

## HABITAT PREFERENCES OF *APOROSA* IN TWO MALAYSIAN FORESTS: IMPLICATIONS FOR ABUNDANCE AND COEXISTENCE

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**Abstract.** Theories accounting for the maintenance of high tree diversity in tropical rain forests range from those proposing that tropical trees are highly co-evolved niche specialists, to those proposing that they are mostly generalist, undergoing random drift. We test these hypotheses at a meaningful, community-wide scale using data on the spatial patterns and habitat preferences of all species of *Aporosa* (Euphorbiaceae) growing on two large rain forest plots in Malaysia. Second-order spatial pattern analyses using a method based on Ripley's *K* function showed that *Aporosa* species formed spatially distinct assemblages, and a randomization procedure suggested that these assemblages were explained by biases in their distributions in relation to habitat types. Soil type, as determined by parent material, was an important determinant of habitat preferences, although topography and forest structure also accounted for some variation. We conclude that niche differentiation is an important mechanism contributing to the coexistence of *Aporosa* species at the community scale. However, spatial separation due to these differential habitat biases accounted for only a portion of the high species richness observed in this genus, so other mechanisms must also be sought to account fully for the maintenance of tropical tree species richness.

**Key words:** *Aporosa*; coexistence; habitat preference; Malaysia; niche; rain forest; random drift; Ripley's *K* function; spatial pattern; species diversity; tropical forest.

### INTRODUCTION

The study of how tree species richness in tropical rain forests is maintained has generated many theories and little consensus. On large geographical scales climatic, altitudinal and edaphic variation may determine species composition, and therefore relative abundance, although these have also been shown to act at small scales (e.g., Newbery et al. 1996, Itoh et al. 1997, Debski et al. 2000). Models developed in the 1970s to address coexistence within rain forest communities focused on density-dependent factors (Janzen 1970, Connell 1971) or random species drift (Hubbell 1979) and have frequently been contrasted with models based on habitat or regeneration niche partitioning (Ashton 1969, Grubb 1977).

The tropical rain forests of Southeast Asia are some of the most diverse terrestrial ecosystems on earth

(Soepadmo 1995), and in such communities great variation in relative abundance and spatial distribution can be observed even for coexisting congeneric tree species (e.g., Manokaran et al. 1992). Because variation in relative abundance can be observed at a number of spatial scales, the scale of analysis is important to consider (e.g., Schupp 1992, He et al. 1996, Cintra 1997). Most tree species in tropical rain forests show clumped distributions (e.g., Condit et al. 1992, 2000, He et al. 1997), i.e., species are not evenly distributed over plots of ~50 ha, and may show large variations in abundance at a scale of a few hectares. In this study we investigated interspecific differences in abundance and distribution between congeneric species, at a range of scales ≤50 ha, a scale that is representative of the forest community (He and Legendre 1996).

In the forests of Sarawak, Malaysia, where edaphic gradients are often readily observable, habitat variation has been proposed as a major factor contributing to the maintenance of diversity (Ashton 1969, Baillie 1978, Baillie et al. 1987). Other factors such as dispersal limitation may also influence distributions (Howe 1989, Hubbell et al. 1999), and uncoupling these factors requires careful analyses. To provide a critical test

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of niche differentiation we studied congeneric species, which minimized interspecific differences in dispersal syndrome, and the effects such differences would have on spatial patterns.

We investigated the spatial patterns in species of the understory tree genus *Aporosa* (also incorrectly spelled *Aporusa*, see Schot 1995) Bl. (Euphorbiaceae) in two rain forest plots in Malaysia: Lambir in Sarawak and Pasoh in Peninsular Malaysia. While both Lambir and Pasoh are tree species rich, and indeed have many taxa in common, the Lambir plot is considerably richer in species than the Pasoh plot, and is located on far more variable terrain (LaFrankie 1995). This comparison enables us to address hypotheses concerning the role of habitat diversity in the maintenance of tree species richness.

Like many understory species, the spatial patterns of *Aporosa* have been very poorly studied in comparison to some common canopy species of the Southeast Asian rain forests (e.g., Kohyama et al. 1994, Itoh et al. 1997, Yamada and Suzuki 1997). A number of factors characteristic of understory species may affect the spatial patterns of *Aporosa* in comparison to canopy species: their small size may give rise to a different scale of distribution patterns, they have bird-dispersed seeds unlike the wind-dispersed Dipterocarpaceae dominating many of the lowland Southeast Asian rain forest canopies, and they exist in a more sheltered environment, less exposed to wind and fluctuations in temperature and moisture than canopy species. Clearly we are not justified in relying on assumptions formed from the study of canopy species to understand spatial patterns of understory trees, and as an important component of the tree biodiversity (e.g., *Aporosa* is the second most common genus in the Pasoh plot after *Shorea*) they deserve independent study.

The aims of this study were to address the following questions: (1) Do *Aporosa* species show limited distributions within a rain forest community? (2) Do *Aporosa* species show a bias in their spatial distribution indicating preferences for microhabitat variables? (3) What are the most important such variables? (4) To what extent may such preferences potentially limit abundance and affect coexistence?

## MATERIALS AND METHODS

### *Study sites and species*

This study was conducted at two established forest dynamics plots in Malaysia: Lambir Hills National Park, Sarawak (4°12' N, 114°00' W), and Pasoh Forest Reserve, Peninsular Malaysia (2°59' N, 102°18' W). Their locations are shown in Fig. 1.

The Lambir 52-ha plot was first enumerated in 1992 (Lee 1995), when all stems  $\geq 1$  cm dbh were mapped, measured, identified, and tagged, following standard methods (Tan 1997), and was recensused in 1997, when some 1200 species were recorded. Lambir Hills Na-

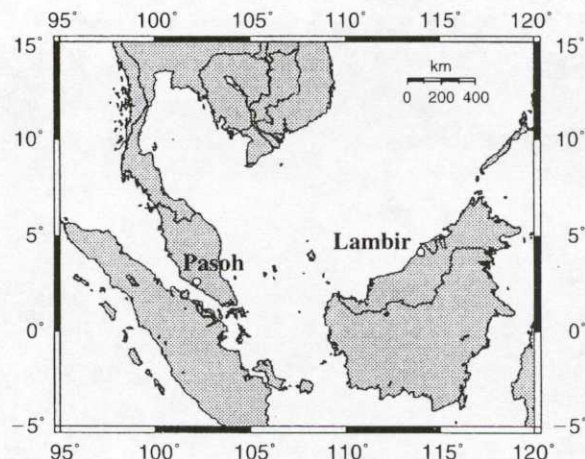


FIG. 1. Map of Southeast Asia showing location of the Pasoh 50-ha and Lambir 52-ha plots. National borders and latitude and longitude indicated.

