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Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest[1]

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Flowerings and flower visitors were observed continuously in a lowland dipterocarp forest in Sarawak, Malaysia, for 53 mo in 1992–1996. Flower visitors of 270 plant species were observed or collected, and pollinators were assessed by observing body contact to stigmas and anthers. We recognized 12 categories of pollination systems. Among them, plants pollinated by social bees included the largest number of species (32%) and were followed by beetle-pollinated species (20%). Pollination systems were significantly related with some floral characters (flowering time of day, reward, and floral shape), but not with floral color. Based on the relationships between pollinators and floral characters, we described pollination syndromes found in a lowland dipterocarp forest. The dominance of social bees and beetles among pollinators is discussed in relation to the general flowering observed in dipterocarp forests of West Malesia. In spite of high plant species diversity and consequent low population densities of lowland dipterocarp forests, long-distance-specific pollinators were uncommon compared with the Neotropics.

Key words: beetle; floral shape; flowering time; general flowering; lowland dipterocarp forest; pollination syndrome; reward; Sarawak; social bee.

Pollination biology at the community level in tropical forests has been studied only in the Neotropics (Bawa et al., 1985; Kress and Beach, 1994). In a tropical rain forest in La Selva, Costa Rica, medium-sized to large bees and small diverse insects are the main pollinators in the canopy (Bawa et al., 1985; Kress and Beach, 1994), while hummingbirds and euglossine bees are prevalent in the forest understory (Janzen, 1971; Stiles, 1978; Endress, 1994; Kress and Beach, 1994). Little information is available on pollination biology in West Malesia, where plant reproductive phenology, fauna, and flora are greatly different from the Neotropics.

On the topic of plant reproductive phenology, the phenomenon known as general flowering has been reported from West Malesia and as might be expected this has consequences for the co-evolutionary processes between plants and pollinators. Over 80% of the emergent and the canopy tree species bloom in short periods of 3–4 mo at irregular intervals of 2–10 yr (Ashton, Givnish, and Appanah, 1988; Appanah, 1993). In general flowering periods (GFP), such a large number of species bloom in so short a period that pollinator shortages might occur unless there are pollinators that can quickly respond to the general flowering (Ashton, Givnish, and Appanah, 1988). According to these authors, thrips are capable of such response. Thrips maintain a low population density using floral resources in gaps during flowerless seasons. They have a short generation time and high fecundity, so as soon as a general flowering starts, they can increase in numbers quickly using the massive floral resources. However, a thrip pollination was only found in the genus *Shorea*, sect. *Mutica* in the Malay Peninsula (Appanah and Chan, 1981). Are all trees that bloom in GFP pollinated by thrips, or are there other types of pollinators that can quickly respond to the general flowering? This is the first question that we address in this paper. Appanah (1990) provided one clue to the answer. Carpenter bees (*Xylocopa* spp.) shift foraging areas in GFP from forest edges to closed forests and pollinate some plants in closed forests. However, we question whether such shifts of for-

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aging areas could provide sufficient pollinator populations.

Bawa (1990) stated that long-distance pollen flow is intensified in species-rich tropical rain forests, because conspecific plants are spatially isolated from each other. Hummingbirds and euglossine bees are the most important long-distance-specific pollinators in the Neotropics (Kress and Beach, 1994), but they are absent in Southeast Asia. From La Selva, Costa Rica, 1287 species of wild flowering plants have been recorded (Hartshorn and Hammel, 1994). The exact number of plant species in Lambir, Sarawak, is unknown, but even when restricted to trees (dbh [diameter at breast height] ≥ 1 cm) found in a 52-ha plot, over 1200 species have been recognized (P. S. Ashton, Harvard University, personal communication). In and around a Canopy Biology Plot (8 ha), 999 species of flowering plants have been collected (Nagamasu and Momose, 1997). In Lambir, species richness is very high, and conspecific plants are considered to be spatially isolated from each other. It would be expected that long-distance specific pollinators have also important roles in the species-rich lowland dipterocarp forest. If so, what types of long-distance-specific pollinators are there in lowland dipterocarp forests? This is our second question.

In tropical rain forests in Borneo, the canopies are sometimes over 70 m above the ground and up to five forest strata are distinguishable (Yamakura, 1992). Higher strata are especially active in primary production and reproduction of plants. Because of technical difficulties, information on plant reproduction and plant–animal interactions in the forest canopy has been very limited (Lowman and Nadkarni, 1995; Lowman and Wittman, 1996). A canopy observation system composed of tree towers and aerial walkways was constructed by the Canopy Biology Program, Sarawak in Lambir Hills National Park, Sarawak, Malaysia (Inoue and Hamid, 1994; Inoue 1995). Using this facility, we are monitoring reproductive phenology of individually marked plants (Yumoto, Inoue, and Hamid, 1996; S. Sakai et al., unpublished data), animal temporal dynamics (Kato et al., 1995), and plant–pollinator interactions (this study).

In this paper we report on plant–pollinator interactions across the whole community of a lowland dipterocarp forest both during the general flowering periods and other periods. Detailed experimental studies on the pollination biology of some plant species and analyses on relationship between pollination systems and other plant characteristics will be reported in other papers.

MATERIALS AND METHODS

Study site—The study was carried out in the Canopy Biology Plot (CBP, 8 ha: 200 × 400 m) and a belt transect along the waterfall trail (5 ha: 1 km × 50 m) established in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°2′ N, 113°50′ E, 150–250 m in altitude). CBP includes humult and udult soils (sandy clay, light clay, or heavy clay in texture), several ridges and valleys, closed (mature-stage) forests, and gaps. At the center of CBP a canopy-access system (two tree towers, nine aerial walkways, and seven tree terraces) was constructed (Inoue et al., 1995). The waterfall trail was located along a stream on yellow sandstone, from the headquarters of the park to the Operation Raleigh Tower (ORT). The belt transect included closed forests and open habitats along river banks. Soils were ultisol or entisol. Waterfalls and wet sandstone cliffs were also included in the transect.

Monitoring of flowering events—A census was carried out continuously for 53 mo from August 1992 (just after a general flowering has finished) to December 1996 (when the next general flowering finished). We monitored 576 individually marked plants (310 species including trees, lianas, and epiphytes) to check their flowering events (Fig. 1; Yumoto, Inoue, and Hamid, 1996; S. Sakai et al., unpublished data), monthly from the forest floor and bimonthly from the canopy using the canopy access system in CBP and the Operation Raleigh Tower. At the same time as the above census we searched flower buds and flowers in CBP and the belt transect. Ad hoc searching was intensfied in the general flowering period (from March to December 1996, when the percentage of flowering individuals among the marked plants continuously exceeded 10%).

Observation and collection—When flowers were found on individually marked plants and those found in ad hoc searching, plant specimens were collected and floral characters (flowering time in day, reward, color, and shape; see below) were recorded. Plant specimens were identified in SAR (Sarawak Herbarium, Sarawak Forest Department). They were sent to some herbaria, among which SAR and KYO (Herbarium, Kyoto University) have complete sets of our collection (Plants of Sarawak, Canopy Biology Program, Sarawak; Appendix).

Flower visitors and their behavior on flowers were observed both in daytime and nighttime on the day on which we found flowering and on following days. When flower visitors made contact with stigmas and anthers, those visitors were regarded as pollinators. When pollinators were vertebrates, they were identified in the field. When pollinators were insects, they were collected as far as possible by flower beating and net sweeping (Fig. 2). All insect specimens were pinned and identified to families. All bees and some beetles were identified to genera. Family Apidae (honey bees and stingless bees, Hymenoptera) were identified to species. Figs (*Ficus* spp., Moraceae) were not included in this study, because they have specialist pollinators, fig wasps (Galil and Eisikowitch, 1968; Compton, Wiebes, and Berg, 1996) whose behavior cannot be observed in the same ways as pollinators of other plants, and they belong to completely independent pollination guilds from the other plants. The fig–fig wasp interaction is being studied separately by R. D. Harrison.

Floral characters—We recorded flowering time, reward, color, and shape.

Flowering time—We defined flowering time of day as the time when

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Figs. 1–6. Monitoring of plant phenology, collection of flower visitors, and various types of flowers and pollinators. **1**. Monitoring of phenology of individually marked plants to check their flowerings from the canopy access system in Lambir Hills National Park, Sarawak, Malaysia. **2**. Sweeping of flower visitors on a temporary wood terrace set at the crown top of *Shorea falciferoides* (Dipterocarpaceae), at 60 m above the ground. **3**. Bat pollination: *Macroglossus minimus* (Pteropodidae) visiting flowers of *Fagraea racemosa* (Loganiaceae). **4**. Bird pollination: *Arachnothera robustra* (Nectariniidae) visiting flowers of *Amylotheca duthiana* (Loranthaceae). **5**. Social bee pollination: a worker of *Apis dorsata* (Apidae) collecting pollen from a flower of *Dryobalanops aromatica* (Dipterocarpaceae). **6**. A worker of *Apis koschevnikovi* visiting a flower of *Dillenia excelsa* (Dilleniaceae) that is mainly pollinated by *Apis dorsata*.


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TABLE 1. Numbers of genera and species, and main pollination systems of the 73 plant families observed in a lowland dipterocarp forest in Sarawak, Malaysia.

Family	No. of genera	No. of species	Pollination systems
Acanthaceae	2	2	*Nomia*
Actinidiaceae	1	3	*Amegilla, Xylocopa, Trigona*
Alangiaceae	1	1	*Apis*
Anacardiaceae	2	2	social bee/diverse insect
Annonaceae	12	22	beetle, etc.
Apocynaceae	1	1	social bee/diverse insect
Araceae	1	1	beetle
Asclepiadaceae	1	1	social bee/diverse insect
Bombacaceae	2	5	bird, etc.
Burmanniaceae	1	1	fly
Burseraceae	4	6	social bee/diverse insect
Celastraceae	1	1	social bee/diverse insect
Compositae	2	2	social bee/diverse insect
Convolvulaceae	1	2	social bee/diverse insect, beetle
Cornaceae	1	1	beetle
Costaceae	1	2	*Amegilla*
Crypteroniaceae	1	1	social bee/diverse insect
Dilleniaceae	2	3	*Apis, Xylocopa*
Dipterocarpaceae	5	27	beetle, *Apis,* etc.
Ebenaceae	1	1	beetle
Elaeocarpaceae	1	2	social bee/diverse insect
Euphorbiaceae	15	23	social bee/diverse insect, *Apis*
Fagaceae	1	2	social bee/diverse insect
Flacourtiaceae	2	2	social bee/diverse insect, etc.
Gesneriaceae	1	1	*Amegilla*
Gnetaceae	1	3	moth, fly
Gramineae	1	1	social bee/diverse insect
Guttiferae	3	5	social bee/diverse insect, *Apis*
Hypericaceae	1	1	social bee/diverse insect
Hypoxidaceae	1	1	social bee/diverse insect
Icacinaceae	1	2	social bee/diverse insect, beetle
Ixonanthaceae	1	1	*Apis*
Lauraceae	2	2	social bee/diverse insect
Lecythidaceae	1	1	moth
Leguminosae	8	13	social bee/diverse insect, *Apis, Megachile,* etc.
Loganiaceae	1	1	bat
Loranthaceae	3	3	bird
Lowiaceae	1	1	beetle
Marantaceae	2	3	*Amegilla, Nomia*
Melastomataceae	3	5	social bee/diverse insect, *Xylocopa*
Meliaceae	2	3	social bee/diverse insect, *Nomia, Apis*
Menispermaceae	1	1	social bee/diverse insect
Moraceae	1	2	social bee/diverse insect
Musaceae	1	1	bird
Myristicaceae	3	5	beetle, thrip
Myrsinaceae	2	2	bird, *Nomia*
Myrtaceae	1	3	social bee/diverse insect
Olacaceae	2	2	social bee/diverse insect
Opiliaceae	1	1	social bee/diverse insect
Orchidaceae	3	3	*Trigona, Apis*
Palmae	2	2	social bee/diverse insect
Pentaphragmataceae	1	2	*Amegilla, Nomia*
Piperaceae	1	2	social bee/diverse insect, beetle
Polygalaceae	1	1	*Amegilla*
Proteaceae	1	1	social bee/diverse insect
Rhamnaceae	1	1	social bee/diverse insect
Rhizophoraceae	1	1	social bee/diverse insect
Rosaceae	1	1	social bee/diverse insect
Rubiaceae	9	13	butterfly, social bee/diverse insect, bird
Rutaceae	1	1	social bee/diverse insect
Sapindaceae	2	3	social bee/diverse insect
Sapotaceae	4	7	bird, etc.
Simaroubaceae	1	1	social bee/diverse insect
Sterculiaceae	4	7	beetle, social bee/diverse insect, *Apis*
Theaceae	1	1	social bee/diverse insect
Tiliaceae	2	4	social bee/diverse insect
Trigoniaceae	1	1	*Nomia*

TABLE 1. Continued.

