils.

Performance of species aggregated on clay resembled those of species aggregated on sandy loam, albeit with somewhat higher overall growth and mortality rates, despite below-ground resources being substantially higher on clay. The role of the irradiance environment may explain this counter-intuitive result, as light availability appears lowest on clay soil both in the Lambir plot and in other Bornean forests on clay soils (P. S. Ashton, personal communication). Clay soils generally occur in low-elevation valleys where erosion has revealed shale deposits. In addition, crown densities of the canopy trees may be higher on clay soils due to the dominance of larger (mesophyll) over smaller (notophyll) leaf sizes on clay, relative to sandy loam (Ashton 1964). Species aggregated on clay may be adapted to these lower light levels; however, quantitative data on irradiance on each soil type at Lambir and experimental tests of responses of clay specialists to increases in light are needed.

Pioneers had higher growth rates than did late-successionals on all soil types, which is consistent with observations that species with high growth rates tend to perform better on both low and high fertility soils (Huante *et al.* 1995; Grubb *et al.* 1996; Palmiotto *et al.* 2004). However, pioneers on loam had significantly lower growth rates than on either clay or fine loam. These results suggest that pioneers were more responsive than late-successional species to the greater below-ground resource levels on clay, but that their growth became relatively limited by the lower availability of below-ground resources on loam. Thus, differences among species in the ability to respond to soil nutrients depend on the irradiance environment (Bungard *et al.* 2002).

This inference is consistent with a study of the pioneer genus *Macaranga*, which found that species distribution patterns in Lambir were mediated by the dual influences of soil texture (a correlate of soil nutrients) and light on growth and mortality (Davies 2001). Furthermore, a reciprocal seedling transplant experiment near Lambir found significantly higher growth rates for all species on clay, but only in gaps (Palmiotto *et al.* 2004). Limitation by soil moisture and nutrients may be greatest for trees that are released from light limitation and achieve high growth rates (Turner 1991; Latham 1992; Burslem *et al.* 1996; Grubb *et al.* 1996; Davies 2001; Bungard *et al.* 2002). However, responses of south-east Asian rain forest seedlings and trees to nutrient addition in pot and field experiments are inconsistent, and may partly reflect the influence of confounding variation in light and species-specific responses (Burslem *et al.* 1996; Turner 1991; Turner *et al.* 1993; Palmiotto *et al.* 2004). Thus, which species are excluded from each soil type at Lambir is likely to depend upon the frequency of disturbance, in combination with limitation by soil moisture and nutrients.

EVIDENCE FOR PERFORMANCE-BASED ECOLOGICAL SORTING

We found strong evidence of ecological sorting based on the significant losses of species with increasing diameter from soils on which they were not aggregated. Losses of species from non-home-soil types exceeded what would be expected based on random mortality. Consequently, as trees aged, species composition became increasingly biased in favour of home-soil species. This effect may be most pronounced on sandy loam, as most trees on this soil were of species that were aggregated on that soil type. This was not the case for any of the other three soil types, which had more equitable representations of species from all five aggregation patterns. Thus, each soil type appears to eliminate species that are not adapted for survival there, but this effect appears strongest on the most resource-poor soil type.

The ecological sorting process at Lambir does not appear to be a simple consequence of specialists consistently having a home-soil performance advantage in terms of both growth and mortality. Rather, a low mortality rate appears to be a requirement for a species to achieve a high abundance on sandy loam, but having a high growth rate is not. Conversely, having a high growth rate appears to be more important than a low mortality rate for a species to achieve high abundance on the three richer soils, particularly loam and fine loam. Thus, a species' responsiveness in terms of rapid exploitation of more abundant local resources by faster growth may be more important on the three richer soils, whereas on sandy loam, species need to tolerate low resources enough to survive. Higher disturbance rates (Palmiotto 1998) and greater below-ground resources on the richer soils would favour faster-growing species, which could reach the canopy sooner and produce more seed earlier than slower-growers, resulting in greater recruitment rates. This conceptual model of ecological sorting at Lambir is consistent with Grime's (1977) characterization of competitive and tolerant species, but could result either from all forms of competition declining in importance with soil resources or from competition for soil resources being relatively more important on the poor soil and for light being more important on the richer soils (Tilman 1988; Campbell & Grime 1992; Fynn *et al.* 2005).

Performance-based ecological sorting among soils was evident despite substantial demographic variability. Such variability is expected given small-scale environmental heterogeneity, plasticity of species' responses, and the many factors that can influence growth and mortality, sometimes in opposing directions (Clark 2003). However, even weak differences in performance of species among soils operating over time periods relevant for recruitment of reproductive adults could nonetheless influence the development of distribution patterns of species. Such effects, if present, appeared to influence all diameter classes uniformly, as the skewness of stem diameter distributions of species did not vary significantly among soil types.

OTHER POTENTIAL MECHANISMS INFLUENCING SPATIAL DISTRIBUTIONS

With the available data, we cannot rule out the possibility that dispersal limitation may enhance these edaphically biased distributions. In addition, it is likely that ecological sorting also occurs before the 1-cm diameter sapling stage (Grubb 1977), as demonstrated in a Panamanian forest (Engelbrecht & Kursar 2003). However, our analyses indicate that, regardless of what may occur before the 1-cm diameter sapling stage, ecological sorting after this stage has a substantial influence on edaphically biased species distribution patterns at Lambir.

We have discussed light as an important unmeasured source of variation in this study, but it is likely that there are others. In particular, these soils may vary substantially in the communities of mycorrhizal fungi they support and their effects on tree growth and survival (Turner *et al.* 1993; Moyersoen *et al.* 2001). The majority of individuals in this forest are in the Dipterocarpaceae, all of which are known to be ectomycorrhizal, and many other species in this community have associations with vesicular-arbuscular mycorrhizas (Alexander 1989). How the mycorrhizal communities vary among the soil types in Lambir, if at all, and how that variation might influence performance and species distributions in relation to soil type is unknown.

Conclusions

Previous studies have suggested that niche differentiation contributes to the maintenance of tropical tree species diversity by documenting the correlation between the distributions of species and environmental variation. Our study is one of the first to test whether performance variation can explain such patterns. We suggest that species' demographic responses to resource variation among soil types plays an important role in generating and maintaining the edaphically biased spatial distributions of tree species at Lambir and thereby contributes to the high beta-diversity observed in this forest.

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