tional Park covers an area of 6823 ha, encompassing a rugged sandstone escarpment on the coastal plain (Watson 1985). The mean annual rainfall at Miri airport ( $\sim 20$  km northeast of the plot) from 1993 to 1997 was 2687 mm (Department of Statistics Malaysia 1998), which is typical of the region, although measurements made over a shorter time interval at the Park headquarters suggests the total there may be somewhat greater (Momose et al. 1994). This difference was attributed to orographic rainfall generated by the Lambir Hills and the more forested environment. The 52-ha plot is situated in an area of highly heterogeneous topography and straddles two main soil types. It is aligned so that the long axis runs parallel to a steep ridge which is encompassed by the plot. Soil texture (Appendix A) ranges from clay to loamy sand, with finer textural classes dominating the south central part of the plot and occurring in distinct patches along the eastern boundary of the plot, and the coarser textured sandy loam and sandy clay-loam soils dominating the remaining two thirds of the plot (Palmiotto 1995). The topography (Appendix A) is hilly and complex, consisting of finely bifurcated steep slopes, ridges and valleys, and land slides on a variety of scales (Yamakura et al. 1995). There is a maximum elevation difference of 137 m across the plot. Both the variation in topography and soil type are expected to cause high soil-nutrient and moisture heterogeneity at the microsite scale. The vegetation of the plot is mixed dipterocarp forest (Chai et al. 1995).

A 50-ha plot was established at Pasoh and first enumerated in 1987, using the same standard methods (Manokaran et al. 1990), with 814 species recorded (Manokaran et al. 1992). The plot was recensused in 1990 and 1995. Pasoh Forest Reserve covers 2650 ha, with 650 ha of primary lowland forest, on flat land and gently rolling ridges. Annual rainfall is  $\sim 2000$  mm, with a dry period often occurring each year either Jan-

TABLE 1. Species names, along with abundance and distribution data for the 17 *Aporosa* species within the Lambir 52-ha plot and 12 species within the Pasoh plot.

Species	Code	Total abundance	Abundance category	Percentage occurrence	Subplot density	
					Median	Maximum
<b>Lambir</b>						
<i>A. benthamiana</i> Hk. f.	BE	1088	common	21	3	25
<i>A. subcaudata</i> Merr.	AC	774	common	40	1	5
<i>A. alia</i> Schot	SY	702	common	31	1	7
<i>A. nitida</i> Merr.	AU	510	common	25	1	5
<i>A. lagenocarpa</i> Airy Shaw	EM	336	intermediate	19	1	6
<i>A. sarawakensis</i> Schot	SA	334	intermediate	13	1	10
<i>A. falcifera</i> Hk. f.	SH	216	intermediate	12	1	8
<i>A. chalarocarpa</i> Airy Shaw	SP	201	intermediate	11	1	5
<i>A. illustris</i> Airy Shaw	AR	191	intermediate	10	1	4
<i>A. nervosa</i> Hk. f.	NE	181	intermediate	10	1	6
<i>A. nigricans</i> Hk. f.	NI	174	intermediate	10	1	7
<i>A. elmerii</i> Airy Shaw	EL	149	intermediate	9	1	4
<i>A. lucida</i> (Miq.) Airy Shaw	LC	118	intermediate	7	1	7
<i>A. bullatissima</i> Airy Shaw	BU	97	rare	7	1	3
<i>A. bracteosa</i> Pax. and Hoffm.	MN	96	rare	6	1	6
<i>A. hosei</i> Ridl.	HY	91	rare	4	1	6
<i>A. frutescens</i> Bl.	LH	56	rare	3	1	4
<b>Pasoh</b>						
<i>A. microstachya</i> (Tul.) M.A.	M1	6357	common	92	5	23
<i>A. subcaudata</i> Merr.	BR	2308	common	62	2	25
<i>A. aurea</i> Hk. f.	AU	1989	common	67	2	12
<i>A. prainiana</i> King ex Gage	PR	1614	common	56	2	11
<i>A. globifera</i> Hk. f.	GL	1099	common	47	1	8
<i>A. nigricans</i> Hk. f.	N1	856	intermediate	43	1	8
<i>A. lucida</i> (Miq.) Airy Shaw	M2	536	intermediate	26	1	12
<i>A. sessiliflora</i>	N2	328	intermediate	14	1	11
<i>A. symplocoides</i> (Hk. f.) Gage	SY	328	intermediate	29	1	4
<i>A. nervosa</i> Hk. f.	NE	265	intermediate	17	1	3
<i>A. lunata</i> (Miq.) Kurz	LU	53	rare	3	1	3
<i>A. confusa</i> Gage	CO	5	rare	0.4	1	1

Notes: Cods are those used in the plot data set (with the prefix "APOR"). Subplots are 20 × 20 m ( $n = 1300$  at Lambir,  $n = 1250$  at Pasoh). Density values are for each species within a subplot. Percentage occurrence is the proportion of subplots in which the species occurs. Abundance categories are relative to each plot.

uary–March or July–August (Kochummen et al. 1991). A total of 10 agricultural soil series occur in the plot, which fall into three classes (Appendix A) based on parent material (Wan Ahmad 2001): alluvial, shale, and laterite (developed on reworked material). There is a maximum difference in elevation across the plot of only 22 m, although a stream dissects the plot, giving rise to a topographical range from valley bottom to hill top (Appendix A; Wan Ahmad 2001). The vegetation covering the Pasoh plot is described as lowland dipterocarp forest with a canopy dominated by species of *Dipterocarpus* and *Shorea* (both Dipterocarpaceae; Manokaran et al. 1992).

*Aporosa* consists of ~80 species, distributed from India to the Solomon Islands (Schot 1995) and is one of the commonest understory genera in Malayan rain forests at least (Whitmore 1972). They are dioecious small to medium trees or shrubs, with small fruits, splitting to expose seeds covered by brightly colored fleshy arils, a characteristic of bird-dispersed seeds (Whitmore 1972; A. M. Schot, unpublished data). All *Aporosa* species considered in this study are listed in Table 1. Due to poor taxonomic agreement over this genus we also list the species codes used in the standardized

plot data sets from the two study sites. For species from Lambir, determinations were made at Kew Herbarium by I. Debski and voucher specimens are deposited in the ABD herbarium (University of Aberdeen Herbarium, Aberdeen, UK). For species from Pasoh, plot data-set names from Manokaran et al. (1999) are given, and can be cross-referenced to voucher specimens at the KEP herbarium (Herbarium of Forest Research Institute Malaysia, Kepong, Malaysia; likewise plot data set names from Lambir can be cross-referenced to collections from that site). Cautionary note should be made of *A. nitida* at Lambir (due to confusion with *A. aurea* which may or may not occur at the site), and *A. elmerii* and *A. subcaudata* which are difficult to distinguish in the field, especially as young plants. Because of these taxonomic difficulties we did not make within species comparisons between the two sites.