Family	No. of genera	No. of species	Pollination systems
Triuridaceae	1	1	fly
Ulmaceae	1	1	social bee/diverse insect
Urticaceae	2	2	*Trigona*
Verbenaceae	6	8	social bee/diverse insect, *Nomia,* etc.
Xanthophyllaceae	1	2	*Megachile, Xylocopa*
Zingiberaceae	10	26	*Amegilla, Nomia,* bird
Total	165	270	

male or female functions are maintained (pollen is served, stigmas are receptive) and flower visitors are attracted. To ensure the latter, we checked the following conditions: flower opening, reward production (except deceit pollination), and odor emission (if it existed). We categorized it into daytime (0600–1800) and nighttime (1800–0600).

Reward—We identified rewards (nectar, pollen, floral tissues, and others).

Floral color—We selected the visually most attractive parts in flowers (corolla, calyx, bracts, etc.), and recorded the color (white, yellow, red-orange, and the others).

Floral shape—We followed Harris and Harris (1994).

Pollination systems—Based on the obligate or dominant pollinators observed, we determined pollination systems (mode of pollination; obligate or main pollinators if zoophilous). Relationships between floral characters and pollination systems were tested by the *G* test (Sokal and Rohlf, 1981) on the basis of the number of plant species. According to the relationships between pollination systems and floral characters, we described plant–pollinator interactions in a lowland dipterocarp forest.

RESULTS

We collected or observed flower visitors of 270 plant species of 73 families (Table 1, Appendix). Flowerings of more species were observed, but flowers of some species were difficult to access. Flower visitors that were regarded as pollinators (attachments to stigmas and anthers were observed) were mammals, birds, and insects. *Gironniera* spp. (Ulmaceae) and *Artocarpus elasticus* (Moraceae) appeared to be wind pollinated, but we did not include them in our results, because this has not been confirmed. Other observed flowers were all animal pollinated.

Based on obligate or dominant pollinators, 12 categories of pollination systems were found: (1) mammal pollination (obligately pollinated by bats and squirrels); (2) bird pollination (obligately pollinated by birds); (3) social bee pollination (dominantly pollinated by the genera *Apis*, *Trigona*, and *Braunsapis*, Apidae, Hymenoptera, but several other insect families also became pollinators); (4) *Xylocopa* pollination (obligately or dominantly pollinated by *Xylocopa* spp. Anthophoridae); (5) *Amegilla* pollination (obligately pollinated by *Amegilla* spp., Anthophoridae); (6) halictid pollination (obligately or dominantly pollinated by *Nomia* spp. or *Thrinchostoma* spp., Halictidae, Hymenoptera); (7) *Megachile* pollination (obligately pollinated by *Megachile* spp., Megachilidae, Hymenoptera); (8) butterfly pollination (obligately pollinated by butterflies); (9) moth pollination (obligately pollinated by moths); (10) beetle pollination (obligately or dominantly pollinated by beetles); (11) diverse insect pollination (pollinated by several families of multiple insect orders and not dominated by any insect families); and (12) others (obligately or dominantly pollinated by thrips, flies, wasps, or cockroaches).

Plants pollinated by social bees included the largest number of species (32%), followed by beetle-pollinated species (20%).

Pollination systems and floral characters—*Flowering time*—Flowering time of day was significantly related with pollination systems ($G = 95.7$, $P < 0.001$; Table 2). Most plants pollinated by mammals and moths and some plants pollinated by diverse insects (*Artocarpus* spp., Moraceae) and social bees (*Dipterocarpus* spp., Dipterocarpaceae, pollinated by *Apis dorsata*) flowered at night. Beetle-pollinated plants flowered both in daytime and nighttime.

Reward—The relationship between pollination systems and rewards was significant ($G = 65.1$, $P < 0.001$; Table 2). In most plant species (78 %) the reward was nectar and/or pollen. The relative importance of nectar and pollen varies among plants, but this was not quantified. Thus, in the above analysis, we treated nectar and pollen as the same category. Flowers offering floral tissues as reward were found in plants pollinated by mammals, beetles, and thrips. Deceit (pollination without reward) was found in *Apis*- and *Trigona*-pollinated orchids (Inoue, Kato, and Inoue, 1995; T. Yumoto et al., unpublished data) and a beetle-pollinated herb (*Orchidantha lambirensis*, Lowiaceae; S. Sakai et al., unpublished data).

Floral color—Floral colors were not significantly related with pollination systems ($G = 45.7$, NS; Table 2). Mammal-pollinated and moth-pollinated flowers were white. However, white flowers did not strongly characterize the two pollination systems, because many flowers pollinated by bees and diverse insects were also white to the human eye.

Floral shape—Floral shapes were significantly related with pollination systems ($G = 92.9$, $P < 0.01$; Table 2). Cup-shaped and rotate flowers were common in plants pollinated by social bees, beetles, and diverse insects. *Amegilla*- and Halictidae-pollinated plants had bilabiate flowers. *Megachile*-pollinated flowers were papilionaceous. Lepidopteran-pollinated flowers were tubular or brush-like.

TABLE 2. Floral characters of 270 plant species in various pollination systems.

Pollination system	No. of plant species	Flowering time[1]			Reward[2]			Floral color[3]				Floral shape[4]					
		d	d, n	n	n, p	fl. t.	Other	White	Yellow	Red, orange	Other	Bilabiate	Tubular	Brush	Urceolate, campanulate	Cup, rotate	Other
Mammal	5	0	2	3	3	2	0	5	0	0	0	1	0	0	0	0	4
Bird	19	18	1	0	19	0	0	7	1	6	5	6	2	0	2	4	5
Social bee	86	78	4	4	83	0	3	46	21	8	11	5	0	13	10	48	10
Xylocopa	8	8	0	0	8	0	0	2	2	1	3	1	0	0	1	2	4
Amegilla	17	17	0	0	17	0	0	8	0	7	2	14	0	0	0	2	1
Nomia	21	21	0	0	21	0	0	18	1	0	2	15	0	1	1	3	1
Megachile	4	4	0	0	4	0	0	1	0	1	2	0	0	0	0	0	4
Butterfly	6	6	0	0	6	0	0	0	0	6	0	0	4	1	0	0	1
Moth	3	0	0	3	2	0	1	2	0	0	1	0	0	1	1	0	1
Beetle	56	4	50	2	14	19	23	15	28	4	9	1	0	0	6	28	21
Diverse insect	37	33	2	2	35	0	2	16	14	2	5	1	0	7	0	22	7
Other	8	5	3	0	4	1	3	3	2	1	2	0	0	0	2	2	4
Total	270	194	62	14	216	22	32	123	69	36	42	44	6	23	23	111	63

[1] d: daytime (0600–1800); n: nighttime (1800–0600); d, n: both in daytime and nighttime. $G = 95.7$, $P < 0.001$.
[2] n, p: nectar and/or pollen; fl. t.: floral tissue; others: stigmatic secretions, deceit, etc. $G = 65.1$, $P < 0.001$.
[3] $G = 45.7$, NS.
[4] $G = 92.9$, $P < 0.01$.

Descriptions of plant-pollinator interactions—*Mammal pollination*—Four species in three families (Leguminosae, Loganiaceae, Sapotaceae) were pollinated by bats (*Macroglossus* spp., Fig. 3) and one species (Sapotaceae; T. Yumoto et al., unpublished data) by squirrels (*Callosciurus prevostii caroli*, *Sundasciurus hippurus inquinantus*, *S. lowii*) and flying squirrels (*Petaurista petaurista rajah*). Rewards were nectar in three bat-pollinated species and a berry-like sweet corolla in one bat-pollinated species (*Ganua beccarii*, Sapotaceae) and the squirrel-pollinated species (*Ganua* sp., Sapotaceae). Flowers of all five species were white and emitted a strong scent, but shapes were various.

Bird pollination—Nineteen species in seven families were pollinated by birds (*Nectarinia jugularis*, *Arachnothera longirostra*, and *A. robusta*, Nectarinidae; Fig. 4). Flowers were bilabiate or tubular in shape (some that burst open); white, red, or orange in color; without scent or with strong scent (Yumoto, Itino, and Nagamasu, 1997; T. Yumoto et al., unpublished data).

Social bee pollination—Flowers of 86 species in 42 families were predominantly visited and pollinated by the genera *Apis* (honey bees), *Trigona* (stingless bees), and *Braunsapis*. Among them, the number of *Apis dorsata* (giant honey bee; Fig. 5) colonies increased greatly during the GFP by migration and colony multiplication, but they were much fewer in non-GFP. In daytime, they were found together with other social bees and diverse insects of several families of Coleoptera, Diptera, and Hymenoptera. However, in the early morning before sunrise (0500–0600) and from evening to early nighttime (1800–2000), only *A. dorsata* among social bees foraged. Two species of *Dryobalanops*, *Dipterocarpus tempehes* (Dipterocarpaceae) and *Dillenia excelsa* (Dilleniaceae) flowered in the early morning (0500). Other species of *Dipterocarpus* flowered in the evening (1800). *Apis dorsata* was an especially important pollinator for those plants (K. Momose et al., unpublished data).

Other social bees (Figs. 6, 7) seldom migrate and were important pollinators especially in non-GFP (Inoue et al., 1984a; Momose, Nagamitsu, and Inoue, 1996; Nagamitsu and Inoue, 1997a), when *A. dorsata* were rare. They were found together with diverse insects of several families of Coleoptera, Diptera, and Hymenoptera. Flowers dominated by social bees were brush-like, rotate, or cup-shaped in shape, and white or yellow in color.

Xylocopa pollination—Eight species in seven families were mainly pollinated by *Xylocopa* spp. (carpenter bees; Fig. 8). They usually had large flowers with long pistils. The arrangement of anthers and stigmas suited to the body sizes of carpenter bees, but other visitors like stingless bees were not excluded (Fig. 9). Some *Xylocopa*-pollinated flowers had porose anthers, from which carpenter bees collected pollen grains by buzzing. Carpenter bees usually foraged at forest edges and open habitats, but were sometimes found in the forest canopy. Although Appanah (1990) reported carpenter-bee pollination of forest trees in the Malay Peninsula, they were not the main pollinators in the forest trees in our study site in Sarawak,

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Figs. 7–14. Various types of flowers and flower visitors. **7**. A stingless bee *Trigona canifrons* (Apidae) visiting a flower of *Dryobalanops aromatica* that is mainly pollinated by *Apis dorsata*. **8**. *Xylocopa* pollination: a female of *Xylocopa* sp. (Anthophoridae) collecting, by buzzing, pollen of a flower of *Melastoma malabathricum* (Melastomataceae). **9**. A stingless bee collecting pollen of *Melastoma malabathricum* from anthers without touching a stigma. **10**. *Amegilla* pollination: *Amegilla insularis* (Anthophoridae) entering a long floral tube of *Zingiber longipedunculatum* (Zingiberaceae). **11**. Halictid pollination: *Thrincostoma afasciatum* (Halictidae) entering a bilabiate flower of *Elettariopsis kerbyi* (Zingiberaceae). **12**. *Megachile* pollination: a female of *Megachile* sp. (Megachilidae) inserting its mouthpart into a papilionaceous flower of *Callerya nieuwenhuisii* (Leguminosae). **13**. Butterfly pollination: *Troides brookiana* (Papilionidae) visiting and sucking nectar from newly opened yellow flowers of *Bauhinia* sp. (Leguminosae). Red flowers were old, remaining for a long time. **14**. Butterfly-pollinated tubular flowers of *Ixora caudata* (Rubiaceae).


