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PLANT ANIMAL INTERACTIONS

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Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand

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Abstract Large frugivores are considered to be important seed dispersers for many tropical plant species. Their roles as seed dispersers are not well known in Southeast Asia, where degraded landscapes typically lack these animals. Interactions between 259 (65 families) vertebrate-dispersed fruits and frugivorous animals (including 7 species of bulbul, 1 species of pigeon, 4 species of hornbill, 2 species of squirrel, 3 species of civet, 2 species of gibbon, 1 species of macaque, 2 species of bear, 2 species of deer, and 1 species of elephant) were studied for 3 years in a tropical seasonal forest in Khao Yai National Park, Thailand. The purpose was to examine the dietary overlaps among the large frugivores and the characteristics of fruits they consumed. Most fruit species are eaten by various kinds of frugivores; no close relationship between a particular fruit and a frugivore was found. The number of frugivore groups that served a given plant species was negatively correlated with seed size. Additionally, the fruit/seed diameters consumed by bulbuls were significantly smaller than consumed by the other nine groups. These trends of fruit characteristics were consistent with those observed elsewhere in Southeast Asia: small fruits and large, soft fruits with many small seeds are consumed by a wide spectrum of frugivores while larger fruits with a single large seed are consumed by relatively few potential dispersers. Importantly, these large, single-seed fruits are not consumed by the small frugivores that thrive in small forest fragments and degraded areas in Southeast Asia. To insure the natural seed dispersal process in the forest, an evaluation of all frugivore groups in the forest is urgently needed in Southeast Asia.

Keywords Dietary overlap · Frugivory · Fruit characteristics · Seed dispersal · Southeast Asia

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Introduction

Basic knowledge about fruit–frugivore interactions, and especially the seed dispersal process in forest ecosystems, is essential for conservation of endangered animals and the forest itself (Corlett 1998; Silva and Tabarelli 2000). In the tropics, where frugivores are the dominant group of vertebrates (Gautier-Hion et al. 1985), there have been few studies about which frugivores disperse which seeds, and the degree to which plants and animals rely on one another.

The characteristics of the fruits themselves are significant in determining which animals disperse them (Jordano 1995; Corlett 1996). Seed and/or fruit size limits the number of frugivores that can disperse the seeds (Leighton and Leighton 1983). In general, large frugivores can handle a wider range of fruit sizes than small frugivores (Noma and Yumoto 1997). These large frugivores are thought to be vulnerable to extinction in the face of selective hunting (Bennett and Robinson 2000) and habitat loss and degradation (Terborgh and Winter 1980). Therefore, plants that produce large-sized fruits and/or seeds may be vulnerable to extinction when they lose their natural seed dispersers.

In Southeast Asia, degraded landscapes typically lack many of the important dispersal agents, such as gibbons and hornbills, increasing the significance of those few individuals that remain (Corlett 1998). However, certain fruits and their seeds can be dispersed by many different vertebrates. Close species-species interactions in seed dispersal are considered very rare, but some do exist (see Tutin et al. 1991). Thus, studies of interactions among fleshy fruit and frugivore assemblages are important to evaluate the relative contribution of different frugivores to the seed dispersal of plant species. Fruit-frugivore interactions at the community level have been studied in several parts of Southeast Asia: Yakushima Island in Japan (Noma and Yumoto 1997), Hong Kong (Corlett 1996), Tamil Nadu in India (Balasubramanian and Bole 1993; Balasubramanian 1996), North Negros Island in the Philippines (Hamann and Curio 1999; Heindl and Curio 1999), and Kutai National Park in Indonesia (Leighton 1982; Leighton and Leighton 1983). All of these studies illustrate the same point: species bearing soft fruits with many small seeds, whether the fruits were small or large, were visited by a wide spectrum of frugivores, whereas fruits with a single large seed were visited by few large frugivores such as primates, fruit pigeons, and hornbills. A review of studies of frugivory and seed dispersal in Southeast Asia (Corlett 1998) also highlighted this pattern. Though their results suggested the relative importance of large frugivores as seed dispersers, these studies were mostly conducted in forest fragments or small islands where some large frugivores are already extinct or have never been present. Given the human pressures on large frugivores, studies on seed dispersal in ecosystems that include them should be undertaken with urgency (Corlett 1998).