#### Data collection

This study utilizes the data sets derived from the censuses at Pasoh in 1995 and Lambir in 1997. At Pasoh one *Aporosa* species (*A. falcifera*) has been excluded from this study because of uncertainty over the consistency of correct identification. For each tree we

used  $x$ - and  $y$ -coordinates to the nearest 0.1 m. Data on soil and topography at the Pasoh plot are those from Wan Ahmad (2001). The soil series were divided into four classes (lateritic soils, shale soils, well drained alluvial soils, and imperfectly drained alluvial soils), and topographic variation into six classes (valley bottom, flat, low slope, midslope, high slope and hill/ridge tops). At Lambir a soil map of the plot was created by sampling the soil at the center of each of 1300  $20 \times 20$ -m subplots and assigning a class based on texture sensu Palmiotto (1995). Six classes were used: 1 (most clay rich), 2, 3, 5, 6, and 7 (most sand rich) and the topographic position of each subplot was classified as one of four classes (valley bottom, low slopes, high slopes and hill/ridge tops). At Pasoh these data were used for analyses by assigning a soil and topography class to each  $10 \times 10$ -m subplot ( $n = 5000$ ). At Lambir these data were analyzed at a resolution of  $20 \times 20$ -m subplots ( $n = 1300$ ).

A relative index of forest phase after gap formation was constructed using the ratio of basal area:stem number in  $20 \times 20$ -m subplots (Appendix A). The phases were defined presuming an increase of basal area and decrease of stem number over time after gap formation (Grau et al. 1997, Oliveira et al. 1997) such that one will observe a low ratio soon after gap formation (i.e., small stems only) to a high ratio in mature forest (i.e., with large stems). These ratios were sorted by rank and divided into four quartile groups, from 1 (shortly after gap formation) to 4 (mature forest). At Lambir kerangas (or heath) forest, which is composed solely of small diameter stems, occurs on the higher ridges, and may be confused with early phases derived from this index. However, mixed dipterocarp forest covers virtually all of the 52-ha plot. Because of missing data in the Lambir data set and to take some account of neighboring areas (e.g., a large gap in one subplot would quite likely affect neighboring subplots), counts of stem number and basal area were buffered in such a way that each subplot value was a weighted mean of its own (half weighting) and its neighboring eight (five for subplots on the plot edge and three for subplots forming the plot corners) subplots (combined half weighting). This smoothing will also make the test more conservative by partially masking differences between subplots.

#### *Statistical analyses and data presentation*

Total abundance of a species is defined as the number of individuals with dbh  $\geq 1$  cm in the plot. Because of the range in tree morphology among *Aporosa* species (Debski 2000) defining populations by a fixed cutoff point (1 cm dbh in this case) will capture different proportions of the entire population for different species (i.e., only larger individuals of small species will be included, indicating an artificially low abundance, and vice versa for large species). The frequency of  $20 \times 20$ -m subplots in which a species occurs is a measure of the extent of its distribution, and is expressed as a

percentage of all subplots (i.e., percentage of the plot over which the species occurs). Together with median and maximum subplot density one can distinguish between widespread but rarer species and locally common, but spatially restricted species, both of which may have equal total abundance within the plot.

The spatial distribution of individuals by species was tested for nonrandomness (i.e., whether distribution is clumped or regular) by a method of univariate second-order spatial pattern analysis based on Ripley's (1976)  $K$  function (methods used follow Haase 1995), using a weighting factor to correct for edge effects, as recommended.  $K(d)$  was calculated separately for each distance  $d$  from 0 to 250 m in 5-m increments. The test statistic used was  $L(d) = \sqrt{[K(d)/\pi] - d}$  and results are displayed as a plot of  $L(d)$  vs.  $d$ . To test for significant deviation away from a random distribution, Monte Carlo computer-generated data were used to construct a 99% confidence envelope for comparison to the sample statistic. If the sample statistic is positive and exceeds the confidence envelope, a clumped distribution can be inferred, if it is negative and exceeds the confidence envelope a regular distribution can be inferred, and if it does not exceed the confidence envelope a random distribution is inferred. These calculations were performed using SPPA 1.1 (Peter Haase, Tecklenburg, Germany). A very similar method of bivariate spatial pattern analysis was used to test for spatial association between the distributions of each combination of two species. The program reported by Moeur (1993) was used for these analyses. When  $L(d)$  exceeds the confidence envelope with positive values the distributions are inferred as significantly attracted, or associated, and with negative values are inferred as significantly repelled, or complementary. Groups of spatially associated species were obtained by combining attracted species pairs together in such a way that each species in a group was randomly distributed or repelled in relation to species in other groups.

To investigate the co-occurrence of species distributions and habitat variation (i.e., habitat preference) we used a torus-randomization method based on that developed by Harms (1997; Harms et al., 2001). Soil type and texture, topography, and successional stage were used to define habitat type in separate analyses using the classification systems described in *Data collection*. The method generates a null distribution of habitat occurrence for each population of trees (i.e., each species) to test whether the observed count for each species of trees on each habitat class is significantly greater or lower than random expectation, i.e., to test for bias indicative of preference. The habitat map is superimposed upon the tree distribution map, and translated (but not rotated or reflected) while the tree distribution map remains fixed. The edges of the habitat map wrap back on either side of the plot. In this way the relative location of a tree to the habitat map changes with each translation, while retaining the



exact same spatial pattern of the trees and the underlying spatial gradient of habitat variation. The randomization procedure is repeated 1000 times. For each species and each habitat class we generated a hypothesis of whether we expected the actual distribution frequency to be higher or lower than by chance, by comparing the proportion of individuals on that habitat class to the proportion of plot covered by that habitat class. A count of how many of these randomizations produced more than or equal to vs. less than or equal to the observed habitat-class count (depending on our hypothesis) was made and a probability value calculated using  $P = (n + 1)/(N + 1)$  where  $n$  is the number of counts and  $N$  is the number of randomizations. In a comparison between Harms' torus-randomization method and chi-squared goodness-of-fit tests for 303 species at the 50-ha Barro Colorado Island plot, Panama, the torus-randomization method was more conservative in identifying habitat preferences (Harms 1997), so we also used findings with  $P < 0.10$  as indicative of a habitat preference when deriving groups of species with similar habitat preference. Note that topography data at Lambir are available for only 51.12 ha, thus sample sizes vary slightly from tests of the other habitat variables, and that results for the very rare species *A. confusa* at Pasoh are not shown.

## RESULTS

### *Species abundance and clumping*

There is a high degree of variation in abundance among *Aporosa* species at both Lambir and Pasoh (Table 1), the most common *Aporosa* species at each site being one of the commonest of all species on that plot (*A. microstachya* is the fifth most common species at Pasoh while *A. benthamiana* is within the most common five percent of species at Lambir). Because of the higher *Aporosa* density at Pasoh than at Lambir, there is some overlap between the definitions of common and intermediate species between the sites. One would expect higher density by species at the lower diversity forest of Pasoh so the definitions are relative to the community species richness. In general the most abundant species have both high subplot frequency and high density within subplots (i.e., they are common over a large part of the plot). However, there are noticeable variations among species in abundance within the plot due to restricted distributions. *Aporosa benthamiana* at Lambir is an extreme example of a clumped species (Appendix B) as it occurs in only 21% of subplots but is the commonest *Aporosa* species. Where *A. benthamiana* occurs it is found at very high density, with a maximum subplot density close to that of the super-abundant *A. microstachya* at Pasoh. *Aporosa subcaudata* at Lambir is a good example of an evenly distributed species (Appendix B); it is the second most common *Aporosa* species in the plot, but never attains a density greater than five trees per subplot.

