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Determinants of Tree Species Distributions: Comparing the Roles of Dispersal, Seed Size and Soil Specialization in a Bornean Rainforest

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Introduction

Understanding the factors influencing plant species distributions in local communities is critical to explaining how these communities are structured. This is evidenced by the prominence of spatial variation in many hypotheses of species diversity, such as the niche differentiation (MacArthur and Levins, 1967; Tilman and Pacala, 1993), dispersal limitation (Levin, 1974; Hurtt and Pacala, 1995) and natural enemies hypotheses (Janzen, 1970; Connell, 1971). From an ecological perspective, spatial distribution patterns (dispersion) are extremely important for sedentary organisms such as plants because they can mediate species coexistence, which influences the maintenance of species diversity. From an evolutionary perspective, a plant's location affects its fitness and the selection pressures it is exposed to, which influence lineage diversification and the origins of species diversity.

Three important factors that influence the dispersion of plants are *seed dispersal* (Nathan and Muller-Landau, 2000; Russo and Augspurger, 2004), *seed size* (Westoby *et al.*, 1996) and *niche specialization* (Tilman and Kareiva, 1997). However, there is little consensus as to the relative magnitude of their effects and how they interact in determining the dispersion of plants in different communities. Through seed size-number trade-offs and interactions with dispersers, dispersal mode and seed size shape spatial patterns of seed deposition, which establish the initial template of offspring dispersion. The pattern of seed deposition determines how many offspring 'lottery tickets' are played in different environments (Dalling *et al.*, 2002; Schupp *et al.*, 2002; Russo and Augspurger, 2004). Over evolutionary time, spatial patterns of seed dispersal can thereby influence the frequency with which a species experiences novel selection regimes as well as gene flow between populations (Herrera, 2002; Holt *et al.*, 2004).

The size of a plant's seed can influence both its dispersal and the abiotic and biotic environments in which it is most successful (Baker, 1972; Grubb, 1977) due to trade-offs between size and either competitive (Levins and Culver, 1971; Tilman, 1994) or establishment (Dalling and Hubbell, 2002; Coomes and Grubb, 2003) ability. For example, compared with smaller seeds, larger seeds often have greater establishment probability in soils with low mineral nutrient availability and in shaded environments (Westoby *et al.*, 2002). Niche specialization after the seedling stage can modify post-dispersal offspring dispersion (Wada and Ribbens, 1997; Dalling and Hubbell, 2002). Functional traits governing resource acquisition determine the environments in which species are most successful (Reich *et al.*, 1995; Wright *et al.*, 2001). Hence, over ecological timescales, seed dispersal, seed size and niche specialization affect dispersion, whereas over evolutionary timescales, they affect the selection pressures and gene flow that facilitate evolution in novel environments (Van Tienderen, 1991; Westoby *et al.*, 1996; Herrera, 2002; Holt *et al.*, 2004).

The research reported in this chapter was conducted on a 52-ha forest dynamics plot (Lambir) in species-rich, mixed dipterocarp rainforest in Borneo. At Lambir, spatial variations in the distribution of tree species are strongly influenced by variations in soil chemistry and topography (Davies *et al.*, 2005). Soils in Lambir range from sandy loams, which are sandstone-derived, nutrient-poor and well drained; to clays, which are shale-derived, more nutrient-rich and less well drained (Lee *et al.*, 2002). The distributions of most species of tree were significantly aggregated on at least one of four distinct soil types identified in Lambir (Davies *et al.*, 2005). Such edaphic niche specialization is widespread and consistent among species of tree in forests across Borneo, making it likely to be a species-level trait (Ashton, 1964; Brunig, 1974; Baillie *et al.*, 1987; Potts *et al.*, 2002). Variation in soil moisture and fertility may be two important factors underlying this floristic variation among soil types (Palmiotto *et al.*, 2004) and may have influenced the evolution of species to different edaphic niches.

Local adaptation of a population to a novel environment depends on many characteristics of the population and traits in question (Holt *et al.*, 2002). One important factor is gene flow between populations in different environments (Wright, 1943; Lenormand, 2002). Furthermore, only a narrow range of successful colonization rates may facilitate adaptive evolution in a novel sink environment (Holt *et al.*, 2004). Gene flow in plants is partly mediated by colonization effected first by immigration and then successful establishment, processes that are influenced by seed dispersal mode, seed size and environmental niche specialization (Gibson and Wheelwright, 1995; Stanton and Galen, 1997; Jordano and Godoy, 2000; see Hardesty, Chapter 12, this volume). Thus, at Lambir, whether a species of tree is a soil specialist or a generalist may depend on its dispersal mode and seed size. In this study we tested this hypothesis by comparing ecological and evolutionary patterns of covariation among dispersal mode, seed size and soil specialization at Lambir. By arraying these species-level traits on a supertree phylogeny of the species of tree, in this community, we assessed whether divergences in

dispersal mode and seed size were associated with divergences in edaphic niche. We also sought to dissect the effects of these factors as determinants of the distributions of species of tree at small and large spatial scales in this rainforest tree community.