The major aim of this study is to obtain data on fruit preferences of large frugivores as a baseline for studies on seed dispersal of fruit bearing plants in the tropical seasonal forest of Khao Yai National Park, Thailand, where an intact fauna and flora survives. More specifically, we ask two questions:

1. Are there particular plant species that appear wholly reliant on one or a few frugivore groups for dispersal? Conversely, how many plant species have interactions that allow for substitution?
2. Do large-gaped frugivores feed on a wide range of plant species or do they ignore small-fruited species?

Materials and methods

Study area

The study was conducted from June 1998 to March 2002 in Khao Yai National Park (KY), established in 1962 as the first national park in Thailand (Smitinand 1977) and covering an area of 2,168 km^2 in lower northeastern Thailand. The park lies at latitudes 14°05'–15'N and longitudes 101°05'–50'E in the Dongruk mountain range. Its elevation ranges from 250 to 1,326 m. Based on stand structure and species composition, the vegetation can be classified into six communities: moist evergreen forest, hill evergreen forest, mixed deciduous forest, dry evergreen forest, tropical grassland and disturbed or secondary forest (Smitinand 1977; Kutintara 1993). The main study area of about 70 km^2 around the headquarters of KY has an altitudinal range of 600–800 m and comprises moist evergreen forest.

The moist evergreen forest of KY covers approximately 64% of the total park area, or 1,375 km^2, ranging from 400 to 1,000 m (Smitinand 1977). The trees reach 45 m in height; the density of trees over 10 cm in diameter at breast height is 371 ha^{-1}, with a basal area of 32 m^2 ha^{-1} (Kutintara 1993). Characteristic species in this forest are *Acrocarpus fraxinifolius*, *Anthocephalus chinensis*, *Balakata baccata*, *Cinnamomum subavenium*, *Dipterocarpus gracilis*, *Elaeocarpus robustus*, *Gironniera nervosa*, *Mastixia pentandra*, *Platymitra macrocarpa*, *Sloanea sigun*, and *Syzygium cumini* (S. Kitamura, unpublished data). The mean annual rainfall is 2,326 mm (1993–2001), with a marked wet season from May through October and relatively dry conditions from November until April. The mean monthly temperature ranges from 21°C (December and January) to 32°C (April and May). Although ripe fruit (*Ficus* spp.) is available year-round (Poonswad et al. 1998a), fruit diversity and abundance are relatively high in the rainy season and reach a trough at the beginning of the dry season (S. Kitamura, unpublished data).

Plant species studied

In this study, we use "fruits" and "seeds" in their ecological, not anatomical sense. Whenever it was possible, ripe fruits were collected in the study area. The following characteristics were recorded: length and transverse diameter of fruit/seed, wet weight of fruit/seed, ripe fruit color (for dehiscent fruits, the color of the inner part of the fruits displayed for animals was described), number of seeds in a fruit, and sugar concentration of the fruit pulp. The latter was measured using a pocket refractometer (Belingham and Stanley, BS-R70) that determined the sucrose equivalents of the juice. In the case of several dehiscent fruits like *Michelia baillonii*, we treated the arillate seeds as the dispersal units since they separate quite easily in the ripe fruit and are apparently removed by animals individually. Such data were collected on at least 15 samples for each fruit species (except *Artocarpus gomezianus*, for which only four intact fruits were found). Fruits with obvious damage were excluded from the measurements. No attempt was made to look at variation among individuals within species; samples were chosen to represent the typical size range. These measurements were performed within a day of when fruits were collected. Some seeds were kept as a reference collection to compare with the seeds from fecal samples and seed traps. The life form and fruit type of each species were defined as follows (cf. Gautier-Hion et al. 1985): life form: EP, epiphyte; HE, herb; LI, liana; SH, arboreal shrub (<7 m); ST, small tree (7–15 m); MT, middle-sized tree (15–30 m); TT, tall tree (>30 m); fruit type: D, dehiscent fruit; I, indehiscent fruit with a thin husk; T, indehiscent fruit with a thick husk. Plant nomenclature follows the Tree Flora of Malaya I–IV (Whitmore 1972, 1973; Ng 1978, 1989), A Field Guide to Forest Trees of Northern Thailand (Gardner et al. 2000), or the incomplete series of the Flora of Thailand, when the studied group was covered therein. Plant specimens were collected as often as possible and matched with the identified specimens in the herbarium of the Royal Forest Department in Bangkok (BKF) or checked in the herbarium of the Department of Botany, Faculty of Science, Kyoto University (KYO). The voucher specimens are kept in our laboratory in KY.

