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Lambir Forest Dynamics Plot, Sarawak, Malaysia

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Site Location, Administration, and Scientific Infrastructure

Lambir Hills National Park is in the Malaysian state of Sarawak, on the island of Borneo. Established in 1975, this 6823-ha park lies about 10 km from the South China Sea and ranges in elevation from ca. 60 m to 465 m above sea level. The totally protected park is managed by the National Parks and Wildlife Branch of the Sarawak Forest Department. The research section of the Forest Department coordinates investigations within the park. The 52-ha Lambir Forest Dynamics Plot is located along the southern edge of the park, 20 km from the town of Miri by a good highway (fig. 31.1). In the immediate vicinity of the plot, there are two permanent residential buildings with rudimentary laboratories and herbaria, three canopy towers, a canopy walkway, and a construction crane equipped for biological canopy research.

In 1963, P. S. Ashton, then of the Sarawak Forest Department, established six 0.6-ha plots within Lambir Hills National Park, four of which were made permanent and recensused every 5 years thereafter (Ashton and Hall 1992). Three and three-quarters of these latter plots are included within the 52-ha Forest Dynamics Plot. The six plots were part of a network of 105 plots (0.6 ha each) laid out throughout apparently mature lowland mixed dipterocarp forest in Sarawak, over a distance of 500 × 150 km (Potts et al. 2002).

Climate

The climate of northwestern Borneo is strongly influenced by the Indo-Australian monsoon. While generally everwet, this region is subject to a shift in monsoonal winds that often triggers brief droughts. A northerly monsoon occurs from December to March and a southerly monsoon from May to October (Proctor et al. 1983). Tropical typhoons do not affect the region.

No long-term weather records in the immediate vicinity of the plot are available. The 30-year mean annual rainfall at the Miri airport, 20 km from the plot, is 2725 ± 72 mm/year (Malaysian Meteorological Service from 1968–98). The heaviest rainfalls in the region coincide with the northerly monsoon. Records of

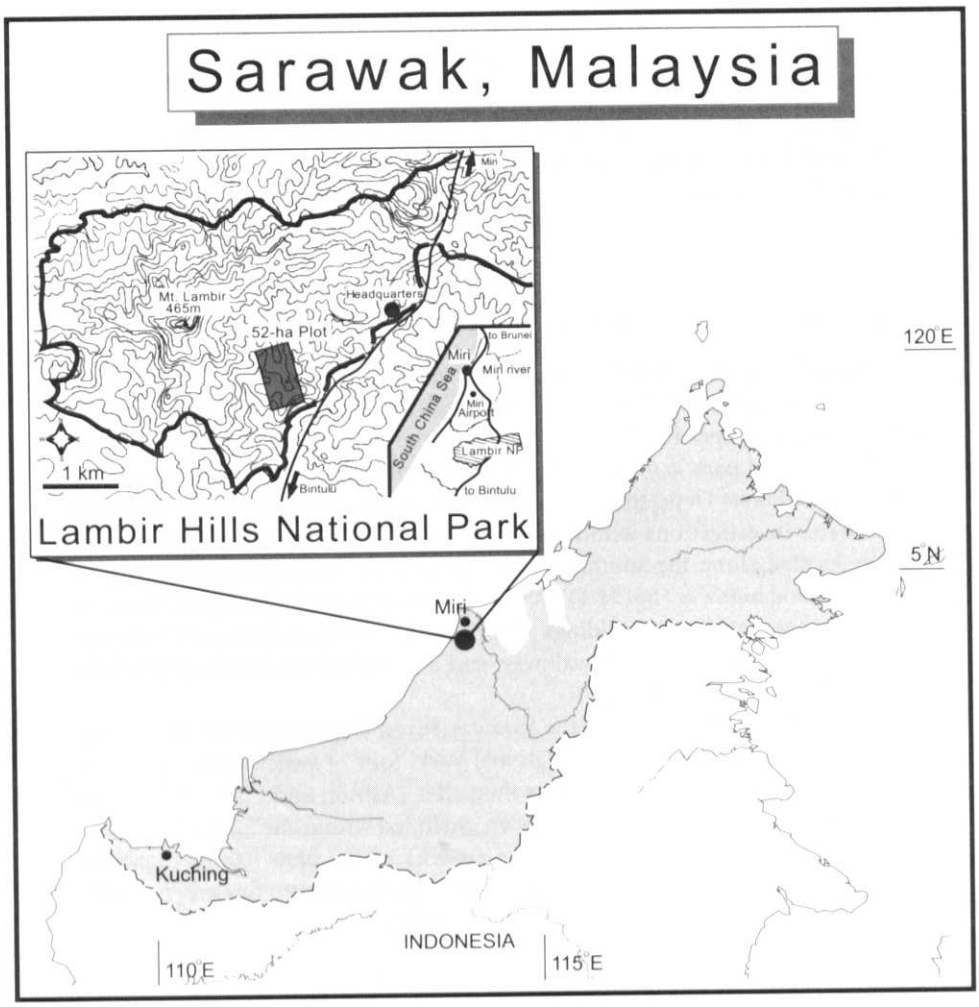

Fig. 31.1. Location of the 52-ha Lambir Forest Dynamics Plot.

monthly rainfall in Miri since 1912 indicate that the recent spate of droughts is unprecedented and the severe drought in 1998 was the worst on record for Miri (Harrison 2001). See table 31.1.

