FLORISTIC AND STRUCTURAL DIVERSITY OF MIXED DIPTEROCARP FOREST IN LAMBIR HILLS NATIONAL PARK, SARAWAK, MALAYSIA

H. S. Lee,

Forest Department, 93660 Kuching, Sarawak, Malaysia

S. J. Davies*,

Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge MA02138, USA. E-mail: sdavies@oeb.harvard.edu

J. V. LaFrankie,

Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Bukit Timah Road, Singapore

S. Tan,

Forest Department, 93660 Kuching, Sarawak, Malaysia

T. Yamakura, A. Itoh,

Osaka City University, Sumiyoshi-ku, Osaka 558, Japan

T. Ohkubo

Utsunomiya National University, Utsunomiya 321-8505, Japan

&

P. S. Ashton

Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge MA02138, USA

Received March 2001

LEE, H. S., DAVIES, S. J., LAFRANKIE, J. V., TAN, S., YAMAKURA, T., ITOH, A., OHKUBO, T. & ASHTON, P. S. 2002. Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. A 52-ha permanent forest plot was established in Lambir Hills National Park Sarawak, Malaysia to begin the long-term study of factors controlling the origin and maintenance of tree diversity. Stand structure and floristic composition of the plot are described.

**Author for correspondence.*

Lambir was found to have the highest diversity of trees anywhere on earth. In the 52-ha plot there were 356 501 trees with a total basal area of 2252 m^2, comprising 1173 tree species in 286 genera and 81 families. The Euphorbiaceae (125 species) and the Dipterocarpaceae (87 species) were the most species-rich families. The Dipterocarpaceae dominated the forest with 42% of the basal area and 16% of the trees. The Burseraceae, Anacardiaceae and Euphorbiaceae were the next most important large trees in the plot. *Shorea* was the most important genus with 53 species and the highest basal area and stem number. As with other Asian tropical forests there were many speciose genera in the plot; 21 genera had ≥ 12 species. In addition to *Shorea, Dipterocarpus* and *Dryobalanops* were important basal area contributors and *Dryobalanops* was the second most abundant genus. *Dryobalanops aromatica* and *Dipterocarpus globosus* were the most important canopy trees. *Fordia splendidissima* was the most abundant understorey tree in the 52 ha. An important finding is the change in floristic composition and stand structure across the 52-ha plot in relation to soil and topographic variation.

Key words: Basal area - Borneo - density - Dipterocarpaceae - resource heterogeneity - species richness - tree species diversity - tropical rain forest

LEE, H. S., DAVIES, S. J., LAFRANKIE, J. V., TAN, S., YAMAKURA, T., ITOH, A., OHKUBO, T. & ASHTON, P. S. 2002. Kepelbagaian flora dan struktur hutan dipterokarpa campur di Taman Negara Bukit Lambir, Sarawak, Malaysia. Petak hutan kekal seluas 52 ha ditubuhkan di Taman Negara Bukit Lambir, Sarawak, Malaysia bagi memulakan kajian jangka panjang tentang faktor yang mengawal asal dan penyenggaraan kepelbagaian pokok. Struktur dirian dan kandungan flora petak ini diterangkan. Lambir mempunyai kepelbagaian pokok yang tertinggi di dunia. Di dalam petak 52 ha terdapat 356 501 pokok dengan jumlah luas pangkal 2252 m^2, dan terdiri daripada 1173 spesies pokok dalam 286 genera dan 81 famili. Euphorbiaceae (125 spesies) dan Dipterocarpaceae (87 spesies) merupakan famili yang mempunyai paling banyak spesies. Dipterocarpaceae menaungi hutan sebanyak 42% daripada luas pangkal dan 16% daripada pokok. Burseraceae, Anacardiaceae dan Euphorbiaceae merupakan jenis pokok besar yang kedua pentingnya di dalam petak tersebut. *Shorea* ialah genus terpenting yang mempunyai 53 spesies dengan luas pangkal dan bilangan batang yang tertinggi. Seperti spesies hutan tropika Asia yang lain, terdapat banyak genera speciose di dalam petak ini, iaitu 21 genera mempunyai ≥ 12 spesies. Di samping *Shorea, Dipterocarpus* dan *Dryobalanops* merupakan dua spesies penting yang menyumbangkan luas pangkal. *Dryobalanops* ialah genus yang kedua banyaknya. *Dryobalanops aromatica* dan *Dipterocarpus globosus* merupakan pokok kanopi yang terpenting. *Fordia splendidissima* merupakan pokok tingkat bawah yang paling banyak di dalam petak 52 ha. Penemuan penting ialah terdapat perubahan dalam kandungan flora dan struktur dirian di sepanjang petak 52 ha apabila dikaitkan dengan variasi tanah dan topografi.

Introduction

Lowland tropical rain forest is among the most diverse vegetation in the world (Whitmore 1984, Richards 1996). The diversity of trees in these forests increases with a decline in climatic seasonality, with the most diverse forests occurring in areas without a significant annual dry period (Clinebell *et al.* 1995, Gaston 2000). Among lowland tropical forests of the aseasonal zone there is nevertheless a wide range in levels of tree diversity. Species richness in these forests may be influenced by variation in soil nutrient status (Ashton & Hall 1992, Duivenvoorden 1996, Sollins 1998), the probability of short-term drought (Walsh 1996), the ability of certain species to become dominant and have a disproportionate access to limited resources (Connell & Lowman 1989, Hart *et al.* 1989, Newbery *et al.* 1997), as well as historical and biogeographic factors (Gunatilleke & Ashton 1987). Resolving the relative influence of these different factors on tropical forest diversity is a central concern of tropical forest ecology (Givnish 1999).

In western Malesia, lowland forests with the highest tree species diversity are thought to occur on soils of intermediate nutrient status (Baillie *et al.* 1987, Ashton 1995, Davies & Becker 1996). Several studies have found lowest tree diversity in edaphically extreme sites, for example, forests on ultrabasic soils (Proctor *et al.* 1988), limestone-derived soils (Proctor *et al.* 1983), or white sand podzols (Brunig 1974, Proctor *et al.* 1983, Davies & Becker 1996). In all these cases low soil nutrient availability appears to strongly influence the floristic composition of the forests, although other resources, particularly soil water availability, may co-limit or may be more important in affecting forest composition (Walsh 1996). Some evidence suggests that forests on soils of high nutrient availability may also have lower species richness than forests on intermediate soils. Ashton and Hall (1992) found lower species richness on deep basalt-derived soils at Bukit Mersing in Sarawak, than on shallower, more nutrient-poor soils at Bukit Lambir. Furthermore, in Brunei, species richness was higher on sandy humult ultisols at Andulau than on more fertile clay-rich ultisols at Ladan (Davies & Becker 1996), although no soil nutrient analyses were conducted in these sites.

Stand structure also varies significantly among lowland tropical forests (Clark *et al.* 1999a). In western Malesia, mixed dipterocarp forests on red-yellow podzolic soils are generally taller in stature and have much greater above-ground biomass than heath (*kerangas*) forests on white-sand podzols (Ashton & Hall 1992). In Gunung Mulu, Sarawak, mixed dipterocarp forest on sandstone-derived soil had 42% greater above-ground biomass than forest over limestone and 28% greater biomass than heath forest on acid podzols (Proctor *et al.* 1983). Heath forests typically also have a more even canopy with fewer emergents, greater densities of trees in the smallest size classes, and a predominance of species with small sclerophyllous leaves (Richards 1936, Browne 1952, Becker *et al.* 1999).

Within these forest formations there is evidence that variation in stand structure and floristic composition is related to environmental gradients. An analysis of 38 small plots in heath forest in Sarawak and Brunei revealed strong differences in floristic composition related to topography and soil properties (Brunig 1974, Newbery 1991). In mixed dipterocarp forests over the broad class of red-yellow podzolic soils, there is also substantial variation in structure and floristics related to variation in topography, drainage, soil clay content (and, by inference, soil nutrients) and geography (Austin *et al.* 1972, Baillie *et al.* 1987, Ashton & Hall 1992). Ashton and Hall (1992), for example, found that stem densities in all but the largest size classes were lower on nutrient-rich soils at Bukit Mersing than on nutrient-poor soils at Bukit Lambir. Furthermore, comparisons of floristic similarity within the dominant family, Dipterocarpaceae, among mixed dipterocarp forests in Sarawak and Brunei found greatest similarity of dipterocarp composition for plots on similar soils and parent materials (Davies & Becker 1996). However, most studies of environmental correlates of forest composition in western Malesia have used small sample plots (usually ≥ 1 ha) that do not account for the effect of local environmental variation on forest structure and composition. Also, in many cases, studies comparing forests on different soils are from geographically distant areas and, therefore, soil fertility differences may covary with other factors such as rainfall.