All *Aporosa* species at both sites (excluding the rare species *A. confusa* at Pasoh) exhibited clumped distributions (Appendices B and C); the univariate Ripley's  $K$  analyses (Table 2, Fig. 2) found significant positive  $L(d)$  values over all or most of the range of  $d$  tested (0–250 m). The few species that showed only limited evidence for clumped distributions were those that showed patchy, rather than restricted, distributions, and spatial randomness was found at high  $d$  values, indicating that these clumps (at a scale of one to a few hundred meters) are located at random with respect to each other (e.g., *A. benthamiana* at Lambir). Because of the prevalence of statistically significant clumping, the range of  $L(d)$  values found for each species are also summarized in Table 2 to help distinguish between the degree of clumping between species, and to indicate the scale at which clumping is greatest (indicated by the maximum value of  $L(d)$ ). Species with distributions restricted to one area of the plot (e.g., *A. sarawakensis* at Lambir or *A. lunata* and *A. sessiliflora* at Pasoh) have the greatest  $L(d)$  values, indicating a high degree of spatial aggregation, or clumping. It should be noted that although widespread species (e.g., *A. subcaudata* at Lambir, *A. microstachya* at Pasoh) exhibited only a low  $L(d)$ , significant clumping was still found. Such patterns can be explained when spatial analyses are conducted separately on adult and juvenile populations: juvenile patches may be found close to randomly dispersed adults.

### *Species groupings*

Bivariate Ripley's  $K$  identified significant species groups (see Appendices D and E for detailed results) and they are summarized in Table 3 for both sites. At Lambir there were three species groups, and at Pasoh we detected two scales of species associations, with two groups at large scales ( $d = \sim 170$ –250 m) and four groups at small scales ( $d = \sim 5$ –80 m). *Aporosa microstachya* did not fit into a larger scale group because it had a ubiquitous distribution across the plot. Additionally, *A. sessiliflora* and *A. microstachya* showed a high degree of association at the smaller scale but not at the larger scale. This phenomenon is explained by the restricted distribution of *A. sessiliflora*: where they both occur, they are spatially associated, but over large scales *A. microstachya* has a far more widespread distribution than *A. sessiliflora*. Examples of species with associated and complementary distributions, respectively, are *A. nigricans* and *A. aurea* at Pasoh (Fig. 3a), and *A. sarawakensis* and *A. lagenocarpa* at Lambir (Fig. 3b). *Aporosa confusa* was not considered because of its rarity (five individuals total).

### *Species distribution on habitat variables*

The torus-randomization method using soil texture at Lambir (Table 4) showed that *A. nitida*, *A. benthamiana*, *A. elmerii*, *A. lucida*, and *A. sarawakensis* were significantly biased in their distribution towards the



TABLE 2. Results of univariate Ripley's *K* spatial pattern analysis on all individuals of each of the 17 *Aporosa* species at Lambir and 12 species at Pasoh.

Species	Pattern	<i>L(d)</i>		
		<i>d</i> = 1	Intermediate max. or min.	<i>d</i> = 250
<b>Lambir</b>				
<i>alia</i>	clumped	7		14
<i>benthamiana</i>	clumped to 195 m	5	11	0
<i>bracteosa</i>	clumped	8	75	28
<i>bullatissima</i>	clumped to 160 m	11	18	-2
<i>chalarocarpa</i>	clumped	10		110
<i>elmerii</i>	clumped to 185 m	6	19	2
<i>falcifera</i>	clumped	8		72
<i>frutescens</i>	clumped	15	72	29
<i>hosei</i>	clumped	40		115
<i>illustris</i>	clumped	12		118
<i>lagenocarpa</i>	clumped	4		44
<i>lucida</i>	clumped	14		82
<i>nervosa</i>	clumped	12		124
<i>nigricans</i>	clumped	12		77
<i>nitida</i>	clumped	4	24	18
<i>sarawakensis</i>	clumped	13		139
<i>subcaudata</i>	clumped	2		17
<b>Pasoh</b>				
<i>aurea</i>	clumped	2		31
<i>confusa</i>	random			
<i>globifera</i>	clumped	2	15	6
<i>lucida</i>	clumped	4	24	21
<i>lunata</i>	clumped	16		74
<i>microstachya</i>	clumped (x 250 m)	2	12	1
<i>nervosa</i>	clumped	2	14	10
<i>nigricans</i>	clumped	3	21	16
<i>prainiana</i>	clumped	2	9	2
<i>sessiliflora</i>	clumped	8	90	56
<i>subcaudata</i>	clumped	2		15
<i>symplocoides</i>	clumped to 240 m (x 220 m)	3	11	4

Note: Generalized pattern and range of values of *L(d)* over *d* (distance from focal individual) indicated (from minimum to maximum *d*, with any intermediate peak); *d* = 0–250 m; "x" indicates "except at."

more clay-rich soils in texture classes 2 or 3. There was an indication that *A. alia* was biased towards class 2 and *A. frutescens* to class 3. If *A. frutescens* is excluded (the rarest species which is distributed across the plot but found at highest density only in one small area on soil-texture class 3) the remaining six species form one of the groups of spatially associated species identified by Ripley's *K* analysis (Table 3). *Aporosa lagenocarpa* showed significant bias towards texture class 6 (the sand-rich soil) with a suggestion of this trend for *A. hosei*. These two species formed another group of spatially associated species according to Ripley's *K*. The remaining species, forming the third group of spatially associated species, showed either no bias in their distribution or a bias away from classes 2 (*A. illustris*) or 3 (*A. nervosa*). An illustrative plot of two species at Lambir with complementary distributions (*A. sarawakensis*, whose distribution is biased towards clay-rich soils, and *A. lagenocarpa*, whose distribution is biased towards sand-rich soils) superimposed on the soil-texture map is shown in Fig. 4. In this case there is almost no overlap in the distributions of these species, and *A. sarawakensis* occurs almost exclusively on

clay-rich soils (classes 1–3). In tests using topography as the habitat variable most species had a significant bias away from ridge-top or towards valley-bottom topography classes. *Aporosa lagenocarpa* was the only species significantly biased towards ridge tops. Tests using the forest-phase index found that most species that showed a significant bias towards any stage were biased towards the earlier stages 1 and 2. *Aporosa hosei* was the only species to show significant bias towards stage 3, although *A. lagenocarpa* exhibited a trend towards this stage also. These two species comprised one of the spatially associated groups found by Ripley's *K*. Additionally, six of the seven species showing a bias towards stage 1 (*A. subcaudata*, *A. illustris*, *A. bullatissima*, *A. nervosa*, *A. nigricans*, and *A. chalarocarpa*) were six of the nine species forming another of the spatially associated groups.