Topography and Soil

The geology of the Lambir Hills area is comprised of sedimentary rocks, bands of clay, and sandstones deposited by rivers and streams in the mid-Miocene era. Steep

Table 31.1. Lambir Climate Data

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total/ Averages
Rain (mm)	229	200	182	222	204	153	165	180	198	290	322	319	2664
ADTMx (°C)	28.7	29.4	30.6	31.1	31.4	31.1	30.8	30.6	30.2	29.9	30.1	29.4	30.3
ADTMn (°C)	22.1	22.5	23.4	23.3	23.4	23.1	22.9	22.9	22.9	22.6	22.7	22.6	22.9

Notes: Mean annual rainfall data were taken from the Telecom tower (1985–1997), a relay station of a Malaysian telephone company located inside the park (Telecom, unpublished data). Some of the monthly temperature means were averaged from only 3 years during this period. Temperature data was collected from the Pasoh field station.

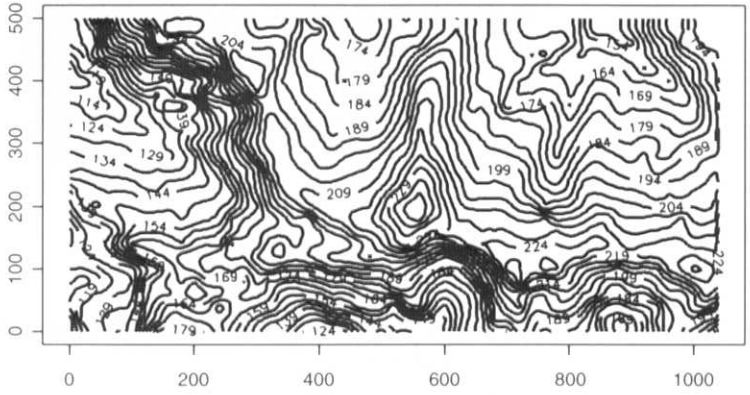

Fig. 31.2. Topographic map of the 52-ha Lambir Forest Dynamics Plot with 5-m contour intervals.

slopes ranging from 23 to 30% cover 85% of the park area (Yamakura et al. 1995; Hazebroek and Abang Kashim 2000). The Lambir Forest Dynamics Plot follows a cuesta ridge, with a gentle dip slope dissected by steep ravines and a precipitous scarp (chap. 19; figs. 31.2 and 31.3). The plot elevation varies from 104 to 244 m above sea level and contains numerous extremely steep slopes and ravines. Most of the plot lies over sandy humult Ultisol soils derived from sandstone. Clay-rich udult Ultisols, derived from shales and bearing relatively high concentrations of phosphorous and magnesium, cover a little less than a third of the plot (Ashton 1973; Baillie et al. 1987; Palmiotto 1998; chap. 14). The plot's udult soils have the following characteristics: Munsell color intensity = 6.0, % clay = 45, % sand = 16, pH = 4.5. HCl extractable concentrations of specific minerals from the udults have the following concentrations (mg/g soil): N = .60, P = 0.12, K = 5.53, Ca = 0.10, Mg = 1.64, % Fe and Al = 11.0. The humult soils have the following characteristics: Munsell color intensity = 6.0, % clay = 21 ± 3, % sand = 69 ± 1, pH = 4.8 ± 0.2. HCl extractable concentrations of specific minerals from the humults have the following concentrations (mg/g soil): N = 0.25 ± 0.03,