Animal species studied

We grouped 25 species of frugivores into ten categories (Table 1): bulbuls (7 spp.); pigeons (1 sp.); hornbills (4 spp.); squirrels (2 spp.); civets (3 spp.); gibbons (2 spp.); macaques (1 sp.); bears (2 spp.); deer (2 spp.); and elephants (1 sp.). The body weight of the focus groups greatly varied from bulbuls (<0.05 kg) to elephants (4,000 kg). Diets of frugivore groups for the plant species studied were obtained from the following observations: direct observation including over 10-h diurnal watches from hides at fruiting trees (35 individuals of 30 species); casual observations of fruit consumption by animals in the forest; identification of seeds in the feces of mammals: three species of civets (*n*=30); white-handed gibbons (*n*=15); pig-tailed macaques (*n*=167); two species of bears (*n*=24); two species of deer (*n*=3,397); elephants (*n*=2,249); and in seed

Table 1 List of animal species studied (nomenclature: Lekagul and Round (1991) for birds and Srikosamatara and Hansel (1996) for mammals). In each family, species are listed by increasing weight (kg). (Daily habit: *A* arboreal, *T* terrestrial, *AT* arboreal-terrestrial, *D* diurnal, *N* nocturnal, *DN* diurnal-nocturnal)

Species	Weight (kg)	Daily habit	Species	Weight (kg)	Daily habit
Bulbuls (Pycnonotidae)			Civets (Viverridae)		
Pycnonotus atriceps	<0.05	A, D	*Paradoxurus hermaphroditus*	2–5	AT, DN
P. finlaysoni	<0.05	A, D	*Paguma larvata*	3–5	AT, DN
P. melanicterus	<0.05	A, D	*Arctictis binturong*	9–20	AT, DN
P. jocosus	<0.05	A, D	Gibbons (Hylobatidae)		
Hypsipetes propinquus	<0.05	A, D	*Hylobates lar*	4–7	A, D
H. flavala	<0.05	A, D	*H. pileatus*	4–7	A, D
Criniger pallidus	<0.05	A, D	Macaques (Cercopithecidae)		
Pigeons (Columbidae)			*Macaca nemestrina*	4–9	AT, D
Ducula badia	0.5–0.6	A, D	Bears (Ursidae)		
Hornbills (Bucerotidae)			*Urus malayanus*	27–65	AT, DN
Anthracoceros albirostris	0.7–0.8	A, D	*U. tibetanus*	100	AT, DN
Anorrhinus austeni	0.8–0.9	A, D	Deer (Cervidae)		
Aceros undulatus	2.0–2.5	A, D	*Muntiacus muntjak*	20–28	T, DN
Buceros bicornis	2.2–3.0	A, D	*Cervus unicolor*	185–260	T, DN
Squirrels (Sciuridae)			Elephants (Elephantidae)		
Callosciurus finlaysoni	0.3	A, D	*Elephas maximus*	4,000	T, DN
Ratufa bicolor	1.4	A, D			

traps (119 traps) under the nests and roosts of hornbills. All samples of feces (except for elephants) were washed through sieves with mesh size of 0.4 mm and dried in the sun. In the case of elephants, dung balls were examined in situ for seeds. Seeds from both feces and traps were identified by comparison to a reference collection of seeds and fruits. These data on frugivore diets, seasonality, and tree visitation will be published separately. Data from the previous studies on frugivore diets in KY were included in the list of fruit species eaten. The quality of the literature was assessed with respect to the type of study from which the data was accumulated: studies of an particular animal's diets: bulbuls (Chaikuad 2000), hornbills (Poonswad 1993; Poonswad et al. 1998b), gibbons (Whitington 1991; Whitington and Treesucon 1991), and macaques (T. Maruhashi, unpublished data), and observations of frugivores visiting fruiting crops: nine species of roadside tree (McClure 1974), ten fruit species of gibbon diets (Whitington 1991), and ten species of strangler figs (Poonswad et al. 1998a). We calculated the dietary overlap among pairs of frugivores using Sorensen's similarity index (Krebs 1989). This index generates a value ranging from 0 to 1, with 0 representing no overlap and 1 representing complete overlap.

