16. Lowland Tropical Rain Forests of Asia and America: Parallels, Convergence, and Divergence

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This chapter primarily compares the forest at Lambir Hills National Park, Sarawak, with other lowland tropical forests in Asia and America. No two tropical forests are exactly alike. But do differences result from histories, often overshadowed by adaptive convergence toward uniform forest ecology? Or do the actual differences reflect fundamental differences in ecological function?

16.1 Introduction

Lowland equatorial wet forests generally display a uniform structure. In each hectare there are 35 m^3 to 45 m^3 of basal area, 400 to 600 trees over 10 cm dbh (diameter at breast height), and 1000 to 3000 trees 1 cm to 2 cm dbh (see comparative tallies in Davies and Becker 1996; Richards 1996; Lieberman et al. 1996). The general range of tree diversity among continents is also roughly similar, although depressed in African wet lowland forest (Gentry 1988).

Parallel familial representation is characteristic of lowland wet forest in all continents. Of the 168 families represented by trees of Southeast Asia, all but 24 are shared with tropical America. Generally speaking, genera are not shared among continents. However, the few of the shared genera are often conspicuous in the ecological uniformity displayed by their species, which reinforces the notion of a similarity among all tropical forests. A naturalist from Central America knowing *Anaxagorea panamensis* (Annonacaeae) as an abundant small treelet with ballistically dispersed seeds and highly aggregated populations would immediately recognize *Anaxagorea luzonensis* at Mount Makiling in the Philippines or *Anaxagorea javanica* in the Malay peninsula. The genus *Xylopia* (Annonaceae) appears on all three continents, as does *Campnosperma* (Anacardiaceae), which forms characteristically dense populations in wet open sites in both America and Asia. *Rinorea* (Violaceae) is recognized in both America and Asia (and in Africa) by flower, fruit, and leaf features, and by the similar clumped distribution among the ballistically dispersed species. *Ormosia amazonica* (Leguminosae) and *Ormosia sumatrana* are quickly recognized as congeners. Other genera of this sort include *Croton* (Euphorbiaceae), *Dacryodes* (Burseraceae), *Elaeocarpus* (Elaeocarpaceae), *Sterculia* (Sterculiaceae), and many smaller Rubiaceae such as *Psychotria*.

It is more typical that a taxonomic family is represented in each continent by regionally endemic genera that display a recognizable suite of ecological features with regard to habit, physiology, flowers, and fruit. The most obvious examples of such families are the Myristicaceae, Sapotaceae, Clusiaceae, Myrtaceae, Malvaceae, and Lauraceae, and many herbs, pteridophytes, orchids, and gingers. Nutmeg trees of the family Myristicaceae are exemplary of such parallel development. The family is easily recognized from vegetative features alone: alternate, entire leaves, the simple leaf stalk, exstipulate, branches typically arranged around the trunk in the pattern of a wagon wheel, and the trunk exuding a red sap. The flowers and fruit are uniform across the family: small, tri-partite, the plants dioecious, and the fruit a single-seeded dehiscent berry with a brightly arilate seed. In Neotropical forests we find the following genera and numbers of species: *Compsoneura* 9, *Virola* 40, *Osteophloeum* 1, *Iryanthera* 23, and *Otoba* 7. In Asian forest, the family is represented by *Horsfieldia* 100, *Endocomia* 4, *Myristica* 72, *Knema* 60, and *Gymnacranthera* 7.

A second factor that implies homogeneity among the rain forests of the world is the convergent adaptation among unrelated taxa, which has yielded so many singular and well-known examples. Those include the high light- and nutrient-demanding mymecophytes *Macaranga* (Euphorbiaceae) in Asia, and *Cecropia* (Cecropiaceae) in America, the hummingbird/sunbird parallels (Karr and James 1975), the Asian pangolin and American anteaters, and the convergent trophic structure among non-volant mammals (Eisenberg 1981). Finding ecological equivalents is a game inevitably played by any naturalist who visits a new continent.

With an eye on uniform physiognomy, on parallel family development, and on ecological convergence of divergent taxa, Gentry (1988) argued for the global similarity of tropical forests. He saw the same tree families dominating lowland wet forests all over the world, with the principal exception of the dipterocarps of Southeast Asia. He further suggested that the ecological role of diptercarps was taken up in the Neotropics by the legumes, especially the caesalpinoid legumes, and particularly on poor soils and/or in seasonal climates. According to Gentry, "Legume trees play essentially the same role in Neotropical forests as the dipterocarps do in Asia"(Gentry 1993).