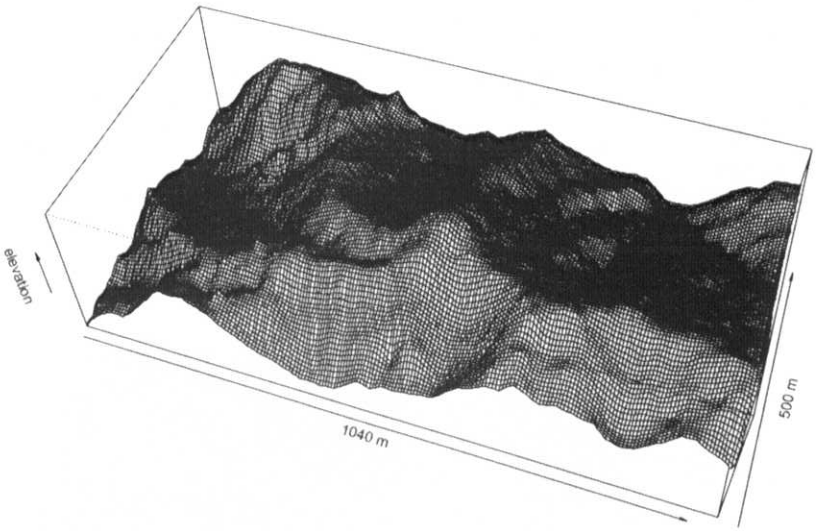

Fig. 31.3. Perspective map of the 52-ha Lambir Forest Dynamics Plot.

P = 0.08 ± 0.04, K = 1.95 ± 1.17, Ca = 0.11 ± 0.06, Mg = 0.61 ± 0.38, % Fe and Al = 8.6 ± 2.5 (Ashton and Hall 1992).

Forest Type and Characteristics

Approximately two-thirds of Lambir Hills National Park, and the entire 52-ha plot, is covered by mature lowland mixed dipterocarp forest. The canopy of this forest type is fairly heterogeneous and tends to be 40–60 m tall, with emergents reaching over 75 m. About 80% of the mixed dipterocarp forest is in a mature phase (Ohkubo et al. 1995). Average aboveground tree biomass in the plot is 520 tons/ha (Yamakura et al. 1996). Mass flowering followed by mass fruiting occurs on a supra-annual cycle, typically beginning in March but also sometimes in August. The park also supports several conspicuously different forest types, such as the lower-stature kerangas forest on white sand near the summit and on the western side of the hills and open secondary forest around the forest margin and on large landslips. The beta diversity of the trees in Lambir Hills is as rich as in any plant community in the Old World. Two of the major factors leading to this diversity are thought to be soil and topographic heterogeneity.

Within the plot, floristic composition and stand structure varies with the change from humult Ultisols in the higher areas of the plot to udult Ultisols in lower portions. The forest community on udult soils, dominated by *Koilodepas*

Table 31.2. Lambir Plot Census History

Census	Dates	Number of Trees (≥1 cm dbh)	Number of Species (≥1 cm dbh)	Number of Trees (≥10 cm dbh)	Number of Species (≥10 cm dbh)
First	October 1991–June 1993	346,061	1179	32,662	1008
Second	May 1997–October 1997	359,603	1182	33,175	1003

Notes: Two censuses have been completed, the enumeration of the third census was initiated in August 2003.

Table 31.3. Lambir Summary Tally

Size Class (cm dbh)	Average per Hectare							52-ha Plot				
	BA	*N*	*S*	*G*	*F*	*H'*	α	*S*	*G*	*F*	*H'*	α
≥1	43.5	6907	618	201	66	2.40	165.3	1182	287	83	2.65	152.2
≥10	37.8	637	247	117	47	2.19	153.6	1003	258	73	2.59	195.1
≥30	26.3	119	67	42	25	1.70	73.6	574	186	60	2.28	154.1
≥60	13.9	26	16	9	6	1.09	24.7	200	80	36	1.77	64.2

Notes: *BA* represents basal area in m^2, *N* is the number of individual trees, *S* is number of species, *G* is number of genera, *F* is number of families, *H'* is Shannon–Wiener diversity index using $\log_{10}$, and α is Fisher's α. Basal area includes all multiple stems for each individual. Individuals are counted using their largest stem. 12,083 individuals were not identified to species or morphospecies. Data are from the second census.

longifolium (Euphorbiaceae), *Millettia vasta* (Leguminosae), *Dryobalanops lanceolata* (Dipterocarpaceae), and *Hopea dryobalanoides* (Dipterocarpaceae), contained a third fewer trees and basal area yet slightly higher species richness than that on humult soils, dominated by *Dipterocarpus globosus* (Dipterocarpaceae), *Elateriospermum tapos* (Euphorbiaceae), *Dryobalanops aromatica* (Dipterocarpaceae), *Whiteodendron moultonianum* (Myrtaceae), and *Shorea acuta* (Dipterocarpaceae) (Lee et al. 2002). For census history and rankings, see tables 31.2–31.7.