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because of their much lower density than social bees. However, carpenter bees sometimes visited papilionaceus flowers (usually *Megachile*-pollinated; see below) and became dominant pollinators, if plants were located in gaps.

Amegilla pollination—Seventeen species in six families (Costaceae, Gesneriaceae, Marantaceae, Pentaphragmataceae, Polygalaceae, and Zingiberaceae) were pollinated only by the trap-lining long-tongued bees, *Amegilla pendleburyi* and *A. insularis* (Fig. 10). They had odorless bilabiate flowers colored white, yellow, purple, or orange with nectar guides. Rich nectar was secreted and protected from other insects by specialized floral shapes (Kato, Itino, and Nagamitsu, 1993). Males of *A. pendleburyi* were observed to make mating territories around flowers. Whereas *A. pendleburyi* and *A. insularis* forage on forest floors only, *A. andrewsi* usually foraged at forest edges and open habitats. *Amegilla andrewsi* often visited *Xylocopa*-pollinated flowers, but were not predominant.

Halictid pollination—Twenty-one species in nine families (Zingiberaceae, Verbenaceae, Acanthaceae, etc.) were pollinated by smaller trap-lining bees, *Nomia* spp. or *Thrincostoma* spp. (Fig. 11). Their flowers were similar to *Amegilla*-pollinated flowers in shape but smaller in size.

Megachile pollination—*Megachile* spp. appeared twice (May-July 1993 and May-July 1996) in the 53-mo census period. Plants with papilionaceous flowers (four species of two families: Leguminosae and Xanthophyllaceae) flowered in synchrony with the emergence of *Megachile* spp. and were pollinated by them (Fig. 12). *Megachile*-pollinated flowers seem to have shorter flowering cycles than the general flowering plants. Nectar and pollen were protected by keels from other visitors. However, after visitations of *Megachile* spp., a small amount of pollen fell from the anthers and was deposited on the surface of petals. Stingless bees and beetles were often found to collect pollen grains on petal surfaces, but they did not touch stigmas.

Butterfly pollination—There were two shapes of butterfly-pollinated flowers, one brush-like (Fig. 13) and the other tubular (Fig. 14). Butterfly-pollinated flowers (six species in three families: Leguminosae, Rubiaceae, and Verbenaceae) were usually odorless, and orange in color when fresh, but they often remained in inflorescences, turning reddish, even after pollination. This phenomenon was common in both brush-like flowers (*Bauhinia* spp., Leguminosae) and tubular flowers (*Ixora* spp., Rubiaceae).

Moth pollination—Moth-pollinated flowers (two species in two families: Dipterocarpaceae and Lecythidaceae) were also blush-like or thinly campanulate (mostly tubular). They had scent and were white or pale yellow in color. Moth pollination of a gymnosperm, *Gnetum gnemon* (Gnetaceae), has been reported in our study site (Kato and Inoue, 1994; Kato, Inoue, and Nagamitsu, 1995).

Beetle pollination—Fifty-six species in 11 families were pollinated by beetles. There were three types of rewards for beetles: floral tissues, stigmatic secretions, and pollen. Beetle-pollinated flowers were rotate, urceolate, or forming a floral chamber, and yellow, white, or pink in color.

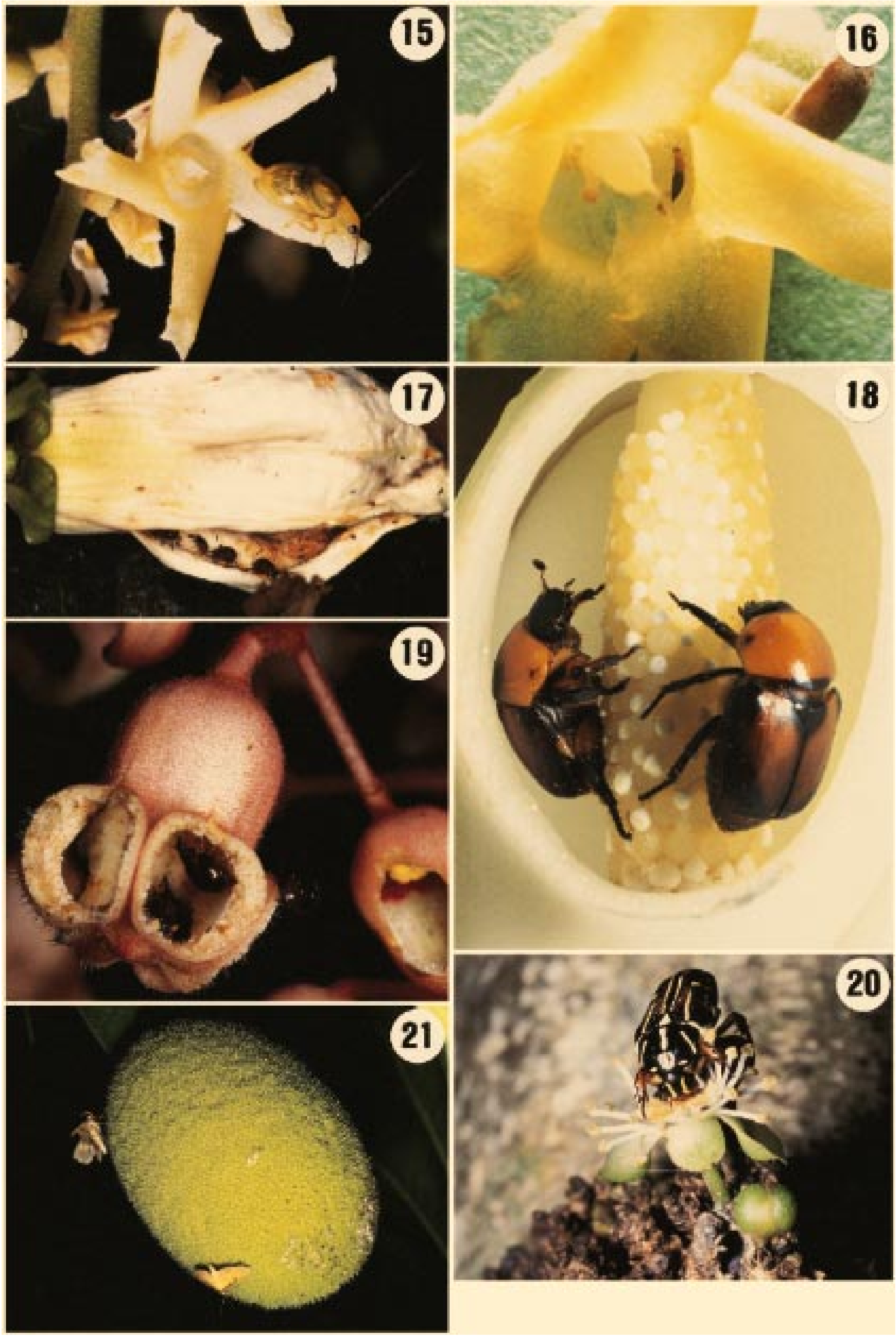
Shorea spp., *Hopea* spp., and *Vatica* spp. (all Dipterocarpaceae) flowered mostly in GFP and were visited by multiple species of beetles that fed on petals and occasionally on pollen and pistils (Fig. 15). Flowers were pale yellow or pink in color, producing scent, and rotate in shape, but sexual parts were located within a central cup-shaped part. The predominant family among visitors was Chrysomelidae, followed by Curculionidae and Nitidulidae. All of these three beetle families were regarded as pollinators, because pollen deposition on the body surfaces and stigmatic contact of beetle bodies were observed. Several flower-visiting chrysomelid species were found on dipterocarp fresh leaves in non-GFP. In Pasoh, Malay Peninsula, thrips pollination of *Shorea* section *Mutica* has been reported (Appanah and Chan, 1981). In our study site in northwestern Borneo, thrips (Fig. 16) were not important pollinators of dipterocarps even in the same species that Appanah and Chan (1981) studied, because the density of thrips per flower was far lower ($\sim$0.3 thrips) than Pasoh ($\sim$3 thrips). Details on beetle-pollinated dipterocarps will be reported by S. Sakai.

Most species of Annonaceae (91% in 22 observed species) were also pollinated by beetles. They were protogynous and had floral chambers (Fig. 17). Beetles were attracted by a strong scent during the female stage and remained in the floral chambers until they were released in the male stage, as reported by Gottsberger (1970). Rewards were stigmatic secretions and/or mating sites. Beetles found in flowers were *Carpophilus* spp. and *Epuraea* spp. (Nitidulidae) and *Endaenidius* spp., *Endaeus* spp. (Curculionidae) in most species. These beetles were not found on flowers of dipterocarps. In two species (*Enicosanthum coreaceum* and *Polyalthia motleyana*) of Annonaceae, Scarabaeidae and Chrysomelidae were found to feed on the petals. Stingless bees often visited male-stage flowers to collect pollen, but they did not visit flowers in the female stage.

Homalomena propinqua (Araceae) had its spathe forming a chamber, and several hundred male and female

→

Figs. 15–21. Various types of flowers and flower visitors. **15**. A chrysomelid beetle, pollinator of *Shorea parvifolia* (Dipterocarpaceae), feeding on the tip of a petal. **16**. A thrip in a flower of *Shorea parvifolia*. **17**. Chrysomelid pollinator beetles in a pollination chamber of *Enicosanthum coriaceum* (Annonaceae). **18**. Pollinator beetles of *Parastasia* (Scarabaeidae) in a spathe of *Homalomena propinqua* (Araceae). **19**. Chrysomelid pollinator beetles in the urceolate calyxes of *Sterculia stipulata* (Sterculiaceae). **20**. A scarabaeid beetle on flowers of *Drypetes longifolia* (Euphorbiaceae), which are pollinated by diverse insects. **21**. Pyralid moths visiting a female spadix of *Artocarpus odoratissimus* (Moraceae), which is pollinated by diverse nocturnal insects.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flowers were located in this chamber (Fig. 18). The inflorescence was protogynous (after female flowers have finished, male flowers open; Young, 1986). It was pollinated by *Parastasia* sp. (Scarabaeidae), which fed on the staminodes and pollen, and *Dercetia* sp. (Chrysomelidae), which fed on pollen and used the spathe chamber as a mating site (Kato, 1996). These beetles also were not found on flowers of dipterocarps.

The genera *Diospyros* (Ebenaceae), *Gymnacranthera*, *Knema* (Myristicaceae), *Heritiera*, and *Sterculia* (Sterculiaceae) were pollinated by beetles (Chrysomelidae were the commonest), which fed on pollen and/or nectar. Flowers were unisexual (monoecy or dioecy), drooping, and sexual parts were located at the bottom of the urceolate corolla / calyx, which had small entrances by which other visitors were excluded (Fig. 19).

Diverse insect pollination—Thirty-seven species in 22 families were visited and pollinated by several orders of insects (Coleoptera, Diptera, Hymenoptera, etc.) and were not dominated by any families (Fig. 20). The floral characters were those common to social bee-pollinated plants (except *Artocarpus* spp.; see below). Large flower patches including rich floral resouces tended to be dominated by social bees. Otherwise no insect families dominated.

Artocarpus spp. has a unisexual spadix containing many tiny flowers. Secretions from the spadix and scent were emitted at night. Several families of insects, Drosophilidae (Diptera), Pyralidae, Geometridae (Lepidoptera), Nitidulidae (Coleoptera), Blatteridae (Blatteria), etc., visited the spadix to feed on the secretions (Momose et al., in press; Fig. 21).