Methods

Study site and data sets

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 and Hall, 1992; Lee *et al.*, 2002). The Park receives *c.*3000 mm of rainfall annually, with all months averaging > 100 mm (Watson, 1985). Animal seed dispersers include primates, birds, small arboreal and terrestrial mammals, and large terrestrial mammals (Shanahan and Debski, 2002). In 1991, a 52-ha research plot (hereafter, Lambir) was established in the Park to monitor all woody plants ≥ 1 cm diameter at breast height (dbh). Methods for this project followed similar studies coordinated by the Centre for Tropical Forest Science (Condit, 1998; Ashton *et al.*, 1999). All trees ≥ 1 cm dbh excluding palms were tagged, mapped, identified, and their diameters measured to the nearest 1 mm. 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). 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 variations in soil nutrients (total C, N and P, and exchangeable K, Ca and Mg) and elevation at a 20 \times 20 m scale (Fig. 23.1). Ranked in ascending order of fertility and moisture, these soil types are here referred to as: sandy loam (30.64 ha in area in the plot), loam (7.36 ha), fine loam (10.80 ha) and clay (3.20 ha), which correspond to habitats A, B, C and D, respectively, in Davies *et al.* (2005). 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 the sandy loam and clay (35.2° and 20.4° versus 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 fastest growing 2% of all stems (Fig. 23.1f).

Davies *et al.* (2005) identified the 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). Species were classified as either

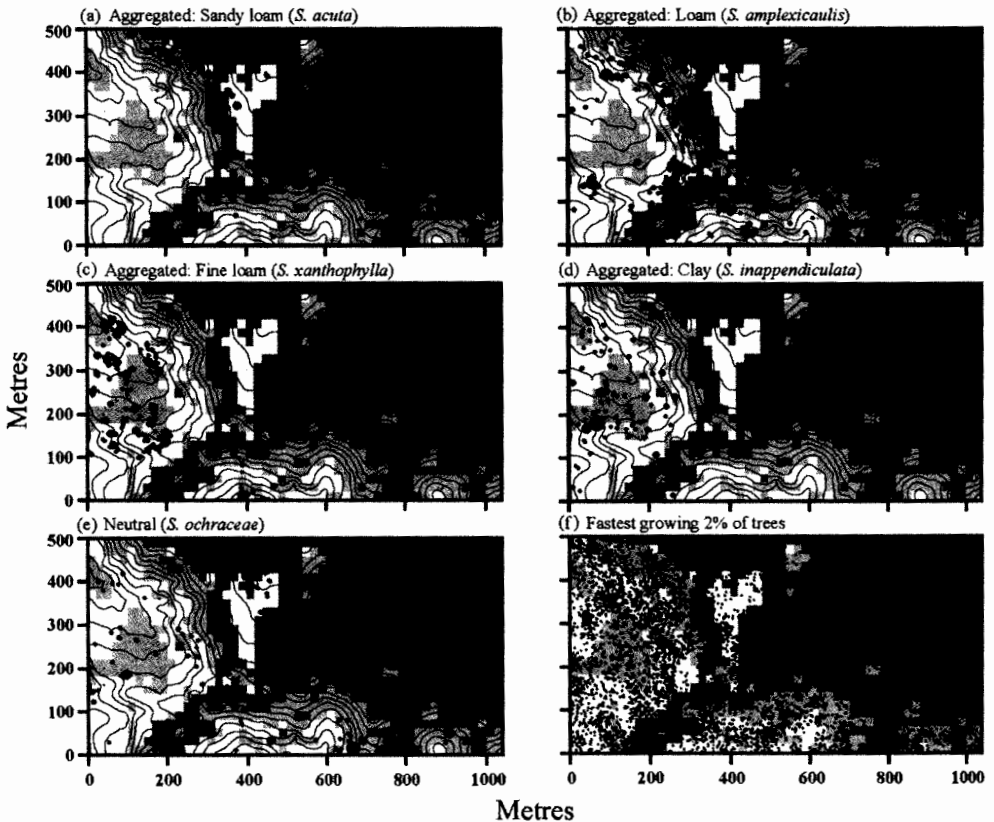


Fig. 23.1. Distributions of five species of *Shorea* (Dipterocarpaceae) that are significantly aggregated on (a) sandy loam, (b) loam, (c) fine loam, or (d) clay soils or (e) with a neutral distribution, in the Lambir plot, Borneo. In parts a–e, circles are scaled according to the diameter of the tree. Locations of the fastest growing 2% of all trees in the Lambir plot are also shown (f). Shading indicates soil types: darkest grey, sandy loam; light grey, loam; white, fine loam; and lightest grey, clay.

aggregated on, repelled from, or having a neutral distribution with respect to each 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 (specialists) on *sandy loam* (285 species), on *loam* (66 species), on *fine loam* (152 species) and on *clay* (57 species), and species showing *neutral* patterns (generalists: 100 species). Five species of *Shorea* (Dipterocarpaceae) showing these distribution patterns are illustrated in Fig. 23.1a–e.

The results of the Poisson cluster model analysis indicated that at larger spatial scales, distributions of tree species within Lambir are strongly determined by edaphic variation (Davies *et al.*, 2005). Visual inspection of species' distributions within the plot (e.g. Fig. 23.1a–e) none the less indicated substantial interspecific variation in dispersion at smaller spatial scales. Here we use spatial statistics (see Statistical analyses section) to test the hypothesis that interspecific variation in small-scale dispersion can be explained by dispersal mode, seed size and niche specialization.

We collected data on primary dispersal mode and seed length on as many as possible of the 764 species for which soil specialization was categorized (308 species in 119 genera and 47 families). The seed was defined as the diaspore with the dispersal morphology removed. Seed weight may be a preferred metric of seed size but we were able to collect seed lengths for more species, allowing stronger tests of covariation between seed size, dispersal mode and soil specialization. We collected data from diverse sources, including measurements of seeds in herbarium specimens, seed measurements reported in the literature, and data from other researchers (see Acknowledgements).