Janzen (1977), however, pointed out a conspicuous contrast between the hemispheres. The understory of Asian forests appears dominated by the saplings of canopy trees which are juvenile and thus sterile, whereas his experience in America, especially in wet lowland forests, indicated an understory rich in small treelets that flowered and fruited frequently. He emphasized the impact that this had on herbivores and seed dispersers (and consequently on pollinators and flower visitors, as discussed in other chapters in the present book).

There has been little formal comparison of tropical forest composition among continents, perhaps chiefly because of scant information on the lower strata, of the trees no more than 1 cm to 2 cm in diameter.

16.2 A Comparative Study of Forest Composition

Here the principal comparison of trees focuses on four forests—two in America and two in Asia—where large-scale plots have been established. These are Lambir Hills, Pasoh Forest in Peninsular Malaysia, Yasuní forest in Ecuador, and Barro Colorado Island in Panama. Additional comparisons are made to the well-studied site of La Selva Field Station, Costa Rica. The tabulations and results are from published sources or re-calculated for comparison from the original data. The large-scale plot methods are found in Manokaran et al. (1990) and Condit (1998). Data for the individual sites can be found for Lambir Hills (Lee et al. 2002, 2003); for Pasoh, in Manokaran and LaFrankie (1990); Kochummen et al. (1990); and Manokaran et al. (1992); for Yasuní, in Valencia et al. (2004a-c); for Barro Colorado Island in Condit (1998); and for La Selva, in Lieberman and Lieberman (1987), Clark and Clark (1992), and McDade et al. (1994).

The four forests are structurally similar (see Table 16.1). BCI is the least similar, having lower density and far lower diversity owing chiefly to its geographic position and more strongly seasonal climate.

Asian forests are distinguished by numerous families of large canopy trees that in tropical America either are represented sparsely or not at all (see Table 16.2). Foremost are the Dipterocarpaceae, Fagaceae, Ebenaceae, and Polygalaceae. Conversely, some families are diverse and abundant among Neotropical canopy trees but poorly represented in the wet equatorial forests of Asia. These include Bignoniaceae, Cecropiaceae, and Malpighiacaeae. However, it will be quickly seen that these are of a different character than the former families, being either trees characteristically of dry habitats (such as Bignoniaceae, well represented in dry forests of the American tropics) or trees of a somewhat ruderal or early successional habit, such as Cecropiaceae. The Old World tropics do not have a family that is easily paralleled with Bignoniaceae.

Table 16.1. Summary comparison of study sites and permanent plots of trees

	Pasoh Malaysia	Lambir Malaysia	Yasuní Ecuador	BCI Panama
Altitude(m)	100	100	235	100
Annual rainfall (mm)	1850	2300	~3000	2500
Months with <100 mm rainfall	0*	0*	0	3
No. trees/ha				
≥1 cm dbh	6477	7068	6094	4707
1–2 cm dbh	2566	3155	2357	2569
<10 cm dbh	5922	6430	5392	4289
≥10 cm dbh	554	637	702	418
Basal Area (m^2)				
Tree Flora				
Families: Plot	93	93	86	62
Genera: Plot	294	288	299	184
Species: Plot	823	1188	1104	304

* Each year may include periods of up to 20 consecutive rain-free days but they are irregular, yielding monthly means over 100 mm.

16.3 Individual Tree Families

Notes on the characteristics of individual families, given below, will be followed by more general findings and summaries.

Annonaceae. While trees of the family Annonaceae display fundamentally parallel ecology among the continents, a profound divergence between America and Asia is seen among lianas. Asian Annonaceae include the following genera and number of species, strictly lianas: *Tetrapetalum* 2; *Rauwenhoffia* 5; *Cyathostemma* 8; *Dasoclema* 1; *Ellipoeiopsis* 2; *Uvaria* 110; *Ellipia* 5; *Anomianthus* 1; *Artobotrys* 100; *Schefferomitra* 1 (PNG); *Desmos* 25; *Friesodielsia* 50; *Melodorum* 5; *Pyramidanthe* 1; *Mitrella* 5; *Fissistigma* 60. In contrast, the Annonaceae are represented among Neotropical lianas by perhaps 3 species of *Annona*, and perhaps a few scrambling shrubs. Besides being species-rich, the annone climbers are also one of the most abundant liana families, which serves to raise their total abundance and species richness to higher levels in Asia than normally found in the Americas (Appanah et al. 1993).