Others—Flies (Culicidae, Lauxaniidae, Drosophilidae, Calliphoridae: Diptera) were attracted to four species in three families (Burmanniaceae, Gnetaceae, and Triuridaceae) of forest floor plants (Kato, Inoue, and Nagamitsu, 1995; Kato, 1996). Wasps (Vespidae) were attracted to *Casearia grewiaefolia* (Flacourtiaceae; Kato, 1996). Cockroaches (Blatteridae) were attracted to *Uvaria* aff. *elmeri* (Annonaceae; Nagamitsu and Inoue, 1997b). Mechanisms of attraction of special pollinators and exclusion of other insects were uncertain in these examples. The genera *Popowia* (Annonaceae; Momose, Nagamitsu, and Inoue, in press) and *Horsfieldia* (Myristicaceae) attracted thrips (Thripidae, Thysanoptera) by scent and offered floral tissues and pollen as rewards. Other visitors were excluded by the small entrances of the pollination chambers.

DISCUSSION

Our observations were intensive for some plants but brief for many others (Appendix). The purpose of this paper was to clarify the characteristics of the plant–pollinator community of a dipterocarp forest. For this purpose it was necessary to observe as many species as possible. Because of the high species diversity and very low population density of many plant species, numerous observations in each plant species were not always possible. Hence, with limited pollinator observations for some species it is possible that we have incorrectly assigned the main pollinator. However, given that we have only used broad categories to describe the pollinator systems and the good fit found between pollinator systems and certain floral characteristics, we believe that this is an accurate characterization of the plant–pollinator interactions in our study site.

We monitored flowering phenology and pollination systems of plants in a fixed area (13 ha in total) of a lowland dipterocarp forest in Sarawak, Malaysia, continuously for 53 mo in 1992–1996. In and around the Canopy Biology Plot (8 ha), 999 species of flowering plants were collected (Nagamasu and Momose, 1997). Pollinators were determined in only 270 plant species (24% of the list by Nagamasu). However, this study is the first systematic observation of pollination systems at the community level in the Asian tropics, although our sampling ratios do not exactly reflect the abundance of species in respective plant habits. As we are continuing these community-level observations and, in addition, several plant groups, e.g., Dipterocarpaceae, Zingiberaceae, *Ficus*, etc, are being intensively studied by individual members in the Canopy Biology Program in Sarawak, much more information will be accumulated in the next decade.

Pollination syndromes—We revealed by statistical tests that the main pollinators were mostly determined by floral characters. Main pollinators were significantly related with flowering time, reward, and floral shape. Such relations among pollination systems and multiple floral characters can be called pollination syndromes (Faegri and van der Pijl, 1979; Table 3). In the study of pollination syndromes, floral characters are understood as mechanisms to attract proper pollinators and exclude low-efficiency visitors.

The reward is an important character to attract pollinators. Most species offered nectar and/or pollen as rewards, but some species had other types of reward (floral tissues, stigmatic secretions, etc.). These species that provided rewards other than nectar and pollen were visited by peculiar pollinators (squirrels, some beetles, etc.). The flowering time is also important for attracting certain pollinators but excluding other visitors. Bat- and moth-pollinated flowers were nocturnal. Some plants pollinated by *Apis dorsata*, which can forage both in daytime and in nighttime (Dyer, 1985), avoided visitations of diurnal insects (other social bees and diverse insects) by flowering in the early morning or evening. The floral color seems to have a role in attraction, but we could not detect a significant relationship with pollination systems from a classification based on colors recognized by humans. In this paper, we did not quantify nor qualify the floral scent, one more factor of pollinator attraction, but we have collected floral odors from various flowers and the analyses are in progress. Floral morphology is important in excluding low-efficiency visitors in some plants. Plants relying on specialized pollinators (solitary bees, lepidopterans, and vertebrates) and offering rich nectar per flower need to protect their rewards from other visitors (Heinrich and Raven, 1972). They usually have tubular, bilabiate, papilionaceous, or urceolate flowers. On the other hand, flowers pollinated by social bees and diverse insects are considered to have no morphological mechanisms to exclude any flower visitors. They have rotate,

TABLE 3. Pollination syndromes found in a lowland dipterocarp forest in Sarawak.

Pollinator group	Phenology[1]	Sex[2]	Time	Reward[3]	Color	Scent[4]	Shape	Protection[5]	Habit[6]
Mammal	g, (n)	h, (m)	night	n, f	white	3	various	flowering time	3, 4
Bird	g, n	h, (m)	day	n	white, orange, red	1–3	bilabiate, tubular, burst open	long floral tube, tightly closed petals before picked	2, 3, G, E
Social bee, diverse insect	g, n	h, m, d	day, (night)	n, p	white, yellow	1–3	brush (small), rotate, cup-shaped	nothing, (flowering time)	2, 3, 4, 5, G, L
Xylocopa	(g), n	h	day	n, p	yellow, purple	1–2	long pistil, large petal, (papilionaceous)	nothing, (keel)	G
Amegilla	n	h	day	n (p)	white, yellow, orange	1	bilabiate	long floral tube	1, G
Nomia	(g), n	h	day	n (p)	white, yellow, orange	1	bilabiate	small fl. with relatively long floral tube	1, G
Megachile	n	h	day	n, p	pink, red	1–2	papilionaceous	keel covering sexual part	1, L
Moth	(g), n	h, (d)	night	n	white, pale yellow	3	brush (large), tubular	flowering time, long slender floral tube	1, L
Butterfly	(g), n	h	day	n	orange turning red	1	brush (large), tubular	long slender floral tube	1, L
Beetle	g, n	h, m, d	day and night	p, f, l	yellow, pink, white	3	rotate, chamber, urceolate	type of reward, floral chamber with small entrance	1, 2, 3, 4, 5, L

[1] g: flowers only in the general flowering period; n: flowers in non-general-flowering periods or both in general and eneral-flowering periods.
[2] h: hermaphrodite, m: monoecy, d: dioecy.
[3] n: nectar, p: pollen; f: floral tissue; 1: liquid (non nectar).
[4] 1: inconspicuous, 2: conspicuous, 3: strong.
[5] Ways of excluding nonpollinating visitors (especially against social bees).
[6] 1: forest floor herbs or treelet, 2: understory, 3: subcanopy, 4: canopy, 5: emergent, G: gap (or open habitat) trees, L: liana, E: epiphyte, in brackets: exist but rare.

cup-shaped, or brush-like flowers. The flowers should have suitable arrangements of sexual parts for efficient transfer of pollen, but such detailed flower measurements were not carried out in this study.

Using the results of this study, as summarized in Table 3, we can, more or less, predict pollination systems from floral characters. However, perfect prediction is impossible, because pollinator guilds are not always clearly separated from each other (Roubik, 1992). For example, *Xylocopa* spp. sometimes dominated on papilionaceus flowers, which are usually pollinated by *Megachile* spp. In this study, we have just shown that there is an overall pattern of significant relationships between floral characters and main pollinators.

General flowering and pollination—In general flowering periods (GFP), such a large number of species bloom in so short a period that pollinator shortage might occur unless pollinators can quickly respond (Ashton, Givnish, and Appanah, 1988). In the case of thrip pollination of *Shorea*, sect. *Mutica* in Malay Peninsula, numbers quickly increase using massive floral resources (Appanah and Chan, 1981). In our study site, their quick increase was not observed and they had limited roles as pollinators (S. Sakai et al., unpublished data). Carpenter bees (*Xylocopa* spp.) shift foraging areas in GFP from forest edges to closed forests in the Malay Peninsula (Appanah 1990), but were not common in closed forests during GFP at our study site.

We hypothesize that some beetles can use such suddenly increasing flower resources, and several plant species reproducing in GFP use those beetles as pollinators. Chrysomelids pollinating some dipterocarps fed on leaves of dipterocarps in non-GFP and shift resources to floral tissues in GFP, because they were collected on dipterocarp leaves in flowerless seasons.

Social bees (*Trigona*, *Apis*, and *Braunsapis*) also had important roles as pollinators in the lowland dipterocarp forest compared to the Neotropical forest in Costa Rica, where medium to large anthophorid bees are dominant (Bawa et al., 1985; Kress and Beach, 1994), and the genus *Apis* is absent. Unlike the predictable annual flowering cycles in Costa Rica (Newstorm et al., 1994), the general flowering of lowland dipterocarp forests is a supra-annual (2–10 yr) cycle, and its intervals are not constant. Social bees can use such unpredictably fluctuating floral resources by long-distance migrations (*Apis dorsata*) or by resource stocking (*Trigona*).

Apis dorsata can migrate over 100 km (Koeniger and Koeniger, 1980). In Sarawak, they migrate to lowland dipterocarp forests as soon as the general flowering starts, and as the general flowering finishes they abscond (T. Nagamitsu and T. Inoue, personal observations). In non-GFP, their nests are found in mountain forests (T. Inoue, personal observations).

The stored excess honey of *Trigona* spp. enables a colony to survive for 2–5 yr without resupply from floral resources (Inoue et al., 1984b). Therefore, by stabilizing the effects of temporal changes in floral resources at a colony level, *Trigona* colonies can maintain forager workers, which can quickly start foraging in response to abrupt increases of ephemeral and massive floral resources in both GFP and non-GFP, and then store these resources in the nest (Inoue et al., 1984b, 1990, 1993; Salmah, Inoue, and Sakagami, et al., 1990). Recruitment behavior of social bees can further increase the quick exploitation of mass flowering trees (Roubik, 1989; Roubik, Inoue, and Hamid, 1995).

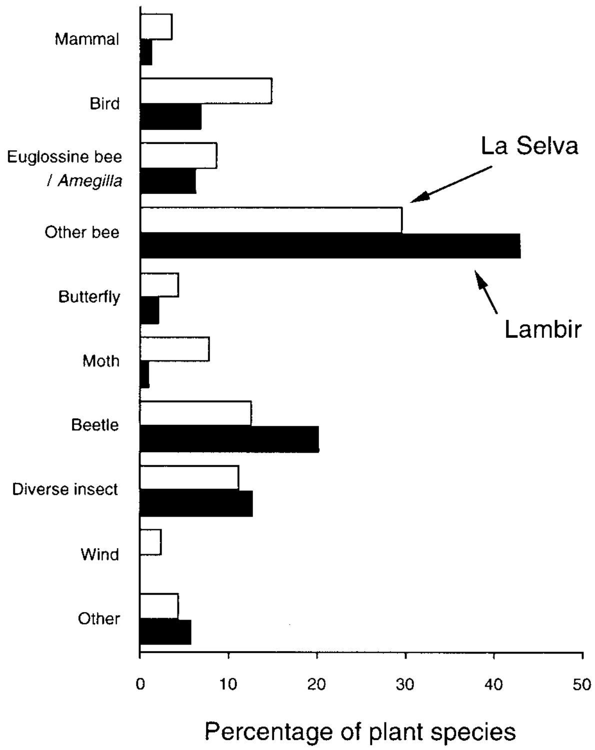

Fig. 22. Comparison of the frequency distributions of pollination systems between the two tropical regions: (top) a Neotropical lowland rain forest in La Selva, Costa Rica (from Kress and Beach, 1994) and (bottom) a Southeast Asian lowland dipterocarp forest in Lambir, Sarawak, Malaysia (this study). The frequency of different pollination syndromes was significantly different between two sites ($G = 18.0$, $P < 0.05$; wind pollination was excluded because of insufficient information in Lambir).

Long-distance-specific pollinators—Hummingbirds (long-billed nectar-feeding birds) and euglossine bees (long-tongued bees) are important long-distance-specific pollinators in the Neotropics (Kress and Beach, 1994). In the Neotropics, hummingbirds and euglossine bees are diversified and coexist by more or less partitioning floral resources (Janzen, 1971; Stiles, 1978). Long-billed nectar-feeding birds and long-tongued bees also are found in Southeast Asia; the former are spiderhunters and sunbirds, and the latter are *Amegilla* spp. However, the species diversity of these long-distance-specific pollinators is much lower in Southeast Asia. Only three species of long-billed nectar-feeding birds (*Arachnothera longirostra*, *A. robusta*, and *Nectarinia jugularis*) and two species of long-tongued bees (*Amegilla pendleburyi* and *A. insularis*) were major pollinators in our study site. The proportion of plant species pollinated by these long-distance-specific pollinators is smaller in Lambir than in La Selva (bird: 7.0 vs. 14.9%; long-tongued bee: 6.3 vs. 8.7%; Fig. 22).