Based on fruit morphology, personal observations, and reports in the literature, we categorized species into four primary dispersal modes: (i) ballistic (i.e. explosive) dispersal; (ii) gravity (i.e. unassisted) dispersal; (iii) dispersal by animals; and (iv) dispersal by wind. Although more finely divided dispersal categories would be preferable, for most species we have little detailed information about species-specific dispersal mechanisms or the distributions of dispersal distances of seeds. In addition, it is likely that many species in each primary dispersal category are secondarily dispersed by small mammals, but insufficient data exist to account for this process.

We constructed a phylogenetic hypothesis of the evolutionary relationships among the 308 species in our analyses, based on phylogenetic hypotheses for these taxa published in the literature. This supertree phylogeny (Sanderson *et al.*, 1998) was assembled using the software Phylomatic (Webb and Donoghue, 2004) and is based on the most recent Angiosperm Phylogeny Group tree, with generic relationships within families based on other published phylogenies. All species within genera are represented as polytomies (unresolved within-genus relationships), which limits our ability to test patterns of trait variation among species within genera. Because the final phylogenetic tree was a composite from multiple sources, branch lengths could not be estimated. We therefore assumed a speciation model of evolution (branch lengths = 1 across the tree; Ackerly, 2004). Some comparative analyses that we used (i.e. those using the software Discrete; Pagel, 1994) do not accept polytomies. For these, we arbitrarily resolved polytomy relationships into a completely bifurcating tree, and gave the branches added in the process very short branch lengths (equal to 10^{-6}). How polytomies were resolved does not influence the outcomes of analyses when the branch lengths are so short. Species values for dispersal mode, seed size and edaphic niche specialization were arrayed on this phylogeny.

Statistical analyses

For non-phylogenetic analyses (analyses using species values), we used general linear models and type III tests (proc mixed in SAS; SAS Institute, 2000) to test the relationships between continuous variables and between continuous and categorical variables. Standard transformations were used to improve normality of continuous dependent variables. We used Poisson regression to test relationships between categorical variables in which the response variable was counts of species in each cross-classification category (proc genmod in SAS). For all tests of association, as a continuity correction, a value of 1 was added to all cell counts in cross-classification tables containing a zero or when 20% of all counts were < 5.

Tests of phylogenetic trait conservatism evaluate whether trait values of closely related species are more similar (trait evolution is conserved) or more dissimilar (traits have diverged evolutionarily) to each other than what would be expected by chance, or whether species' traits are randomly distributed across the phylogenetic tree (Blomberg *et al.*, 2003). Phylogenetic trait conservatism was tested using the methods implemented in the software Phylocom (Webb *et al.*, 2005). The methods in Phylocom are similar to those for independent contrasts but are modified to handle polytomies by calculating the standard deviation of the descendent trait values at each node from the observed species' values on the phylogeny. Significance is assessed based on 1000 randomizations of species' values across the tips of the phylogeny.

Phylogenetic independent contrasts (PICs) (Felsenstein, 1985), as calculated in the software Phylocom (Webb *et al.*, 2005), were used to test for correlated evolution between two continuous variables and to compare mean contrast values between two groups. In the first case, PICs were analysed using general linear models (proc mixed in SAS) with the intercept forced through the origin. In the second case, PICs were analysed using either Student's *t* or sign tests in two-way comparisons between levels of a factor (e.g. for dispersal modes: wind versus animal dispersal, wind versus ballistic dispersal, wind versus gravity dispersal, and so on). The phylogenetic tree was pruned so as to include only the species appropriate for the particular two-way comparison, and separate tests were run for each comparison.

Correlated evolution between categorical variables was analysed using a likelihood ratio test of whether the transition rates between different character states of a trait on the phylogeny are best modelled as independent of or dependent upon each other, as implemented in the software Discrete (Pagel, 1994). Multistate categorical variables were analysed by transforming them into a series of binary state categorical variables, as described above.

We used the neighbourhood density function (Ω) to analyse species dispersion within soil types (Condit *et al.*, 2000; Dale *et al.*, 2002). This statistic is a modification of the second-order spatial statistic known as Ripley's K (Ripley, 2003) but the value of the statistic is calculated within annuli surrounding a focal tree. Many annuli included areas outside of the

52-ha plot, necessitating an edge correction so that only the area inside the plot was used (Condit *et al.*, 2000).

Dispersion is defined relative to an Ω value of 1, which indicates Poisson random dispersion within the tested annulus; values significantly >1 indicate clumped dispersion, and values <1 indicate over-dispersion (i.e. regularity). Significance was assessed by calculating Ω from 100 realizations of a Poisson random process. The number of times that Ω from the randomized data exceeded the observed value of Ω was tallied and the probability calculated as above. We calculated this statistic for all species with at least 50 saplings across the plot in each of three size classes (1–2 cm, 2–4 cm and 1–5 cm) and within each of three annuli (0–10 m, 10–20 m and 0–20 m). The results from analyses based on 1–5 cm saplings and the 0–20 m annulus are presented here. The results from this subset of data are consistent with the others tested. Because all species were significantly clumped at this scale, Ω can be considered a measure of small-scale clumping.

Results

Phylogenetic trait conservatism

Seed size, dispersal mode, and small-scale clumping intensity (Ω) were highly conserved phylogenetically (Table 23.1). In contrast, soil specialization was randomly distributed phylogenetically, meaning that related species were neither more nor less likely to share edaphic niches than distantly related species. This was true regardless of whether soil specialization categories were broken out individually (four soil specialists plus generalists) or whether all specialists were lumped into one category (specialists versus generalists; Table 23.1).