Arecaceae. While the palm family is species-rich and abundant in most parts of the tropical world, their ecological representation in forests contrasts sharply among continents. In almost all American forests, palms are an important part of the lower canopy and collectively may comprise a large fraction of basal area. Lambir Hills is typical of Asian forests because palm trees are a minor component of the tree flora over 10 cm dbh. While the 52 ha plot includes nearly 1200 species of trees, no more than 25 are palms, and no palm is especially

Table 16.2. Comparison of tree composition in four lowland tropical forests: Pasoh Forest, Peninsular Malaysia; Lambir Hills, Sarawak Malaysia; Yasuní, Ecuador (based on re-calculations from data summarized in Valencia et al. 2004a,b, and LaFrankie et al. (in review); and Barro Colorado Island, Panama). Tallies are based on 50 ha samples (25 ha in Yasuní) but are presented as equivalent 25 ha values. Tallies are made for each species and are summed across families. Saplings are trees 1 cm to 2 cm dbh belonging to a species that exceeds 30 cm dbh. Treelets are trees 1 cm to 2 cm dbh belonging to species that do not exceed 30 cm dbh. Ratio in parentheses indicates saplings over 30 cm recorded per adult tree.

	PASOH				LAMBIR				YASUNÍ				BCI			
	SPP	>30 cm	Sapling (ratio)	Treelet	SPP	>30 cm	Sapling (ratio)	Treelet	SPP	>30 cm	Sapling (ratio)	Treelet	SPP	>30 cm	Sapling (ratio)	Treelet
Total	827	2004	27540 (13.74)	34128	1194	3036	49189 (16.20)	29879	1104	1678	10644 (6.34)	42884	304	2133	21479 (10.07)	42741
Families of canopy trees more abundant in Asia																
Dipterocarpaceae	33	576	5952 (10.33)	5	88	1198	12627 (10.54)	101	.	.	.(.)	.	.	.	.(.)	.
Fagaceae	15	100	684 (6.84)	34	21	28	340 (12.14)	36	.	.	.(.)	.	.	.	.(.)	.
Ebenaceae	23	15	299 (19.93)	2706	35	37	1519 (41.05)	429	5	2	11 (5.50)	20	1	.	.(.)	7
Polygalaceae	10	23	725 (31.52)	2	25	10	157 (15.70)	1374	.	.	.(.)	.	.	.	.(.)	.
Dilleniaceae	3	4	4 (1.00)	37	5	10	494 (49.40)	352	1	.	.(.)	1	.	.	.(.)	.
Memecylaceae	12	3	19 (6.33)	1241	12	5	236 (47.20)	204	.	.	.(.)	.	.	.	.(.)	.
Anisophylleaceae	1	1	68 (68.00)	0	5	5	453 (90.60)	492	.	.	.(.)	.	.	.	.(.)	.
Alangiaceae	4	4	471 (117.75)	1	4	1	87 (87.00)	66	.	.	.(.)	.	.	.	.(.)	.
Ixonanthaceae	2	59	516 (8.75)	0	1	51	1781 (34.92)	0	.	.	.(.)	.	.	.	.(.)	.
Families of canopy trees more abundant in Ameria																
Bignoniaceae	2	.	.(.)	0	.	.	.(.)		6	7	15 (2.14)	1043	3	79	90 (1.14)	0
Cecropiaceae	.	.	.(.)	.	.		.(.).		16	104	297 (2.86)	719	3	52	52 (1.00)	0
Araliaceae	1	.	.(.)	3	1		.(.)	4	4	13	35 (2.69)	294	3	39	11 (0.28)	0
Malpighiaceae	.	.	.(.)	.	.		.(.).		7	4	18 (4.50)	131	2		.(.)	25
Boraginaceae	2	0	5 (.)	0	1	0	75(.)	0	9	4	.(.)	598	3	34	121 (3.56)	224
Nyctaginaceae	.	.	.(.)	.	.		.(.).		22	17	319 (18.76)	889	2	22	19 (0.86)	30
Hippocrateaceae	.	.	.(.)	.	.		.(.).		5	16	57 (3.56)	416	.	.	.(.)	.
Shared Families																
Euphorbiaceae	84	98	1999 (20.40)	6101	125	150	3926 (26.17)	7002	34	127	215 (1.69)	2697	11	81	580 (7.16)	592
Legumes																
Mimosoideae	9	23	344 (14.96)	51	9	5	20 (4.00)	163	54	156	984 (6.31)	2371	18	24	481 (20.04)	562
Caesalpinioideae	11	154	597 (3.88)	110	6	43	202 (4.70)	9	15	35	129 (3.69)	1582	6	78	1492 (19.13)	58
Phaseoideae	4	33	151 (4.58)	0	4	11	42 (3.82)	1201	32	48	176 (3.67)	243	14	93	1481 (15.92)	696
Dialium-group	4	31	262 (8.45)	0	5	14	112 (8.00)	48	1	7	41 (5.86)	0	.		.(.).	
Bauhinia-group	.	.	.(.)	.	.		.(.).		2	.	.(.)	218	.		.(.).	