Plant species pollinated by mammals and lepidopterans (other types of long-distance-specific pollinators) are also less frequent in Lambir than La Selva (mammal: 1.5 vs. 3.6%; lepidopteran: 3.3 vs. 12.3%; Fig. 22). *Xylocopa*, Halictidae, and *Megachile* are also long-distance-specific pollinators in Lambir (not specified in the data set of Kress and Beach, 1994). However, plant species pollinated by them in Lambir represent only 2.9, 7.7 , and 1.5% of the whole, respectively (Table 2). Some (maybe not all) beetles can move long distances (Young, 1988). However, if dipterocarps, which are pollinated by beetles feeding on floral tissues in GFP are excluded, the frequency of beetle pollination is similar between Lambir (10.7%) and La Selva (12.7%).

Long-distance-specific pollinators have less important roles in the species-rich lowland dipterocarp forest of Lambir than in the Neotropical forest. They require a continuous supply of rich resources, because their costs for body maintenance and foraging are high (Heinrich and Raven, 1972), and irregular and ephemeral floral resources in lowland dipterocarp forests are inadequate for their survival.

Highly eusocial bees (*Apis* spp. and *Trigona* spp.) are not specific pollinators but generalists in the sense that they use a wide range of floral resources. They communicate with colony members and can harvest floral resources effectively (Seeley, 1985; Roubik, 1989). According to pollen analyses at bee nests by T. Nagamitsu (unpublished data), at any one time, they often major in one or a few plant species that offer the richest floral resources (see also Seeley, 1985). In this case, conspecific plant individuals can be selectively visited by social bees. Especially, honey bees are considered to have wide foraging area (5 km or more), and enable long-distance pollen transfer (Seeley, 1985). To attract them, plants must have a reproductive phenology of the mass flowering type (set large amount of flowers within a short period). This might be another way of achieving effective long-distance pollen transfer and is a more favored strategy in lowland dipterocarp forests.

The plant-pollinator community of a lowland dipterocarp forest—Some plants have mechanisms to attract specific pollinators (mammals, birds, solitary bees, lepidopterans, beetles, etc.) and exclude low-efficiency visitors. Such mechanisms were partly detected as the set of floral characters (flowering time, reward, and floral shape). Otherwise, flowers were visited by diverse insects, and if plants had large flower patches with a rich reward, social bees dominated. Some pollinators can respond to the sudden increase of floral resources in the general flowering by shifting resources (beetles), long-distance migrations (*Apis dorsata*), or maintaining forager workers using stored resources (other social bees). Long-distance-specific pollinators were less common than in a Neotropical forest, probably because of the unpredictably fluctuating environment. Instead, at any one time, highly eusocial bees often major in one or a few plant species that offer the richest floral resources, and enable long-distance pollen transfer. To attract them, plants must have a reproductive phenology of the mass flowering type.

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APPENDIX. Reproductive traits, floral characters and pollinators of 270 plant species (73 families) in a lowland dipterocarp forest in Sarawak, Malaysia.[a]

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)		10
ACANTHACEAE												
Borneacanthus grandiflorus Brem.	Momose 25	1	s	N	h	d	n	white	bilabiate	*Nomia*		3
Ptyssiglottis dispar Hallier	Nyambong 124	1	s	N	h	d	n	white	bilabiate	*Nomia*		3
ACTINIDIACEAE												
Saurauia sp.	Momose 7015	1	i	N	h	d	n	pink	rotate	*Amegilla*		1
Saurauia glabra Merr.	Maeda 672	G	i	N	h	d	n, p	white	cup	*Xylocopa*		1
Saurauia ridleyi Merr.	Nagamasu 4866	1	b	N	h	d	n	pink	rotate	*Trigona*		1
ALANGIACEAE												
Alangium ridleyi King	Yumoto 7	2	s	G	h	d	n	white	campanulate deeply lobed	*Apis dorsata*		2
ANACARDIACEAE												
Buchanania sessilifolia (Bl.) Bl.	Momose 7102	3	s	G	h	d	n, p	greenish	rotate	d	Canaceidae, Syrphidae, several fam. of Coleoptera, Diptera	2
Gluta laxiflora Ridl.	Momose 5019	3	s	G	h	d	n, p	white	rotate	*Trigona*		1
ANNONACEAE												
Cathostemma aff. *hookerii* King	Momose 56	L	i	N	h	d, n	s	purple	cup	bs	*Endaenidius* spp., *Endaeus* spp. (Curculionidae)	1
Enicosanthum coriaceum (Ridl.) Airy Shaw	Momose 1019	3	b	N	h	d, n	c, s	white	chamber	bs, bf	Scarabaeidae, Chrysomelidae	4
Enicosanthum macranthum (King)	Momose 115	3	b	N	h	d, n	s	white	chamber	bs	*Endaenidius* spp., *Endaeus* spp. (Curculionidae)	2
Fissistigma paniculatum (Dunal) Merr.	Nyambong 101	L	s	N	h	d, n	s	yellow	chamber	bs	*Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3
Friesodielsia glauca (Hk. f. et Th.) van Steenis	Johan 207	L	s	N	h	d, n	s	yellow	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculioniae)	3
Friesodielsia filipes (Hk. f. et Th.) van Steenis	Yamauch 382	L	s	N	h	d, n	s	yellow	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3
Goniothalamus sp. nov.	Momose 7039	2	b	N	h	d, n	s	yellow	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	1
Goniothalamus uvarioides King	Momose 5250	1	b	N	h	d, n	s	white	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3
Goniothalamus velutinus Airy Shaw	Nagamasu 4836	1	b	N	h	d, n	s	yellow	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	4
Meiogyne cylindrostigma (Burck) van Heusden	Momose 87	2	i	N	h	d, n	s	pink	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	2
Monocarpia euneura Miq.	Nyambong 169	3	1	N	h	d, n	s	yellow	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3
Polyalthia cauliflora Hk. f. et Th.	Nagamasu 4606	2	b	N	h	d, n	s	yellow	chamber	bs	*Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3
Polyalthia hypogaea King	Momose 620	2	b	N	h	d, n	s	white	chamber	bs	*Endaenidius* spp., *Endaeus* spp. (Curculionidae)	2
Polyalthia motleyana (Hk. f.) Airy Shaw	Johan 260	1	i	N	h	d, n	c, s	white	chamber	bs, bf	Chrysomelidae	3
Polyalthia rumphii (Bl.) Merr.	Momose 517	2	i	N	h	d, n	s	yellow	chamber	bs	*Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
Polyalthia sp. nov.	Momose 383	1	s	N	h	d, n	s	yellow	chamber	bs *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	1
Polyalthia sp. nov. 2	Momose 76	1	i	N	h	d, n	s	purple	chamber	bs *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	1
Popowia pisocarpa (Bl.) Endl.	Momose 310	2	s	N	h	d, n	p, c	yellow	urceolate	Thripidae	5
Pyramidanthe prismatica (Hk. f. et Th) Sincliar	Momose 380	L	s	N	h	d, n	s	yellow	chamber	bs Chrysomelidae	3
Sphaerothalamus insignis Hk. f.	Momose 5049	1	b	G	h	d, n	s	red	chamber	bs *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	1
Uvaria aff. *elmeri* Merr.	Yamauch 55	L	b	N	h	d, n	p, s	white	rotate	Blattellidae	3
Uvaria sp. nov.	Momose 158	L	s	N	h	d, n	s	yellow	chamber	bs *Carpophilus* spp. (Nitidulidae), *Endaenidius* spp., *Endaeus* spp. (Curculionidae)	3
APOCYNACEAE											
Urceola sp.	Momose 7328	L	s	N	h	d	n	white	cup	d Vespidae, Halictidae, several fam. of Hymenoptera, Diptera	3
ARACEAE											
Homalomena propinqua Schott	Kato	1	b	N	m	d, n	staminode, p	white*	chamber*	bp, bf Scarabaeidae, Chrysomelidae	3
ASCLEPIADACEAE											
Gongonema sp.	Nyambong 133	L	s	N	h	d	n	yellow	rotate	d Chrysomelidae, Cleridae, several fam. of Coleoptera, Diptera	3
BOMBACACEAE											
Coelostegia griffithii Benth.	Momose 540	3	i	N	h	d, n	p	brown	cup	bp Elateridae, Chrysomelidae	3
Durio grandiflorus (Mast.) Kost et Soegeng	Yumoto	3	i	G	h	d	n	white	rotate, brush	Spiderhunter (*Arachnothera robusta*)	5
Durio griffithii (Mast.) Bakh.	Sakai 78	2	i	G	h	d	n, p	white	rotate	*Nomia*	1
Durio kutejensis (Hassk.) Becc.	Momose 7329	3	i	G	h	d, n	n	red	cup, brush	Bird	2
Durio oblangus Mast.	Yumoto	3	i	G	h	d	n	white	cup, long stamen tube	Spiderhunter (*Arachnothera robusta*)	2
BURMANNIACEAE											
Burmannia lutescens Becc.	Kato	1	s	N	d	d	n	white	cup	Culicidae	3
BURSERACEAE											
Canarium denticulatum Bl.	Momose 7012	3	s	N	d	d	p	yellow	rotate	d Chrysomelidae, several fam. of Hemiptera, Hymenoptera	3
Dacryodes laxa (Benn.) H. J. Lam	Momose 5038	3	s	G	d	d	p	red	rotate	*Trigona*	2
Dacryodes incurvata (Engl.) H. J. Lam	Sakai	3	s	G	d	d	n, p	white	rotate	*Apis dorsata*, *Apis koschevnicovi*	2
Santiria griffithii (Hk. f.) Engl.	Momose 371	3	s	N	d	d	n, p	orange	cup	*Trigona*, *Apis dorsata*	3
Santiria laevigata Bl.	Momose 553	4	s	N	d	d	n, p	green	rotate	*Trigona*	3
Triomma malaccensis Hk. f.	Nagamasu 4688	5	s	G	d	7-7+		white	rotate	d Chrysomelidae, several fam. of Hemiptera, Hymenoptera	2
CELASTRACEAE											
Lophopetalum glabrum Ding Hou	Momose 7211	3	s	N G′	h	d	n, p	orange	rotate	*Trigona* d Elateridae, Chrysomelidae, several fam. of Coleoptera, Diptera	3