In this paper, we describe floristic composition and stand structure of the mixed dipterocarp forest at Lambir Hills National Park, Sarawak, East Malaysia. Following similar projects initiated in Barro Colorado Island, Panama (Hubbell & Foster 1983) and Pasoh Forest Reserve in Peninsular Malaysia (Kochummen & LaFrankie 1990, Manokaran & LaFrankie 1990), this study encompasses a large forest area (52 ha) to facilitate demographic analyses of a significant proportion of the tree species, and to enable analyses of the importance of spatial heterogeneity of resource availability for tree species and forest community distribution patterns (Condit 1995, Ashton *et al.* 1999). Studies at Lambir have revealed considerable local-scale heterogeneity in resource availability, and this variation has been shown to have a significant effect on the distribution and abundance of several common tree species (Itoh *et al.* 1997, Davies *et al.* 1998, Yamada *et al.* 2000). Here we describe the major components of floristic and structural variation in the Lambir forest. First, we analysed overall stand structure and floristic composition of the forest to investigate whether stand structure, species diversity and floristic composition vary predictably across the 52-ha plot. Then we analysed in detail the dramatic differences in floristics and stand structure between two distinct tree communities that co-occur within Lambir. This paper provides an important basis for more detailed functional and comparative ecological studies of factors contributing to the maintenance of diversity in the world's richest tropical rain forest.

Materials and methods

Study site

Lambir Hills National Park, hereafter Lambir, (4° 20' N, 113° 50' E) (Figure 1) includes 6800 ha of lowland mixed dipterocarp forest (MDF) with patches of heath forest on the highest ridges. Lambir ranges from near sea level to 465 m altitude (Watson 1985). The forest is 40–70 m tall, with a heterogeneous canopy and high stem turnover rates (Phillips *et al.* 1994), which contribute to making it the most diverse forest in tree species recorded for the Palaeotropics (Ashton & Hall 1992, Phillips *et al.* 1994, Davies & Becker 1996). Lambir receives 3000 mm of rainfall per year, with all months averaging > 100 mm (Watson 1985). However, periodic short-term droughts may have a significant impact on floristic patterns in this region (Becker 1992). Temperatures are high and typical of the region with mean daily maximum of 32 °C and minimum of 24 °C, and no significant seasonal variation.

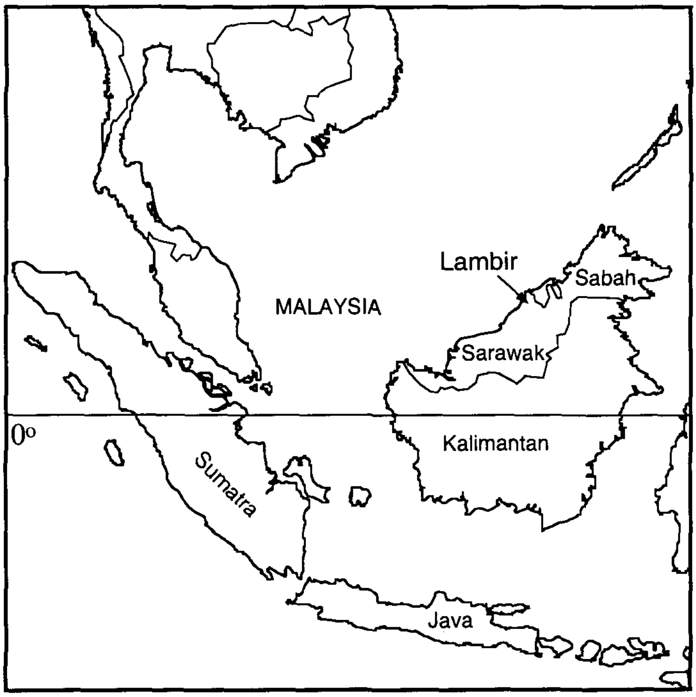

Figure 1 Location of Lambir Hills National Park, Sarawak, Malaysia

The Lambir hills consist of a series of cuestas comprised of Neogene sediments, dominated by soft erodable sandstone (Liechti *et al.* 1960). These sediments overlie the calcareous Setap shale formation of the lower Miocene, which is exposed along the southern boundary of the park. The soils of Lambir are derived from this complex lithology of interbedded sandstone and shale parent materials. Sandstone-derived soils are humult ultisols, or sandy haplic acrisols in FAO-UNESCO-ISRIC terminology (Anonymous 1998), with a surface horizon of loosely matted and densely rooted raw humus, low nutrient status and low water retention capacity (Ashton 1964, Baillie *et al.* 1987, Ashton & Hall 1992, Davies *et al.* 1998, Palmiotto 1998). Shale-derived soils are friable, relatively fertile, clay-rich udult ultisols (clay-rich haplic acrisols) with greater water holding capacity, and only a shallow layer of leaf litter. These two ultisols represent extremes in the range of lowland soils overlying sediments in north-west Borneo. The shale-derived soils cover 15% of the 52-ha plot (Davies *et al.* 1998) and occur mostly in the low-lying gullies; the humult ultisols occur on slopes and ridges. In areas where the shale is exposed the soil types form a mosaic, providing excellent opportunities for studies of the relationship between soils and forest variation. However, it must be pointed out that many soil factors appear to be intercorrelated at Lambir, for example, soil clay content, topography and water availability (Figure 2) (Yamakura *et al.* 1995, 1996).

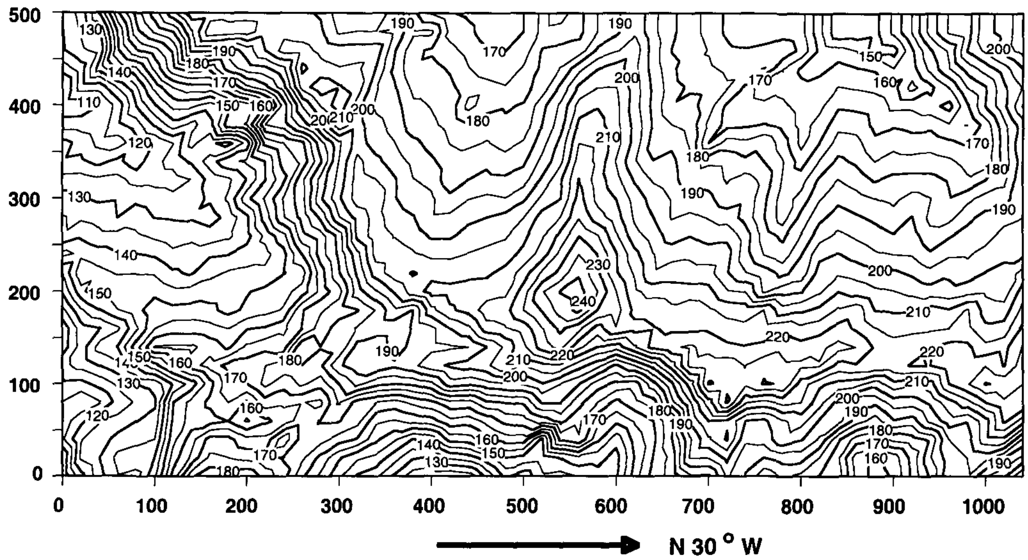

Figure 2 Topography of the 52-ha plot at Lambir. Contour lines are drawn at 5-m intervals

Data collection and analysis

In 1991, a long-term research project was initiated at Lambir to monitor all woody plants ≥ 1 cm diameter at breast height (dbh) in 52-ha of forest. The methods for this project closely followed similar studies already initiated in Barro Colorado Island, Panama (Hubbell & Foster 1983) and Pasoh Forest Reserve, West Malaysia (Manokaran *et al.* 1990; see also Ashton *et al.* 1999). In short, all trees ≥ 1 cm dbh (excluding palms and lianas) were tagged, mapped to ± 10 cm, identified, and their diameters measured to ± 1 mm (Condit 1998).

In 1997, a recensus of the 52-ha plot was undertaken, in which all extant trees were remeasured and their identifications confirmed. Newly recruited trees (≥ 1 cm dbh) were mapped, tagged and identified as for all trees in 1991. In contrast to a preliminary summary of stand structure and species composition based on a partial uncorrected data set (Lee *et al.* 1999), in this paper, we used the final 1999 version of the data as archived on CD-ROM. All tallies are for the forest as of 1997.