The data set comprises accounts of which frugivore group consumes each fruit species and how they handle the fruit. The categories of fruit consumers were classified according to Gautier-Hion et al. (1985). Dispersers (D) are frugivores that disperse intact seeds by either endozoochory or synzoochory. Neutral consumers (N) are those who leave the seed intact under the parent tree. Predators (P) destroy the seeds, whether the remains are spat out, eliminated in feces, or rotted whole in a food hoard. When we found that a seed without obvious damage was regurgitated, defecated, or spat out by a frugivore, we defined it as a disperser. Of course, it is not so easy to generalize a species' effect on the fate of the seeds of fruits that it ate; a consumer may have several effects whose relative importance can vary (Gautier-Hion et al. 1985). In this study, we did not consider the variation of diets among frugivore species within groups, or their respective effects on seeds. Our reasons were practical. It has been shown that fruit consumption patterns and effects are quite similar within groups such as hornbills and gibbons (Poonswad et al. 1998b; Srikosamatara and Hansel 1996); perhaps more important, it is difficult to distinguish between the feces of the different species of civets, bears, and deer. The dietary overlap of bulbuls (7 spp.) was assumed to be high, because they were often observed to feed on fruits in the mixed flocks of several species at the fruiting plants (S. Kitamura, personal observation). Since several researchers have conducted ecological studies of hornbills and gibbons since the 1980s in the same area, fruits eaten by both groups may have been more thoroughly sampled than the other groups. Animal nomenclature follows Lekagul and Round (1991) for birds, and Srikosamatara and Hansel (1996) for mammals.

Results

Fruit characteristics in KY

Fruit characteristics were determined for 259 species in 65 families (Appendix). The distribution of most fruit characteristics was highly skewed (Fig. 1). Median fruit weight for the species investigated was 1 g (range 0.02–275) and the median fruit diameter was 10 mm (range 2–84). The median value of the sugar concentration was 12% (range 2–26: *n*=126). Half of the species did not have enough juice in the pulp to measure sugar content using the refractometer. The median weight of seeds was

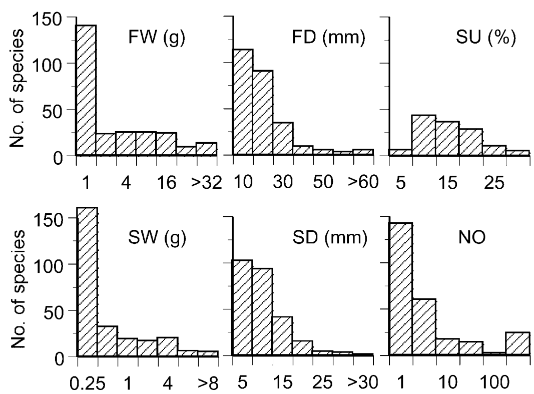

Fig. 1 Frequency distribution of fruit characteristics in KY. [*FW* fruit weight (g), *FD* fruit diameter (mm), *SU* sugar concentration of the fruit pulp (%), *SW* seed weight (g), *SD* seed diameter (mm), *NO* number of seeds per fruit]

0.1 g (range 0.01–21) and the median seed diameter was 6 mm (range 0.1–28). Half the fruit species had a single seed (55%). Most of the fruits were indehiscent with a thin husk (75%), followed by dehiscent fruits (16%; Celastraceae, Euphorbiaceae and Meliaceae), and indehiscent fruits with a thick husk (9%; Annonaceae, Meliaceae and Sapindaceae). Percentages of each life form among the collected fruit species were 2% (EP), 3% (HE), 21% (LI), 27% (SH), 13% (ST), 22% (MT), and 12% (TT). The commonest fruit colors in the forest were black (27%) and red (22%), followed by yellow (14%).

Frugivore diet and fruit preference

We categorized the 259 fruit species into three groups according to the quality of data (Appendix). Fairly observed (F) species' fruit characteristics were recorded and fruit consumption by frugivores was observed for more than 10 h per fruit species (53 spp.). Casually observed (C) species' fruit characteristics were recorded and fruit consumption by frugivores was casually observed (151 spp.). Not observed (N) species were those for whom only fruit characteristics were recorded (55 spp.). Among the 53 fairly observed plant species, there were no fruit species consumed by only one frugivore group. The minimum number of frugivore groups recorded for a given fruit species was two (hornbills and squirrels) for *Sterculia balanghas* and three (mostly pigeons, hornbills and/or squirrels) for 9 species. The most widely consumed fruits were *Ficus altissima* and *F. subcordata* (10 groups each), *Elaeagnus latifolia* (9 groups), and *Bridelia insulana* and *Syzygium cumini* (9 groups each). Of these, the *Ficus* species bear soft fruits with many small seeds, *E. latifolia* bears large soft fruit with a single large seed, and *B. insulana* and *S. cumini* bear small soft fruits with a single seed. The number of frugivore groups that served a given plant species declined with seed size (Fig. 2). The correlation was not significant for fruit size (Fig. 2a; Spearman rank correlation: P=0.74), but was significant for seed size (Fig. 2b; Spearman rank correlation: r=–0.27, P<0.05). The number of frugivore groups in one-seeded fruits (n=39 spp.)