The random distribution of soil specialization on the phylogeny is illustrated by the fact that 73% of the families and 48% of the genera with > 1 species that were analysed for soil specialization contained at least one specialist and one generalist. Furthermore, 36% of families and 15% of

Table 23.1. Phylogenetic niche conservatism in dispersal mode, seed size and small-scale clumping intensity (Ω) for 1–5 cm saplings at 0–20 m spatial scale, for 308 tree species in a Bornean rainforest. Probabilities are based on randomization of the standard deviations of trait values across the supertree phylogeny of the 308 species. The multistate trait, soil specialization, was transformed into a series of binary traits to meet assumptions of the analysis, and the range of probabilities for possible pairwise comparisons for different binary combinations is given.

Trait	Conserved?	Probability
Dispersal mode	Yes	0.002
Seed size	Yes	0.002
Small-scale clumping intensity	Yes	0.002
Soil specialization	No (random)	0.1118–0.882
Generalists versus specialists	No (random)	0.498

genera with > 4 species had at least one representative of every soil specialist and one generalist. In fact no genus or family with five or more species was composed of only one kind of soil specialist or only of generalists. These results indicate that soil specialization is evolutionarily far more labile than dispersal mode, seed size or small-scale clumping intensity, all of which were more conserved.

Covariation between dispersal mode, seed size and soil specialization

We next tested whether dispersal mode and soil specialization showed significant covariation in ecological and evolutionary contexts. From an ecological perspective, soil specialists and generalists had similar overall frequencies of species in each of the four dispersal modes (Table 23.2). In other words, generalists did not have proportionally more species that were good dispersers (wind- or animal-dispersed), relative to poor dispersers (ballistically or gravity-dispersed). This result held whether soil specialists were all tested separately ($\chi^2 = 12.39$, $\nu = 12$, $P = 0.415$) or grouped together ($\chi^2 = 4.86$, $\nu = 3$, $P = 0.182$). Similarly, from an evolutionary perspective, transitions between different dispersal modes on the phylogenetic tree were not significantly associated with transitions from being a generalist to a specialist species (likelihood ratio test for a model of independent versus dependent trait transitions $\nu = 4$ for all tests; animal versus gravity: $\chi^2 = 3.03$, $P = 0.554$; animal versus ballistic: $\chi^2 = 0.83$, $P = 0.935$; wind versus ballistic: $\chi^2 = 1.72$, $P = 0.787$; wind versus animal: $\chi^2 = 1.44$, $P = 0.838$; wind versus gravity: $\chi^2 = 0.77$, $P = 0.9426$; ballistic versus gravity: $\chi^2 = 2.76$, $P = 0.175$). Furthermore, transitions on the phylogeny from being a well-dispersed species (wind- or animal-dispersed) to being a poorly dispersed species (ballistically or gravity-dispersed) were not associated with transitions from being a generalist to a specialist (likelihood ratio test for a model of independent versus dependent trait transitions; $\chi^2 = 6.984$, $\nu = 4$, $P = 0.137$). Thus, evolutionary transitions between modes of dispersal and soil specialization categories were relatively independent.

Table 23.2. Numbers of tree species in a Bornean rainforest in each cross-classification of dispersal mode and soil specialization categories. There was no significant association ($P > 0.05$) between dispersal mode and soil specialization categories, either with all five soil specialization categories tested separately or with all specialist categories grouped and compared with generalists.

Dispersal mode	Soil specialization				
	Sandy loam	Loam	Fine loam	Clay	Generalist
Ballistic	7	1	4	2	1
Gravity	8	0	1	1	4
Animal	79	20	53	12	24
Wind	18	7	10	7	9

We used a general linear model to test for main effects of both dispersal mode, soil specialization, and their interaction on interspecific variation in seed length. Seed size varied significantly among dispersal modes ($F_{(3, 260)} = 7.57, P < 0.001$; Fig. 23.2a) and among soil specialization categories ($F_{(4, 260)} = 7.29, P < 0.001$; Fig. 23.2b), but there was no significant interaction between these factors ($F_{(11, 249)} = 0.72, P = 0.720$). In other words, species with the same dispersal mode had similar seed sizes across the different soil specialization categories.

When ranked by increasing mean seed length, ballistic-dispersed species had the smallest seeds, followed by animal-, wind- and gravity-dispersed species (Fig. 23.2a). Seed size of wind-dispersed species was somewhat larger than expected, probably due to an effect of species in the Dipterocarpaceae, 83% of which have winged fruits with large seeds (33 of 40 species). Specialists of both the poorest (sandy loam) and the richest (clay) soils and generalists had the largest seeds (Fig. 23.2b). The smallest seeds were of species specializing on the two soils with intermediate fertility and moisture, the loam and fine loam soils.

We used PICs to test for correlated evolution between changes in seed length and either dispersal modes or soil specialization categories, using binary codings of these categorical variables. The results were similar to those of the non-phylogenetic analyses. Among the species contrasted, smaller seeds had an evolutionary association with specialists of loam compared with specialists of sandy loam (17 of 19 contrasts; sign test $P < 0.001$) and compared with specialists of clay (10 of 12 contrasts; sign test $P = 0.039$). No other seed length–soil specialization pairwise combinations were significantly correlated (sign tests, $P > 0.05$), even when specialists of the two richer soils (fine loam and clay) were grouped and compared with specialists of the two poorer soils grouped (sandy loam and loam; 20 of 43 contrasts, sign test, $P = 0.761$). In addition, larger seeds had no significant evolutionary