Methods of tree identification followed the general procedures described in Manokaran *et al.* (1990) and Condit (1998). Details particular to Lambir were as follows. All trees were subjected to a confirmation or correction of the 1991 identification during the second census in 1997. Approximately 20% of the trees, representing common and conspicuous species, were identified in the field. Trees >10 cm dbh were subjected to two independent identifications between 1991 and 1996. For the remaining trees, a numbered leaf collection was taken, dried, sorted to morphospecies and assigned a six-letter identification code. Approximately 5000 permanent herbarium specimens representing all morphospecies were stored in the research herbarium at Lambir. Morphospecies were assigned scientific names by comparison with reference material in Kuching (SAR) and Singapore (SING) herbaria. Since the taxonomy of trees in Borneo did not have a standard reference, the ongoing *Tree Flora of Sabah and Sarawak* (Soepadmo & Wong 1995, Soepadmo *et al.* 1996), the checklist for Brunei (Coode *et al.* 1996), *Flora Malesiana*, and other monographic treatments were followed where possible. In the course of the identification work, a computer-based list of six-letter morphospecies codes for all species was developed, complemented by technical notes on the tree descriptions and the currently assigned binomial.

In total 356 501 individual trees (359 207 stems) were alive in the 52-ha plot in 1997. Of these 95.3% (339 732 trees) were identified to species, 4.3% (15 409 trees) were identified to family or genus without a specific epithet (e.g. Burseraceae sp. or *Syzygium* sp.), and 0.4% (1360 trees) were unnamed. Unidentified or partially identified trees resulted mainly from clerical errors, rather than taxonomic or biological uncertainty. Therefore, missing identifications are no more likely to include "new" species than the same number of randomly chosen trees from anywhere in the plot. Based on species-tree number accumulation curves for the rest of the plot, adding the 4.7% of unidentified trees increased total plot species number by only 0.1% or 1.2 species.

Statistical analysis

Patterns of variation in community composition within the 52-ha plot were analysed using multivariate techniques. Principal components analysis (PCA) and cluster analysis based on both stem density and basal area for 50 samples, of 1-ha each, from within the plot demonstrated strong floristic pattern across the 52-ha plot. For the comparisons of floristic composition and stand structure presented in this paper, we used the PCA along with the topographic map and a preliminary soil map of the 52-ha plot (Palmiotto 1998) to select representative 4-ha subplots on udult and humult ultisol soils. The 4-ha subplots, hereafter the udult plot (coordinates: x = 50–250 m, y = 150–350 m, within the 52-ha plot) and the humult plot (x = 700–900 m, y = 200–400 m) were selected to illustrate the extremes of variation in stand structure and species composition across the 52-ha plot. The humult subplot was on the higher part of the plot and the udult subplot was on the lower part of the plot, so soil variation was correlated with topographic position as will be discussed below.

Results

Floristic composition and stand structure of the 52-ha plot

The 52-ha plot included 356 501 trees ≥ 1 cm dbh (mean = 6856 trees ha^{-1}), comprising 81 families, 286 genera and 1173 species. Total basal area for all trees in the 52-ha plot was 2251.52 m^2 (mean = 43.30 m^2 ha^{-1}). Almost 80% of the trees were < 5 cm dbh, and only 1372 trees (~ 26 trees ha^{-1}) were > 60 cm dbh (Table 1).

The Euphorbiaceae with 125 species was the richest family in the plot. However, the 87 species of Dipterocarpaceae dominated the composition with 54 089 trees (15.6% of the total) and basal area of 918.41 m^2 (41.6%) (Table 2). The Lauraceae, Rubiaceae and Annonaceae were also exceptionally species-rich with ≥ 54 species. In all, 21 families had ≥ 20 species in the plot. The Euphorbiaceae with 51 556 trees contributed almost as many trees as the Dipterocarpaceae but considerably less basal area (6.6%). The Burseraceae and Anacardiaceae were among the four most important families in tree number (> 5–7%) and basal area contribution (> 5–7%).

Table 1 Size class distribution for all trees ≥ 1 cm dbh in the 52-ha plot at Lambir

Size class (cm dbh)	Tree number	%	Mean tree (± SD) number ha^{-1}
1–2	146 712	41.15	2809.7 (537.7)
2–5	134 010	37.59	2580.0 (363.0)
5–10	43 187	12.11	831.9 (103.2)
10–20	20 518	5.76	394.3 (56.2)
20–30	5912	1.66	113.3 (20.7)
30–60	4790	1.34	91.5 (21.7)
> 60	1372	0.38	26.1 (6.7)
All trees	356 501		

Table 2 Floristic composition of families for all trees in the 52-ha plot at Lambir

Family	Basal area m^2	Family	Species n	Family	Trees n
Dipterocarpaceae	918.41 (41.6)	Euphorbiaceae	125 (10.7)	Dipterocarpaceae	54 089 (15.6)
Burseraceae	146.49 (6.6)	Dipterocarpaceae	87 (7.4)	Euphorbiaceae	51 556 (14.9)
Euphorbiaceae	144.76 (6.6)	Lauraceae	78 (6.6)	Burseraceae	23 118 (6.7)
Anacardiaceae	133.08 (6.0)	Rubiaceae	59 (5.0)	Anacardiaceae	19 381 (5.6)
Myrtaceae	99.64 (4.5)	Annonaceae	54 (4.6)	Rubiaceae	17 417 (5.0)
Lauraceae	77.00 (3.5)	Myrtaceae	53 (4.5)	Annonaceae	15 148 (4.4)
Clusiaceae	53.68 (2.4)	Meliaceae	52 (4.4)	Myristicaceae	12 584 (3.6)
Myristicaceae	52.69 (2.4)	Clusiaceae	50 (4.3)	Myrtaceae	12 550 (3.6)
Leguminosae	47.72 (2.2)	Burseraceae	40 (3.4)	Lauraceae	12 205 (3.5)
Sapotaceae	39.35 (1.8)	Myristicaceae	40 (3.4)	Clusiaceae	10 065 (2.9)
Moraceae	37.45 (1.7)	Moraceae	38 (3.2)	Ebenaceae	9471 (2.7)
Annonaceae	36.16 (1.6)	Ebenaceae	34 (2.9)	Leguminosae	7684 (2.2)
Simaroubaceae	34.81 (1.6)	Sapotaceae	33 (2.8)	Simaroubaceae	7484 (2.2)
Rubiaceae	30.17 (1.4)	Anacardiaceae	32 (2.7)	Meliaceae	7084 (2.0)
Ebenaceae	29.93 (1.4)	Polygalaceae	25 (2.1)	Flacourtiaceae	6794 (2.0)
Tiliaceae	28.66 (1.3)	Leguminosae	24 (2.0)	Polygalaceae	6654 (1.9)
Sterculiaceae	26.91 (1.2)	Fagaceae	21 (1.8)	Tiliaceae	5594 (1.6)
Labiatae	19.98 (0.9)	Melastomataceae	21 (1.8)	Moraceae	5512 (1.6)
Meliaceae	19.18 (0.9)	Sapindaceae	21 (1.8)	Sapotaceae	5510 (1.6)
Bombacaceae	19.06 (0.9)	Flacourtiaceae	20 (1.7)	Melastomataceae	5454 (1.6)
		Sterculiaceae	20 (1.7)		

Only families with the greatest total basal area, number of species and tree number are listed, with percentages given in parentheses.

Shorea was the most important genus in the 52-ha plot in terms of species richness (55 species, 4.7% of all species), tree number (23 813 trees, 6.9% of all trees), and basal area (467.8 m^2, 21% of total basal area) (Table 3). *Syzygium, Diospyros, Litsea* and *Xanthophyllum* were also exceptionally species-rich with ≥ 25 species. A total of 21 genera had ≥ 12 species. For basal area contribution, two other dipterocarp genera, *Dipterocarpus* (9.7%) and *Dryobalanops* (7.4%), were the second and third most important genera, and *Dryobalanops* had the second greatest number of trees (3.3%). Several genera of small to subcanopy trees had substantial numbers in the forest (e.g. *Diospyros, Vatica* and *Macaranga*).

The 20 most abundant species and those contributing most to total basal area are listed in Table 4. The emergent dipterocarp, *Dryobalanops aromatica,* was the dominant tree species, with 10 503 trees (3.0%) and basal area of 152.8 m^2 (6.9%). *Dipterocarpus globosus* also contributed significantly to basal area, and together with *D. aromatica* accounted for > 13% of total basal area. The six species with the largest contribution to basal area were all dipterocarps, as were 13 of the top 20 basal area contributors. In tree numbers, individual dipterocarp species were less dominant (Table 4), with several very common understorey non-dipterocarps, the more important of which were the legume, *Fordia splendidissima,* and the shade-tolerant euphorbs, *Croton oblongus* and *Macaranga brevipetiolata.*

Variation in forest structure and diversity

Stand structure and floristic composition varied significantly across the 52-ha plot (Figures 3 and 4). Mean tree density per hectare was 6899 (SD = 987, range = 4861–8866 trees, based on 50 single hectares), and mean basal area was 43.14 m^2 ha^{-1} (SD = 6.6; range = 28.1–54.2 m^2 ha^{-1}. Total basal area and tree density, mapped on a 20 × 20 m scale, were substantially greater in the higher areas of the plot (Figure 3). These areas are dominated by the sand-rich humult ultisol soils (Figure 2).