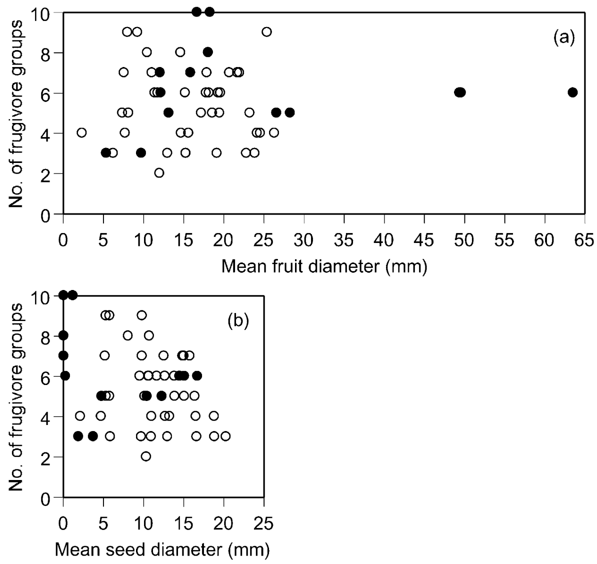

Fig. 2 Number of frugivore groups plotted against **a** mean fruit diameter and **b** mean seed diameter of their diet species. *Open circles* one seed per fruit (n=39 spp.); *solid circles* two or more seeds per fruit (n=14 spp.)

was not significantly different from that of the groups in many-seeded fruits (n=14 spp.; Mann-Whitney U-test, P>0.19). For the 151 casually observed species, 45 species were consumed by only one frugivore group (in most cases, bulbuls: 67% of 45 spp.). Forty-six species were recorded by two groups (mostly shared with bulbuls: 66% of 46 spp. or macaques: 53%). Most of these fruits were arboreal shrubs (SH: 41 spp.) or small trees (ST: 15 spp.).

The number of fruit species consumed by each frugivore group ranged from 9 species consumed by elephants to 122 species consumed by macaques (Table 2). Frugivore groups shared between 2 and 76 fruit species in their diet; Sorensen's similarity index between frugivore groups varied from 0.03 to 0.74 (Table 2). Dietary overlap between phylogenetically close groups was greater than that between distant groups. The highest value was obtained between gibbons and macaques

Table 2 Diet overlap between each pair of consumer groups. Number of fruit species consumed by each frugivore group is shown in parentheses. *Above diagonal* Number of fruit species shared between pairs of the groups. *Below diagonal* The dietary overlap values calculated by Sorensen's similarity index

	Bulbuls	Pigeons	Hornbills	Squirrels	Civets	Gibbons	Macaques	Bears	Deer	Elephants
	(118)	(62)	(71)	(104)	(56)	(84)	(122)	(13)	(46)	(9)
Bulbuls		43	39	40	24	34	63	9	11	2
Pigeons	0.48		47	45	22	39	45	10	17	2
Hornbills	0.41	0.71		55	27	43	48	11	18	2
Squirrels	0.36	0.54	0.63		42	64	73	13	38	8
Civets	0.28	0.37	0.43	0.53		45	48	9	25	6
Gibbons	0.34	0.53	0.55	0.68	0.64		76	12	36	7
Macaques	0.53	0.49	0.50	0.65	0.54	0.74		13	40	7
Bears	0.14	0.27	0.26	0.22	0.26	0.25	0.19		10	3
Deer	0.13	0.31	0.31	0.51	0.49	0.55	0.48	0.34		9
Elephants	0.03	0.06	0.05	0.14	0.18	0.15	0.11	0.27	0.33	

Table 3 Mean, range, and coefficient of variance (*CV*) of fruit/seed diameters (mm) consumed by each frugivore group