Fauna

Lambir Hills National Park has 366 species of vertebrates (not including fish) (Shanahan and Debski 2002). Sixty-one species of mammals have been recorded, ranging from sun bear (*Helarctos malayanus*) to slow loris (*Nycticebus coucang*), including five fruit bats and five insectivorous bats. The largest herbivores are the sambar deer (*Cervus unicolor*), bearded pig (*Sus barbatus*), and two species of Muntjak or barking deer (*Muntiacus muntjac* and *M. atherodes*). The largest canopy herbivores are the langurs (*Presbytis hosei* and *P. melalophos*). Important frugivores include, on the ground, two species of mouse deer (*Tragulus javanicus* and *T. napu*) and, in the canopy, fruit bats including the large flying fox (*Pteropus*

Table 31.4. Lambir Rankings by Family

Rank	Family	Basal Area (m^2)	% BA	% Trees	Family	Trees	% Trees	Family	Species
1	Dipterocarpaceae	908.1	41.0	15.5	Dipterocarpaceae	53,696	15.5	Euphorbiaceae	125
2	Burseraceae	144.5	6.5	6.5	Euphorbiaceae	49,724	14.3	Dipterocarpaceae	87
3	Euphorbiaceae	140.8	6.3	14.3	Burseraceae	22,749	6.5	Lauraceae	77
4	Anacardiaceae	134.5	6.1	5.6	Anacardiaceae	19,322	5.6	Rubiaceae	58
5	Myrtaceae	96.8	4.4	3.4	Rubiaceae	15,669	4.5	Myrtaceae	57
6	Lauraceae	76.3	3.4	3.5	Annonaceae	14,987	4.3	Meliaceae	55
7	Guttiferae	52.8	2.4	2.9	Myristicaceae	12,251	3.5	Annonaceae	54
8	Myristicaceae	51.5	2.3	3.5	Lauraceae	12,053	3.5	Guttiferae	51
9	Leguminosae	46.1	2.1	2.1	Myrtaceae	11,713	3.4	Burseraceae	40
10	Sapotaceae	38.7	1.7	1.6	Guttiferae	9,945	2.9	Myristicaceae	40

Notes: The top 10 families for trees ≥1 cm dbh ranked in terms of basal area, number of individual trees, and number of species, with the percentage of trees in the plot. Data are from the second census.

Table 31.5. Lambir Rankings by Genus

Rank	Genus	Basal Area (m^2)	% BA	% Trees	Genus	Trees	% Trees	Genus	Species
1	*Shorea* (Dipterocarpaceae)	455.4	20.5	6.7	*Shorea* (Dipterocarpaceae)	23,415	6.7	*Shorea* (Dipterocarpaceae)	56
2	*Dipterocarpus* (Dipterocarpaceae)	213.4	9.6	1.5	*Dryobalanops* (Dipterocarpaceae)	11,497	3.3	*Syzygium* (Myrtaceae)	53
3	*Dryobalanops* (Dipterocarpaceae)	166.8	7.5	3.3	*Dacryodess* (Burseraceae)	11,292	3.2	*Diospyros* (Ebenaceae)	34
4	*Santiria* (Burseraceae)	61.5	2.8	2.1	*Diospyros* (Ebenaceae)	9,419	2.7	*Litsea* (Lauraceae)	28
5	*Gluta* (Anacardiaceae)	60.3	2.7	2.5	*Vatica* (Dipterocarpaceae)	8,890	2.6	*Aglaia* (Meliaceae)	25
6	*Dacryodes* (Burseraceae)	60.0	2.7	3.2	*Gluta* (Anacardiaceae)	8,629	2.5	*Xanthophyllum* (Xanthophyllaceae)	25
7	*Syzygium* (Myrtaceae)	52.8	2.4	2.1	*Macaranga* (Euphorbiaceae)	8,096	2.3	*Garciniaa* (Guttiferae)	23
8	*Allantospermum* (Ixonanthaceae)	34.3	1.5	2.2	*Allantospermum* (Ixonanthaceae)	7,473	2.2	*Ficus* (Moraceae)	21 21
9	*Whiteodendron* (Myrtaceae)	32.0	1.4	1.0	*Santiria* (Burseraceae)	7,450	2.1	*Aporusa* (Euphorbiaceae)	18
10	*Vatica* (Dipterocarpaceae)	31.4	1.4	2.6	*Syzygium* (Myrtaceae)	7,415	2.1	*Knema* (Myristicaceae)	17
11								*Santiria (Burseraceae)*	17

Notes: The top 10 tree genera for trees ≥1 cm dbh are ranked by basal area, number of individual trees, and number of species with the percentage of trees in the plot. Data are from the second census.