Table 16.2. *Continued*

	PASOH				LAMBIR				YASUNÍ				BCI			
	SPP	>30 cm	Sapling (ratio)	Treelet	SPP	>30 cm	Sapling (ratio)	Treelet	SPP	>30 cm	Sapling (ratio)	Treelet	SPP	>30 cm	Sapling (ratio)	Treelet
Meliaceae	43	14	511 (36.50)	1297	55	13	636 (48.92)	932	39	106	490 (4.62)	2299	6	301	3891 (12.93)	1
Rubiaceae	47	15	688 (45.87)	4618	59	18	801 (44.50)	3952	80	58	464 (8.00)	2729	32	144	2654 (18.43)	9173
Annonaceae	42	38	647 (17.03)	4035	54	28	842 (30.07)	2915	40	16	173 (10.81)	1575	9	41	475 (11.59)	3928
Burseraceae	25	123	2203 (17.91)	141	40	234	4463 (19.07)	161	17	61	818 (13.41)	133	6	105	2540 (24.19)	215
Anacardiaceae	32	66	592 (8.97)	548	33	215	3291 (15.31)	453	7	36	187 (5.19)	14	4	36	49 (1.36)	0
Myrtaceae	48	75	897 (11.96)	506	58	186	2002 (10.76)	249	56	7	113 (16.14)	1321	7	14	938 (67.00)	427
Lauraceae	49	25	210 (8.40)	923	78	116	1879 (16.20)	918	81	119	1128 (9.48)	1872	10	114	1379 (12.10)	21
Clusiaceae	34	46	1341 (29.15)	536	50	80	1317 (16.46)	735	19	9	104 (11.56)	197	8	15	204 (13.60)	1517
Sapotaceae	15	30	119 (3.97)	268	33	61	538 (8.82)	398	54	38	469(12.34)	903	5	41	663 (16.17)	0
Moraceae	25	51	299 (5.86)	33	45	60	595 (9.92)	486	51	90	1272 (14.13)	1173	21	106	593 (5.59)	1210
Myristicaceae	31	39	1884 (48.31)	472	40	58	1541 (26.57)	735	17	162	395 (2.44)	435	3	63	505 (8.02)	0
Verbenaceae	8	1	38 (38.00)	97	9	37	883 (23.86)	16	9	.		502	1			19
Chrysobalanaceae	7	35	113 (3.23)	20	8	18	89 (4.94)	1	19	23	281 (12.22)	177	4	27	1174 (43.48)	0
Apocynaceae	7	20	43 (2.15)	71	7	12	50 (4.17)	5	11	16	48 (3.00)	185	4	72	404 (5.61)	20
Lecythidaceae	4	8	734 (91.75)	1	8	10	161 (16.10)	44	15	154	520 (3.38)	306	1	18	29 (1.61)	0
Elaeocarpaceae	8	1	13 (13.00)	77	11	7	148 (21.14)	22	17	25	367 (14.68)	77	1	8	134 (16.75)	0
Combretaceae	4	1	0 (0.00)	2	3	3	7 (2.33)	0	9	13	33 (2.54)	14	2	18	16 (0.89)	0
Celastraceae	7	11	86 (7.82)	132	14	17	653 (38.41)	463	3	2	6 (3.00)	24	1	1	15 (15.00)	0
Sapindaceae	20	43	2918 (67.86)	1472	19	17	930 (54.71)	180	18	7	68 (9.71)	147	7	1	64 (64.00)	697
Malvaceae	27	88	652 (7.41)	492	47	113	2227 (19.70)	729	29	62	880 (14.19)	3183	16	334	436 (1.31)	147
Flacourtiaceae	12	15	640 (42.67)	89	20	26	1227 (47.19)	670	30	7	36 (5.14)	1428	14	52	212 (4.08)	896
Rutaceae	6	1	45 (45.00)	164	6	12	3 (0.25)	126	12	2	16 (8.00)	155	4	35	126 (3.60)	0
Ulmacease	4	5	123 (24.60)	392	4	14	306 (21.86)	8	4	15	79 (5.27)	2	2	2	1 (0.50)	22
Olacaceae	8	17	86 (5.06)	384	7	14	548 (39.14)	164	9	19	81 (4.26)	110	2	8	157 (19.63)	21
Families of shrubs and treelets																
Monimiaceae	1	.	.(.)	5	1.		.(.)	11	17	.	.(.)	898	2.		.(.)	89
Myrsinaceae	8	.	.(.)	3142	9.		.(.)	960	4	.	.(.)	225	4.		.(.)	286
Melastomataceae	3	0	41 (.)	67	9.		.(.)	558	59	8	31 (3.88)	2069	13	2	173 (86.50)	3400
Piperaceae	.	.	.(.)	. .			.(.).		22	.	.(.)	3144	8.		.(.)	1787
Solanaceae	.	.	.(.)	. .			.(.)		14	.	.(.)	247	5.		.(.)	137
Violaceae	3	.	.(.)	1657	4.		.(.)	153	9	.	.(.)	2644	2.		.(.)	14298
Acanthaceae	.	.	.(.)	..			.(.).		2	.	.(.)	55	2.		.(.)	3
Capparidaceae	.	.	.(.)	.	.		.(.).		3	.	.(.)	449	1.		.(.)	1149
Pandaceae	3	.	.(.)	456	1.		.(.)	257	.	.	.(.)	.	.		.(.).	