	Fruit diameter			Seed diameter		
	Mean	Range	CV	Mean	Range	CV
Bulbuls	10	2–37	55	4	0.1–13	59
Pigeons	14	2–23	45	8	1.0–20	69
Hornbills	16	5–69	56	8	0.3–20	62
Squirrels	19	2–69	63	9	1.0–28	67
Civets	18	5–64	65	8	0.1–17	60
Gibbons	20	5–84	69	8	0.1–19	59
Macaques	18	2–84	78	7	0.1–28	70
Bears	17	8–26	36	7	0.3–13	67
Deer	28	8–84	61	11	0.1–28	58
Elephants	38	17–64	48	11	1.0–23	65

(0.74), followed by hornbills and pigeons (0.71). The lowest value was obtained between bulbuls and elephant (0.03) followed by hornbills and elephant (0.05). The dietary overlaps within bird groups were relatively high compared with those of mammalian groups. Observations for nocturnal animals (civets, bears, and deer) were relatively few; their diet lists are likely to be incomplete.

The ranges of the fruit/seed diameter consumed by each frugivore group showed greatly overlap for many groups, especially for seeds (CV: 36–78 for fruit and 58–70 for seeds in Table 3). These findings can be explained by the facts that (1) most frugivore groups, except for elephants, consumed small fruit (less than 10 mm) as well as large fruits despite their body sizes and (2) the most commonly consumed larger fruits were generally soft with many small seeds. The mean diameters of the fruit/seed were significantly different among frugivores (Kruskal-Wallis test, H=150.1, P<0.001 for fruit; H=71.9, P<0.001 for seed). Pair-wise comparisons of the mean fruit/seed diameter consumed by each frugivore group revealed that those of bulbuls were significantly smaller (Mann-Whitney U test with Bonferroni-corrected P-values: a=0.0011); comparing fruit diameters: P<0.001 for each bulbul group paring and comparing seed diameters: P<0.001 for each bulbul group pairing except for bears (P>0.07) and elephants (P>0.006). The mean fruit diameter consumed by deer was significantly larger than for other groups (P<0.001 for pigeons, P<0.001 for hornbills, P<0.001 for squirrels, P<0.001 for civets, P<0.001 for gibbons, and P<0.001 for macaques), except for bears (P>0.017) and elephants (P>0.109). The seed diameter consumed by deer was significantly larger than for macaques (P<0.001). The fruit diameter consumed by elephants was significantly larger than for bulbuls (P<0.001), pigeons (P<0.001), hornbills (P<0.001), civets (P<0.001), and macaques (P<0.001).

All birds and mammals consumed the thin-husk indehiscent fruits (I) that are the most common fruit types in the forest (Table 4). Mammals tended to consume the thick-husk indehiscent fruits (T) and to avoid the dehiscent fruits (D); birds preferred the dehiscent fruits and avoided the thick-husk indehiscent fruits (Table 4). Most frugivores consumed the fruits of taller trees (TT and MT) or lianas (LI), and ignored those of the smaller trees (ST and SH), except for bulbuls and macaques. Deer and elephants consumed the fallen fruits of large-sized trees (MT and TT) on the forest floor. All the target groups, except for elephants, tended to consume black or red fruits (Table 4). Yellow fruits were preferred by mammals but not by birds. Although the effects on seeds for several frugivore groups (pigeons and deer) were largely unknown, most groups (except for squirrels and macaques) dispersed some seeds of the fruits that they ate (Table 4).

Discussion

Are there any close relationships between a particular species and a frugivore group?

It is clear that many animals rely on fruits as essential food resources and that conversely they provide valuable dispersal services to many of these fruit bearing plants (Gautier-Hion et al. 1985). No close relationship between a particular fruit and a frugivore was found in this study. Our results indicate that most fruit species are eaten by various kinds of frugivore groups. Of the 53 fairly observed species, 43 species are consumed by four or more frugivore groups. Studies in intact forests report that it is typical for numerous frugivorous animals to disperse the fruit of any particular plant species (Leighton and

Table 4 Fruit type, life form, fruit color, and effects on seeds consumed by each frugivore group. Variables listed for fruit type, life form, and fruit color are responsible for more than 15% of the consumed fruit for each frugivore group. The number of fruit species whose seeds are dispersed (*D*), not dispersed (*N*), predated (*P*), or unknown (*X*) by the different frugivore groups are shown in effects on seeds. See Appendix for abbreviations of life form and fruit type