Species richness was also highly variable across the plot (Figure 4). For all stems the mean number of species per hectare was 610 (SD = 53.0, range = 436–713 species ha^{-1}), and mean Fisher's α was 162.5 (range = 116–198). For trees ≥ 10 cm dbh, the mean number of species ha^{-1} was 238.6 (range = 172–290), and the mean Fisher's α was 155.6 (range = 84–230). In contrast to floristic composition and stand structure, variation in species richness was not strongly correlated with variation in topography or soils across the plot. However, the single hectares with the highest species richness and Fisher's α values were in relatively steep areas along the basal margin of the plot (Figure 4).

Table 3 Generic composition of all trees ≥ 1 cm dbh in the 52-ha plot at Lambir

Genus	Family	Basal area m^2	Genus	Family	Species n	Genus	Family	Tree number n
Shorea	Dipterocarpaceae	467.76 (21.2)	*Shorea*	Dipterocarpaceae	55 (4.7)	*Shorea*	Dipterocarpaceae	23 813 (6.9)
Dipterocarpus	Dipterocarpaceae	213.53 (9.7)	*Syzygium*	Myrtaceae	49 (4.2)	*Dryobalanops*	Dipterocarpaceae	11 453 (3.3)
Dryobalanops	Dipterocarpaceae	164.03 (7.4)	*Diospyros*	Ebenaceae	34 (2.9)	*Dacryodes*	Burseraceae	11 252 (3.2)
Santiria	Burseraceae	60.67 (2.8)	*Litsea*	Lauraceae	29 (2.5)	*Diospyros*	Ebenaceae	9471 (2.7)
Gluta	Anacardiaceae	60.03 (2.7)	*Xanthophyllum*	Polygalaceae	25 (2.1)	*Vatica*	Dipterocarpaceae	8889 (2.6)
Dacryodes	Burseraceae	59.65 (2.7)	*Aglaia*	Meliaceae	24 (2.0)	*Gluta*	Anacardiaceae	8616 (2.5)
Syzygium	Myrtaceae	56.18 (2.6)	*Garcinia*	Clusiaceae	23 (2.0)	*Syzygium*	Myrtaceae	8281 (2.4)
Allantospermum	Simaroubaceae	34.14 (1.6)	*Ficus*	Moraceae	21 (1.8)	*Macaranga*	Euphorbiaceae	8046 (2.3)
Whiteodendron	Myrtaceae	31.83 (1.4)	*Aporosa*	Euphorbiaceae	18 (1.5)	*Santiria*	Burseraceae	7430 (2.1)
Vatica	Dipterocarpaceae	31.48 (1.4)	*Knema*	Myristicaceae	17 (1.5)	*Allantospermum*	Simaroubaceae	7368 (2.1)
Diospyros	Ebenaceae	29.93 (1.4)	*Santiria*	Burseraceae	17 (1.5)	*Xanthophyllum*	Polygalaceae	6654 (1.9)
Calophyllum	Clusiaceae	28.24 (1.3)	*Calophyllum*	Clusiaceae	16 (1.4)	*Cleistanthus*	Euphorbiaceae	6128 (1.8)
Artocarpus	Moraceae	28.08 (1.3)	*Macaranga*	Euphorbiaceae	15 (1.3)	*Aporosa*	Euphorbiaceae	5989 (1.7)
Alseodaphne	Lauraceae	27.69 (1.3)	*Baccaurea*	Euphorbiaceae	14 (1.2)	*Dipterocarpus*	Dipterocarpaceae	5338 (1.5)
Swintonia	Anacardiaceae	27.57 (1.2)	*Madhuca*	Sapotaceae	14 (1.2)	*Litsea*	Lauraceae	5262 (1.5)
Canarium	Burseraceae	22.64 (1.0)	*Polyalthia*	Annonaceae	14 (1.2)	*Knema*	Myristiaceae	5138 (1.5)
Mangifera	Anacardiaceae	22.44 (1.0)	*Palaquium*	Sapotaceae	13 (1.1)	*Anisophyllea*	Rhizophoraceae	4640 (1.3)
Elateriospermum	Euphorbiaceae	22.03 (1.0)	*Artocarpus*	Moraceae	12 (1.0)	*Urophyllum*	Rubiaceae	4507 (1.3)
Palaquium	Sapotaceae	21.56 (1.0)	*Drypetes*	Euphorbiaceae	12 (1.0)	*Aglaia*	Meliaceae	4289 (1.2)
Pentace	Tiliaceae	18.97 (0.9)	*Lithocarpus*	Fagaceae	12 (1.0)	*Ixora*	Rubiaceae	4238 (1.2)
			Memecylon	Melastomataceae	12 (1.0)			

Only genera with the greatest total basal area, number of species and tree number are listed, with percentages given in parentheses.

Table 4 The 20 most important species (≥1 cm) in the 52-ha plot

Tree Number

Species	Family	Frequency n
Dryobalanops aromatica Gaertn. f.	Dipterocarpaceae	10 503 (3.0)
Allantospermum borneense Form.	Simaroubaceae	7368 (2.1)
Vatica micrantha V. Sl.	Dipterocarpaceae	6261 (1.8)
Fordia splendidissima (Bl.) Buijsen	Fabaaceae	3717 (1.1)
Gluta laxiflora Ridl.	Anacardiaceae	3646 (1.1)
Whiteodendron moultonianum (W.W. Sm.) v. Steen.	Myrtaceae	3387 (1.0)
Shorea beccariana Burck	Dipterocarpaceae	3361 (1.0)
Shorea laxa V. Sl.	Dipterocarpaceae	3328 (1.0)
Dipterocarpus globosus Vesq.	Dipterocarpaceae	3311 (1.0)
Dacryodes expansa (Ridl.) Lam	Burseraceae	3287 (1.0)
Shorea amplexicaulis Ashton	Dipterocarpaceae	3131 (0.9)
Dacryodes rostrata (Bl.) Lam	Burseraceae	3119 (0.9)
Croton oblongus Burm. f.	Euphorbiaceae	2935 (0.9)
Macaranga brevipetiolata Airy-Shaw	Euphorbiaceae	2869 (0.8)
Mangifera parvifolia Boerl. & Koord.	Anacardiaceae	2752 (0.8)
Macaranga praestans Airy-Shaw	Euphorbiaceae	2647 (0.8)
Strombosia ceylanica Gardner	Olacaceae	2523 (0.7)
Ixora glomerulifera Brem.	Rubiaceae	2376 (0.7)
Santiria laevigata Bl.	Burseraceae	2183 (0.6)
Diospyros mindanensis Merr.	Ebenaceae	2124 (0.6)

Basal area

Species	Family	Basal area m^2
Dryobalanops aromatica Gaertn. f.	Dipterocarpaceae	152.75 (6.9)
Dipterocarpus globosus Vesq.	Dipterocarpaceae	137.91 (6.3)
Shorea beccariana Burck	Dipterocarpaceae	59.55 (2.7)
Shorea laxa V. Sl.	Dipterocarpaceae	47.96 (2.2)
Shorea acuta Ashton	Dipterocarpaceae	41.12 (1.9)
Shorea smithiana Sym. complex	Dipterocarpaceae	39.23 (1.8)
Allantospermum borneense Form.	Simaroubaceae	34.14 (1.6)
Whiteodendron moultonianum (W.W. Sm.) v. Steen.	Myrtaceae	31.83 (1.4)
Shorea curtisii Dyer	Dipterocarpaceae	27.86 (1.3)
Elateriospermum tapos Bl.	Euphorbiaceae	22.03 (1.0)
Dacryodes expansa (Ridl.) Lam	Burseraceae	20.52 (0.9)
Swintonia schwenkii Teijsm. & Binn.	Anacardiaceae	20.46 (0.9)
Santiria laevigata Bl.	Burseraceae	19.35 (0.9)
Shorea kunstleri King	Dipterocarpaceae	18.45 (0.8)
Dipterocarpus acutangulus Vesq.	Dipterocarpaceae	18.36 (0.8)
Shorea parvifolia Dyer	Dipterocarpaceae	18.04 (0.8)
Dipterocarpus geniculatus Vesq.	Dipterocarpaceae	17.68 (0.8)
Vatica micrantha V. Sl.	Dipterocarpaceae	16.06 (0.7)
Dipterocarpus confertus V. Sl.	Dipterocarpaceae	15.81 (0.7)
Gluta laxiflora Ridl.	Anacardiaceae	15.58 (0.7)

Percentages given in parentheses.