numerous. However, we must add an important qualifier. Asian lowland forests are very often rich in caespetose palms with large fan leaves—the genus *Licuala* foremost among these. *Licuala* is often abundant to the point of local physical dominance. Individual leaves can be 2 meters across, and the 50-ha plot in Pasoh included more than 17,000 individuals. Furthermore, in most humid forests of the Sunda Shelf we find palms richly and abundantly represented among climbing plants. More than 20 species of rattans occur at Lambir (K. Ickes, unpublished report). While noting the relative absence of large tree palms in Asian forests, we should bear in mind that palms may nevertheless show a globally identical presence in terms of leaf area and/or biomass.

Bignoniaceae. In American tropical forests, Bignoniaceae can become relatively abundant both as trees and as lianas. The family is poorly represented in Asian wet forests. In Pasoh, among the trees were three species in two genera, but these were represented by only a few individual saplings, all of which had died before the 1995 census. In the Lambir Hills plot the family did not appear at all.

Dipterocarpaceae. Dipterocarps are ecologically unique and have no equivalent in America (see Plates 2, 5). They represent the most profound ecological divergence among the continents. (Technically, the family is represented in the Americas by two species of subfamily Pakaraimaeoideae, but it is absent from most of the land area and absent in all lowland forests.) The family chiefly comprises tall trees of large diameter—although most genera include a few species of small stature—and they collectively represent a large fraction of the basal area of forests in the lowland wet areas of the Sunda Shelf. The plant body is highly resinous, the leaves pinnate-veined, evergreen, the roots ectomycorrhizal, associated with a rich basidiomycoflora; the flower is variously sized, bell-shaped and malvalean in form, pollinated by insects, presumably obligately outcrossing (Ashton 1989); the single-seeded fruit, variously sized from very large to small, is either non-dispersed, falling in dense clusters around the mother tree, or dispersed opportunistically via thick calyx wings during rare, high winds, or perhaps dispersed secondarily by animals through scatter hording; the phenology is exemplary of the exaggerated masting habit, with three to five or more years of vegetative growth followed by species-specific synchronous flowering (Ashton et al.1988; LaFrankie and Chan 1991); the saplings are highly aggregated. The geography is also indicative of the ecology. In mixed dipterocarp forest of the Sunda Shelf, individual species often have a restricted distribution. For example, the most abundant species of *Shorea* and *Dipterocarpus* in the 52 ha plot at Lambir are *Shorea acuta* and *Dipterocarpus globosus*, species that are not widespread. Among the five most abundant species of Dipterocarpaceae in Lambir and Pasoh forests, we find no species in common (see Okuda et al., editors, 2003).

Fagaceae. The oaks and chestnuts often dominate forests in the high latitudes. While a few species of *Quercus* are found in the Mesoamerican mountains, where they sometimes dominate (Guariguata and Saenz 2002), they are essentially absent from the Neotropics below 1000 meters, or south of Panama. In contrast to their absence in tropical America and Africa, Fagaceae play a significant role in the lowland forests of Asia. The Lambir plot includes 21 species, while the plot at Pasoh has 15 species, thus representing the ninth-ranked family in basal area (Kochummen et al. 1990). They share with dipterocarps a masting habit and produce large and essentially non-dispersed seeds, presumably subject to scatter-hording by squirrels and small rodents.