At Pasoh all species tested showed significant bias towards one (or both shale and laterite for *A. subcaudata* and *A. lucida*) of the four soil types (Table 5). *Aporosa subcaudata*, *A. microstachya*, *A. sessiliflora*, *A. nervosa*, *A. prainiana*, and *A. symplocoides* all showed significant bias towards shale or lateritic soils,



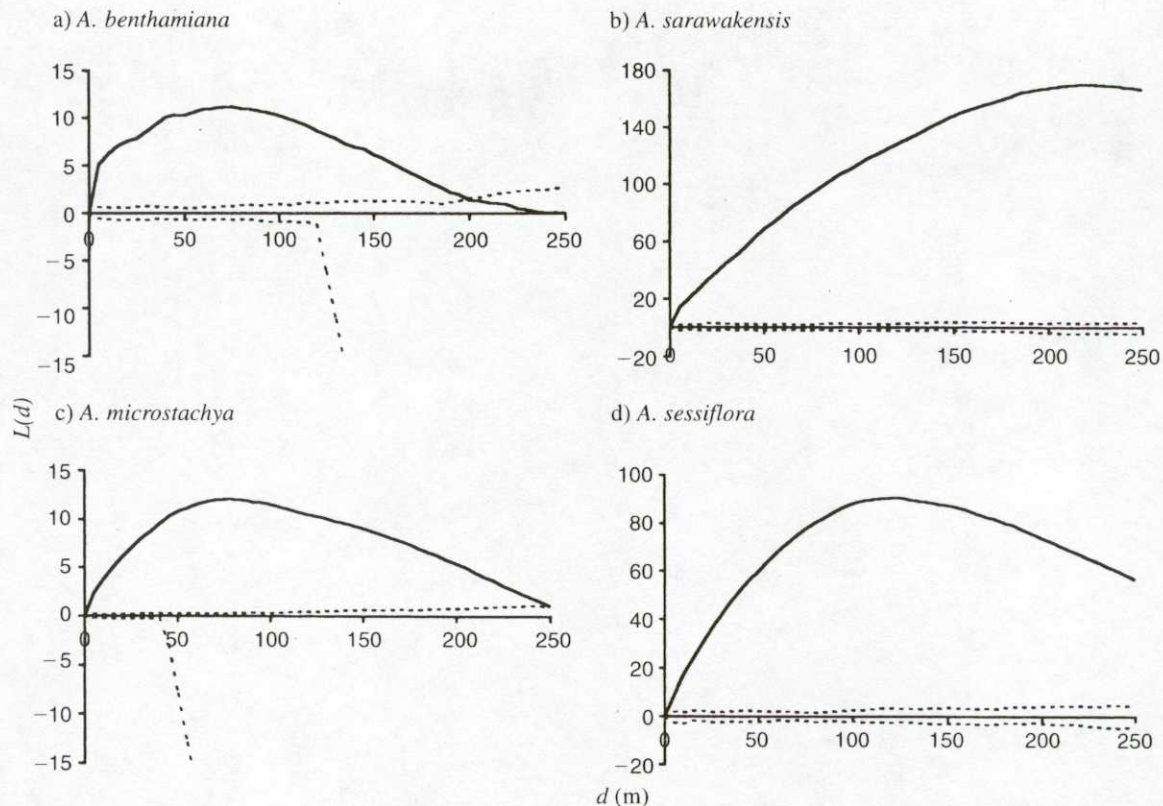


FIG. 2. Plots of spatial-pattern analysis of all individuals of selected *Aporosa* species using univariate Ripley's  $K$ : (a) *A. benthamiana* at Lambir, (b) *A. sarawakensis* at Lambir, (c) *A. microstachya* at Pasoh, and (d) *A. sessiflora* at Pasoh. Solid lines show test statistic  $L(d)$ ; dashed lines show 99% confidence envelopes.

while *A. aurea*, *A. globifera*, *A. lunata*, *A. lucida*, and *A. nigricans* all showed significant bias towards one of the alluvial soil types. This division into two species groups corresponds to the larger scale species spatial-association groups found by Ripley's  $K$  (Table 3), with the exception of *A. microstachya* which did not fit into either group. Tests using topography as the habitat variable showed *A. globifera*, *A. lunata*, and *A. lucida* to be significantly biased towards valley-bottom topography (and flat for *A. globifera*); *A. aurea* and *A. nigricans* towards flat topography only; *A. subcaudata*, *A. nervosa*, *A. prainiana*, and *A. symplocoides* towards low and intermediate slopes; and *A. microstachya* and *A. sessiflora* towards high slopes (and intermediate slopes for *A. microstachya*). These species groupings correspond to the smaller scale species spatial-pattern associations found using Ripley's  $K$ . Tests using the forest-phase index as the habitat variable showed all species to be significantly biased towards one stage, except *A. lunata* (a rare species) and *A. sessiflora* which was near significant ( $P = 0.060$ ). The species can be divided into those with a bias towards the earlier stages 1 and 2 (*A. aurea*, *A. globifera*, *A. microstachya*, *A. lucida*, and *A. nigricans*) and those towards the later stages 3 and 4 (*A. subcaudata*, *A. sessiflora*, *A. nervosa*, *A. prainiana*, and *A. symplocoides*). These group-

ings correspond well to the larger scale species spatial-association groups found by Ripley's  $K$ , although here again *A. microstachya* is included in a group.

Patterns also emerged when we investigated the frequency of co-occurrence of soil and topography classes with forest phase classes at Pasoh and Lambir. At Pasoh, when soil type was classified as two types, alluvial soils co-occurred more frequently with early forest phases, and shale/lateritic soils with later phases ( $\chi^2 = 164.87$ ,  $df = 3$ ,  $P < 0.001$ ). Flat topography also co-occurred more frequently with early phases ( $\chi^2 = 171.11$ ,  $df = 17$ ,  $P < 0.001$ ). At Lambir lower topography (valley bottom and low slopes) co-occurred more frequently with earlier phases (1 and 2) and higher topography with later phases ( $\chi^2 = 105.79$ ,  $df = 9$ ,  $P < 0.001$ ). Soil-texture classes were less clearly associated with forest-phase classes, although the earliest phase co-occurred more frequently with the most clay-rich soils ( $\chi^2 = 17.46$ ,  $df = 9$ ,  $P < 0.05$ ).

## DISCUSSION

### *Abundance and spatial distribution*

*Aporosa* was an appropriate understory genus to study spatial patterns in relation to abundance across the two plots at Lambir and Pasoh: it is speciose at



TABLE 3. Summary of spatial-association groups found by bivariate Ripley's *K* (see Appendices D and E for full results summary).