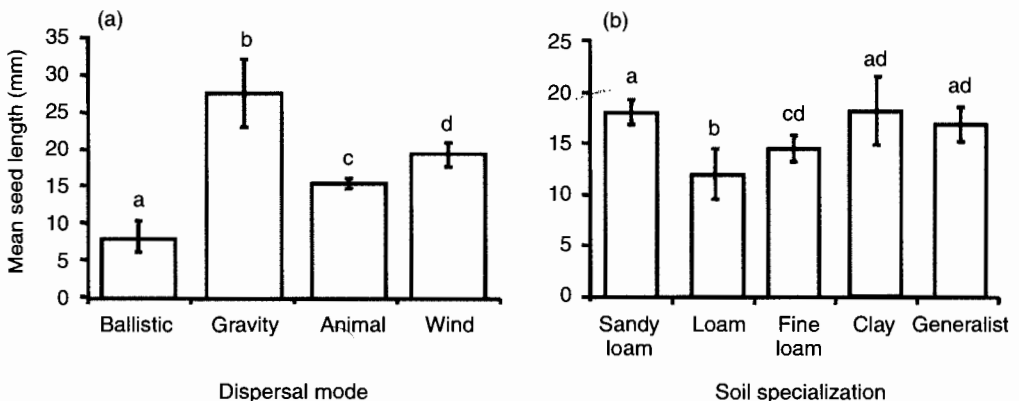


Fig. 23.2. Variation in seed length (mm) among tree species with different (a) dispersal modes and (b) soil specializations in a Bornean rainforest. Error bars are ± 1 SE. Lower-case letters indicate statistically significant differences among means within each panel.

association with being a generalist compared to a specialist (19 of 30 contrasts, sign test; $P = 0.201$).

Among the species contrasted in dispersal mode, larger seeds had an evolutionary association with animal- compared with gravity-dispersed species (3 of 3 contrasts; t -test, $P < 0.001$) and weakly for wind- compared with gravity-dispersed species (5 of 5 contrasts; sign test, $P = 0.063$). Other seed length-dispersal mode pairwise combinations were either not significantly correlated (wind versus animal dispersal: 4 of 9 contrasts; and ballistic versus animal dispersal: 1 of 3 contrasts; sign tests $P > 0.05$) or there were too few contrasts to test (wind versus ballistic and gravity versus ballistic dispersal).

Effects of dispersal mode, seed size and soil specialization on small-scale dispersion

The most intensely clumped families (largest values of Ω) were Violaceae (mean $\Omega = 37.6$), which consists of two ballistic-dispersed, understory tree species in the genus *Rinorea*, followed by the Dipterocarpaceae (mean $\Omega = 23.4$), with 40 gravity- and wind-dispersed species, and lastly, Theaceae (mean $\Omega = 13.1$), with two animal-dispersed, pioneer species in the genus *Adinandra*. The two most clumped species were dipterocarps, *Shorea macrophylla* ($\Omega = 113.28$) and *Dipterocarpus kunstleri* ($\Omega = 109.27$), both wind-dispersed pioneers that are specialists of clay soil. The least clumped species were in the families Anisophylleaceae (mean $\Omega = 1.9$; one animal-dispersed and one gravity-dispersed species) and Bombacaceae (mean $\Omega = 2.1$), Annonaceae (mean $\Omega = 3.0$) and Burseraceae (mean $\Omega = 3.0$), all three of which contain only animal-dispersed species. The gravity-dispersed species in the Anisophylleaceae has quite large seeds that germinate from within the leathery fruit, which suggests that it may be secondarily dispersed by small mammals.

The effects of seed length, dispersal mode and soil specialization on small-scale clumping intensity were tested using a general linear model. All two-way interactions were tested, except the soil specialization \times dispersal mode interaction, because some factor combinations had less than two observations. In addition to the significant main effects (dispersal mode: $F_{(3, 216)} = 8.42$, $P < 0.001$; soil specialization: $F_{(4, 216)} = 6.55$, $P < 0.0001$), the only interaction that was significant was that between seed length and dispersal mode (seed length \times dispersal mode: $F_{(3, 216)} = 5.15$, $P = 0.002$; seed length \times soil specialization: $F_{(4, 212)} = 0.56$, $P = 0.692$).

Variation due to dispersal mode was significant, with animal-dispersed species being the least intensely clumped, wind and gravity-dispersed species being most intensely clumped, and ballistically dispersed species having intermediate clumping intensity (Fig. 23.3a). The intense clumping of wind-dispersed species is somewhat surprising, but can be explained by the importance of the large-seeded Dipterocarpaceae in the wind-dispersal category (80% of wind-dispersed species).

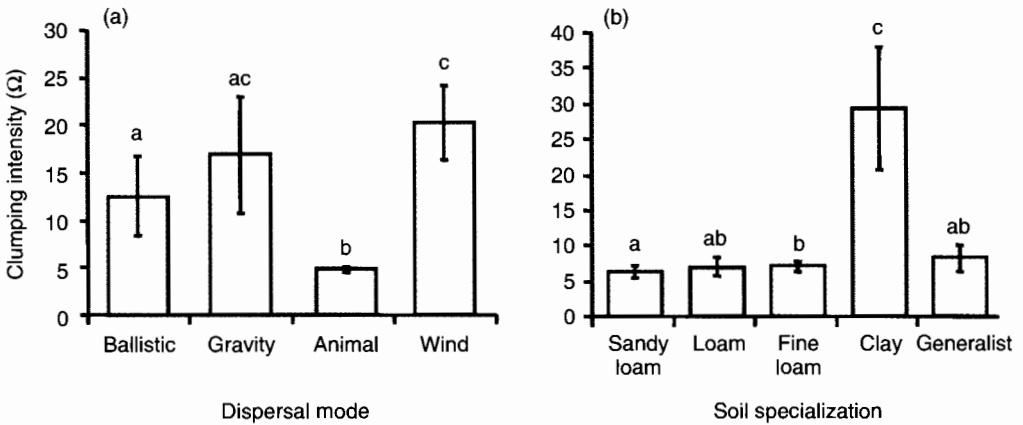


Fig. 23.3. Variation in Ω , the intensity of small-scale (0–20 m) clumping of juveniles (1–5 cm dbh saplings), among tree species with different (a) dispersal modes and (b) soil specializations in a Bornean rainforest. Error bars are ± 1 SE. Lower-case letters indicate statistically significant differences among means within each panel.