Lecythidaceae. This family is easily recognized in all tropical forests by the candelabra of branches bearing dense, spiraling rosettes of oblanceolate leaves, with the twigs often hollow. Lecythids are typically a minor element in the lowland forests of Asia, and also in much of America, but collectively are near dominant in the more seasonal habitats such as near Manaus, Brazil. However, America and Asia are represented by different clades, with different ecologies (Morton et al. 1997). In Southeast Asia the family is represented by the Barringtoniae. The flowers are open powder puffs. Some riparian and littoral species have red flowers opening during the day, but species of the closed forest are all (or, almost all) night blooming, presumably pollinated by bats or large moths. The fruit is invariably indehiscent and fleshy. The following genera and species are typically found: *Barringtonia* 40; *Careya* 4; *Chydenanthus* 1; *Petersianthes* 1; *Planchonia* 5. In America the flowers of Lecythidaceae are diverse in symmetry and the fruit varied, but especially abundant are those with dehiscent capsules, seeds winged or not, or arilate or not: *Gustavia* 40, *Grias* 6, *Asteranthos* 1; *Allantoma* 1; *Cariniana* 15; *Couroupita* 3; *Bertholettia* 1; *Couratari* 19; *Eschweilera* 83; *Lecythis* 26. Lecythidaceae is represented in Lambir by *Barringtonia* and in Yasuní and BCI by genera such as *Gustavia*. While the trees can be recognized as con-familial, the reproductive ecology differs sharply and, in light of the great difference in sapling abundance, the population ecology also likely differs.

Melastomataceae. The family Melastomataceae is nearly cosmopolitan, but recent phylogenetic work (Renner et al. 2001), together with the compositional data from the Center for Tropical Forest Science/Smithsonian Tropical Research Institute large plot network, make clear the strong asymmetry of familial representation. Asian forests are most richly represented by *Memecylon*, which forms a sister clade of the rest of the melastomes. It is the latter that are so well represented in the understory of the Americas. *Melastoma* itself is found in Asia but typically in gaps and wet, open forest. The tribes Kibessieae and Astronieae—the basal-most clade within the melastomes—are sometimes represented, but chiefly at altitudes approaching 1000 meters. The other true melastomes found in Asia include some abundant herbs of the forest floor, such as *Sonnerlila* and *Phyllagathis*. Nowhere in Asia do we find an assemblage of shrubs and treelets comparable to the family's representation in BCI and Yasuní (see Table 16.2).

Piperaceae. Pipers can be found all over Asia, but chiefly as small plants <1 meters tall, or, more often, as weak-stemmed climbing plants. More than one million trees have been recorded in the CTFS Asian plot network, but not a single individual of *Piper* has been found. This is in stark contrast to the rich diversity and abundance of *Piper* on BCI, and in most of wet tropical America. La Selva is perhaps the premier location for *Piper*, with more than 40 species of shrubs and treelets.

Sapindaceae. This family is a vexing confusion of small trees. The family is more often than not represented by the most abundant species at each of the CTFS-AA forest sites: Pasoh (*Xerospermum noronhianum*); Huai Kha Khaeng, Thailand (*Dimocarpus longan*); and Palanan, Philippines (*Nephelium ramboutan-ake*). In Lambir the family is best represented by the many species of rambutan of the genus *Nephelium.* The American tropical forests sometimes include a few abundant trees in the Sapindaceae, but they are far more important as lianas, where they typically rank as one of the most diverse and abundant families. Sapindaceae are not represented among lianas in Asia. Perhaps associated with the contrasting habit, the American Sapindaceae that grow as lianas are primarily wind-dispersed, whereas the trees of wet Asian forests almost all bear seeds with fleshy arils, which attract animals as dispersers.

16.4 Other Ecological Elements of Divergence

No pretense is made to formally review a subject so large and involving such a heterogenous mass of complex data. Rather, the intention is to note contrasting ecological features that have recently come to light, through either the CTFS plot program or other work.

Lianas. Family composition of lianas differs between Asia and America. Other than legumes, which are among the most species-rich and abundant families in both hemispheres, the tropical forests of Old and New Worlds share few dominant liana families. In Asia the dominant families are Annonaceae, Arecaceae, Connaraceae, Celastraceae and Icacinaceae (Appanah et al. 1992; Putz and Chai 1987). The composition of lianas at BCI (Foster and Hubbell 1990), La Selva (Hammel 1990), and Manu, Perú (Foster 1990) is fairly uniform; dominant families are Bignoniaceae, Sapindaceae, Malpighiaceae, Dilleniaceae, Aristolochiaceae, Cucurbitaceae, Menispermaceae, and Passifloraceae. The contrasting taxonomy is not as important as the contrasting ecology. Whereas in America the bulk of liana seeds are wind-dispersed, in Asia the majority are fleshy fruited.