Table 31.6. Lambir Rankings by Species

Rank	Species	Number Trees	% Trees	Species	Basal Area (m^2)	% BA	% Trees
1	*Dryobalanops aromatica* (Dipterocarpaceae)	10,562	3.0	*Dryobalanops aromatica* (Dipterocarpaceae)	155.3	7.0	3.0
2	*Allantospermum borneense* (Ixonanthaceae)	7,473	2.2	*Dipterocarpus globosus* (Dipterocarpaceae)	138.5	6.3	1.0
3	*Vatica micrantha* (Dipterocarpaceae)	6,274	1.8	*Shorea beccariana* (Dipterocarpaceae)	61.6	2.8	1.1
4	*Fordia splendidissima* (Leguminosae)	3,764	1.1	*Shorea laxa* (Dipterocarpaceae)	47.3	2.1	1.0
5	*Shorea beccariana* (Dipterocarpaceae)	3,761	1.1	*Shorea acuta* (Dipterocarpaceae)	41.8	1.9	0.3
6	*Gluta laxiflora* (Anacardiaceae)	3,615	1.0	*Allantospermum borneense* (Ixonanthaceae)	34.3	1.6	2.2
7	*Whiteodendron moultonianum* (Myrtaceae)	3,405	1.0	*Whiteodendron moultonianum* (Myrtaceae)	32.0	1.4	1.0
8	*Shorea laxa* (Dipterocarpaceae)	3,322	1.0	*Shorea curtisii* (Dipterocarpaceae)	28.0	1.3	0.1
9	*Dipterocarpus globosus* (Dipterocarpaceae)	3,318	1.0	*Elateriospermum tapos* (Euphorbiaceae)	22.2	1.0	0.3
10	*Dacryodes expansa* (Burseraceae)	3,302	0.9	*Swintonia schwenkii* (Anacardiaceae)	21.2	1.0	0.3

Notes: The top 10 tree species for trees ≥1 cm dbh are ranked by number and percentage of trees and basal area. Data are from the second census.

Table 31.7. Lambir Tree Demographic Dynamics

Size Class (cm dbh)	Growth Rate (mm/yr)	Mortality Rate (%/yr)	Recruitment Rate (%/yr)	BA Losses (m^2/ha/yr)	BA Gains (m^2/ha/yr)
1–9.9	0.52	1.74	2.72	0.07	0.20
10–29.9	1.63	1.3	1.96	0.14	0.32
≥30	2.7	1.01	1.34	0.23	0.39

Notes: Data recorded between the 1992 and 1997 censuses. Climbers, including free-standing hemi-epiphytic figs, and all palms were not enumerated in the first two censuses.

vampyrus), nine species of squirrel (*Ratufa affinis, Callosciurus prevostii caroli, C. notatus, C. adamsi, Sundasciurus hippurus, S. lowi, Dremomys everetti, Exilisciurus exilis, Rheithrosciurus macrotis*), five species of flying squirrel (*Petaurillus hosei, Petinomys setosus, P. vordermanni, Petaurista petaurista, Aeromys thomasi*), the colugo (*Cynocephalus variegatus*), two macaques (*Macaca fascicularis* and *M. nemstrina*), the Bornean gibbon (*Hylobates muelleri*), and the binturong (*Arctitis binturong*). The largest mammal predators are civets (*Viverra tangalunga, Paradoxurus hermaphroditus,* and *Hemigalus derbyanus*) and the Oriental small-clawed otter (*Aonyx cinerea*). Some mammals characteristic of Borneo, such as the orangutan, are not found in Lambir, and there is no evidence that they were ever found there. Lambir Hills also hosts 237 species of birds (Shanahan and Debski

2002). Pythons (*Python curtus* and *P. reticulatus*) are important predators and can reach very large sizes (a 6-m skin was collected from the plot).

Invertebrates are also very diverse and include such distinctive species as Rajah Brooke's birdwing (*Trogonoptera brookiana brookiana*) and the giant moth, *Antheraea celebensis* (Saturnidae), but are generally poorly cataloged. With 361 species, ants are one well-studied group that illustrates the great diversity within the park (Yamane unpublished data).

Natural Disturbances

The most important natural disturbances within Lambir Hills National Park are landslips. With continuous heavy rain, the steep soils give way and patches of forest as large as 1-ha can collapse. The very wet winter of 1963 (daily rainfall of 560 mm in May) led to such a large number of slips that today, nearly 40 years later, they are still only in the early stages of recovery (Ohkubo et al. 1995). Unpredictable, severe droughts, usually associated with El Niño Southern Oscillation events, are also very important for their impact on seedling regeneration, tree mortality (especially among larger size classes) (Nakagawa et al. 2000), and phenology with consequences for organisms dependent on plant resources. Harrison (2000) has also demonstrated a breakdown of the fig/fig-wasp pollination system during an El Niño event.

Human Disturbance

Humans have lived in the vicinity of Lambir National Park for a very long time. The Niah Cave archeological site, 50 km down the coast, includes the oldest records of human settlements in southeast Asian rainforest, dated at 40,000 years before present. Within the park boundary, however, no record of cultivation exists. The main products extracted from the forest have been animals—deer, pigs (*Sus barbatus*), porcupine (*Trichys fasciculate*)—timber, rattan, and wild fruits and shoots. While the park is a totally protected area, hunting and extraction of timber and rattan continue from time to time. On the eastern side of the park, illicit entry and encroachment are continuing problems. Sanctioned projects that reduced the park's area include the construction of a radio tower, the main highway (which divided the park in two), and the excavation for a major water pipeline.

