

## CONTRASTING STRUCTURE AND COMPOSITION OF THE UNDERSTORY IN SPECIES-RICH TROPICAL RAIN FORESTS

JAMES V. LAFRANKIE,<sup>1,15</sup> PETER S. ASHTON,<sup>2</sup> GEORGE B. CHUYONG,<sup>3</sup> LEONARDO CO,<sup>4</sup> RICHARD CONDIT,<sup>5</sup>  
STUART J. DAVIES,<sup>2</sup> ROBIN FOSTER,<sup>6</sup> STEPHEN P. HUBBELL,<sup>7</sup> DAVID KENFACK,<sup>8</sup> DANIEL LAGUNZAD,<sup>9</sup> ELIZABETH C. LOSOS,<sup>10</sup>  
NOOR SUPARDI MD. NOR,<sup>11</sup> SYLVESTER TAN,<sup>12</sup> DUNCAN W. THOMAS,<sup>13</sup> RENATO VALENCIA,<sup>14</sup> AND GORKY VILLA<sup>14</sup>

<sup>1</sup>Smithsonian Tropical Research Institute, c/o National Institute of Education, 1 Nanyang Walk, 637616 Singapore

<sup>2</sup>Arnold Arboretum, Harvard University, Cambridge, Massachusetts 02138 USA

<sup>3</sup>Department of Life Sciences, University of Buea, P.O. Box 63, Buea, Republic of Cameroon

<sup>4</sup>Conservation International, #5 South Lawin Road, PhilAm Homes, Quezon City, Philippines

<sup>5</sup>Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948 USA

<sup>6</sup>Botany Department, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605-2496 USA

<sup>7</sup>Department of Plant Biology, University of Georgia, Athens, Georgia 30602-7271 USA

<sup>8</sup>Missouri Botanical Garden, Department 43, 4500 Shaw Boulevard, St. Louis, Missouri 63110 USA

<sup>9</sup>Institute of Biology, University of the Philippines, Diliman, Manila, Philippines

<sup>10</sup>Center for Tropical Forest Science, 1100 Jefferson Drive, Suite 3123, P.O. Box 37012, MRC 705,  
Washington, DC 20013-7012 USA

<sup>11</sup>Forest Research Institute of Malaysia, Kepong, 52109 Malaysia

<sup>12</sup>Sarawak Forest Corporation, Research Center, Kuching, Sarawak, Malaysia

<sup>13</sup>Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA

<sup>14</sup>Department of Biological Sciences, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador

**Abstract.** In large samples of trees  $\geq 1$  cm dbh (more than 1 million trees and 3000 species), in six lowland tropical forests on three continents, we assigned species with  $>30$  individuals to one of six classes of stature at maturity (SAM). We then compared the proportional representation of understory trees (1–2 cm dbh) among these classes. The understory of the three Asian sites was predominantly composed of the saplings of large-canopy trees whereas the African and American sites were more richly stocked with trees of the smaller SAM classes. Differences in class representation were related to taxonomic families that were present exclusively in one continent or another. Families found in the Asian plots but not in the American plot (e.g., Dipterocarpaceae, Fagaceae) were predominantly species of the largest SAM classes, whereas families exclusive to the American plots (e.g., Melastomataceae sensu stricto, Piperaceae, and Malvaceae [Bombacacoidea]) were predominantly species of small classes. The African plot was similar to Asia in the absence of those American families rich in understory species, while similar to America in lacking the Asian families rich in canopy species. The numerous understory species of Africa were chiefly derived from families shared with Asia and/or America. The ratio of saplings (1–2 cm dbh) to conspecific canopy trees ( $>40$  cm dbh) was lower in American plots than in the Asian plots. Possible explanations for these differences include phenology, moisture and soil fertility regimes, phyletic constraints, and the role of early successional plants in forest development. These results demonstrate that tropical forests that appear similar in tree number, basal area, and the family taxonomy of canopy trees nonetheless differ in ecological structure in ways that may impact the ecology of pollinators, dispersers, and herbivores and might reflect fundamental differences in canopy tree regeneration.

**Key words:** Cameroon; Ecuador; Malaysia; regeneration; tropical forest; understory.

### INTRODUCTION

High-diversity tropical forests share a broad structural uniformity that includes basal area of 30–45 m<sup>2</sup>/ha, densities of trees  $\geq 10$  cm dbh of 400–500 trees/ha, with  $\sim 10$  times that density of trees  $< 10$  cm dbh (see comparative tables in Gentry [1988], Davies and Becker [1996], Richards [1996], Dallmeier and Comiskey [1998],

Phillips et al. [1998], and Losos and Leigh [2004]). Such forests also share several dominant taxonomic families of canopy trees such as the Fabaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Annonaceae, and Rubiaceae (Gentry 1988). Those families that predominate in only one hemisphere, most significantly the Dipterocarpaceae in Asia, are sometimes seen to have an “ecological equivalent” in, for example, the caesalpinoid Legumes in the Neotropics (Gentry 1993). Within this orthodoxy, individual species are considered fungible elements representing a series of ecological types, each defined in large measure by the phyletic limitations of the family

Manuscript received 29 November 2004; revised 3 January 2006; accepted 4 January 2006. Corresponding Editor: K. D. Woods.