Understory treelets. LaFrankie et al. (2002) compared the large permanent forest plots at Lambir and Pasoh with Yasuní in Ecuador and Korup in Cameroon. They found profound differences in the understory composition, regarding the proportions of tree species of large and small stature. In the understory of the American and African forest, roughly 70% of the small trees belong to species that reach a maximum diameter of less than 10 cm dbh. By contrast, in the two Asian forests nearly 60% of understory trees are saplings of canopy trees that reach a maximum diameter of over 20 cm. Florisitc information from other Neotropical sites reinforces this picture. The shrub flora of La Selva, Costa Rica (Hammel 1990), and Manu, Peru (Foster 1990) are similar. Some abundant shrubs and treelets are of families also abundant in Asia. These include Rubiaceae, Myrtaceae, Myrsinaceae, and Arecaceae, but their abundance is often less in the Asian forests. However, the rich and abundant families of Piperaceae, Solanaceae, Acanthaceae, and Melastomataceae are poor or absent in the Asian forest understory.

Canopy saplings. While the Asian understory is generally depauperate in shrubs and treelets, it is very rich in canopy tree saplings. This appears to be a general phenomenon. The contrast with the Neotropics appears to be quantitatively significant and taxonomically broad (see Table 16.2). Lambir is more than 25% richer than Pasoh in saplings among all trees over 30 cm dbh, but it is 60% richer than BCI and 250% richer than Yasuní. The result is not solely due to families of canopy trees exclusive to Asia, and the difference persists even without Dipterocarpaceae. The nutmegs (Myristicaceae) are instructive. The family is well represented among trees over 30 cm dbh in all four forests, but the two Asian forests have 26 saplings per adult at Lambir, and 48 at Pasoh, versus 8 at BCI and only 2 at Yasuní. A similar trend is seen in the Annonaceae. Additional data from other Neotropical sites are few, but studies that are somewhat comparable tend to show similar results. For example, Clark and Clark (1992) surveyed 150 ha for six emergent tree species at La Selva, Costa Rica. All six species had more trees above 10 cm dbh than the number in the class of 1 cm to 4 cm dbh. While the abundance of those trees over 30 cm dbh would place them within the 50 most abundant species at Lambir, the number of saplings 1 cm to 4 cm dbh is nearly ten times less than any such species at Lambir. This finding suggests a profound and general divergence between continents, in the nature of canopy tree regeneration.

Termites. Davies et al. (2003) examined termite communities in tropical forests of the world and found large inter-regional differences in the ecological composition, suggesting large differences in related ecosystem processes at the soil surface.

Mammals. Eisenberg (1981) saw in the small non-volant mammals a clear pattern of convergence among trophic guilds between Asia and America. Nevertheless, there is also evidence of strong divergence among mammals. Bats typically have two to three times more species in Neotropical than in Asian forests, and typically include a large fraction of strictly frugivorous species. Primate ecology also shows strong divergence among continents. Species richness exhibits a strong positive correlation with the area of tropical forest on each continent (Reed and Fleagle 1995). However, while in South America, Africa, and Madagascar, species diversity shows a strong positive correlation with mean annual rainfall, no such relation exists within Asia. Kappeler and Heyman (1996) examined convergence of life history traits of primates. They found basic aspects of primate life history varied significantly among the continents. New World primates are significantly smaller than primates in other regions and lack species larger than about 10 kg; only in Asia do we find strictly frugivorous primates. Asia lacks primarily sap-feeding primate species, whereas the Neotropics lacks primarily folivorous primates, nor do the Americas have solitary species.

Birds. Lists of birds cannot always be sensibly compared, because birds are highly mobile and use various parts of the landscape in different ways. A so-called resident species can mean different things to different observers. Nevertheless, tropical forests sites in America appear to have on the order of 30% more resident bird species than comparable forest in Asia. Robinson and Terborgh (1990) cite one of richest Neotropical locations having 239 resident species, while Pasoh, Malaysia, with 180 species, is 75% of that Neotropical locale (Francis and Wells 2003).