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
COMPOSITAE											
Mikania micrantha H., B. et K.	Kato	G	s	N	h	d	n, p	white	brush*	*Trigona*	3
Vernonia arborea Ham.	Momose 536	G	s	N G′	h	d	n, p	white	brush*	*Ceratina, Braunsapis Nomia, Apis dorsata*	3
CONVOLVULACEAE											
Erycibe sp. 1	Momose 5111	L	s	G	h	d	p	yellow	cup	*Trigona*	1
Erycibe sp. 2	Momose 7311	L	s	G	h	d	p	yellow	cup	bp Mordellidae	1
CORNACEAE											
Mastixia rostrata Bl.	Kato	2	i	G	h	d	n, p	white	rotate	bp Chrysomelidae	1
COSTACEAE											
Costus globosus Bl.	Sakai 105	1	i	N	h		n, p	orange*	bilabiate	*Amegilla*	3
Costus speciosus (Koenig.) J. E. Sm.	Sakai	G	b	N	h	6-18	n, p	white, yellow*	bilabiate	*Amegilla*	3
CRYPTERONIACEAE											
Crypteronia cumingii Endl.	Momose 492	3	s	N	h	d	p	white	rotate, brush	*Ceratina, Braunsapis*	3
DILLENIACEAE											
Dillenia exelsa (Jack) Gilg.	Momose 5222	G	s	G	h	5-17	p	yellow	rotate	*Apis dorsata*	2
Dillenia suffruticosa (Griff.) Mart.	Nagamasu 4943	G	s	N	h	d	p	yellow	rotate	*Xylocopa*	4
Tetracera akara (Brum. f.) Merr.	Kato KL 1	L	s	G	h	d	p	white	rotate	*Apis koschevnikovii*	2
DIPTEROCARPACEAE											
Dipterocarpus geniculatus Vesque	Momose 402	5	s	G	h	18:30-18	p, c	orange	campanulate deeply lobed	*Apis dorsata*, bp (Scarabaeidae)	2
Dipterocarpus globosus Vesque	Momose 7011	5	s	G	h	18:30-18	p, c	white, purple	campanulate deeply lobed	*Apis dorsata*	2
Dipterocarpus pachyphyllus Meijer	Momose 571	5	s	G	h	n	n	white	campanulate deeply lobed	Geometridae	2
Dipterocarpus tempehes Slooten	Momose 354	5	s	G	h	5-4:30	p	yellow	campanulate deeply lobed	*Apis dorsata*	2
Dryobalanops aromatica Gaertn. f.	Nagamasu 4637	5	s	G	h	5-12	p	white	campanulate deeply lobed	*Apis dorsata*	3
Dryobalanops lanceolata Burck	Momose 215	5	s	N G′	h	5-12	p	white	rotate rotate	*Trigona* *Apis dorsata*	3
Hopea pterigota Ashton	Momose 7007	3	s	N	h	d, n	c, (p)	yellow	rotate, cup	bf Chrysomelidae, Curculionidae	2
Hopea sphaerocarpa (Heim.) Ashton	Nagamasu 4616	1	s	G	h	d, n	p	red	rotate, cup	*Trigona*, Sciaridae	2
Shorea agami Ashton	Momose 5100	5	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf Chrysomelidae, Curculionidae	1
Shorea beccariana Burck	Kato KL6	5	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf Chrysomelidae, Curculionidae	1
Shorea bullata Ashton	Momose 5508	5	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf Chrysomelidae, Curculionidae	2
Shorea confusa Ashton	Johan 272	5	s	G	h	7-18	n, p, c	purple	rotate, cup	bf Chrysomelidae, Curculionidae	2
Shorea balanocarpoides Symington	Momose 7322	4	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf Chrysomelidae, Curculionidae	2

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)		10
Shorea falciferoides Foxw.	Momose 7220	5	s	G	h	d, n	c, (p)	white	rotate, cup	bf	Chrysomelidae, Curculionidae	2
Shorea ferruginea Dyer ex Brandis	Momose 401	5	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf	Chyrsomelidae, Curculionidae, Nitidulidae	2
Shorea havilandii Brandis	Nagamitsu 136	3	s	G	h	d, n	c, (p)	white	rotate, cup	bf	Chyrsomelidae, Curculionidae	2
Shorea macrophylla (D. Vr.) Ashton	Momose 7217	4	s	G	h	d, n	c, (p)	pink	rotate, cup	bf	Chrysomelidae, Curculionidae	3
Shorea macroptera Dyer	Momose 362	5	s	G	h	d, n	c, (p)	pink	rotate, cup	bf	Chrysomelidae, Curculionidae	3
Shorea ochracea Symington	Harrison RDH52 1	5	s	G	h	6:30-6	n, p, c	yellow*	rotate, cup	bf	Chrysomelidae, Curculionidae	2
Shorea parvifolia Dyer	Momose 7303	5	s	G	h	17:30- 17:30+	c, (p)	yellow	rotate, cup	bf	Chrysomelidae, Curculionidae	5
Shorea patoiensis Ashton	Momose 7008	4	s	G	h	n	c, (p)	white	rotate, cup	bf	Chrysomelidae, Curculionidae	1
Shorea pilosa Ashton	Momose 609	5	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf	Chrysomelidae, Curculionidae, Nitidulidae	2
Shorea smithiana Symington	Momose 520	5	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf	Chrysomelidae, Curculionidae, Nitidulidae	1
Shorea superba Symington ex Wood	Yamauch 306	5	s	G	h	d, n	c, (p)	white	rotate, cup	bf	Chrysomelidae, Curculionidae	2
Shorea xanthophylla Symington	Momose 5073	4	s	G	h	d, n	c, (p)	yellow	rotate, cup	bf	Chrysomelidae, Curculionidae, Cleridae	2
Vatica micrantha Slooten.	Momose 7371	4	s	N	h	d, n	c, (p)	yellow	rotate, cup	bf	Chrysomelidae, Curculionidae	3
Vatica aff. *parvifolia* Ashton	Momose 70	4	s	N	h	d, n	c, (p)	white	rotate, cup	bf	Chrysomelidae, Curculionidae	3
EBENACEAE												
Diospyros dicotyoneura Hiern	Momose 7312	3	i	G	d	d, n	p	white	urceolate	bp	Staphylinidae, Nitidulidae	2
ELAEOCARPACEAE												
Elaeocarpus nitidus Jack	Momose 293	G	s	N	h	d	n, p	white	rotate	*Ceratina*, *Braunsapis*		4
Elaeocarpus stipularis Bl.	Momose 5419	G	s	N	h	d	n, p	white	cup	*Braunsapis*, *Trigona*, *Apis koschevnikovi*		4
EUPHORBIACEAE												
Agrostistachys longifolia (Wight) Benth. ex. Hk. f.	Nagamasu 4701	1	b	N	d	d	n, p	yellow*	brush*	*Trigona*		3
Aporusa nitida Merr.	Momose 5099	2	s	N	d	d	p	yellow*	brush*	*Trigona*		2
Aporusa prainata King ex Gage	Nyambong 156	3	s	N	d	d	p	yellow*	brush*	d	Scarabaeidae, several fam. of Coleoptera, Diptera	2
Aporusa sarawakensis Schott	Momose 5036	2	s	N	d	d	p	yellow*	brush*	*Trigona*		2
Baccaurea racemosa (Reinw.) Muell. Arg.	Momose 5044	2	b	N	d	d	p	yellow*	brush*	d	Cantharidae, Muscidae, several fam. of Coleoptera, Diptera	2
Cephalomappa beccariana Baill.	Momose 5027	4	s	G	m	d	p	yellow*	brush*	d	Curculionidae, Chrysomelidae, several fam. of Coleoptera, Diptera	1
Cleistanthus pseudopodocarpus Jabl.	Momose 5061	3	s	N G′	m	d	n, p	yellow	cup	*Trigona* *Apis dorsata*		3

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
Cleistanthus sumatranus (Miq.) Muell. Arg.	Momose 500	3	s	G	m	d	n, p	yellow	cup	*Trigona*	3
Cleistanthus venosus C. B. Rob.	Momose 106	3	s	G	m	d	n, p	yellow	cup	*Apis dorsata*	3
Dimorphocalyx denticulatum Merr.	Momose 5104	2	i	N	d	d	p	red	rotate	*Trigona*	3
Drypetes longifolia (Bl.) Pax ex Hoffman	Yamauch 402	2	b	N	d	d	n, p	white*	rotate	d Scarabaeidae, Chrysomelidae, several fam. of Coleoptera, Diptera	4
Drypetes xanthophyloides Airy Shaw	Momose 5033	2	s	G	d	d	n, p	white*	rotate	d Mordellidae, several fam. of Coleoptera, Hemiptera, Diptera	2
Endospermum peltatum Merr.	Yamauch 123	G	s	G	d	d	n, p	yellow	brush*	*Trigona, Apis koschevnikovi*	1
Homalanthus populneus (Geisel.) Pax	Nagamitsu 444	G	s	N	m	d	p	yellow*		d *Rhopalomelissa* (Halictidae), *Allodape* (Anthophoridae), *Hylaeus* (Colletidae), Eumenidae, several fam. of Diptera, Hymenoptera	3
Koilodepas laevigatum Airy Shaw	Nyambong 137	3	s	N	m	d	p	yellow*	brush*	*Trigona*	4
Macaranga brevipetiolata Airy Shaw	Momose 5001	2	s	G	d	d	n, p	green*		*Trigona*	2
Macaranga winkleri Pax et Hoffman	Momose 5046	G	s	N	d	d	n, p	green*		*Trigona*	2
Mallotus griffithianus (Hk. f.) Muell. Arg.	Nyambong 224	2	s	N	d	d	p	yellow*	brush*	*Trigona*	2
Mallotus penangensis Muell. Arg.	Nyambong 134	3	s	N	d	d	p	yellow*	brush*	*Trigona*	3
Mallotus wrayi King ex Hk. f.	Momose 7004	2	s	N	d	d	p	yellow*	brush*	*Trigona*	4
Moultonianthus leembrugianus (Boerl. et Koord.) van Steenis	Momose 5021	3	s	G	m	d	p	white*	rotate	*Trigona*	2
Tapoides villamilii (Merr.) Airy Shaw	Momose 539	3	s	N	m	d	n, p	white	cup	d Anthicidae, Scarabaeidae, Elateridae, several fam. of Coleoptera, Diptera	3
Trigonopleura malayana Hk. f.	Momose 156	G	s	G	d	d	n, p	white	cup	*Apis dorsata*	2
FAGACEAE											
Lithocarpus lucidus (Roxb.) Rehd.	Momose 5058	G	s	G	m	d	p	yellow*	brush	d Braconidae, *Trigona*, several fam. of Hymenoptera, Diptera	3
Lithocarpus ferrugineus Soepadmo	Johan 184	4	s	N	m	d	p	yellow*	brush	d Chrysomelidae, Elateridae, several fam. of Coleoptera, Diptera	3
FLACOURTIACEAE											
Casearia grewiaefolia Vent	Johan 155	1	s	N	h	d	n	red	cup	Eumenidae	3
Hydnocarpus borneensis Sleum.	Momose 5034	2	s	G	h	d, n	n	yellow*	rotate	d Chrysomelidae, several fam. of Coleoptera, Diptera	1
GESNERIACEAE											
Didissandra sp.	Kato	1	s	N	h	d	n	white	bilabiate	*Amegilla*	3

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
GNETACEAE											
Gnetum cuspidatum Bl.	Kato	L	b	N	d	morning	droplet	green*		fly (Lauxaniidae)	3
Gnetum gnemon L.	Kato	1	s	N	d	n	droplet	green*		Pyralidae, Geometridae	3
Gnetum leptostachyum Markgraf	Kato	L	b	N	d	morning	droplet	green*		fly (Muscidae, Conopidae, Drosophilidae)	3
GRAMINEAE											
Dinochloa sp.	Kato	L	s	N	h	d	p	pink*		*Trigona*	3
GUTTIFERAE											
Calophyllum sp.	Momose 5054	2	s	G	h	d	n, p	white	rotate	*Trigona*	1
Garcinia penangiana Pierre	Nagamasu 6055	2	s	G	h	d	n, p	white	rotate	*Trigona*	2
Garcinia nervosa Miq.	Nyambong 300	2	i	G	h	d	n, p	white	rotate	d Curculionidae, Chrysomelidae	2
Mesua grandis (King) Kosterm.	Momose 7116	2	s	G	h	d	p	white	rotate	*Apis koschevnikovi*	2
Mesua oblongifolia (Ridl.) Baill.	Momose 7009	2	s	G	h	daytime	p	white	rotate	*Apis koschevnikovi*	2
HYPERICACEAE											
Cratoxylum sumatranum (Jack) Bl.	Nagamitsu 543	G	s	N	h	d	n, p	pink	rotate	*Trigona*	3
HYPOXIDACEAE											
Curculigo villosa Wall.	Kato	G	b	N	h	d	n	yellow	rotate	*Trigona*	3
ICACINACEAE											
Gomphandra cumingiana (Miers) F. Vill.	Momose 5433	2	s	N	d	n	n, p	white	campanulate	*Trigona*	2
Iodes sp.	Momose 5045	L	s	G	h	n	p	green	rotate	bp Nitidulidae, Chrysomelidae	1
IXONANTHACEAE											
Allantospermum borneense Forman	Momose 5028	4	s	G	h	n	n	white	rotate	*Apis dorsata*	2
LAURACEAE											
Endiandra clavigata Kosterm.	Momose 502	3	s	N	h	d	p	yellow	cup	d Curculionidae, several fam. Coleoptera, Diptera	3
Litsea sp.	Momose 7358	2	s	N	d	d	n, p	white	cup	d Chrysomelidae, Vespidae, several fam. Diptera, Coleoptera	3
LECYTHIDACEAE											
Barringtonia sarcostachys Bl. (Miq.)	Momose 690	1	s	N	h	n	n	white*	brush	Sphingidae	2
LEGUMINIOSAE											
Afzelia borneensis Harms	Momose 5077	2	s	G	h	d	n	red, white*	Caesalpinia-like	d Chrysomelidae, several fam Diptera, Coleoptera	2
Bauhinia sp.	Momose	L	s	G	h	d	n	orange	Caesalpinia-like	Several fam. of Lepidoptera (butterfly)	3
Caesalpinia sp.	Momose	G	s	N	h	d	n, p	orange	Caesalpinia-like	*Xylocopa*	1
Callerya niewenhuisii (J. J. Sm.) Schot.	Momose 61	L	b	N	h	d	n, p	orange	papilionaceous	*Megachile*	4
Callerya vasta (Kosterm.) Schot.	Momose 7354	4	s	N	h	d	n, p	purple	papilionaceous	*Megachile*	2
Fordia sp.	Momose 303	2	s	N	h	d	n, p	pink	papilionaceous	*Megachile*	4
Parkia singularis Miq.	Momose 372	3	s	G	m	n	n	white	tubular, brush	Bat	1