<sup>15</sup> E-mail: jlafrankie@yahoo.com

type. The perception of ecological congruence is reinforced by remarkable instances of ecological convergence across continents, e.g., the ruderal myrmecophytes *Macaranga* (Euphorbiaceae) and *Cecropia* (Cecropiaceae), nectivorous birds (Karr and James 1975), the trophic structure of non-volant mammals (Eisenberg 1981), and the nutmegs (Myristicaceae) dispersed by toucans in America (Howe 1982) and hornbills in Asia (Kinnaird 1998). Such a view of tropical forest uniformity and ecological equivalence is amenable to a neutral hypothesis of community organization (Hubbell 2001).

Most of the data available for global comparisons of tropical forest structure are based on samplings of the mature trees that form the forest canopy. The free-standing woody plants of the understory with stems 1–2 cm dbh are less well known with regard to comparative ecology. Some species have a small stature at maturity (SAM) and reproduce without ever exceeding a few centimeters in diameter. Other understory trees are the juveniles of forest giants and, should they live, grow for decades before reaching reproductive size. If forests should differ in the proportion of these stature classes then this will influence the ecology of the understory with regard to the number of flowers and fruits and availability of sugars and lipids. Differences may also suggest differences in forest dynamics. Teasing apart such a compositional difference is difficult because the thousands of small individuals must be segregated to species in the field using only sterile characters and then considered in light of the adult stature of the species.

In this paper we compare the relative understory abundance of species that differ in their stature at maturity in six tropical rain forests from around the world in order to test the uniformity of forest composition and indirectly to compare likely dynamics. We ask: (1) Does the relative importance of stature types differ among forests? (2) Do the differences relate to taxonomy? (3) Are there differences among forests in the density of juveniles of those species that reach a large stature at maturity?

#### METHODS AND STUDY SITES

We established large permanent plots in six forests, one in Africa, two in America, and three in Asia. The African site is in Korup National Park, along the western border of Cameroon. The Neotropical sites are in Barro Colorado Island, Panama, and Yasuni National Park, Ecuador. The three Asian sites are in Pasoh Forest Reserve in south-central Peninsular Malaysia, Lambir Hills National Park, Sarawak, East Malaysia, and Palanan Wilderness Area (Northern Sierra Madre Nature Reserve), Luzon Island, Philippines. Details of the site descriptions, basic forest and plot composition, and references to more extensive ecological findings from the plots can be found in Losos and Leigh (2004) and in Okuda et al. (2003) for Pasoh and in Roubik and Sakai (2004) for Lambir.

Plots were of 50 ha area (25 ha in Yasuni, 16 ha in Palanan). All trees  $\geq 1$  cm dbh were tagged and identified to species, their location mapped to the nearest 10 cm, and the trunk measured to 1 mm dbh. Individual trees were enumerated with identical methods (Manokaran et al. 1990, Condit 1998, Losos and Leigh 2004).

The plots include more than 1 million trees and 3500 species. Species were determined by comparison of fertile plot specimens with annotated material in herbaria. However, most individual trees in the samples (and all juveniles) were identified using sterile characters by teams assembled specifically for the purpose. Identification methods, quality control, and level of documentation were similar at all sites and  $>97\%$  of the trees could be identified to known species or recognized as a species new to science. Lists of voucher specimens have been published (see references in Losos and Leigh [2004]) except for Korup and Palanan. Family taxonomy follows current phylogenetic information (APG, 1998 and associated updates).

Stature at maturity was determined for species with  $>30$  individuals by dropping the largest diameter and taking the mean of the next three largest diameters. The SAM classes were determined at the following dbh intervals: (1) 1–5 cm; (2)  $>5$ –10 cm; (3)  $>10$ –20 cm; (4)  $>20$ –40 cm; (5)  $>40$ –80 cm; and (6)  $\geq 80$  cm. In some cases ( $<2\%$ ) species were assigned to a larger class when a much larger conspecific individual was known from outside the plot. Alternative quantitative methods of assessing SAM from diameter data, such as D. A. King (1996 and *personal communication*) or Thomas' (1996) asymptotic method are preferable when the aim is comparative allometry, that is, when examining the growth trajectories of individual species. However, here we aim at class comparison among species, and alternative methods of determining specific maximum diameters did not alter the relative class positions.

Analysis for Yasuni and Korup was based on the single census so far taken, while at other sites analysis was based on the following census years: Pasoh, 1987; Lambir, 2003; Palanan, 2003; and BCI, 1995. Statistical comparisons among sites tallied the 50 1-ha sample plots at Korup, Lambir, and Pasoh and 25 1-ha plots at Yasuni and 16 1-ha plots in Palanan. Tabulations and statistics were calculated with SAS version 8 (SAS Institute, Cary, North Carolina, USA).

#### RESULTS

##### *Representation of stature classes in the understory*

The sites are generally comparable with regard to forest structure (Table 1). Individual paired comparisons of mean densities within dbh doubling classes among sites ( $t$  test, Bonferroni [Dunn]-corrected, 0.001 level with similar results for GT2 [SAS version 8] or Tukey) do not differ for diameter class 1–2 cm dbh. The largest departure from uniformity lies in the very rich stocking of very large trees in the Bornean plot, Lambir, which

TABLE 1. Summary comparison of study sites and permanent plots of all trees  $\geq 1$  cm dbh.