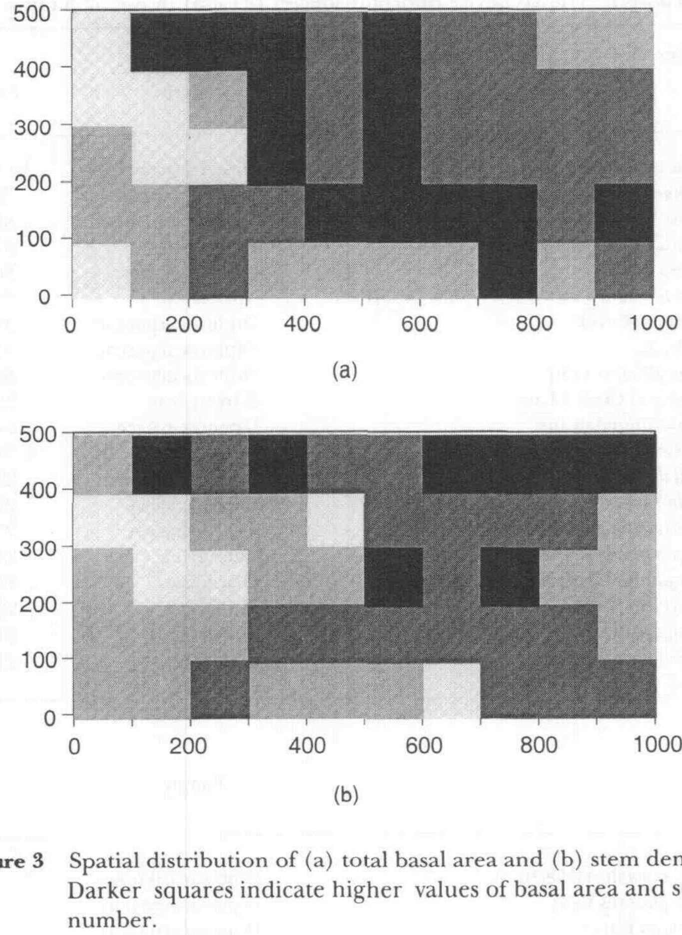

Figure 3 Spatial distribution of (a) total basal area and (b) stem density. Darker squares indicate higher values of basal area and stem number.

Community diversity in the 52-ha plot

Multivariate analyses found a strong gradient in floristic composition across the plot associated with the change from humult ultisols in the higher areas to udult ultisols in the lower parts of the plot (Figure 5, unpublished data). Analysis of two 4-ha subplots from areas dominated by humult and udult soils was conducted to illustrate the strong spatial patterning of floristic composition and stand structure across the 52-ha plot. The 4-ha udult subplot included 33% fewer trees and 32% less basal area than the 4-ha humult subplot (Table 5). In addition, tree size-class distributions differed among the two 4-ha samples ($p < 0.01$) (Figure 6). The humult subplot had greater proportions of stems in the smallest (1–2 cm dbh) and larger (> 30 cm dbh) size classes, whereas the udult subplot had greater proportions of stems in the intermediate size classes, particularly in the 2–10 cm dbh size classes. Despite the much larger number of trees in the humult subplot, species richness was slightly higher in the udult subplot (Table 5). For 30 random samples of 15 000 adjacent trees there were on average 2.7% more species in the udult plot, although these values were statistically indistinguishable.

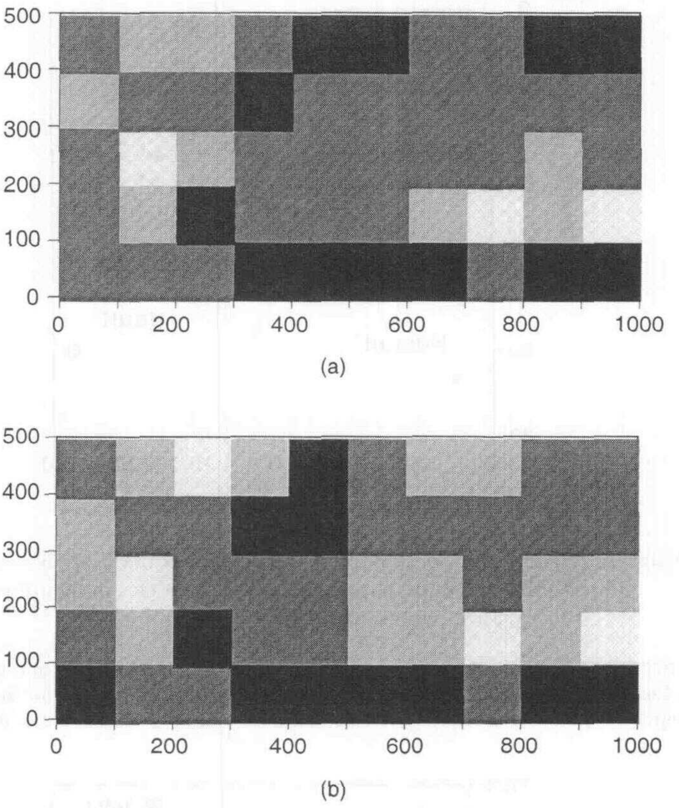

Figure 4 Spatial distribution of (a) species richness and (b) the Fisher's α diversity index. Darker squares indicate higher values of species richness and Fisher's α.

Table 5 Comparison of stand structure and floristics in two 4-ha subplots from within the 52-ha plot at Lambir

	4-ha subplot			
	Udult		Humult	
Total stem number	20449		30405	
Total stem basal area (m^{-2})	122.38		180.61	
Species number in:				
1000 trees	345.1	(7.0)	344.5	(9.7)
5000 trees	608.8	(7.8)	596.2	(7.6)
10 000 trees	711.2	(7.4)	688.0	(7.9)
15 000 trees	761.3	(4.0)	740.8	(8.7)
All trees	781		816	

The plots were chosen to represent the vegetation of the two extremes of soil-type variation (udult versus humult ultisols) within the plot based on Figure 6. Species richness was calculated in 30 randomly selected samples of 1000, 5000, 10 000 and 15 000 trees for each subplot. Standard deviations are given in parentheses.

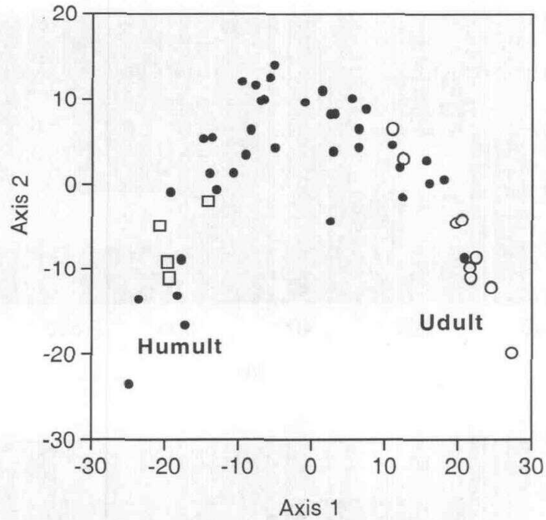

Figure 5 The first two axes of the principal components analysis (PCA) of abundance values for each of 1173 species in 50 individual 1-ha quadrats within the 52-ha plot at Lambir.

The first two axes accounted for 28% of the variation. The 4-ha humult and udult plots used for comparison in Tables 5, 6 and 7 are indicated by open squares for humult hectares and open circles for udult hectares. Parts of nine hectares were included in the 4-ha udult plot.