By far the most intensely clumped species were among specialists of the clay soil, whereas the least-clumped species were specialists of the two poorer soils, sandy loam and loam soils, and generalists (Fig. 23.3b). This result is partly due to the fact that of the 17 species for which we had seed size and dispersal information that were also clay specialists, seven were from the two most-clumped families, Violaceae and Dipterocarpaceae, and included the two most intensely clumped species on the entire plot. Even after removing species in these two families from the analysis, the clay specialists still remained the most intensely clumped. Thus, these two families were not completely responsible for this significant effect, but rather make the underlying difference of the clay specialists relative to the others even stronger.

Slopes of the relationship between small-scale clumping intensity and seed length were significantly different from zero for all dispersal modes except for ballistically dispersed species (Fig. 23.4a; $b = -0.013$, $SE_b = 0.023$, $P = 0.586$). Animal- and gravity-dispersed species had significantly negative, but shallow, slopes (animal: $b = -0.012$, $SE_b = 0.006$, $P = 0.044$; gravity: $b = -0.042$, $SE_b = 0.013$, $P = 0.001$). In contrast, wind-dispersed species had a significantly positive slope ($b = 0.026$, $SE_b = 0.008$, $P = 0.002$). The negative slopes indicate that animal- and gravity-dispersed species with larger seeds have less intense small-scale clumping than do those with smaller seeds, whereas the reverse is true for wind-dispersed species.

Some analyses of small-scale clumping intensity based on PICs differed from those based on species values. Among the species contrasted, increased clumping was not an evolutionary pattern associated with specialist, compared with generalist, species (17 of 26 contrasts; sign test, $P = 0.169$), parallel to analyses based on species values. Based on PICs, species with

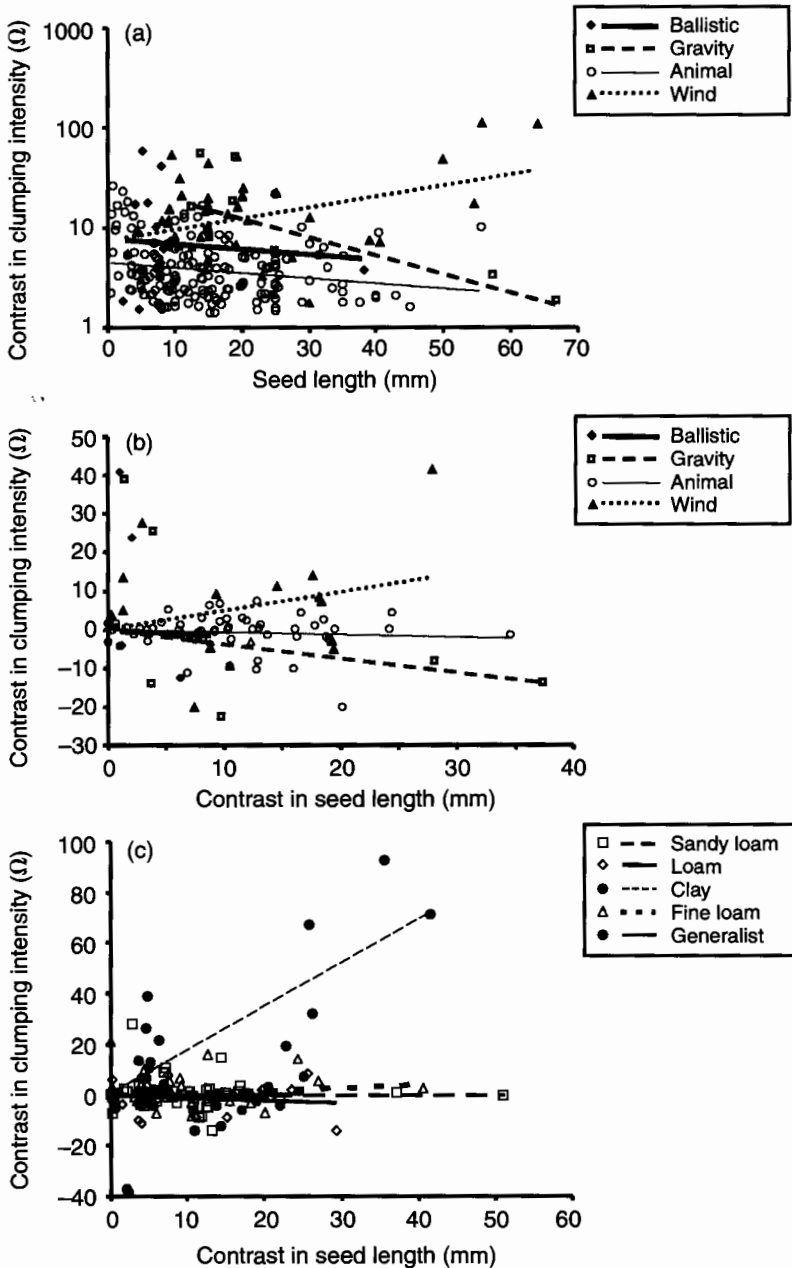


Fig. 23.4. Variation in Ω , the intensity of small-scale (0–20 m) clumping of juveniles (1–5 cm dbh saplings) as a function of seed length (mm) for tree species in a Bornean rainforest, distinguishing dispersal mode (a, non-phylogenetic analysis; and b, phylogenetic analysis) and soil specialization (c, phylogenetic analysis). Lines are best-fit lines based on ordinary least-squares regression. Non-phylogenetic analyses were based on species' values; phylogenetic analyses were based on independent contrasts with the intercept forced through the origin (see Methods for details).