Frugivore	Fruit type	Life form	Fruit color	Effects on seeds			
				D	N	P	X
Bulbuls	D, I	MT, LI, SH	Black, red, purple	98	1	0	19
Pigeons	D, I	TT, MT, LI	Black, red, purple	23	0	0	39
Hornbills	D, I	TT, MT, LI	Black, red	71	0	0	0
Squirrels	I, T	TT, MT, LI	Black, red, yellow	0	33	78	13
Civets	I, T	TT, MT, LI	Black, red, yellow	46	3	0	9
Gibbons	I, T	TT, MT, LI	Black, red, yellow	72	23	1	7
Macaques	I, T	TT, MT, LI, SH	Black, red, yellow	84	35	36	14
Bears	I, T	TT, MT	Black, red, purple, yellow	10	0	0	3
Deer	I, T	TT, MT	Black, red, yellow	10	1	0	35
Elephants	I, T	TT, MT	Yellow	6	0	1	3

Leighton 1983; Gautier-Hion et al. 1985). As long as the fruit is soft with many seeds (e.g. figs), size has no negative effect on the number of dispersers (Fig. 2a). In contrast, the size of seed does limit the number of consumer groups (Fig. 2b). In this respect, our results reflect the same relationship between frugivores and tropical plants noted elsewhere in Southeast Asia (e.g. Leighton and Leighton 1983; Corlett 1998; Hamann and Curio 1999; Heindl and Curio 1999). The remaining 10 F species are consumed by two or three groups (pigeons, hornbills and/or squirrels) and are mostly one-seeded fruits (8 of 10 species). The dietary overlaps among these frugivores are relatively high (0.71 for pigeons-hornbill, 0.63 for hornbills-squirrels and 0.54 for squirrels and pigeons: Table 2). As squirrels are considered the major seed predators in KY (Table 4), pigeons and hornbills are important seed dispersers for some species. Indeed, an intensive study on fruit consumption of *Aglaia spectabilis* (the largest of the 53 seed species) corroborates the finding that fruit/seed size may limit the number of available frugivorous bird species; in this case, only large frugivorous birds (pigeons and hornbills) disperse the seeds (S. Kitamura, unpublished data).

Of the 151 casually observed species (C), 91 species were observed being eaten by only one or two frugivores (mostly bulbuls and macaques). Although the observation effort compromises these findings, it seems evident that large frugivores ignore these species, mostly small trees and arboreal shrubs. Most of the studied groups are canopy dwelling animals (pigeons, hornbills, squirrels and gibbons) or large terrestrial herbivores that consume fallen fruits off the forest floor (deer and elephants). These animals are less likely to eat the fruits of the smaller trees because they mostly provide smaller crops compared with the taller trees. Since most studied groups ignore the fruits and macaques mainly act as seed predators for them (Appendix), bulbuls seem to be the only seed dispersers for them. However, this does not necessarily indicate the uniqueness of bulbuls as seed dispersers in KY. Because our focus was on large frugivores, we do not have sufficient data on the diets of small, highly frugivorous birds found in Southeast Asia (Corlett 1998), including green pigeons (5 species recorded in KY), barbets (5 spp.), white-eyes (2 spp.), laughing-thrushes (3 spp.), babblers (10 spp.), and flowerpeckers (5 spp.). Like bulbuls, these small birds are sometimes observed to consume the fruits of SH or ST as well as large soft fruits with small tiny seeds such as figs. Therefore they seem to be vital as seed dispersal agents for small trees and understory shrubs that other large animals ignore in KY.

Do large frugivores take a wider range of fruit species?

In this study, we focus on the size of fruits and seeds because both dimensions interact with frugivore consumption; for instance, fruit size is most critical for birds that swallow fruit whole (Leighton and Leighton 1983). Although the ranges of the mean fruit and seed diameters consumed by each frugivore group show broad similarities (Table 3), the mean diameters of fruit/seed consumed by bulbuls are significantly smaller than those consumed by other groups. The fruits consumed by the larger birds (pigeons and hornbills) are not significantly different from those of mammals in terms of mean fruit/seed diameters, with the exception of fruit size for elephants and deer. Our results indicate that several large-sized fruits are inaccessible for small birds in KY. The potentially available number of fruit species, estimated from the relationship between gape width of frugivorous birds (13 mm for bulbuls, 30 mm for pigeons and 50 mm for hornbills; Leighton 1982) and the fruit diameter, are quite high (157 spp. for bulbuls, 238 spp. for pigeons and 252 spp. for hornbills). In practice, a smaller number of fruit species were used by each frugivorous bird species, especially for larger groups (28% of potentially available fruit species for hornbills, 62% for pigeons and 66% for bulbuls). It is to be expected that frugivore behavior and hence seed dispersal rely on the phenology and life form of each visited fruiting plant, its crop size, pulp-to-seed ratio, fruit/seed size, pulp mass, pulp chemistry, and ease of harvest (Corlett 1998). Thus, factors other than fruit/seed size may have a strong influence on the fruit selection by large frugivorous birds.