Site	Location	Plot size (ha)	Altitude (m)	Annual rainfall (mm)	No. months <100 mm rainfall	Tree density (no./ha <sup>-1</sup> )		
						$\geq 1$ cm dbh	1–2 cm dbh	<10 cm dbh
Korup: Cameroon	5°0' N, 8°52' E	50	500	~5000	2–3	6580 (987)	2760 (498)	6088 (989)
BCI: Panama	9°9' N, 79°51' W	50	140	2551	3	4882 (480)	1964 (260)	4299 (451)
Yasuní: Ecuador	0°41' S, 76°24' W	25	235	2826	0	6094 (820)	2357 (473)	5392 (792)
Lambir: Malaysia	4°20' N, 113°50' E	50	100	2300	0	7068 (974)	3155 (562)	6430 (927)
Pasoh: Malaysia	2°58' N, 102°18' E	50	100	1850	0	6477 (872)	2566 (523)	5922 (870)
Palanan: Philippines	17°02' N, 122°22' E	16	100	3379	0	5378 (742)	2097 (402)	5822 (750)

Notes: Tallies are the mean (with SD in parentheses) for the 50 1-ha plots at each site (25 1-ha plots in Yasuní and 16 1-ha plots at Palanan, Philippines). “BCI” indicates Barro Colorado Island.

yields the largest basal area. Otherwise, Lambir is similar to Yasuní in structure as well as species richness and diversity values. These two sites record the greatest tree diversity yet documented. The principal anomaly was the high dominance values (Berger-Parker index) at BCI, Panama, where in most 1-ha<sup>2</sup> areas two or three species comprise 30% of the trees.

Representation of SAM classes differed significantly among the sites (Fig. 1). In general, at each site the middle classes (2–5) were more abundant than the extremes; however, the mode differed among sites: class 2 at BCI, class 3 at Yasuní and Korup, and class 4 at Pasoh, Lambir, and Palanan. The understory at Korup, BCI, and Yasuní included more individuals of classes 1

and 2 (849, 1121, and 977 trees/ha or 39.9%, 28.8%, and 34.4 % of individuals, respectively) than did the understory in Lambir, Pasoh, or Palanan (394, 574, and 474 or 17.6%, 16.8%, and 23.1%, respectively; paired Dunn *t* test, Bonferroni corrected,  $P < 0.0001$ ; reciprocal paired comparisons of percentage differences, Komolgorov-Smirnov,  $P < 0.0001$ ). The three Asian sites were generally similar to one another in the relatively low representation of small SAM classes and high representation of large SAM classes in the understory. The SAM classes 5 and 6 were well represented in the understory of the Asian plots of Lambir, Pasoh, and Palanan, where the fraction was 34.6%, 18.7%, and 30.5%, respectively. In Yasuní the representation of these largest two classes

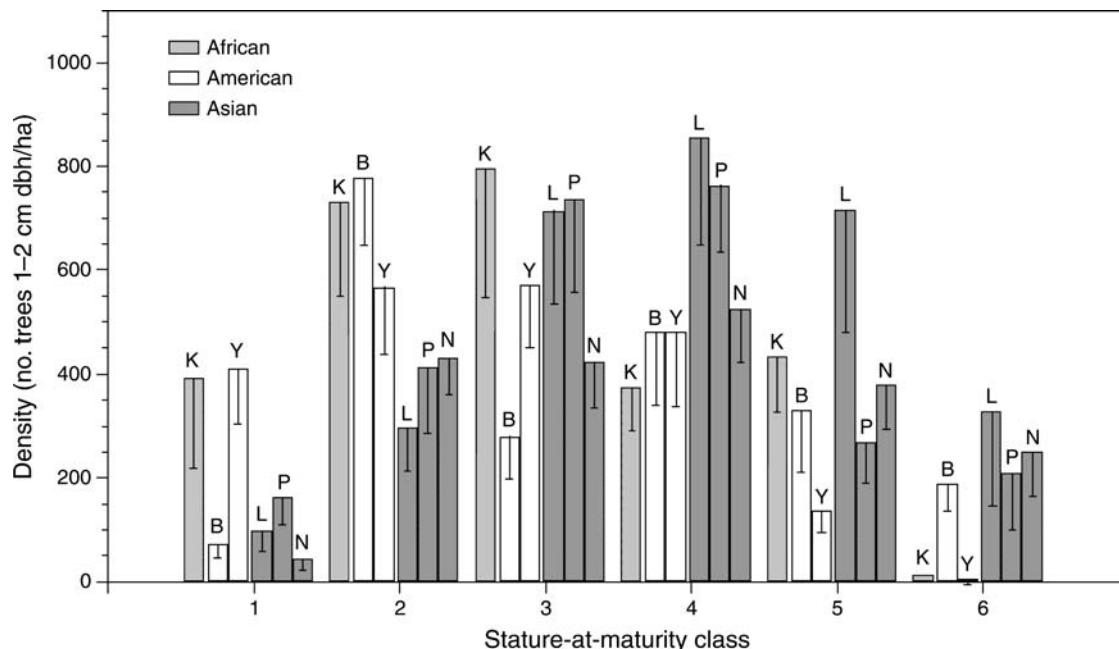


FIG. 1. Density (mean and SD) of trees 1–2 cm dbh (no./ha) per site by stature-at-maturity (SAM) class based on 50 1-ha samples per site except Yasuní (25 1-ha samples) and Palanan (16 1-ha samples). From left to right, the African site is Korup (K); the American sites are Yasuní (Y) and Barro Colorado Island (B); the Asian sites are Lambir (L), Pasoh (P), and Palanan (N, Northern Sierra Madre Natural Park). All classes reject the hypothesis of equal means within class (*t* test, Bonferroni [Dunn] corrected,  $P < 0.001$  level with similar results for GT2 or Tukey); 99% confidence intervals are given as a guide to significance of pairwise comparisons. The SAM classes were determined at the following dbh intervals: (1) 1–5 cm; (2) >5–10 cm; (3) >10–20 cm; (4) >20–40 cm; (5) >40–80 cm; and (6)  $\geq 80$  cm.