different dispersal modes varied in their relationship between seed length and small-scale clumping intensity (Fig. 23.4b). Slopes of the relationship between PICs in small-scale clumping intensity and seed length were not different from zero for ballistically dispersed ($b = -0.189$, $SE_b = 0.964$, $P = 0.845$), gravity-dispersed ($b = -0.374$, $SE_b = 0.222$, $P = 0.096$) and animal-dispersed species ($b = -0.038$, $SE_b = 0.114$, $P = 0.742$). In contrast, wind-dispersed species had a significantly positive slope ($b = 0.486$, $SE_b = 0.188$, $P = 0.012$), as was found in analyses based on species values.

In contrast to analyses based on species values, there was significant variation among soil specialists in the relationship between PICs for seed length and for small-scale clumping intensity (Fig. 23.4c). This effect was due to the significant positive slope for clay specialists ($b = 1.742$, $SE_b = 0.141$, $P < 0.001$). For all other soil specialists, there was no significant relationship (sandy loam: $b = -0.008$, $SE_b = 0.102$, $P = 0.936$; loam: $b = -0.113$, $SE_b = 0.177$, $P = 0.526$; fine loam: $b = 0.106$, $SE_b = 0.141$, $P = 0.453$, generalists: $b = 0.014$, $SE_b = 0.171$, $P = 0.933$).

Discussion

We found no strong ecological or evolutionary relationships between the probability of being a soil specialist or generalist and either dispersal mode or seed size. Dispersal modes occurred with equal frequency among the five different soil specialization categories, and seed sizes of species in the same dispersal mode were consistent across soil specialization categories, findings that are consistent with patterns from neotropical forests (Hammond and Brown, 1995). In addition, there were no significant associations between evolutionary transitions between different dispersal modes and soil specialization on the phylogenetic supertree of the species in this Bornean rainforest community. Therefore, generalists were not significantly better dispersers than specialists. Using these broad categories to estimate 'good' versus 'poor' dispersing species is clearly inferior to having more detailed information on the actual spatial patterns of seed dispersal, but we lack such information in this forest.

There was significant variation in seed size among soil specialization categories. None the less, the patterns we observed in this Bornean rainforest were inconsistent with the hypotheses that:

1. Larger seeds enhance establishment on soils with low fertility and moisture, restricting smaller-seeded species to richer soils;
2. Larger seeds enhance establishment on any soil type, facilitating evolution of a generalist strategy;
3. Smaller seeds enhance dispersal, facilitating evolution of a generalist strategy.

Although specialists of the poorest soil (sandy loam) and generalists had the largest seeds, they were not alone, as specialists of the richest soil (clay) also had large seeds. Specialists of loam and fine loam had the smallest seed sizes,

which are often observed among tropical tree species with fast growth rates (Bazzaz and Pickett, 1980). These two soils, particularly loam, are located on steep slopes with greater frequency of disturbance from landslips. Consequently, they are likely to have greater light availability, which may favour species with faster growth responses. Hence, seed size variation among soil specialization categories may be better explained by light availability and disturbance on the different soil types, rather than soil fertility and moisture, which is consistent with similar analyses in New World tropical forests (Foster and Hanson, 1985; Hammond and Brown, 1995).

Tree species with different dispersal modes varied in seed size. Wind-dispersed seeds are generally smaller than seeds having other dispersal modes (Hammond and Brown, 1995; Westoby *et al.*, 1996). In contrast, as a group, wind-dispersed trees in this community had the largest seed sizes. This surprising result is simply because the dipterocarps, which comprise a majority of species in this forest, are large-seeded, yet most have wings for dispersal by wind (Webber, 1934).

Dispersal mode and seed size were highly conserved on this phylogeny of species in this forest community, as has been observed in temperate floras (Lord *et al.*, 1995). In contrast, soil specialization was evolutionarily labile. Consistent with this result, many families and genera contained representatives of multiple soil specialist and generalist species, but this was not true of dispersal mode. Taken together, these results indicate that tree species' occurrence in, and possibly diversification into, different edaphic niches in this forest may not depend strongly on dispersal mode or seed size. These results raise the possibility that edaphic niche specialization may have had a central role in the more recent diversification of these Bornean tree species, as has been found for the Burseraceae in Amazonia (Fine *et al.*, 2005). In contrast, divergences at deeper nodes in the phylogeny are more associated with differences among lineages in life history traits that are often viewed as more conserved, such as seed size and dispersal mode. A large-scale phylogenetic analysis of seed size variation also found that deeper divergences were associated with large shifts in seed size (Moles *et al.*, 2005). However, studies in a temperate conifer community and an African tropical forest found that variation in seed size was randomly distributed on the phylogenies of species in those communities (Veech *et al.*, 2000; Zanne *et al.*, 2005), suggesting that in some communities there may be ecological sorting to minimize similarity in seed size among species, which may be important for community assembly. In contrast, in this Bornean rainforest, ecological sorting via edaphic niche specialization (Russo *et al.*, 2005) appears to play a more prominent role.