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
Parkia speciosa Hask.	Momose 7351	3	s	G	m	n	n	white	tubular, brush	Bat	2
Sindora beccariana Backer ex de Wit	Nagamitsu 141	4	s	N	h	d	n	brown	Caesalpinia-like	*Trigona, Megachile*	2
Sindora cf. *irpicina* de Wit	Momose 7324	4	s	G	h	d	n	brown	Caesalpinia-like	*Trigona, Nomia,* Vespidae	2
Spatholobus ferrugineus (Zoll. et M.) Benth. ex Miq.	Momose 7368	L	s	G	h	d	n	red	papilionaceous	*Apis dorsata, Apis koschevnikovi*	2
Spatholobus macropterus Miq.	Johan 219	L	s	G	h	d	n	white	papilionaceous	*Apis dorsata*	2
Spatholobus multiflorus Ridder	Momose 7370	L	s	G	h	d	n	red	papilionaceous	d Curculionidae, Chrysomelidae, several fam. Hemiptera, Coleoptera	2
LOGANIACEAE											
Fagraea racemosa Jack ex Wall.	Sakai	G	s	N	h	n	n	white	bilabiate	Bat	2
LORANTHACEAE											
Amylotheca duthieana (King) Danser	Yumoto	E	s	N	h	d	n	red	tubular	Spiderhunter (*Arachnothera robusta*)	4
Macrosolen cochinchinensis (Lour.) van Tiegh.	Yumoto	E	s	G	h	d	n	yellow	burst open	Birds (*Dicaeum trigonostigma, Chloropsis*	2
Tritecanthera xyphostachys Tirgh.	Yumoto	E	s	N	h	d	n	pink	tubular	Spiderhunter (*Arachnothera robusta*)	3
LOWIACEAE											
Orchidantha lambirensis Nagamasu unpub.	Sakai	1	b	N	h	d, n	deciet	purple*	bilabiate	Scarabaeidae	2
MARANTACEAE											
Phacelophrynium maximum (Bl.) K. Schum.	Kato	1	b	N	h	d	n	white	bilabiate	*Amegilla*	3
Stachyphrynium cylindricum (Ridl.) K. Schum.	Kato	1	b	N	h	d	n	white	bilabiate	*Nomia*	3
Stachyphrynium griffithii (Bak.) K. Schum.	Kato	1	b	N	h	d	n	white	bilabiate	*Nomia*	3
MELASTOMATACEAE											
Melastoma beccariana Cogn.	Nagamasu 4643	G	s	N	h	8-12	n	purple	Caesalpinia-like	*Xylocopa*	4
Melastoma malabathricum L.	Momose 83	G	s	N	h	8-12	n	purple	Caesalpinia-like	*Xylocopa*	4
Memecylon sp. 1	Momose 7214	3	s	N	h	d	p	white	rotate	d Curculionidae, Chrysomelidae, Anthicidae	2
Memecylon sp. 2	Yamauch 137	G	s	N	h	d	p	purple	rotate	*Trigona*	1
Pternandra multiflora Cogn.	Maeda 489	G	s	N	h	d	n, p	yellow	rotate	d Acrididae, several fam. Coleoptera, Diptera	2
MELIACEAE											
Aglaia palembanica Miq.	Nyambong 201	2	2	N	d	d	p	yellow	cup	d Syrphidae	2
Dysoxylum cauliflorum Heim.	Kato	3	b	N	h	d	n, p	white	campanulate	*Nomia*	3
Walsura sp.	Momose 5089	3	s	N	h	d	n	white	cup	*Apis koschevnikovi*	2

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
MENISPERMACEAE											
Diploclisia kunstleri (King) Diels	Kato	L	b	N	d	d	n, p	white	cup	d Syrphidae, several fam. of Diptera, Coleoptera, Hymenoptera	3
MORACEAE											
Artocarpus integer L.	Momose 7326	4	b	G	m	n	liquid	green*		d Geometridae, Blattellidae, several fam. of Diptera, Lepidoptera, Orthoptera	2
Artocarpus odoratissimus Blanco	Nagamitsu 156	G	s	G	m	n	liquid	brown*		d Drosophilidae, Geometridae, Nitidulidae, several fam. of Diptera, Lepidoptera, Coleoptera	2
MUSACEAE											
Musa campestris Becc.	Kato	G	s	N	m	d	n	pink	tubular	Spiderhunter (*Arachnothera robusta*)	3
MYRISTICACEAE											
Gymnacranthera contracta Warb.	Momose 506	4	s	N	d	d, n	p	white	campanulate	bp Curculionidae, Chrysomelidae	3
Horsfieldia grandis (Hk. f.) Warb.	Momose 7204	3	s	N	d	d, n	p	yellow	urceolate	Thripidae	3
Kema tridactyla Airy Shaw	Nagamasu 6057	1	i	N	d	d, n	p	yellow	cup	bp Curculionidae	2
Knema cinerea (Poir.) Warb. var. *sumatrana* (Miq.) Sinclair	Nagamasu 4845	4	s	G	d	d, n	p	yellow	cup	bp Staphylinidae	1
Knema latifolia Warb.	Momose 509	2	i	N	d	d, n	p	yellow	cup	bp Curculionidae	2
MYRSINACEAE											
Ardisia macrophylla Reinw.	Momose 4976	3	i	N	h	d	n	white	rotate	Sunbird (*Nectarinia jugularis*)	1
Labisia pumila (Bl.) Benth. et Hk. f.	Kato KL2	1	b	G	h	d	n, p	pale purple	rotate	*Nomia*	3
MYRTACEAE											
Eugenia (=SAN73069)	Momose 5008	4	s	G	h	d	n, p	white*	brush	*Trigona*	1
Eugenia sp.4 (KYO)	Johan 127	4	s	N G′	h	d	n, p	white*	brush	d Chrysomelidae, Elateridae, several fam. Coleoptera, Diptera, *Apis dorsata*	3
Eugenia subrufa King	Momose 147	4	s	G	h	d	n, p	white*	brush	d Chrysomelidae, Curculionidae, several fam. of Coleoptera, Lepidoptera, also *Apis dorsata*	2
OLACACEAE											
Scorodocarpus borneensis Becc.	Momose 548	4	s	N	h	d	n	white	campanulate	*Braunsapis*, *Trigona*	2
Strombosia ceylanica Gardner	Nyambong 184	3	s	N	h	d	n	white	cup	d Culicidae, several fam. of Diptera, Hemiptera	1
OPILIACEAE											
Lepionurus sylvestris Bl.	Kato	1	s	N	d	d	n, p	white	rotate	*Trigona*	3
ORCHIDACEAE											
Coelogyne foerstermanii Ridl.	Momose	E	s	G	h	d	deciet	white	bilabiate	*Apis dorsata*	3
Dendrobium setifolium Reichb. f.	K. Inoue	E	s	N	h	d	deciet	white	bilabiate	*Trigona*	3
Neuwiedia borneensis	K. Inoue	1	s	N	h	d	deciet	white	bilabiate	*Trigona*	3

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
PALMAE											
Caryota sp.	Momose	2	s	N	h	d	p	yellow	cup	*Trigona*	2
Licuala sp.	Momose	1	b	N	h	d	n, p	white	cup	*Trigona*	2
PENTAPHRAGMATACEAE											
Pentaphragma lambirensis Kiew	Kato	1	s	N	h	d	n	orange	cup	*Amegilla*	3
Pentaphragma viride Staph et Green	Kato	1	s	N	h	d	n	white	cup	*Nomia*	3
PIPERACEAE											
Piper vestitum C. DC.	Kato KL107	1	s	N	h	morning	n	white*		d Muscidae, Drosophilidae, Anthicidae	3
Piper sp.	Nagamitsu	1	s	N	h	d	p	yellow*		bp Curculionidae	2
POLYGALACEAE											
Polygala venosa Juss. ex Poir.	Kato	1	b	N	h	d	n	purple	papilionaceous	*Amegilla*	3
PROTEACEAE											
Heliciopsis artocarpoides (Elmer) Sleum.	Kato	2	b	N	h	d	n, p	white	campanulate deeply lobed	*Trigona*	3
RHAMNACEAE											
Ventilago malaccensis Ridl.	Momose 7353	4	s	N	h	d	n, p	yellow	rotate	*Trigona*	2
RHIZOPHORACEAE											
Carallia brachiata (Loer.) Merr.	Momose 538	3	s	N	h	d	n, p	green	rotate	d Chrysomelidae, Cantharidae, several fam. of Coleoptera, Hymenoptera, Diptera	3
ROSACEAE											
Parastemon urophyllum A. DC.	Kato KL7	4	s	N	h	d	n, p	white	cup, zygomorphic	*Trigona*, *Apis koschevnikovi*	2
RUBIACEAE											
Chasalia sp.	Kato	1	s	N	h	d	n, p	white	cup	*Trigona*	3
Ixora brevicaudata Brem.	Momose 2102	1	s	N	h	d	n	orange	tubular	Several fam. of Lepidoptera (butterfly)	3
Ixora stenophylla (Korth.) Kuntze	Momose 1	1	s	N	h	d	n	orange	tubular	Several fam. of Lepidoptera (butterfly)	4
Ixora urophylla Brem.	Momose 7410	1	s	N	h	d	n	orange	tubular	Several fam. of Lepidoptera (butterfly)	3
Ixora woodii Brem.	Momose 1501	1	s	N	h	d	n	orange	tubular	Several fam. of Lepidoptera (butterfly)	3
Ophiorrhiza axillaris Ridl.	Kato	1	i	N	h	d	n, p	white	cup	*Trigona*	3
Pavetta cf. *petiolaris* Craib. ex Brem.	Yumoto 9	2	s	G	h	d	n	white	tubular	Sunbird (*Nectarinia jugularis*)	2
Praravinia sp.	Kato	G	i	N	h	d	n	purple	tubular	Sunbird (*Nectarinia jugularis*)	3
Steenisia pleurocarpa (Airy Shaw) Bakh. f.	Kato	1	s	N	h	d	n, p	white	rotate	*Trigona*	3
Uncaria longiflora Merr.	Momose 251	L	s	N	h	d	n	white	tubular	d Otitidae, Chalcididae, several fam. of Diptera, Hymenoptera	2
Urophyllum hirsutum Hk. f.	Momose 11	2	i	N	d	d	n, p	white	cup	*Trigona*	2
Urophyllum pelacalyx Ridl.	Momose 3016	2	i	N	d	d	n, p	yellow	cup	*Trigona*	2
Xanthophytum brookei Aexelius	Momose 5031	1	s	N	h	d	n, p	white	cup	*Trigona*	2