TABLE 1. Extended.

Tree density (no./ha <sup>-1</sup> )				Flora (no./ha)			Diversity indices for trees >1 cm dbh/ha		
≥10 cm dbh	≥20 cm dbh	≥30 cm dbh	Basal area (m <sup>2</sup> /ha)	Families	Genera	Species	Fisher's alpha	Shannon	Berger-Parker
491 (50)	192 (17)	83 (15)	31.3 (4.2)	46	142	228	44.4	3.91	14.74
424 (44)	155 (15)	82 (11)	32.1 (4.0)	48	120	169	34.6	3.65	17.3
702 (53)	219 (23)	81 (17)	33.0 (3.9)	73	227	639	190.5	5.59	5.24
637 (91)	234 (43)	119 (26)	43.5 (6.6)	70	194	634	158.0	5.39	5.68
554 (42)	174 (17)	78 (10)	32.2 (2.9)	73	210	484	120.0	5.28	4.07
627 (55)	215 (20)	97 (15)	39.15 (3.5)	56	130	235	47.7	4.57	6.16

was very poor by comparison, with a total of 6.5% of the 1–2 cm dbh trees. Barro Colorado Island, Panama, showed a relatively high representation of class 6 saplings, although densities were still below those for the Asian sites. Korup differed from the other five sites in that instead of showing a peak of abundance in the middle stature classes, Korup had a larger fraction (15.8%) of plants in class 5 (>40–80 cm dbh) compared with 12% in class 4 (>20–40 cm dbh).

The contrast in class representation between Lambir (Asia) and Yasuní (South America) was especially marked and is emphasized when we compared rankings of the species from most abundant to least abundant. The most abundant understory plant at Lambir was the sapling of the class 6 tree *Dryobalanops aromatica* (Dipterocarpaceae). Furthermore, four of the 10 most abundant species were class 6, and no species of classes 1 or 2 were among the top 10. In contrast, at Yasuní the most abundant species was the class 1 *Matisia oblongifolia* (Malvaceae: Bombacoideae), while the first seven species in abundance were either class 1 or 2, the first class 5 species was ranked 24th, and the first class 6 species was ranked at 103rd place.

#### SAM and taxonomic family

The differences in SAM representation among sites were related to taxonomic composition at the family level. Twenty-four families were represented in American plots but not in Asian plots, while 37 families were in Asian plots but not in American. The differences were strongly asymmetric with regard to the stature at maturity (Fig. 2). Families distinctively Asian are predominantly of species in large-stature classes (Dipterocarpaceae, Fagaceae, Alangiaceae, Ixonanthaceae, Symplocaceae, and Theaceae), while families distinctively South American are much more likely to be species in small-stature classes (Piperaceae, Solanaceae, and Acanthaceae.) The family Dipterocarpaceae, dominant in Asia and not found in Yasuní, was an important contributor to this trend, comprising 54% of the 1–2 cm dbh trees in families exclusively in the Asian plots and dominating stature class 6. However, the effect remains even with the exclusion of the Dipterocarps.

The Africa plot composition was more complicated. Families found exclusively in Korup were few and, of

these, only the Scytopetalaceae was at all abundant. Most of the class 1 and class 2 species at Korup were of families shared among all sites, such as Malvaceae: Sterculioidae and Euphorbiaceae. The African plot was similar to the Asian plots in the absence or paucity of those American families rich in understory species, while Korup was similar to the American plots in lacking those Asian families rich in canopy species.

#### Number of canopy tree saplings

When we considered only species with at least one tree ≥40 cm dbh and calculated the log of the ratio of saplings (1–2 cm dbh) to large trees we found great