Tree species dispersion within the 52-ha Lambir plot was determined by different mechanisms operating at different ecological scales. At larger spatial scales, distributions are largely determined by edaphic variation (Davies *et al.*, 2005). At small spatial scales of 0–20 m, clumping intensity of juveniles was significantly associated with variation in dispersal mode, seed size and soil specialization, but most strongly by dispersal mode and seed size. The fact that small-scale clumping intensity was strongly phylogenetically conserved in

this community may be due to its strong association with dispersal mode and seed size, which were likewise very well-conserved traits on this phylogeny.

Spatial extent of soil types in the plot may affect our estimates of clumping intensity of soil specialists, especially since sample size requirements for spatial statistics necessitated using species with at least 50 stems on the plot. For example, specialists of the soil with the smallest area, clay, were by far the most intensely clumped. It is clear that area does not explain all soil-related variation in clumping intensity because clay specialists were over four times more intensely clumped than specialists of loam, which has only twice the area of clay and is distributed in a narrow band through the plot.

For gravity- and animal-dispersed species, larger seeds were associated with less intense clumping of juveniles. This negative relationship between clumping and seed size may be explained by at least a few processes.

- Small mammals that secondarily disperse seeds by scatter- or larder-hoarding them may prefer larger seeds (Jansen *et al.*, 2002), which would reduce clumping intensity.
- Depending on predator size, larger seeds may experience higher predation rates, especially near parents, which would also reduce clumping, although there is evidence both for and against larger-seeded species suffering greater predation (Kollmann *et al.*, 1998; Coomes and Grubb, 2003; Moles and Westoby, 2004).
- If different species of trees in this community experience a strong trade-off between seed size and number, species with larger seeds may produce fewer seeds, which could reduce clumping of their seed shadows relative to more fecund, smaller-seeded species, particularly if fruits with smaller seeds are more often multi-seeded. The reductions in potential recruitment that large-seeded species suffer (due to seed size–number trade-offs) may be greater than the establishment advantages gained from having larger seeds (Grubb and Coomes, 1997; Coomes and Grubb, 2003; Moles and Westoby, 2004).

For animal-dispersed species, the size of the effect of seed size on clumping intensity was relatively small. This result may be a consequence of the fact that many large-gaped dispersal agents often co-disperse large numbers of both large and small seeds, which could therefore be similar in their spatial patterns of seed deposition (Julliot, 1996; Whitney *et al.*, 1998; Galetti *et al.*, 2000; McConkey, 2000; Poulsen *et al.*, 2002; see Stevenson, Chapter 15, this volume; see Dennis and Westcott, Chapter 9, this volume). Thus, for animal-dispersed species, variation in seed deposition patterns due to seed size alone may be more strongly affected by seed size–number trade-offs (i.e. seed limitation) than by effects of seed size on dispersal agent behaviour (Muller-Landau *et al.*, 2002). In addition, neither negative relationship remained significant after incorporating phylogeny.

In contrast, for wind-dispersed species, seed size explained more variation in small-scale clumping intensity, which increased with increasing seed size. This finding is consistent with larger seeds being harder to

disperse well by wind because of the tendency towards higher wing loading and faster terminal velocities with increasing seed size (Augspurger and Franson, 1987). Of course, larger wind-dispersed species may also be preferentially secondarily dispersed, have higher predation rates, and be subject to the same kinds of seed size–number trade-offs as species with other dispersal modes, but the positive slope suggests that the effects of poorer wind dispersal may be relatively greater.

Based on species values, the relationship between clumping intensity and seed size did not vary among soil specialists and generalists. On the other hand, in analyses with PICs, clay specialists showed steeply increasing clumping intensity with seed size. PICs of clay specialists were the highest values in the analysis. Six of the 17 clay specialists were dipterocarps, including the three most extreme PICs, suggesting that taxon sampling strongly influenced the dramatic increase in clumping with seed size on clay. Indeed, for all dipterocarps, there was a significant increase in small-scale clumping with seed size ($b = 0.026$, $SE_b = 0.009$, $n = 40$, $P = 0.011$, $r^2 = 0.16$), whereas this relationship was not different from zero for all other families with at least 10 species (Euphorbiaceae, $n = 40$; Myristicaceae, $n = 14$; Annonaceae, $n = 13$; Sapotaceae, $n = 12$; Moraceae, $n = 11$). Although a likely explanation for the intense small-scale clumping of dipterocarps is poor wind dispersal due to their large seeds, this is not the only possible explanation, particularly given reports of dipterocarp fruits being uplifted over the canopy (Webber, 1934). Because all dipterocarps are ectomycorrhizal (Alexander, 1989), spatial distributions of mycorrhizae may also play a role (see Theimer and Gehring, Chapter 21, this volume).

Conclusions and Future Directions

This study demonstrated that different mechanisms operate at different spatial scales in shaping the distribution patterns of tree species. Our analyses suggest that smaller-scale dispersion of juveniles is more strongly controlled by variation in dispersal mode and seed size, whereas larger-scale variation is more influenced by edaphic variation in this Bornean rainforest. Further tests of this hypothesis will include spatial analyses conducted at a larger set of spatial scales and sapling size classes. In addition, the role of small-scale variation in light, soil fertility and moisture is unaccounted for, and may also contribute to variation in smaller-scale dispersion.

We also found evidence that, in this rainforest tree community, species' occurrence in, and possibly diversification into, edaphic niches are relatively independent of constraints from dispersal mode and seed size. Because this preliminary conclusion is an explicit statement of trait evolution, a more robust test would use fully resolved phylogenies of several monophyletic groups of tree species combined with data on their comparative ecologies.

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