Species	Spatial association		Soil preference	Topographic preference
	Large scale	Small scale		
<b>Lambir</b>				
<i>alia</i>	1		clay rich	
<i>benthamiana</i>	1		clay rich	
<i>elmerii</i>	1		clay rich	
<i>lucida</i>	1		clay rich	
<i>nitida</i>	1		clay rich	
<i>sarawakensis</i>	1		clay rich	
<i>bracteosa</i>	2		intermediate	
<i>bullatissima</i>	2		intermediate	
<i>chalarocarpa</i>	2		intermediate	
<i>falcifera</i>	2		intermediate	
<i>frutescens</i>	2		intermediate	
<i>illustris</i>	2		intermediate	
<i>nervosa</i>	2		intermediate	
<i>nigricans</i>	2		intermediate	
<i>subcaudata</i>	2		intermediate	
<i>hosei</i>	3		sand rich	
<i>lagenocarpa</i>	3		sand rich	
<b>Pasoh</b>				
<i>globifera</i>	1	a	alluvial	valley bottom
<i>lucida</i>	1	a	alluvial	valley bottom
<i>lunata</i>	1	a	alluvial	valley bottom
<i>aurea</i>	1	b	alluvial	flat
<i>nigricans</i>	1	b	alluvial	flat
<i>nervosa</i>	2	c	shale/lateritic	low slopes
<i>prainiana</i>	2	c	shale/lateritic	low slopes
<i>subcaudata</i>	2	c	shale/lateritic	low slopes
<i>symplocoides</i>	2	c	shale/lateritic	low slopes
<i>sessiliflora</i>	2	d	shale/lateritic	high slopes
<i>microstachya</i>	...	d	...	high slopes

Notes: At Pasoh, associations were found at two scales, large (170–250 m) and small (5–80 m). Soil and topographic preferences are also shown. *A. confusa* at Pasoh is not shown due to its rarity.

both sites and species vary considerably in their abundance and spatial patterns. Because of the long time spans involved in rain-forest dynamics it is impracticable in the short term to study fully factors affecting distribution and abundance of tree species in these communities experimentally. Deductions from observable characteristics, such as spatial distributions, are therefore of great use, but care must be taken in the analysis and interpretation of static data such as these.

In agreement with most recent studies which find tropical tree species to be distributed either at random or clumped, rather than regularly dispersed (e.g., Connell et al. 1984, He et al. 1997, Condit et al. 2000) we found all *Aporosa* species at both sites (with the exception of *A. confusa*, due to its extreme rarity) to have clumped distributions over at least some spatial scales. Many factors can lead to clumped or restricted distributions. Seed dispersal by birds, as in *Aporosa*, is likely to lead to the majority of seeds falling under or close to adults (Howe 1989), and thus may promote a clumped distribution. Associations with habitat variables such as soil nutrients (Gartlan et al. 1986, Baillie et al. 1987), topography (Newbery et al. 1996), or light availability (Lieberman et al. 1995) can lead to re-

stricted or patchy distributions, even over small spatial scales (Debski et al. 2000). Other, biotic, factors, such as mycorrhizal infection of the juvenile plants, which influences seedling growth (Ahmad 1996, Bereau et al. 1997), can also explain differences in species distributions (Bowman and Panton 1993, Asbjornsen and Montagnini 1994). Therefore some factors, biotic or not, may be influencing the distribution of *Aporosa* species, potentially limiting their abundance and thus promoting coexistence.

We found that not only were the distributions of *Aporosa* species limited across the plots, but that at both plots groups of species shared similar limited distributions (Table 3). The existence of these species groups suggests a common cause to the limitation of species distributions within groups, rather than spatially random clumps that may have been caused by dispersal limitation or other similarly acting biotic factors. Given that the plots at Lambir and Pasoh are non-homogenous in the availability of critical resources, such as water, soil nutrient status, and light (Palmiotto 1998; Wan Ahmad 2001) we would expect differing adaptations to the acquisition of these resources, acting through competition or otherwise, to lead to patterns



TABLE 4. Distribution of the 17 *Aporosa* species at Lambir on four soil-texture, topographic-position, and forest-phase classes.

Aporosa species	Soil-texture class†				Topographic position‡				Forest phase§			
	2	3	5	6	val	low	high	top	1	2	3	4
<i>alia</i>	103 (+)	105	64	428	29 (--)	43	557 (++)	68	196	166	172	168
<i>benthamiana</i>	185	216 (++)	117	569 (--)	30 (--)	58	837 (++)	163	288	319	286	195 (-)
<i>bracteosa</i>	17	12	12	55	0 (---)	3	73 (++)	19	25	30	12	29
<i>bullatissima</i>	13	14	12	57	1 (--)	11	71 (+)	11	43 (+++)	31 (+)	17 (-)	6 (---)
<i>chalarocarpa</i>	26	21	19	132	3 (---)	11	128 (--)	51 (+++)	107 (+++)	48	31 (--)	15 (---)
<i>elmerii</i>	27 (+)	35 (++)	16	70 (---)	3 (--)	15	109 (+)	22 (+)	39	51 (++)	37	22 (--)
<i>falcifera</i>	13 2	27 14	19 4	157 32	13 0	13 2	164 36	22 17	46 17	51 15	53 17	66 7
<i>frutescens hosei</i>	0 (--)	4 (-)	12	75 (+)	5 (--)	3	77 (++)	3	24	13 (-)	37 (++)	17 (-)
<i>illustris</i>	4 (--)	26	17	142	5 (--)	13	138 (+)	27 (+)	72 (++)	49	45	25 (--)
<i>lagenocarpa</i>	8 (---)	37	26	265 (+++)	59 (+++)	21	224 (--)	25	85	76	98 (+)	77
<i>lucida</i>	17	27 (++)	14	60 (-)	15	15 (+)	78 (-)	10	24	38	25	31
<i>nervosa</i>	10	13 (--)	20	138	5 (-)	8	116 (-)	45 (+++)	86 (+++)	47	32 (-)	16 (---)
<i>nigricans</i>	14	18	24	118	3 (--)	8	127 (++)	30 (+++)	77 (+++)	44	28 (--)	25 (-)
<i>nitida</i>	91 (++)	84	70 (++)	262 (---)	15 (---)	28	392 (+)	74 (+++)	189 (+++)	147 (+)	94 (--)	80 (---)
<i>sarawakensis</i>	128 (++)	78 (++)	23	105 (---)	9 (-)	32	246 (+)	47 (+++)	108	92	79	55
<i>subcaudata</i>	74	105	82	509	39 (---)	57	565 (++)	93 (++)	230 (++)	205	196	143 (--)

Notes: Results are from 1000 simulations using the torus-randomization method. Observed count of the species on the habitat class is given, with an indication of whether this is less than or equal to (-) or more than or equal to (+) the randomized distributions: one symbol if near significant ( $P < 0.1$ ), two if significant ( $P < 0.05$ ), and three if highly significant ( $P < 0.01$ ).