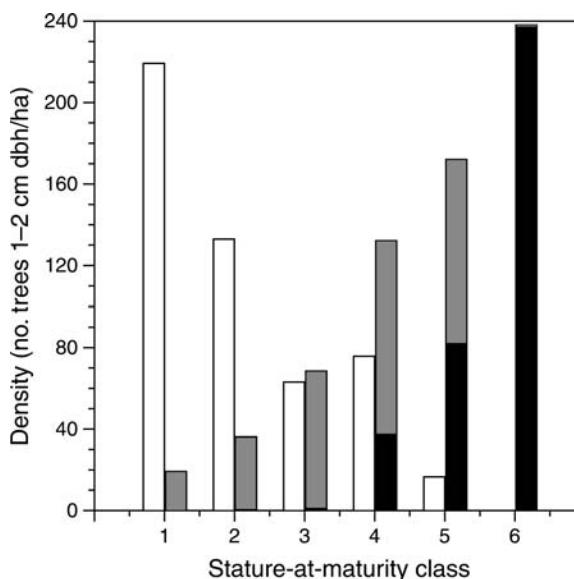


FIG. 2. Comparison of stature distribution of trees 1–2 cm dbh for families differing in continental distribution; open bars show the mean values for families in either of the two Neotropical plots but not in the Asian plots; the gray bars show the mean values for those families in any Asian plot and not in Neotropical plots (the black portion represents the family Dipterocarpaceae); distributions differ between one another and in comparison with the stature distribution of all 1–2 cm dbh individuals (i.e., Fig. 1), chi-square probability is  $P < 0.0001$ . The stature-at-maturity classes were determined at the following dbh intervals: (1) 1–5 cm; (2) >5–10 cm; (3) >10–20 cm; (4) >20–40 cm; (5) >40–80 cm; and (6) ≥80 cm.

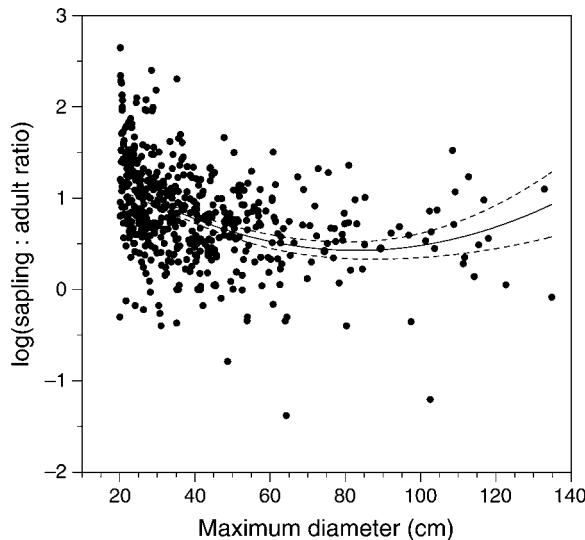


FIG. 3. Polynomial regression of the log of the ratio of number of saplings (1–2 cm dbh) to number of canopy trees ( $\geq 20$  cm dbh) vs. the maximum dbh for species in the 50-ha plot in Lambir, Sarawak, plotted with 95% confidence interval (dashed lines). Ratio data are normally distributed ( $P < 0.0001$ ); regression coefficients including quadratic coefficients are highly significant ( $P < 0.0001$ ). All individual coefficients differ significantly between Lambir and Yasuní ( $P < 0.0001$ ).

differences among sites in the mean (median) values: Lambir, 3.05 (3.03); Palanan, 2.82 (2.73); Pasoh, 2.44 (2.20); Yasuní, 2.12 (2.20); Korup, 1.92 (1.75); and BCI, 1.51 (1.39).

The mean value treats equally all species irrespective of their quantitative importance in the canopy composition, and this obscures the most striking contrast among sites, which was sapling representation of the abundant species. In Lambir, 70.1% of canopy species had a sapling/canopy tree ratio  $>10:1$ , and these species represented 54.9% of trees  $>40$  cm dbh. Similarly, at Pasoh, species with  $>10:1$  ratio represented 62.2% of species and 55.5% of the canopy. In contrast to Asia, at Yasuní, only 38.4% of species had a sapling canopy ratio  $>10:1$ , and these species accounted for only 24% of the canopy. Thus, about three-fourths of the canopy trees in the Yasuní plot were of species with relatively few saplings.

The exact relationship of sapling abundance to canopy abundance is more quantitatively complicated than the above summary might imply. Individual species vary in size at first reproduction and in maximum diameter, as well as in the number of large and small trees. Some of this complexity can be teased out by examining the two most sharply contrasting sites: Lambir (Asia) and Yasuní (America). We compared the relative sapling abundance by maximum diameter in the following way. For each site we calculated the log of the ratio of saplings 1–2 cm dbh to conspecific trees  $>20$  cm dbh and plotted the polynomial regression of that ratio against the maximum dbh (Figs. 3 and 4). The

regressions of the two sites differed significantly in all coefficients ( $P < 0.0001$ ). Lambir had a significant quadratic coefficient, while Yasuní was not significantly different from linear. Species of large stature at Lambir were represented by up to 10 times more saplings than similar-sized species at Yasuní. While the family Dipterocarpaceae, with many large-statured species and often dense sapling populations, contributed greatly to this difference, Lambir and Yasuní still differed when the family was removed.

#### DISCUSSION

The results demonstrate that lowland tropical forests can share nearly identical outward form with regard to the number of trees of different diameter classes and share a broad range of families among their canopy trees and yet still differ in fundamental ways. Lambir and Yasuní are exemplary of that point. The two forests are nearly identical in the stocking of trees of different diameters, excepting only the higher density of very large trees at Lambir. The species diversity is nearly identical, and the taxonomic composition of the canopy, excepting the abundant Dipterocarpaceae at Lambir, is similar at the family level. And yet the mature-size-class apportionment of the understory is sharply contrasting, as is the number of saplings per conspecific canopy tree.