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
RUTACEAE											
Glycosmis sp.	Momose 108	1	i	N	h	d	p	yellow	rotate	*Trigona*	1
SAPINDACEAE											
Allophyllus cobbe (L.) Laeusch.	Momose 1283	1	s	N	h	d	p	white	rotate	d Curculionidae	2
Nephelium cuspidatum Bl.	Momose 5042	3	s	G	ad	d	n, p	white	brush	*Trigona*	2
Pometia pinnata Forst.	Momose 5203	4	s	N	am	d	n, p	white	brush	*Braunsapis*	2
SAPOTACEAE											
Ganua (B16)	Momose 5025	4	i	G	h	d, n	c	white	berry-like	Mammal (*Callosciurus prevostii caroli, Sundasciurus hippurus inquinantus, S. lowii, Petaurista petaurista rajah*)	2
Ganua beccariana Pierre ex Dubard	Momose 5057	3	i	G	h	d, n	c	white	berry-like	Bat	1
Madhuca (T1)	Nyambong 173	3	i	G	h	morning	n, p	white	campanulate, brush	*Xylocopa*	1
Madhuca (Y141)	Momose 5074	3	i	G	h	d	n	white	campanulate, brush	Sunbird (*Nectarinia jugularis*)	2
Palaquium beccarianum (T. et B.) Pierre	Momose 5020	3	s	G	h	d	n	white	campanulate, brush	Spiderhunter (*Arachnothera robusta*)	2
Palaquium sp.	Momose 5090	3	s	G	h	d	n	white	burst open, cup	Bird (*Loriculus galgulus*)	2
Payena acuminata (Bl.) Pierre	Momose 5053	4	s	G	h	d	n	white	cup	*Apis dorsata*	1
SIMAROUBACEAE											
Quassia borneensis Nooteboom	Momose 7452	4	s	N	h	d	n, p	yellow	rotate	d Staphylinidae, Elateridae, several fam. of Diptera, Coleoptera	2
STERCULIACEAE											
Heritiera borneensis (Merr.) Kosterm.	Nyambong 147	5	s	G	m	d, n	p	white*	campanulate	bp Curculionidae, Chrysomelidae	2
Heritiera sumatrana Kosterm.	Momose 5003	3	s	G	m	d, n	p	red*	campanulate	bp Curculionidae, Chrysomelidae	2
Pterocymbium tubulatum (Mast.) Pierre	Momose 5254	5	s	G	m	7-14	n	white*	campanulate	*Apis koschevnikovi, Trigona*	2
Scaphium borneensis (Merr.) Beumee	Momose 7465	4	s	G	m	7-14	n	white*	campanulate	*Apis dorsata*	2
Scaphium longipetiolatum (Kosterm.) Kosterm.	Momose 1216	5	s	G	m	7-14	n	red*	bilabiate	*Trigona, Nomia, Megachile*	2
Sterculia laevis Wall.	Momose 1712	2	s	N	m	d, n	p	red*	urceolate	bp Chrysomelidae	3
Sterculia stipulata Korth.	Nagamitsu 645	1	s	N	m	d, n	p	red*	urceolate	bp Chrysomelidae	3
THEACEAE											
Eurya acuminata (DC.) Merr.	Momose 533	G	s	N	m	d	n, p	white	cup	*Trigona*	2
TILIACEAE											
Grewia sp.	Momose 5016	2	s	G	h	d	n, p	white	cup	*Trigona*	2
Grewia latistipula Ridl.	Nyambong 401	3	s	N	h	d	n, p	yellow	cup	*Trigona, Ceratina, Nomia*	2

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
Grewia stylocarpa Warb. ex Perkins	Momose 4977	3	s	N	h	d	n, p	yellow	cup	d Vespidae, several fam. of Hymenoptera, Diptera, Coleoptera	2
Schoutenia glomerata King	Momose 7364	3	s	G	h	d	n, p	white	cup	d Chrysomelidae, Staphylinidae, several fam. of Hymenoptera, Diptera, Coleoptera	2
TRIGONIACEAE											
Trigoniastrum hypoleucum Miq.	Momose 5022	G	s	G	h	d	n	white	papilionaceous	*Nomia*	2
TRIURIDACEAE											
Sciaphila secundiflora Thw. ex Bth.	Kato	1	s	N	h	d	n	white	rotate	Culicidae, Calliphoridae	3
ULMACEAE											
Trema tomentosa (Roxb.) H. Hara	Nagamitsu	G	s	N	h	d	n, p	white*	rotate	*Trigona*	2
URTICACEAE											
Pipturus argentenus (Forst.) Wedd.	Nagamitsu 387	G	s	N	d	n	p	white*	rotate	*Trigona*	2
Dendrocnide stimulans (L. f.) Chew	Momose 5098	1	s	N	d	n	p	white*	rotate	*Trigona*	3
VERBENACEAE											
Callicarpa pentandra Roxb.	Nyambong 167	G	s	N	h	d	n, p	purple	brush	*Trigona*	2
Callicarpa havilandii (King et Gamble) H. J. Lam	Nagamasu 4611	G	s	N	h	d	n, p	purple	brush	*Trigona*	2
Clerodendron phyllomega Steud.	Rapi 44	1	s	N	h	d	n	red	brush	Several fam. of Lepidoptera (butterfly)	1
Sphenodesma triflora Wight	Momose 159	L	s	G	h	d	n, p	purple, purple*	brush	*Nomia*	1
Stachytarpheta indica (L.) Vahl	Nagamitsu	G	s	N	h	d	n, p	yellow	bilabiate	*Braunsapis*, *Ceratina*, *Trigona*	2
Teijsmanniodendron simplicifolia Merr.	Momose 542	2	s	N	h	d	n, p	purple	bilabiate	d Curculionidae, several fam. of Coleoptera, Hemiptera	2
Vitex pubescens Vahl	Momose 7420	G	s	N	h	d	n	purple	bilabiate	*Xylocopa*	2
Vitex vestita Wall.	Nyambong 200	G	s	N	h	d	n	yellow	bilabiate	*Nomia*	2
XANTHOPHYLLACEAE											
Xanthophyllum sp.	Yamauch 389	1	s	N	h	d	n, p	white	papilionaceous	*Megachile*	2
Xanthophyllum velutinum Chod.	Momose 7200	3	s	G	h	d	n, p	yellowish	papilionaceous	*Xylocopa*, *Megachile*	2
ZINGIBERACEAE											
Alpinia glabra Ridl.	Sakai 132	1	s	N	h	d	n, p	red*	bilabiate	*Amegilla*	3
Amomum calyptratum Nagam. et S. Sakai	Sakai 156	1	b	N	h	d	n, p	orange*	bilabiate	*Amegilla*	3
Amomum coriaceum R. M. Sm.	Sakai 88	1	b	N	h	d	n, p	white*	bilabiate	*Nomia*	3
Amomum durum S. Sakai et Nagam.	Sakai 94	1	b	N	h	d	n, p	white*	bilabiate	*Nomia*	3
Amomum gyrolophos R. M. Sm.	Sakai 75	1	b	N	h	d	n, p	orange*	bilabiate	*Amegilla*	3
Amomum oliganthum K. Schum.	Sakai 187	G	b	N	h	d	n, p	orange*	bilabiate	*Amegilla*	3

APPENDIX. Continued.

Species	Voucher	1	2	3	4	5	6	Color (7)	Fl. shape (8)	Main pollinators (9)	10
Amomum polycarpum (K. Schum.) R. M. Sm.	Sakai 82	G	b	N	h	d	n, p	white*	bilabiate	*Nomia*	3
Amomum angustipetalum S. Sakai et Nagam.	Sakai 192	1	b	N	h	d	n	white*	bilabiate	*Amegilla*	3
Amomum roseisquamosum Nagam. et S. Sakai	Sakai 188	3	b	N	h	d	n	pink*	bilabiate	Spiderhunter (*Arachnothera longirostra*)	3
Amomum somniculosum S. Sakai et Nagam.	Sakai 46	1	b	N	h	10-16	n, p	white*	bilabiate	*Nomia*	3
Boesenbergia grandiflora (Val.) Merr.	Sakai 77	G	b	N	h	6-18	n, p	white*	bilabiate	*Nomia*	3
Boesenbergia gracilipes (K. Schum.) R. M. Sm.	Sakai 79	1	b	N	h	6-15	n, p	white*	bilabiate	*Nomia*	3
Boesenbergia sp.	Sakai 173	1	b	N	h	6-18	n, p	white*	bilabiate	*Nomia*	3
Elettaria longituba (Ridley) Holt.	Sakai 201	G	b	N	h	6-18	n, p	white*	bilabiate	*Nomia*	3
Elettariopsis kerbyi R. M. Sm.	Sakai 114	1	b	N	h	morning	n, p	white*	bilabiate	*Nomia*	3
Elettariopsis sp.1	Sakai 122	1	b	N	h	d	n, p	white*	bilabiate	*Amegilla*	3
Elettariopsis sp.2	Sakai 190	1	b	N	h	morning	n, p	white*	bilabiate	*Nomia*	3
Etlingera metriocheilos (Griff.) R. M. Sm.	Sakai 40	G	b	N	h	6-18	n	red*	bilabiate	Spiderhunter (*Arachnothera longirostra*)	3
Etlingera punicea (Roxb.) R. M. Sm.	Sakai 226	G	b	N	h	d	n	red*, yellow*	bilabiate	Spiderhunter (*Arachnothera longirostra*)	3
Globba brachyanthera K. Schum.	Sakai 065	1	s	N	h	d	n, p	orange*	bilabiate	*Amegilla*	3
Hornstedtia reticulata (K. Schum.) K. Schum.	Sakai 228	G	b	N	h	d	n	red*	bilabiate	Spiderhunter (*Arachnothera longirostra*)	3
Hornstedtia conica Ridl.	Sakai 245	G	b	N	h	6-18	n	red*	bilabiate	Spiderhunter (*Arachnothera longirostra*)	3
crocydocalyx (K. Schum.) Burtt et Smith	Sakai 232	G	b	N	h	d	n, p	white*	bilabiate	*Amegilla*	3
Plagiostachys sp.1	Sakai 234	G	b	N	h	d	n, p	white*	bilabiate	*Amegilla*	3
Plagiostachys strobilifera (Bak.) Ridl.	Sakai 198	G	s	N	h	6-18	n	pink*, yellow*	bilabiate	Spiderhunter (*Arachnothera longirostra*)	3
Zingiber longipedunculatum Ridl.	Sakai 248	G	b	N	h	12-18	n, p	white*, red*	bilabiate	*Amegilla*	3

[a] (1) Plant habit; 1: forest floor; 2: understory; 3: subcanopy; 4: canopy; 5: emergent; G: gap; L: liana; E: epiphyte. (2) Position of flowers; s: on crown surface; i: inside of crown; b: below the crown (cauliflorous). (3) Reproductive phenology; N: flowers in non-general-flowering periods only, or both in non-general- and general-flowering periods; G: flowers in general-flowering periods only; G′: pollinators differ in general-flowering periods. (4) Sexual expression; h: harmaphrodite; d: dioecy; m: monoecy; ad: androdioecy; am: andromonoecy. (5) Flowering time; d: daytime; n: nighttime. (6) n: nectar; p: pollen; c: corolla; s: stigmatic secretion. (7) *: color of calyx, stamen, stigma, bract, inflorescence; no mark: color of corolla. (8) *: shape of inflorescence; no mark: shape of corolla or calyx. (9) bs: beetles mainly feeding on stigmatic secretions; bf: beetles mainly feeding on floral tissues; bp: beetles mainly feeding on pollen; d: diverse insects. (10) Intensity of observations; 1: brief observations; 2: intense but single observation; 3: a few observations (no. individuals × no. reproductive events); 4: several to many observations; 5: field experiments of pollinator introduction, selective exclusion of flower visitors.