† Soil-texture class 2 is clay rich; 6 is sand rich (see *Materials and Methods: Data collection* for full explanation). Results from soil-texture classes 1 and 7 are not shown due to small sample sizes. Soil-texture class 4 did not occur within the plot.

‡ Abbreviations: val, valley bottom; low, low slopes; high, high slopes; top, ridge tops.

§ See *Materials and methods: Data collection* for forest-phase definition.

of distribution limited by preferential habitat type. If more than one species had similar adaptations to one or more critical resource(s) we would expect these species to show a similar distribution, being limited in a similar way by the availability of said resource(s). Results from the torus-randomization method found that most species showed a significant bias in their distribution towards or away from one or more of the microhabitat variables tested: soil type, topography, and forest phase (Tables 4 and 5). Furthermore, when we grouped species with similar habitat preference (Table 3) we found that species sharing a habitat preference exhibited a similar spatial distribution, as hypothesized. We conclude that *Aporosa* species do indeed show variation in their responses to limiting resources, resulting in spatially limited distributions.

#### Habitat variation and species associations

Given that variation in microhabitat across the plots is important in determining species distributions, the

third aim of this study was to determine which are the most important microhabitat variables at each site. At both Lambir and Pasoh we found that variation in soil type corresponded closely to patterns of spatial distribution. At Pasoh, smaller scale patterns of distribution were explained by position on topography. However, there was substantial covariance between the habitat variables tested. At Pasoh, early forest phases co-occur with alluvial soils, and late phases with shale and lateritic soils. Similarly, early phases co-occur with flat topography, which occurs mainly on the low areas adjacent to the stream which dissects the plot, and therefore also co-occurs with alluvial soils. Soil type and topography are both products of underlying geology and the weathering processes, and thus co-occur and have indistinguishable effects on forest structure. At Lambir there was no clear pattern of association between soil texture and forest phase, although across the plot soil texture varies with position on topography,



TABLE 5. Distribution of the 12 *Aporosa* species at Pasoh on four soil-texture, six topographic-position, and four forest-phase classes.

<i>Aporosa</i> species	Soil type†				Topographic position		
	Shale	Lateric	alv1	alv2	Valley bottom	Flat	Low slopes
<i>aurea</i>	227 (---)	171 (---)	1269 (+++)	322	124 (---)	1271 (+++)	272 (--)
<i>globifera</i>	104 (---)	34 (---)	600	361 (+++)	204 (+++)	670 (++)	147 (--)
<i>lucida</i>	42 (---)	26 (---)	255	213 (+++)	111 (+++)	320 (+)	47 (---)
<i>lunata</i>	4	2	14	33 (+++)	18 (+++)	25	5
<i>microstachya</i>	1480	1450 (+++)	3085	342 (---)	273 (---)	2863	1269
<i>nervosa</i>	99 (+++)	72 (+)	79 (--)	15 (-)	21	68 (---)	92 (+++)
<i>nigricans</i>	116 (---)	87 (--)	526 (+++)	127	59	540 (+++)	111 (---)
<i>prainiana</i>	65	220 (+++)	39 (--)	4 (--)	100 (--)	439 (---)	484 (+++)
<i>sessiliflora</i>	632 (+++)	389 (+)	529 (--)	64 (---)	13	33 (---)	50
<i>subcaudata</i>	945 (+++)	713 (++)	527 (---)	123 (--)	208	475 (---)	655 (++)
<i>symplocoides</i>	126 (+++)	87 (+)	104 (--)	11 (---)	28	85 (---)	89 (++)

Notes: Results are from 1000 simulations using the torus-randomization method. Observed count of the species on the habitat class is given, with an indication of whether this is less than or equal to (-) or more than or equal to (+) the randomized distributions: one symbol if near significant ( $P < 0.1$ ), two if significant ( $P < 0.05$ ), and three if highly significant ( $P < 0.01$ ); See *Materials and methods: Data collection* for forest-phase definition.

† Soil type abbreviations: alv1, alluvial imperfectly drained; alv2, alluvial well drained.

with coarser soils (i.e., sand rich) occurring on higher topography and finer textured soils (i.e., clay rich) occurring on lower topography (Palmiotto 1998). Similarly, we found co-occurrence of valley-bottom topography with early forest phases and ridge top with late phases, in correspondence with the findings of Palmiotto (1998). It is therefore unrealistic to consider one factor in isolation of the others.

One can consider the three main limiting plant resources in the forest understory to be soil-nutrient availability, water availability, and light. We can broad-

ly generalize an association between these limiting resources and the microhabitat variables tested. Soil parent material largely determines soil-nutrient status and has been shown to be important in determining species distributions in the lowland forests of Sarawak (Baillie et al. 1987). Soil water potential is known to vary with position on topography (Becker et al. 1988, Baker 2000). However, as we have seen, these factors covary. As well as such abiotic factors, we also need to consider the biotic neighborhood of a tree, which we have investigated by developing a forest-phase index. As well

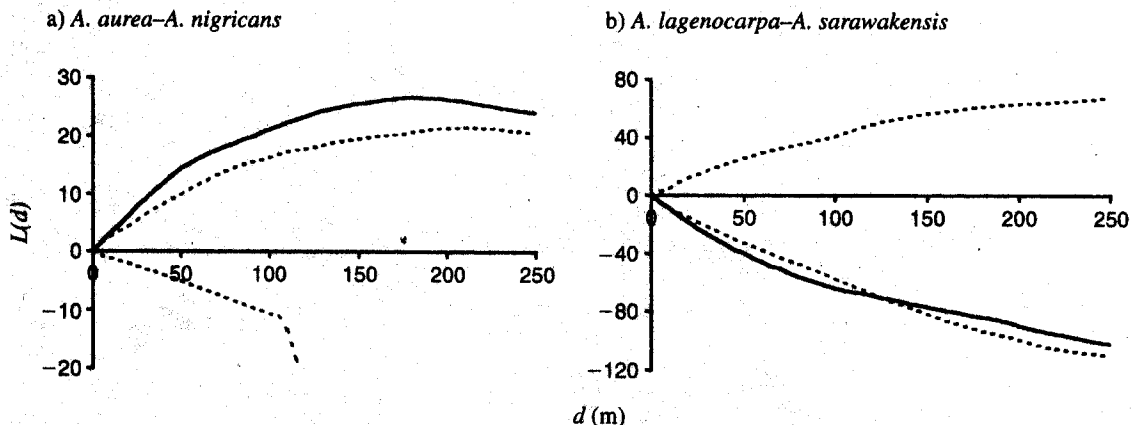


FIG. 3. Plots of spatial-pattern analysis of species associations for selected species pairs using bivariate Ripley's  $K$ : (a) *A. aurea*/*A. nigricans* at Pasoh and (b) *A. lagenocarpa*/*A. sarawakensis* at Lambir. Solid lines show test statistic  $L(d)$ ; dashed lines show 99% confidence envelopes.



TABLE 5. Extended.