There has been a significant increase in the proportion of montane and open- or disturbed-habitat bird species recorded in recent years. Nine mammal and 13 bird species have not been seen since the original park survey in 1985 (Shanahan and Debski 2002). Hornbills, which are richly abundant in the nearby forests of Brunei, are conspicuous in their paucity in Lambir. One species, the vocal helmeted hornbill (*Buceros vigil*) was recorded in 1985 but has not been seen recently, almost certainly as a consequence of illegal hunting. Some of the disappearances

and the increase in open- or disturbed-habitat bird species are likely to be a consequence of two factors: the small size of the park and the dominance of nearby secondary vegetation. Forty-five percent of frogs and 37% of reptiles recorded in 1985 (Watson 1985) have not been recorded since, perhaps due to undersampling.

The southeastern side of the plot is about 200 m from the Miri–Kuching truck road, now abandoned, and faces an area of shifting cultivation fields. The rest of the plot is surrounded by relatively undisturbed forest.

Plot Size and Location

The 52-ha, 1040 × 500 m plot lies north-south on its long axis. The northwest corner of the plot is located at 4°11′20″ N, 114°00′56″ E. The northeast corner of the plot is located at 4°11′20.4″ N, 114°00′55.9″ E. The southeast corner of the plot is located at 4°10′59.1″ North, 114°01′26.7″ East. The southwest corner of the plot is located at 4°10′51.0″ N, 114°01′12.6"″ E (T. Ohkubo and A. Itoh, unpublished data).

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References

Ashton, P. S. 1973. Sarawak mixed dipterocarp forest ecology. Unpublished report to the Government of Sarawak, Malaysia.

Ashton, P. S., and P. Hall. 1992. Comparison of structure among mixed dipterocarp forests of north-west Borneo. *Journal of Ecology* 80:459–81.

Baillie, I. C. 1976. Further studies on drought in Sarawak, East Malaysia. *Journal of Tropical Geography* 43:20–29.

Baillie, I. H, P. S. Ashton, M. N. Court, J. A. R. Anderson, E. A. Fitzpatrick, and J. Tinsley. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forests on tertiary sediments in central Sarawak. *Journal of Tropical Ecology* 3:201–20.

Davies, S. J. 1998. Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life-history. *Ecology* 79:2292–2308.

———. 2001. Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology* 82:920–32.

Davies, S. J., and P. S. Ashton. 1999. Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. *American Journal of Botany* 86:1786–95.

Davies, S. J., P. Palmiotto, P. S. Ashton, H. S. Lee, and J. V. LaFrankie. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: Tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86:662–73.

Harrison, R. D. 1999. *Phenology and Wasp Population Dynamics of Several Species of Dioecious Fig in a Lowland Tropical Rain Forest in Sarawak, Malaysia.* Ph.D. thesis. Kyoto University, Kyoto, Japan.

———. 2000. Repercussions of El Niño: Drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society (London) Series B* 267:911–15.

———.2001. Drought and the consequences of El Niño in Borneo: A case study of figs. *Research in Population Ecology* 43:63–75.

Harrison, R. D., N. Yamamura, and T. Inoue. 2000. Phenology of a common roadside fig in Sarawak. *Ecological Research* 15:47–61.

Hazebroek, H. P., and Abang Kashim bin Abang Morshidi. 2000. Lambir Hills National Park. Pages 147–76 in *National Parks of Sarawak, Natural History Publications (Borneo).* Kota Kinabalu, Sabah, Malaysia.

Hirai, H., H. Matsumura, H. Hirotani, K. Sakurai, K. Ogino, and H. S. Lee. 1997. Soils and the distribution of *Dryobalanopes aromatica* and *D. lanceloata* in mixed dipterocarp forest: A case study at Lambir Hills National Park, Sarawak, Malaysia. *Tropics* 7:21–33.

Inoue, T., T. Yumoto, A. A. Hamid, H. S. Lee, and K. Ogino. 1995. Construction of a canopy observation system in a tropical rainforest of Sarawak. *Selbyana* 16:24–35.

Inoue, K., M. Kato, and T. Inoue. 1995. Pollination ecology of *Dendrobium setifolium, Neuwiedia borneensis,* and *Lecanorchis multiflora* (Orchidaceae) in Sarawak. *Tropics* 5:95–100.