How general are these differences, and do they reflect general differences among continents? The main result for Yasuní, an understory rich in flowering trees of small

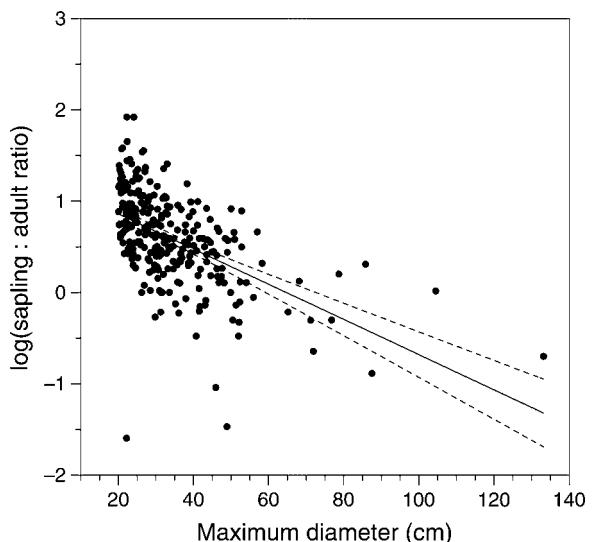


FIG. 4. Linear regression of the log of the ratio of the number of saplings (1–2 cm dbh) to the number of canopy trees ( $\geq 20$  cm dbh) vs. the maximum dbh for species in the 25-ha plot in Yasuní, Ecuador, plotted with 95% confidence interval (dashed lines). Ratio data are normally distributed ( $P < 0.0001$ ), the quadratic coefficient of polynomial regression was not significant, and the linear regression is plotted; all regression terms are highly significant ( $P < 0.0001$ ). All individual coefficients differ significantly between Lambir and Yasuní ( $P < 0.0001$ ).

stature, is consistent with published information from Meso-America and northern South America that suggests that a rich abundance of class 1 and class 2 species are found wherever the sites are wet and the soils moderately rich (Gentry and Emmons 1987, Duivenvoorden 1994, Hartshorn and Hammel 1994:82, McDade et al. 1994). It also extends the results of Pitman et al. (2002), who found that trees of smaller mature stature were richer at Yasuni than at Manu in Peru, a difference they partially attributed to the greater moisture at Yasuni. (This study, however, concerned only trees >10 cm dbh.) However, in seasonal Neotropical sites on poor soils the class 1 and class 2 trees appear to be fewer in number (Gentry and Emmons 1987).

The floristic component of stature differences among the plots is more easily confirmed as general. For example, while the genus *Piper* (Piperaceae) includes many class 1 and class 2 trees in the Neotropics, the many Asian species in this family, 120 species in the Philippines alone (Merrill 1926), are exclusively small herbs and climbers and never freestanding trees. Similarly, the advanced clades of the Melastomes, which are so abundant in the Neotropics, are represented in Asia by herbs and climbers rather than by trees. The families Malvaceae [Bombacoidae], Bignoniaceae, Nyctaginaceae, Solanaceae, and Acanthaceae are all poorly represented or absent in the Asian understory, and these are significant contributors to the class 1 flora in America.

The finding of a relatively low number of saplings of many canopy species at Yasuni, and to a lesser extent at BCI, requires confirmation from a broader range of sites. However, such data that do exist are in general conformity with the findings presented here. For example, Clark and Clark (1992) surveyed 150 ha at La Selva, Costa Rica, and noted all saplings and adults for six common emergent tree species. All six of the species had more trees in the large class (>10 cm dbh) than the number in the small class (1–4 cm dbh). These species would be among the most abundant canopy species at any of our study sites; however, the number of saplings 1–4 cm dbh is nearly one-tenth that of any of the 50 most abundant species at Lambir, and the Lambir tallies were restricted to only 1–2 cm dbh.

These differences in patterns of understory abundance across stature-at-maturity classes might be explained in several ways. A phenological hypothesis for the observed differences follows from Janzen's (1970, 1974, 1977) claim that Asian tropical forest trees are more prone to produce seeds in synchronized, irregular mast crops (documented also by Sakai et al. [1999], Yasuda et al. [1999], and Sakai 2002), while species of wet, fertile Neotropical forests flower more frequently (Bawa et al. 2003). The resulting seed predator satiation in Asian forests may allow establishment of canopy saplings at high densities, which would, in turn, competitively suppress class 1 trees. In Neotropical forests, continu-

ously high seed predation may lead to low densities of canopy saplings. Phenological differences may, in turn, spring from different selective regimes. For example, flowering cycles in Borneo generally coincide with the El Niño Southern Oscillation cycle (Curran et al. 1999), but it is not known whether such climatic cycles produce less consistent environmental cues in Africa or South America.

An alternative explanation is that the composition of the understory is driven by environmental factors of moisture and soil fertility (Gentry and Emmons 1987). An understory with greater density and greater diversity is generally considered to be a feature of pre-montane forests, especially over volcanics (P. S. Ashton, *personal communication*), and was the chief explanation offered by Pitman et al. (2002) to explain the rich class 1 flora at Yasuni. Testing this would require a broader range of understory samples from varied sites with species described with respect to their stature at maturity.