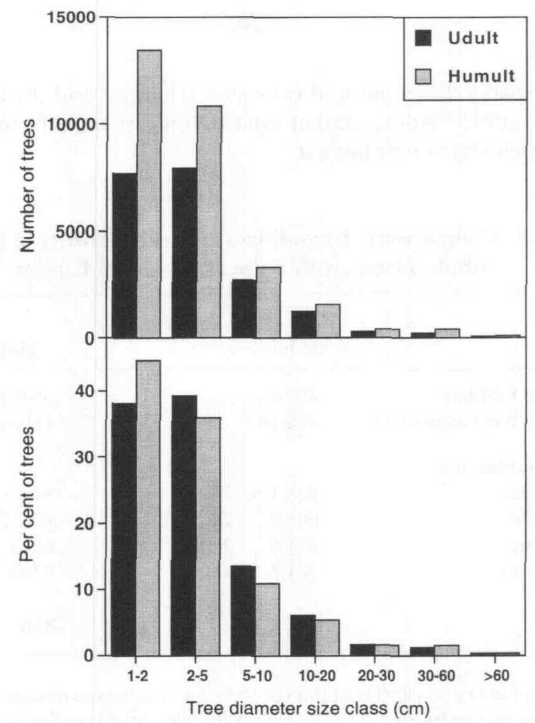

Figure 6 Tree size-class distributions for 4-ha udult and humult subplots within the 52-ha plot at Lambir. Size-class distributions are shown as total and relative number of trees in each size class for the two subplots.

Floristic composition of the canopy, subcanopy and understorey all differed significantly between the 4-ha subplots (Table 6). Among the most common species in each subplot, only the understorey tree, *Fordia splendidissima*, was common to both plots. The canopy of the forest on udult soils was dominated by *Koilodepas longifolium, Millettia vasta, Dryobalanops lanceolata* and *Hopea dryobalanoides*, whereas the humult forest canopy was dominated by *Dipterocarpus globosus, Elateriospermum tapos, Dryobalanops aromatica, Whiteodendron moultonianum* and *Shorea acuta* (Table 7). Among the 20 most common trees ≥ 20 cm dbh only *Shorea smithiana* and *Allantospermum borneense* occurred in both subplots. The subcanopy and understorey of both subplots were dominated by species with ballistically dispersed seeds, *Dimorphocalyx denticulatus* and *Rinorea bengalensis* in the udult subplot and *Cleistanthus beccarianus* and *Macaranga brevipetiolata* in the humult subplot (Table 6).

Table 6 Common species by size-class in representative udult and humult 4-ha subplots of the 52-ha plot at Lambir

Udult	Tree number	Humult	Tree number
Emergent and canopy trees			
Hopea dryobalanoides	764	*Allantospermum borneense*	762
Dryobalanops lanceolata	462	*Whiteodendron moultonianum*	699
Gluta wallichii	205	*Dryobalanops aromatica*	692
Dillenia excelsa	201	*Dipterocarpus globosus*	571
Hopea pterygota	187	*Gluta laxiflora*	447
Millettia vasta	132	*Dacryodes rostrata*	403
Subcanopy trees			
Dimorphocalyx denticulatus	797	*Vatica micrantha*	633
Koilodepas longifolium	237	*Macaranga brevipetiolata*	434
Drypetes xanthophylloides	145	*Diospyros mindanensis*	317
Hydnocarpus borneensis	142	*Anisophyllea corneri*	312
Semecarpus rufovelutinus	140	*Baccaurea sarawakensis*	270
Croton oblongus	137	*Xanthophyllum velutinum*	230
Trigonostemon capillipes	127	*Dillenia sumatrana*	184
Understorey small trees and treelets			
Rinorea bengalensis	321	*Cleistanthus beccarianus*	484
Fordia splendidissima	216	*Fordia splendidissima*	297
Aporosa sarawakensis	171	*Urophyllum* sp. 1	242
Cleistanthus pubens	152	*Ardisia* sp. 3	225
Drypetes myrmecophila	147	*Anisophyllea disticha*	191
Polyalthia glabrescens	142	*Agrostistachys longifolia*	162
Ficus stolonifera	132	*Casearia grewiaefolia*	159
Aporosa benthamiana	111	*Antidesma linearifolium*	125
Hopea mesuoides	102	*Fagraea spicata*	114

Table 7 Common species ≥ 20 cm dbh in representative udult and humult 4-ha subplots of the 52-ha plot at Lambir

Udult	Tree number	Humult	Tree number
Koilodepas longifolium	21	*Dipterocarpus globosus*	70
Millettia vasta	18	*Elateriospermum tapos*	63
Dryobalanops lanceolata	17	*Dryobalanops aromatica*	54
Hopea dryobalanoides	10	*Whiteodendron moultonianum*	44
Parashorea parvifolia	8	*Shorea acuta*	43
Dipterocarpus kunstleri	7	*Santiria laevigata*	26
Eusideroxylon zwageri	7	*Allantospermum borneense*	24
Schoutenia glomerata	7	*Dacryodes expansa*	19
Dacryodes cuspidata	6	*Shorea laxa*	19
Dillenia excelsa	6	*Gluta woodsiana*	18
Macaranga hosei	6	*Shorea quadrinervis*	15
Shorea inappendiculata	6	*Teijsmanniodendron simplicifolium*	14
Shorea parvifolia	6	*Artocarpus nitidus*	13
Shorea smithiana	6	*Koompassia malaccensis*	13
Allantospermum borneense	5	*Shorea smithiana*	13
Dacryodes incurvata	5	*Dacryodes rostrata*	11
Microcos blattaefolia	5	*Hydnocarpus pinguis*	10
Mallotus leucodermis	5	*Mangifera parvifolia*	10
Phoebe macrophylla	5	*Santiria rubiginosa*	10
Saurauia hooglandii	5	*Shorea beccariana*	10
Shorea falciferoides	5	*Shorea curtisii*	10
		Swintonia schwenkii	10

Discussion

Floristic diversity

The 52-ha plot in Lambir Hills National Park has more species of trees than any other area of a similar size anywhere in the world. In comparison with the five other large permanent plots that have been established in association with the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute (Table 8) (Ashton *et al.* 1999), the Lambir plot includes 30% more species than the second richest plot at Pasoh Forest Reserve, Peninsular Malaysia (Kochummen & LaFrankie 1990).

Table 8 Comparison of stand structure and species richness in six large-scale permanent forest dynamics plots that have been established in tropical rain forests

Plot	Location	Plot size (ha)	Rain (cm)	Dry season (months)	Species richness	Fisher's α	Basal area (m^2 ha^{-1})	Total stem number	Mean stem number ha^{-1}
Lambir	Sarawak, Malaysia	52	3000	0	1173	151.0	43.4	356 449	6855
Pasoh[1]	Peninsular Malaysia	50	1800	0	818	101.5	30.3	320 382	6408
Huai Kha Keng[2]	Thailand	50	1500	5	266	34.2	32.0	81 145	1623
Mudumalai[3]	India	50	1200	6	72	9.1	23.7	25 306	506
Sinharaja[3]	Sri Lanka	25	5000	0	203	22.2	-	206 227	8249
BCI[3]	Panama	50	2500	4	299	33.9	31.8	229 071	4581

References: [1] Kochummen & LaFrankie (1990); [2] Bunyavejchewin *et al.* (1998); [3] Condit *et al.* (2000).

Compared with smaller plots, Lambir is also among the world's most diverse forests. A comparison of the Fisher's index of diversity, which accounts for differences in stem numbers among plots (Condit *et al.* 1996), illustrates the exceptional diversity of the Lambir forest. Turner (2001) recently reviewed Fisher's α values for forest plots in Asia and in other tropical areas. Fisher's α values exceeding the plot-wide value of 151 at Lambir have been found in only two other forest plots in Asia, one in Jambi Province, Sumatra (Rennolls & Laumonier 2000), and one in a forest very similar to Lambir at Andulau in Brunei (Davies & Becker 1996). Several plots in South America as well as the Jambi plot have Fisher's α values over 200 (Turner 2001). Analysis of fifty 100 × 100 m (1 ha) samples from within the Lambir plot found a maximum Fisher's α of 230 for trees ≥ 10 cm dbh. As far as we are aware, this is the highest Fisher's α ever recorded for one hectare of tropical rain forest anywhere in the world.

The flora of north-west Borneo (Sarawak, Sabah and Brunei) is estimated to include around 5000 tree species (Soepadmo, pers. comm.). The 52-ha plot at Lambir includes almost one quarter of this estimated flora. The 50-ha plot at Pasoh in Peninsular Malaysia included a similarly large proportion of the dryland Malayan tree flora (LaFrankie 1996). Since Lambir Hills National Park is the only major lowland protected area within the north-west Borneo Geosyncline, it is a critically important conservation area, including the most biodiverse region in the Old World. This area of Borneo, north of a line between Pontianak and Kota Kinabalu, is part of an area that has been referred to as the Riau pocket, a putative Pleistocene refugium comprising coastal Perak, the Riau Archipelago, the peninsular east coast, as well as north-west Borneo (Corner 1960, Ashton 1995, Morley 2000). Preliminary analyses of species composition within the Lambir plot as well as earlier plots in Brunei by Ashton (1964) suggest that many species restricted to the humult ultisols are endemic to this area, further emphasising the conservation importance of Lambir. These species include *Dipterocarpus globosus, Shorea acuta, S. laxa* and *Gluta laxiflora.*

Despite the exceptional species diversity of the Lambir forest, the floristic composition of the 52-ha plot is typical of the dryland forests on red-yellow soils in aseasonal western Malesia. The Dipterocarpaceae dominate much of the lowland forests in this region (Ashton 1988). The 87 species of Dipterocarpaceae in the Lambir plot is extraordinary for a such a small area. However, the relative contribution of dipterocarps within single plots is often in the range of 3–10% for species richness, 8–18% for stem number and 20–56% for basal area contribution (Proctor *et al.* 1983, Kochummen & LaFrankie 1990, Newbery *et al.* 1992, Davies & Becker 1996). The Lambir figures fall on the slightly higher side of these ranges, but illustrate that Lambir is typical of many other dipterocarp forests in western Malesia.