Ishizuka, S., S. Tanaka, K. Sakurai, H. Hirai, H. Hirotani, K. Ogino, H. S. Lee, and J. J. Kendawang. 1998. Characterization and distribution of soils at Lambir Hills National Park in Sarawak, Malaysia, with special reference to soil hardness and soil texture. *Tropics* 8:31–44.

Itoh, A. 1995a. Effects of forest floor environment on seedling establishment of co-occurring Bornean rainforest emergent species. *Journal of Tropical Ecology* 11:517–27.

———. 1995b. Population structure and canopy dominance of two emergent dipterocarp species in a tropical rain forest of Sarawak, East Malaysia. *Tropics* 4:113–41.

———. 1995c. Regeneration processes and coexistence mechanisms of two Bornean emergent dipterocarp species. Ph.D. thesis. Kyoto University, Kyoto, Japan.

Itoh, A., T. Yamakura, K. Ogino, and H. S. Lee. 1995. Survivorship and growth of seedlings of four dipterocarp species in a tropical rainforest of Sarawak, East Malaysia. *Ecological Research* 10:327–38.

Itoh, A., T. Yamakura, K. Ogino, H. S. Lee, and P. S. Ashton. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. *Plant Ecology* 132:121–36.

Itoh A., T. Yamakura, M. Kanzaki, T. Ohkubo, P. A. Palmiotto, J. V. LaFrankie, J. J. Kendawang, and H. S. Lee. 2002. Rooting ability of cuttings relates to phylogeny, habitat preference and growth characteristics of tropical rain forest trees. *Forest Ecology and Management* 168:275–87.

Itoh A., T. Yamakura, T. Ohkubo, M. Kanzaki, P. A. Palmiotto, J. V. LaFrankie, P. S. Ashton, and H. S. Lee. 2003. Importance of topography and soil texture in spatial distribution of two sympatric dipterocarp trees in a Bornean rain forest. *Ecological Research* 18:307–320.

Itoh A., T. Yamakura , T. Ohkubo, M. Kanzaki, P. A. Palmiotto, S. Tan, and H. S. Lee. 2003. Spatially aggregated fruiting in a Bornean emergent tree. *Journal of Tropical Ecology* 19:531–538.

Itioka, T., M. Nomura, Y. Inui, T. Itino, and T. Inoue. 2000. Difference in intensity of ant defense among three species of *Macaranga* myrmecophytes in a southeast Asian dipterocarp forest. *Biotropica* 32:318–26.

Kato, M. 1996. Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany* 83:732–43.

Kato, M., and T. Inoue. 1994. The origin of insect pollination. *Nature (London)* 368:195.

Kato, M., T. Itioka, K. Momose, S. Sakai, S. Yamane, A. A. Hamid, M. B. Merdek, H. Kallang, and T. Inoue. In press. Various population fluctuation patterns of light–attracted beetles in a tropical lowland dipterocarp forest in Sarawak. *Research on Population Ecology.*

LaFrankie, J. V., S. Tan, and P. S. Ashton. 1995. *Species List for the 52-ha Forest Dynamics Research Plot: Lambir Hills National Park, Sarawak, Malaysia.* Miscellaneous Internal Report. Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Singapore.

Lee, H. S., J. V. LaFrankie, S. Tan, T. Yamakura, A. Itoh, and P. S. Ashton. 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, Malaysia.

Lee, H. S., S. J. Davies, J. V. LaFrankie, S. Tan, T. Yamakura, A. Itoh, T. Ohkubo, and P. S. Ashton. 2002. Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. *Journal of Tropical Forest Science* 14:379–400.

Lesslar, P., and M. Wannier. 1998. *Destination—Miri: A Geological Tour, Northern Sarawak's National Parks and Giant Caves.* Interactive CD. http://www1.sarawak.com.my/ecomedia_software/

Mabberley, D. J. 1997. *The Plant-Book: A Portable Dictionary of the Vascular Plants.* Cambridge University Press, Cambridge, U.K.

Maschwitz, U., B. Fiala, S. J. Davies, and K. E. Linsenmair. 1996. A south-east Asian myrmecophyte with 2 alternative inhabitants: *Camponotus* or *Crematogaster* as partners of *Macaranga lamellata. Ecotropica* 2:29–40.

Momose, K., T. Nagamitsu, and T. Inoue. 1996. The reproductive biology of an emergent dipterocarp in a lowland rain forest in Sarawak. *Plant Species Biology* 11:189–98.

Momose, K., R. Ishii, S. Sakai, and T. Inoue. 1998. Reproductive intervals and pollinators of tropical plants. *Proceedings of the Royal Society of London* 265:2333–39.

Momose, K., T. Yumoto, T. Nagamitsu, M. Kato, H. Nagamasu, S. Sakai, R. D. Harrison, T. Itioka, A. A. Hamid, and T. Inoue. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85:1477–1501.