Topographic position			Forest phase			
Mid-slopes	High-slopes	Hill/ridge top	1	2	3	4
251	55	16	772	535	399	283
(-)	(--)	(---)	(+++)		(--)	(---)
71	5	2	378	295	239	187
(---)	(---)	(---)	(+++)		(-)	(---)
46	8	4	146	167	120	103
(---)	(--)	(---)		(++)		(-)
4	0	1	15	17	13	8
		(--)				
1324	567	61	1945	1503	1651	1258
(++)	(+++)	(---)	(++)			(---)
59	22	3	47	54	86	78
		(---)		(-)	(++)	
115	27	4	349	202	171	134
(-)	(--)	(---)	(+++)		(--)	(---)
455	130	6	306	385	446	477
(+++)		(---)				(+)
116	101	15	34	94	131	69
(+)	(+++)	(-)			(++)	
748	201	21	290	597	734	687
(+++)		(---)	(--)		(++)	
85	34	7	50	102	101	75
(++)	(+)	(---)	(--)	(++)	(+)	

as amounts of irradiance reaching the understory, gap formation has been shown to affect other microclimate variables, and localized soil-nutrient and water availability (Denslow 1980, 1987, Denslow et al. 1998). In early phases (i.e., shortly after gap formation) higher irradiance is transmitted to the forest floor, water availability may be reduced (Ashton 1992) or increased (Denslow et al. 1998), nutrient availability may be greater because of decomposition of fallen vegetation (Denslow et al. 1998), and mortality due to fungal pathogens may be reduced (Augsburger 1984). However,

at Lambir, where landslides create 33.7% of open areas (Palmiotto 1998), gaps may occur on nutrient poor sub-soil, leading to very slow rates of succession. Decomposition rates also vary between soil types at Lambir, with faster rates on the more nutrient-rich, higher-moisture, clay-rich soils (Palmiotto 1995). Gap dynamics are likely to have a major influence on community-wide spatial-distribution patterns, although it is impossible to assign causal mechanisms for the limitation of spatial distribution from an analysis such as this.

We conclude that while variation in soil type ap-

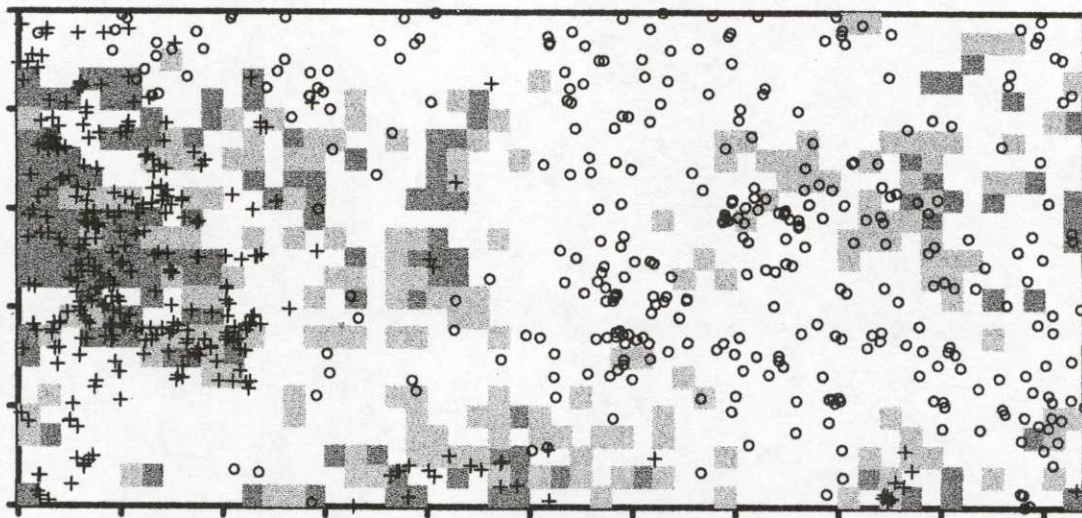


FIG. 4. Distribution of two species over soil texture at the Lambir plot. All individuals ( $\geq 1$  cm dbh) of *A. sarawakensis* ("plus" symbols) and *A. lagenocarpa* (open circles) at Lambir are shown over a soil-texture distribution map. Dark gray shows the most clay-rich soil; white shows the most sand-rich soil.



peared to have the greatest influence in determining species distributions, it is unrealistic to consider any one habitat variable independently, as they are inextricably linked and may affect tree distributions in many interrelated ways.

#### *Implications for coexistence and species abundance*

We have shown that congeneric *Aporosa* species show patterns of spatial partitioning across species at two sites. We have identified possible microhabitat variables responsible for this differentiation. Variation in species distribution and floristic composition reflecting edaphic and topographic variation in the rain forests of Sarawak has already been shown (Ashton 1969, Baillie 1978, Baillie et al. 1987). Such spatial separation of species into distinct assemblages of habitat specialists at small, within-community, scales will enable greater coexistence at the forest-wide, or community, scale. Indeed, the Lambir plot has both a higher tree diversity, and more heterogeneous topography and edaphic properties than the Pasoh plot. We hypothesize that this difference in diversity is due, to some extent, to the greater microhabitat variation at the more species-rich site. Furthermore, spatial limitation by availability of preferred habitat types will thus also be an important factor limiting relative abundance of a species at a community scale. As discussed previously, there is a large suite of interacting habitat variables that could operate through various mechanisms to generate the required spatial separation of species. Intensive experimental testing is required to isolate individual factors.

Although habitat preference is undoubtedly an important mechanism for the maintenance of species richness, the overall contribution must be viewed conservatively. At most we found four spatial assemblages of coexisting species, but  $\leq 17$  *Aporosa* species were found within one community, or landscape, suggesting that habitat preference may account for perhaps one quarter of total species richness in *Aporosa* in these forests. Evidence has also been found that other factors, such as density dependent mortality may also operate on these species (Debski 2000). It is therefore clear that multiple factors such as these, as well as hypotheses of random species drift sensu Hubbell and Foster (1986) must be considered if we are to understand fully, and explain, the maintenance of the high species richness among tropical rain-forest trees.

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#### APPENDIX A

The distribution of habitat variables in four classes across the two plots, with graded shading, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-035-A1.

#### APPENDIX B

Distribution maps (of all individuals greater than or equal to 1 cm dbh) for the 17 *Aporosa* species in the Lambir 52-ha plot are available in ESA's Electronic Data Archive: *Ecological Archives* E083-035-A2.

#### APPENDIX C

Distribution maps (of all individuals greater than or equal to 1 cm dbh) for the 17 *Aporosa* species in the Pasoh 50-ha plot are available in ESA's Electronic Data Archive: *Ecological Archives* E083-035-A3.

#### APPENDIX D

The summary of results from a bivariate Ripley's *K* analysis at Lambir is available in ESA's Electronic Data Archive: *Ecological Archives* E083-035-A4.

#### APPENDIX E

The summary of results from a bivariate Ripley's *K* analysis at Pasoh is available in ESA's Electronic Data Archive: *Ecological Archives* E083-035-A5.