Community diversity

Forest structure and composition varied greatly across the 52-ha plot at Lambir. Tree basal area and stem density were substantially higher in the north-western end of the plot, and comparisons of two 4-ha subplots illustrated huge differences in floristic composition over a distance of less than 800 m. These differences in forest structure and composition are strongly related to habitat variation across the plot (Ashton & Hall 1992, Davies *et al.* 1998). However, the implication that floristic and structural variation across the plot at Lambir is a direct result of different soil nutrient availabilities needs to be examined with detailed experimental studies. The clay-rich udult soils are abundant in the lower areas of the plot and are likely to have greater water-holding capacity. In contrast, the humult soils only occur at higher elevations within the plot and are sandy and probably well drained. Forests on the humult soils on the upper slopes and ridges within the plot may therefore be exposed to short-term droughts during rain-free periods (Becker *et al.* 1998, Nakagawa *et al.* 2000). Differences in drought sensitivity among species could also explain the floristic gradient within the plot. Furthermore, other factors correlated with soil and topographic variation may also have a role in explaining the floristic and structural gradients across the plot.

Differences in forest structure between udult and humult subplots may also have been influenced by variation in disturbance history across the plot. The south-eastern end of the plot in the lower areas is close to the edge of the forest. Increased rates of forest disturbance associated with the forest edge may have resulted in the different structural characteristics of the forest on the udult subplot. However, several other studies of mixed dipterocarp forest have also found higher stem densities on nutrient-poor humult ultisols than in forests over richer substrates (Ashton & Hall 1992, Davies & Becker 1996), suggesting that different structural properties are typical of these different subtypes of the mixed dipterocarp formation. This hypothesis needs further examination with comparative analyses of structural characteristics across a wider range of forests in Borneo.

There was almost no overlap between the common species in the udult and humult subplots, suggesting that these species are specialists of the respective habitats. However, aggregated spatial distributions are widespread in tropical tree species (Condit *et al.* 2000) and may result from processes other than habitat association, such as limited seed dispersal (Clark *et al.* 1999b). Further tests of habitat association of tree species at Lambir that incorporate dispersal characteristics are required to assess the importance of habitat features in producing the floristic gradients across the plot (Harms *et al.* 2001). An alternative test may be provided by examining the distribution of individual species across the whole of north-west Borneo to examine whether species-habitat associations persist across a mosaic of humult and udult ultisol habitats (see also Baillie *et al.* 1987). An analysis of the floristic composition of 105 plots of size 0.6-ha from across Sarawak and Brunei revealed strong correlations between species' distributions and soils (Potts *et al.* 2002). In that study, common species were classified as either generalists, udult specialists or humult specialists based on their repeated occurrence in the different plots. Interestingly, quite a few of the species common to a large proportion of humult and udult plots across Sarawak and Brunei were also abundant in the humult and udult 4-ha subplots within the 52-ha plot at Lambir. Humult specialists that were abundant in the humult 4-ha subplot at Lambir included *Vatica micrantha*, *Allantospermum borneense, Dryobalanops aromatica, Dipterocarpus globosus* and *Gluta laxiflora.* Udult specialists common in the 4-ha udult subplot at Lambir included *Dryobalanops lanceolata* and *Hopea dryobalanoides.* This provides evidence for strong species-habitat associations in the mixed dipterocarp forests of north-west Borneo. Further experimental analyses are required with these species to investigate the mechanistic basis of these habitat associations.

Management implications

Forests over humult soils in the upper part of the 52-ha plot had more trees and greater basal area than the forests on udult soils lower in the plot. It has also been reported that maximum growth rates among pioneer and light-demanding climax species are up to two times greater on udult soils than on humult soils (Ashton & Hall 1992, Davies 2001). This may be the result of higher soil nutrient concentrations on the udult than on the humult ultisols although, as mentioned above, it may also be related to differences in other soil properties, such as water availability differences between udult and humult soils. If further substantiated this result may be of particular significance to forest management as it implies that the silvicultural characteristics and management requirements for timber on the two soils differ in important ways. As policy priorities change towards multiple purpose management with emphasis on the conservation of service values including hydrology, carbon storage, biodiversity and recreation, a new management paradigm which stresses habitat-specific treatments will be required. Research at Lambir aims to generate the basic information needed for the implementation of multiple purpose forest management.

Acknowledgements

The 52-ha Long-Term Ecological Research project is a collaborative project of the Forest Department of Sarawak, Malaysia, Harvard University, USA (under NSF awards DEB-9107247 and DEB-9629601 to P. S. Ashton) and Osaka City University, Japan (under Monbusho grant 06041094 to T. Yamakura, 08NP0901 to S. Tamura and 09NP0901 to S. Sasaki), and is facilitated by the Center for Tropical Forest Science, Smithsonian Tropical Research Institute. The authors would like to thank the Sarawak Government for permission to conduct the project, and for providing research permission to SJD, JVL, TY, AI and PSA. We also thank the National Parks and Wildlife Division of the Forest Department for assistance at Lambir.

References

ANONYMOUS. 1998. FAO-UNESCO soil map of the world. Revised legend. World Soil Research Report 60, FAO, Rome.

ASHTON, P. S. 1964. *Ecological Studies in the Mixed Dipterocarp Forests of Brunei State.* Oxford Forest Memoirs, Volume 25. 74 pp.

ASHTON, P. S. 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. *Annual Review of Ecology and Systematics* 19: 347–370.

ASHTON, P. S. 1995. Biogeography and ecology. Pp. XLIII-LI in Soepadmo, E. & Wong, K. M. (Eds.) *Tree Flora of Sabah and Sarawak.* Volume 1. Forest Research Institute Malaysia, Kepong.

ASHTON, P. S. & HALL, P. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* 80: 459–481.

ASHTON, P. S., BOSCOLO, M., LIU, J. & LAFRANKIE, J. V. 1999. A global programme in interdisciplinary forest research: The CTFS perspective. *Journal of Tropical Forest Science* 11: 180–204.

AUSTIN, M. P., ASHTON, P. S. & GREIG-SMITH, P. 1972. The application of quantitative methods to vegetation survey. III. A re-examination of rain forest data from Brunei. *Journal of Ecology* 60: 305–324.

BAILLIE, I. C., ASHTON, P. S., COURT, M. N., ANDERSON, J. A. R., FITZPARTICK, E. A. & TINSLEY, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3: 201–220.

BECKER, P. 1992. Seasonality of rainfall and drought in Brunei Darussalam. *Brunei Museum Journal* 7: 99–109.

BECKER, P., LYE, O. C. & GOH, F. 1998. Selective drought mortality of dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica* 30: 666–671.

BECKER, P., DAVIES, S. J., MOKSIN, M., ISMAIL, M. Z. & SIMANJUNTAK, P. M. 1999. Leaf size distributions of understorey plants in mixed dipterocarp and tropical heath forests of Brunei. *Journal of Tropical Ecology* 15: 123–128.

BROWNE, F. G. 1952. The kerangas lands of Sarawak. *Malayan Forester* 15: 61–73.

BRUNIG, E. F. 1974. *Ecological Studies in the Kerangas Forests of Sarawak and Brunei.* Borneo Literature Bureau, Kuching, Sarawak. 237 pp.

BUNYAVEJCHEWIN, S., LAFRANKIE, J. V., PATTAPONG, P., KANZAKI, M., ITOH, A., YAMAKURA, T. & ASHTON, P. S. 1998. Topographic analysis of a large-scale research plot in a seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Tropics* 8: 45–60.

CLARK, D. B., PALMER, M. W. & CLARK, D. A. 1999a. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80: 2662–2675.

CLARK, J. S., SILMAN, M., KERN, R., MACKLIN, E. & HILLERISLAMBERS, J. 1999b. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80: 1475–1494.