Nakagawa, M., K. Tanaka, T. Nakashizuka, T. Ohkubo, T. Kato, T. Maeda, K. Sato, H. Miguchi, H. Nagamasu, K. Ogino, S. Teo, A. A. Hamid, and H. S. Lee. 2000. Impact of a severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16:355–67.

Nomura, M., T. Itioka, and T. Itino. 2000. Variations in abiotic defense within myrmecophytic and non-myrmecophytic species of *Macaranga* in a Bornean dipterocarp forest. *Ecological Research* 15:1–11.

Ohkubo, T., T. Maeda, T. Kato, M. Tani, T. Yamakura, H. S. Lee, P. S. Ashton, and K. Ogino. 1995. Landslide scars in canopy mosaic structure as a large scale disturbance to a mixed dipterocarp forest at Lambir Hills National Park, Sarawak. Pages 172–84 in H. S. Lee, P. S. Ashton, and K. Ogino, editors. *Long Term Ecological Research of Tropical Rain Forest in Sarawak.* Ehime University, Matsuyama, Japan.

Palmiotto, P. A. 1995. Preliminary characterization of soil texture and organic matter thickness in 52 ha of lowland mixed dipterocarp forest, Lambir Hills National Park, Sarawak Malaysia. Pages 61–67 in H. S. Lee, P. S. Ashton, and K. Ogino, editors. *Long Term Ecological Research of Tropical Rain Forest in Sarawak.* Ehime University, Matsuyama, Japan.

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, CT.

Potts, M. D., P. S. Ashton, L. S. Kaufman, and J. B. Plotkin. 2002. The effect of habitat and distance on tropical tree species: A floristic comparison of 105 plots in Northwest Borneo. *Ecology* 83:2782–97.

Primack, R. B., P. S. Ashton, P. Chai, and H. S. Lee. 1985. Growth rates and population structures of Moraceae trees in Sarawak, East Malaysia. *Ecology* 66:577–88.

Proctor, J., J. M. Anderson, P. Chai, and H. W. Vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu national park, Sarawak. *Journal of Ecology* 71:237–60.

Putz, F. E., and P. Chai. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75:523–31.

Sakai, S. 2000. Reproductive phenology of gingers in a lowland dipterocarp forest in Borneo. *Journal of Tropical Ecology* 16:337–54.

Sakai, S., and T. Inoue. 1999. A new pollination system: Dung-beetle pollination discovered in *Orchidantha inouei* (Lowiaceae, Zingiberales) in Sarawak, Malaysia. *American Journal of Botany* 86:56–61.

Sakai, S., M. Kato, and T. Inoue. 1999. Three pollination guilds and variation in floral characteristics of Bornean gingers (Zingiberaceae and Costaceae). *American Journal of Botany* 86:646–58.

Sakai, S., M. Kato, and H. Nagamasu. 2000. *Artocarpus* (Moraceae)—gall midge pollination mutualism mediated by a male-flower-parasitic fungus. *American Journal of Botany* 87:440–45.

Sakai, S., K. Momose, T. Yumoto, M. Kato, and T. Inoue. 1999. Beetle pollination of *Shorea parvifolia* (section Mutica, Dipterocarpaceae) in a general flowering period in Sarawak, Malaysia. *American Journal of Botany* 86:62–69.

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* 86:1414–36.

Shanahan, M., and S. G. Compton. 2001. Vertical stratification of figs and fig-eaters in a Bornean lowland rainforest: How is the canopy different? *Plant Ecology* 53:121–32.

Shanahan, M., and I. Debski. 2002. Vertebrates of Lambir Hills National Park, Sarawak. *Malayan Nature Journal* 56:103–18.

Watson, H. 1985. *Lambir Hills National Park: Resource Inventory with Management Recommendations.* National Parks and Wildlife Office, Forest Department, Kuching, Sarawak, Malaysia.

Yamada, T., and E. Suzuki. 1999. Comparative morphology and allometry of winged diaspores among the Asian Sterculiaceae. *Journal of Tropical Ecology* 15:619–35.

Yamakura, T., A. Hagihara, S. Sukardjo, and H. Ogawa. 1990. Aboveground biomass of tropical rain forest stands in Indonesian Borneo. *Vegetatio* 68:71–82.

Yamakura, T., M. Kanzaki, A. Itoh, T. Ohkubo, K. Ogino, E. O. K. Chai, H. S. Lee, and P. S. Ashton. 1995. Topography of a large-scale research plot established within a tropical rain forest at Lambir, Sarawak. *Tropics* 5:41–56.

———. 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.

Yumoto, T. 2000. Bird pollination of three *Durio* species (Bombacaceae) in a tropical rainforest in Sarawak, Malaysia. *American Journal of Botany* 87:1181–88.