Continental differences in avifauna are perhaps more important than differences in diversity, with regard to abundance and trophic organization. Frugivores make up about 30% of the species in the Neotropics, and they are almost always among the most abundant species caught in mist nets (Robinson and Terborgh 1990). On a per gram basis, frugivores might make up a majority of the avian biomass in the Neotropical forest understory. In contrast, perhaps no bird of the Asian tropical forest understory is an obligate frugivore. Similar differences are likely for nectivorous birds. Although sunbirds and spiderhunters are often considered Asian ecological equivalents of Neotropical hummingbirds, the former are far less diverse, less abundant and evidently vastly less important as pollinators.

Dispersal ecology. Ingle (2003) found that many elements of dispersal ecology in montane forest in Mindanao, Philippines, were contrary to findings that appear uniform across the Neotropics (e.g., Foster et al. 1986; Uhl 1987; Gorchov et al. 1993, 1995; Medellin and Gaona 1999). For example, Ingle found that small wind-dispersed seeds dominated seed traps. Birds dispersed more seeds and species of successional plants than did bats. Ingle emphasized that, contrary to the common view that Neotropical and Asian fruit bats are ecological equivalents, Asian fruit bats belong to a separate suborder and cannot echo-locate. Furthermore, the frugivorous bird communities of Asia and the Neotropics are taxonomically distinct. This point was clearly made by Corlett (1998), who states that "On current evidence, it appears that most seeds in the Oriental Region . . . are dispersed by vertebrate families which are either endemic to the region . . . or to the Old World." Thus, dispersal ecology of the Old and New World Tropics has been evolving along independent lines for millions of years.

Phenology. A great deal is still uncertain about phenological patterns in Asia, especially as one leaves the ever-wet equatorial forests. Nevertheless, it is increasingly clear that Asia is characterized by supra-annual masting (Curran et al. 1999, Sakai et al. 1999c, Chapter 4). American tropical forests are characterized by a diversity of phenological habits, with a large proportion of species that flower annually (Bawa et al. 2003).

The comparative chemistry of Asian and American tropical forest trees is poorly investigated and yet suggests today (as it did to Janzen almost 30 years ago) an area of major divergence among the ecosystems. Contrasting sugars in flowers and fruit, and relative lipid content, could also vary both in absolute quantity and temporal and spatial pattern, in tropical Asia compared to America.

16.5 Lambir Hills Compared to La Selva

These miscellaneous notes can be summarized by a synoptic comparison of Lambir Hills forest with the well-studied wet forest at La Selva, Costa Rica. About half the basal area at Lambir is composed of some 80 species of Dipterocarpaceae, none of which dominates, and the most abundant are geographically restricted and of patchy occurrence. At La Selva, half the basal area is composed of *Pentaclethra macroloba* (Mimosoideae) and three species of palms; all four species are geographically widespread. Palms are well represented at Lambir, but not as trees. Instead, they appear as numerous, stemless understory plants and as abundant climbers. The lianas as a class differ sharply between forests. Other than legumes found in both forests, woody climbers at Lambir are chiefly palms, Annonaceae and Icacinaceae—all of which bear fleshy fruit. At La Selva the principal lianas are Bignoniaceae, Sapindaceae, and Malpighiaceae, most having dry, wind-dispersed fruit and seeds. At Lambir the plants in the understory that have 1 cm to 2 cm dbh include 2000 to 3000 individuals in a hectare, of which nearly 70% are the saplings of trees that will exceed 10 cm dbh at maturity. The similar size class at La Selva is much more sparse, and as far as current evidence shows, more than half the individuals are of species that will flower and bear fruit at tree sizes of less than 10 cm dbh. Related to that compositional difference is a difference in abundance of canopy saplings.

Large emergents at La Selva are about as evenly abundant as emergent species at Lambir, but the number of saplings of such species at Lambir is three to ten times greater than their counterparts in La Selva. Lambir Hills has forest that lies almost entirely sterile for many years before displaying a general flowering, whereas La Selva includes a majority of species that flower and fruit more frequently. Pollinators at La Selva appear to be far more diverse with a higher fraction of bird, bat, and species-specific long-distance pollinators. In contrast, the plants at Lambir (with some exceptions) are predominantly pollinated by less-specific fauna of beetles, Lepidoptera, and bees (see Corlett 2004). The birds and bats at Lambir are about 60% as rich as the community at La Selva and include few if any obligate frugivores.

Thus, while Lambir Hills in Sarawak and La Selva in Costa Rica are both lowland wet tropical rain forests of comparable physiognomy, rich diversity, parallel families, a few shared genera, and many examples of convergence, they nevertheless are profoundly different forests. Almost every aspect of ecological dynamics differs between these American and Asian tropical forests. A better description and understanding of such differences will impact basic ecological conundrums as well as influence management decisions aimed at conservation or timber.