CLINEBELL, R. R., PHILLIPS, O. L., GENTRY, A. H., STARK, N. & ZUURING, H. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* 4: 56–90.

CONDIT, R. 1995. Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution* 10: 18–22.

CONDIT, R. 1998. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots.* Springer-Verlag, Berlin. 211 pp.

CONDIT, R., HUBBELL, S. P., LAFRANKIE, J. V., SUKUMAR, R., MANOKARAN, N., FOSTER, R. B. & ASHTON, P. S. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-hectare plots. *Journal of Ecology* 84: 549–562.

CONDIT, R., ASHTON, P. S., BAKER, P., BUNYAVEJCHEWIN, S., GUNATILLEKE, S., GUNATILLEKE, N., HUBBELL, S. P., FOSTER, R. B., ITOH, A., LAFRANKIE, J V., LEE, H. S., LOSOS, E., MANOKARAN, N., SUKUMAR, R. & YAMAKURA, T. 2000. Spatial patterns in the distribution of tropical trees. *Science* 288: 1414–1418.

CONNELL, J. H. & LOWMAN, M. D. 1989. Low diversity tropical rain forests: some possible mechanisms for their existence. *American Naturalist* 134: 88–119.

COODE, M. J. E., DRANSFIELD, J., FORMAN, L., KIRKUP, D. W. & SAID, I. M. 1996. *A Checklist of the Flowering Plants and Gymnosperms of Brunei Darussalam.* Ministry of Industry and Primary Resources, Bandar Seri Begawan, Brunei Darussalam. 477 pp.

CORNER, E. J. H. 1960. The Malayan flora. Pp. 21–24 in Purchon, R. D. (Ed.) *Proceedings of the Centenary and Bicentenary Congress of Biology.* University of Malaya Press, Singapore.

DAVIES, S. J. 2001. Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology* 82: 920–932.

Davies, S. J. & Becker, P. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. *Journal of Tropical Forest Science* 8: 542–569.

Davies, S. J., Palmiotto, P., Ashton, P. S., Lee, H. S. & LaFrankie, J. V. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86: 662–673.

Duivenvoorden, J. F. 1996. Patterns of tree species richness in rain forests of middle Caqueta area, Colombia, NW Amazon. *Biotropica* 28: 142–158.

Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405: 220–227.

Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87: 193–210.

Gunatilleke, C. V. S. & Ashton, P. S. 1987. New light on the plant geography of Ceylon. II. The ecological biogeography of lowland endemic tree flora. *Journal of Biogeography* 14: 295–327.

Harms, K. E., Condit, R., Hubbell, S. P. & Foster, R. B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.

Hart, T. B., Hart, J. A. & Murphy, P. G. 1989. Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *American Naturalist* 133: 613–633.

Hubbell, S. P. & Foster, R. B. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. Pp. 25–41 in Sutton, S. L., Whitmore, T. C. & Chadwick, C. (Eds.) *Tropical Rain Forest: Ecology and Management.* Serial Publication Number 2 of the British Ecological Society, U.K.

Itoh, A., Yamakura, T., Ogino, K., Lee, H. S. & Ashton, P. S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rain forest in Sarawak, Malaysia. *Plant Ecology* 132: 121–136.

Kochummen, K. M. & LaFrankie, J. V. 1990. Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3: 1–13.

LaFrankie, J. V. 1996. The distribution and abundance of Malaysian trees: The significance of family characteristics for conservation. *Bulletin of the Singapore Botanic Gardens* 48: 1–22.

Lee, H. S., LaFrankie, J. V., Tan, S., Yamakura, T., Itoh, A. & Ashton, P. S. 1999. The 52-ha forest research plot at Lambir Hills National Park, Sarawak, Malaysia. Volume 2: Maps and diameter tables. Sarawak Forest Department, Kuching, Sarawak. Unpublished report. 601 pp.

Liechti, P., Roe, F. W. & Haile, N. S. 1960. *The Geology of Sarawak, Brunei and the Western Part of North Borneo.* British Territories in Borneo Geological Survey. 360 pp.

Manokaran, N. & LaFrankie, J. V. 1990. Stand structure of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3: 14–24.

Manokaran, N., LaFrankie, J. V., Kochummen, K. M., Quah, E. S., Klahn, J. E., Ashton, P. S. & Hubbell, S. P. 1990. *Methodology for the 50-ha Research Plot at Pasoh Forest Reserve.* Research Pamphlet No. 104. Forest Research Institute Malaysia, Kepong. 75 pp.

Morley, R. J. 2000. *Origin and Evolution of Tropical Rain Forests.* John Wiley & Sons, New York. 362 pp.

Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T., Sato, K., Miguchi, H., Nagamasu, H., Ogino, K., Teo, S., Hamid, A. A. & Lee, H. S. 2000. Impact of severe drought associated with the 1997–1998 El Nino in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16: 355–367.

Newbery, D. M. 1991. Floristic variation within kerangas (heath) forest: re-evaluation of data from Sarawak and Brunei. *Vegetatio* 96: 43–86.

Newbery, D. M., Alexander, I. J. & Rother, J. A. 1997. Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. *Ecological Monographs* 67: 367–409.

Newbery, D. M., Campbell, E. J. F., Lee, Y. F., Ridsdale, C. E. & Still, M. J. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Philosophical Transactions of the Royal Society, London, Series B.* 335: 341–356.

Palmiotto, P. A. 1998. The role of specialization in nutrient-use efficiency as a mechanism driving species diversity in a tropical rain forest. Ph.D. thesis, Yale University, New Haven, USA. 282 pp.

Phillips, O. L., Hall, P., Gentry, A. H., Sawyer, S. A. & Vasquez, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Science* 91: 2805–2809.

POTTS, M. D., ASHTON, P. S., KAUFMAN, L. S. & PLOTKIN, J. B. 2002. Habitat patterns in tropical rain forests: A comparison of 105 plots in northwest Borneo. *Ecology* 83.

PROCTOR, J., ANDERSON, J. M., CHAI, P. & VALLACK, H. W. 1983. Ecological studies in four contrasting rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *Journal of Ecology* 71: 237–260.

PROCTOR, J., LEE, Y. F., LANGLEY, A. M., MUNRO, W. R. C. & NELSON, T. N. 1988. Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *Journal of Ecology* 76: 320–340.

RENNOLLS, K. & LAUMONIER, Y. 2000. Species diversity structure analysis at two sites in the tropical rain forest of Sumatra. *Journal of Tropical Ecology* 16: 253–270.

RICHARDS, P. W. 1936. Ecological observations on the rain forest of Mt. Dulit, Sarawak. Part I. *Journal of Ecology* 24: 1–37.

RICHARDS, P. W. 1996. *The Tropical Rain Forest: An Ecological Study.* Cambridge University Press, Cambridge. 575 pp.

SOEPADMO, E., & WONG, K. M. 1995. *Tree Flora of Sabah and Sarawak.* Volume 1. Forest Research Institute Malaysia, Kepong. 513 pp.

SOEPADMO, E., WONG, K. M. & SAW, L. G. 1996. *Tree Flora of Sabah and Sarawak.* Volume 2. Forest Research Institute Malaysia, Kepong. 443 pp.

SOLLINS, P. 1998. Factors influencing species composition in tropical lowland rain forest: Does soil matter? *Ecology* 79: 23–30.

TURNER, I. M. 2001. An overview of the plant diversity of Southeast Asia. *Asian Journal of Tropical Biology* 4: 1–16.

WALSH, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of Borneo since the late nineteenth century and possible implications for rain forest dynamics. *Journal of Tropical Ecology* 12: 385–407.

WATSON, H. 1985. Lambir Hills National Park: Resource inventory with management recommendations. National Parks and Wildlife Office, Forest Department, Kuching, Sarawak, Malaysia.,

WHITMORE, T. C. 1984. *Tropical Rain Forests of the Far East.* Oxford University Press, Oxford. 352 pp.

YAMADA, T., ITOH, A., KANZAKI, M., YAMAKURA, T., SUZUKI, E & ASHTON, P. S. 2000. Local and geographical distributions for a tropical tree genus, *Scaphium* (Sterculiaceae) in the Far East. *Plant Ecology* 148: 23–30.

YAMAKURA, T., KANZAKI, M., ITOH, A., OHKUBU, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1995. Topography of a large-scale research plot established within a tropical rain forest at Lambir, Sarawak. *Tropics* 5: 41–56.

YAMAKURA, T., KSANZAKI, M., ITOH, A., OHKUBO, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1996. Forest structure of a tropical rain forest at Lambir, Sarawak with special reference to the dependency of its physiognomic dimensions on topography. *Tropics* 6: 1–18.