The relation of the size class differences to family-level taxonomic differences suggests that there might be an explanation found in deep phyletic differences among the continents. Although many taxonomic families are found in lowland forests around the world (Gentry 1988), the ecological representation is not always parallel. Palm trees are an abundant part of the lowland tropical forest of America, especially Meso-America and northern South America. At least a few species, such as *Welfia*, *Socotrea*, and *Iriartea*, are typically among the most abundant species at 10 cm dbh and above. Nothing parallel to those examples is found in the lowland forests of Asia, where palms are often abundant as caespitose understory plants and especially as climbers, the latter habit in turn being largely absent in America. Similarly, the Sapindaceae are abundant trees in most Asian forests but in America they are conspicuous principally as climbers, a habit that in turn is not developed in Asia. Other examples of deep ecological differences within a taxonomic family between Asia and America, including Annonaceae, Fagaceae, and Lecythidaceae, are described in LaFrankie (2004). Webb et al. (2002) describe how the relationship between phylogeny and ecology might be pursued in the future.

These differences might also be based on differences in succession history. Forests in America and Africa have well-documented large-scale disturbance histories dating back several millennia. There is evidence from rain forests in Cameroon and Nigeria, for example, that current vegetation remains influenced by previous disturbance history hundreds of years ago (Richards 1973, White and Oates 1999, van Gemerden et al. 2003). It may be that proliferation of small-statured species in forests is favored by frequent human disturbance.

Irrespective of the explanation for these differences in understory class composition, the most conspicuous consequence of the differences is that Yasuni, BCI, Korup, and similar forests of America and Africa must have a much larger number of flowers and fruit in the

understory than do forests in Asia. When combined with the differences in phenology, we would anticipate that the understory of American tropical forests will provide relatively abundant, or at least more consistently available, volumes of sugars and lipids in sharp contrast to the relative sterility of the Asian understory. This difference in resource availability could explain the lower number and diversity of frugivorous bats in Asia (Francis 1990) and the near-absence of obligate frugivorous birds in the understory, which in turn would impact selection on plant dispersal syndromes (see Ingle 2003, Corlett 1998).

The results here add to the growing list of studies that demonstrate major differences in the ecology of widely separated tropical forests (see LaFrankie 2004, Primack and Corlett 2004). These differences include termite ecology (Davies et al. 2003), primate ecology (Reed and Fleagle 1995, Kappeler and Heymann 1996), the role of bees (Michener 1979), dispersal ecology (Francis 1990, Corlett 1998, Ingle 2003 and citations therein), and pollination ecology (Corlett 2004). Such differences challenge the orthodox view of a generalized form, structure, and dynamics among lowland tropical forests (Gentry 1988), as well as the neutral theory of community assembly (Hubbell 2001).

#### ACKNOWLEDGMENTS

The Center for Tropical Forest Science is an administrative unit of the Smithsonian Tropical Research Institute dedicated to the development and maintenance of large-scale long-term tropical forest plots. The program is co-sponsored in Asia by the Arnold Arboretum of Harvard University. Funding sources since 1985 for the overall program and the four relevant sites include: Arnold Arboretum of Harvard University, Smithsonian Tropical Research Institute, the Government of Malaysia, the National Science Foundation (USA), Monbusho of Japan, Conservation Food and Health, Rockefeller Foundation, Celerity Foundation, National Institute of Health, and the National Institute of the Environment Japan. We thank the Director of STRI, Ira Rubinoff, and Director of the Arnold Arboretum, Robert Cook, for their long-standing personal support of the program. At individual sites, we thank: at Pasoh, N. Manokaran (retired), Salleh Mohd. Nor (retired), the late K. M. Kochummen, and Quah Eng Seng (retired); at Lambir, Lee Hua Seng (retired), T. Yamakura, and Akira Itoh; at Yasuni, K. Romoleroux, H. Balslev, Jens-C. Svenning, and E. Magård; at Korup, George Angher, S. N. Moses, and N. C. Songwe.

#### LITERATURE CITED

- APG [Angiosperm Phylogeny Group]. 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* **85**:531–553.
- Bawa, K. S., H. S. Kang, and M. H. Grayum. 2003. Relationships among time, frequency, and duration of flowering in tropical rain forest trees. *American Journal of Botany* **90**:877–887.
- Clark, D. A., and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* **62**:315–344.
- Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer-Verlag, Berlin, Germany.
- Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalaysian) Region. *Biological Reviews* **73**:413–448.
- Corlett, R. T. 2004. Flower visitors and pollination in the Oriental (Indomalaysian) Region. *Biological Reviews* **79**:497–532.
- Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita, and H. Haeruman. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**:2184–2188.
- Dallmeier, F. and J. Comiskey, editors. 1998. Forest biodiversity in North, Central and South America, and the Caribbean. United National Educational Scientific and Cultural Organization Man and the Biosphere series. Volume 21. Parthenon, Paris, France.
- Davies, R., P. Eggleton, D. Jones, F. Gathorne-Hardy, and L. Hernandez. 2003. Evolution of termite functional diversity: analysis and synthesis of local, ecological and regional influences on local species richness. *Journal of Biogeography* **30**:847–877.
- Davies, S. J., and P. Becker. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. *Journal of Tropical Forest Science* **8**: 542–569.
- Duivenvoorden, J. F. 1994. Vascular plant-species counts in the rain-forests of the middle Caqueta area, Colombian Amazonia. *Biodiversity and Conservation* **3**:685–715.
- Eisenberg, J. 1981. The mammalian radiations. University of Chicago Press, Chicago, Illinois, USA.
- Francis, C. M. 1990. Trophic structure of bat communities in the understory of lowland dipterocarp forest in Malaysia. *Journal of Tropical Ecology* **6**:421–431.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on geographic and environmental gradients. *Annals of the Missouri Botanical Garden* **75**:1–34.
- Gentry, A. H. 1993. A field guide to the families and genera of woody plants of northwest South America. Conservation International, Washington, D.C., USA.
- Gentry, A. H., and L. H. Emmons. 1987. Geographical variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* **19**:216–227.
- Hartshorn, G. S., and B. E. Hammel. 1994. Vegetation types and floristic patterns. Pages 73–89 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. *La Selva: ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Howe, H. F. 1982. Fruit production and animal activity in two tropical trees. Pages 189–200 in E. G. Leigh, A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term change*. Smithsonian Institution Press, Washington, D.C., USA.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology. Princeton University Press, Princeton, New Jersey, USA.
- Ingle, N. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia* **134**:251–261.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501–528.
- Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* **4**:69–103.
- Janzen, D. H. 1977. Promising directions of study in tropical animal–plant interactions. *Annals of the Missouri Botanical Garden* **64**:706–736.
- Kappeler, P. M., and E. W. Heymann. 1996. Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal of the Linnean Society* **59**:297–326.
- Karr, J. R., and F. C. James. 1975. Ecomorphological configurations and convergent evolution. Pages 258–291 in M. L. Cody and J. M. Diamond, editors. *Ecology and*

- evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.
- King, D. A. 1996. Allometry and life history of tropical trees. *Journal of Tropical Ecology* **12**:25–44.
- Kinnaird, M. F. 1998. Evidence for effective seed dispersal by the Sulawesi red-knobbed hornbill, *Aceros cassidix*. *Biotropica* **30**:50–55.
- LaFrankie, J. V. 2004. Lowland tropical rain forests of Asia and America: parallels, convergence and divergence. Pages 178–190 in D. Roubik and S. Sakai, editors. *Ecology of Lambir Hills National Park, Sarawak*. Springer Verlag, Tokyo, Japan.
- Losos, E. C., and E. G. Leigh, editors. 2004. *Forest diversity and dynamism: findings from a network of large-scale tropical forest plots*. Chicago University Press, Chicago, Illinois, USA.
- Manokaran, N., J. V. La Frankie, K. M. Kochummen, E. S. Quah, J. E. Klahn, P. S. Ashton, and S. P. Hubbell. 1990. Methodology for the fifty hectare research plot at Pasoh Forest Reserve. Forest Research Institute Malaysia, Kepong, Malaysia.
- McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn. 1994. *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Merrill, E. 1926. An enumeration of Philippine flowering plants. Bureau of Science, Manila, Philippines.
- Michener, C. D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Garden* **66**:277–347.
- Okuda, T., N. Manokaran, S. C. Thomas, and P. S. Ashton, editors. 2003. *Pasoh: ecology and natural history of a lowland rain forest in Southeast Asia*. Springer-Verlag, Tokyo, Japan.
- Phillips, O. L., Y. Malhi, N. Higuchi, W. F. Laurance, P. V. Nunez, R. M. Vasquez, S. G. Laurance, L. V. Ferreira, M. Stern, S. Brown, and J. Grace. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* **282**:439–442.
- Pitman, N. C., J. W. Terborgh, M. R. Silman, P. Nunez, D. A. Neill, C. E. Ceron, W. A. Palacios, and M. Aulestia. 2002. A comparison of tree species diversity in two upper Amazonian forests. *Ecology* **83**:3210–3224.
- Primack, R., and R. Corlett. 2004. *Tropical rainforests: an ecological and biogeographical comparison*. Blackwell Science, New York, New York, USA.
- Reed, K. E., and J. G. Fleagle. 1995. Geographic and climatic control of primate diversity. *Proceedings of the National Academy of Sciences (USA)* **92**:7874–7876.
- Richards, P. W. 1973. Africa, the 'odd man out.' Pages 21–26 in B. J. Meggers, E. S. Ayensu, and W. D. Duckworth, editors. *Tropical forest ecosystems in Africa and South America: a comparative review*. Smithsonian Institution, Washington, D.C., USA.
- Richards, P. W. 1996. *The tropical rain forest*. Second edition. Cambridge University Press, Cambridge, UK.
- Roubik, D., and S. Sakai, editors. 2004. *Ecology of Lambir Hills National Park, Sarawak*. Springer Verlag, Tokyo, Japan.
- Sakai, S. 2002. General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biological Journal of the Linnean Society* **75**:233–247.
- Sakai, S., K. Momose, T. Yumoto, T. Nagamitsu, H. Nagamasu, A. A. Hamid, T. Nakashizuka, and T. Inoue. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* **86**:1414–1436.
- Thomas, S. C. 1996. Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos* **76**:145–154.
- van Gemerden, B. S., H. Olf, M. P. E. Parren, and F. Bongers. 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *Journal of Biogeography* **30**:1381–1390.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**:475–505.
- White, L. J. T., and J. F. Oates. 1999. New data on the history of the plateau forest of Okomu, southern Nigeria: an insight into how human disturbance has shaped the African rain forest. *Global Ecology and Biogeography* **8**:355–361.
- Yasuda, M., J. Matsumoto, N. Osada, S. Ichikawa, N. Kachi, M. Tani, T. Okuda, A. Furukawa, A. R. Nik, and N. Manokaran. 1999. The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology* **15**:437–449.