Corlett (1998) mentioned that fruit diameters over 30 mm may exclude all birds but hornbills and imperial pigeons, yet such fruit can still be harvested by most fruit eating mammals with teeth. In the case of mammals in KY, the number of fruit species consumed is not greatly different from those consumed by birds (Table 2). Large terrestrial frugivores such as deer and elephants only consume the fallen fruits under the fruiting trees. The diverse fruits they ate seem to be similar in their occurrence in large patches on the ground, in keeping with the large body mass. Most fruits that are not consumed by these animals seem to be too small or too sparse to eat efficiently, especially for elephants. Mammals consumed the thick-husk fruit that are too large for birds along with the fruits consumed by birds, but they (except for squirrels) avoid several dehiscent fruits such as the Meliaceae. Those fruits are known as “lipid-rich fruits” and are not preferred by mammals in Southeast Asia (Corlett 1998). Both birds and mammals in KY consume a limited number of fruit species. In general, most fruit consumed by birds in KY are black or red and have no thick husk. Birds cannot use the thick-husk fruit that mammals in KY do (Table 4). These results are similar to previously reported “bird-fruits” and “mammal-fruits” (e.g. Leighton and Leighton 1983; Corlett 1998) and suggest that the fruits in KY might comprise three dispersal assemblages (birds, birds and mammals, mammals), each with relatively distinctive fruit characteristics.

Effects of human impact on fruit-frugivore interactions in tropical forests

In order to sustain the natural interaction between fleshy fruits and frugivores in KY, it is necessary to estimate the minimum suitable size of a protected area and the tolerance of forest fragmentation, based on knowledge of diet, frugivore population density and home range requirements. According to Corlett (1998), the tolerance of forest fragmentation for each group rates as follows: high (bulbuls and squirrels), medium (some civets and macaques) and low (pigeons, hornbills, some civets, gibbons, bears, deer and elephants). If major large forest fragmentation were to occur in KY, intolerant large frugivores that require larger areas for their long-term survival might disappear quickly, leaving only a few frugivore groups such as bulbuls and squirrels, which are tolerant of forest fragmentation. Indeed, large frugivorous animals such as elephants and hornbills have become locally extinct in small conservation areas in Thailand, although they still exist in large conservation areas (over 2,000 km^2). One extreme example in Southeast Asia is reported from the highly degraded landscape of Hong Kong and Singapore (Corlett and Turner 1997). Much of the tree flora is no longer effectively dispersed after the disappearance of forest-dependent vertebrate species.

Hunting adds to the challenges of maintaining the survival of fruit-bearing species. Poulsen et al. (2002) reported that primate populations in Africa face greater declines than hornbill populations due to hunting pressures. They consider it unlikely that seed dispersal by hornbills will compensate for the loss of primates in maintaining forest structure, as the dietary overlap between hornbills and primates is relatively low. Our findings in KY support their results; there is no reason to consider that seed dispersal by a certain frugivore group will compensate for the loss of other frugivore groups, as the dietary overlap between large frugivores, especially between bird and mammal groups, tends to be low (Table 2). Even gibbons and macaques, with the highest dietary overlaps in KY, have different dispersal methods: gibbons usually disperse the seeds via defecation and macaques usually disperse the seeds via their cheek pouches. The different treatments of fruit and seeds may increase the chance that a seed is disseminated in a favorable site whose location is unpredictable (Wheelwright and Orians 1982).

Despite the wide range of frugivorous animals included in this study, we do recognize certain limitations in our study of the relative importance of frugivore groups. First, we did not include bats and rodents, despite their importance for seed dispersal in a tropical forest. Most of the observations were conducted in the daytime and the fallen fruits consumedby rodents were mostly ignored. The consumption by nocturnal animals and secondary dispersal of fallen fruits may be important processes of seed dispersal in Southeast Asia (Yasuda et al. 2000). Second, we concentrated on the interactions between fleshy fruits and their consumers. The supra-annual fruiting patterns of the Dipterocarpaceae in Southeast Asia are also considered to have a huge impact on frugivores (Curran and Leighton 2000). Further studies are needed to evaluate the seed dispersal and/or predation by nocturnal animals such as porcupines and rodents in KY. To insure natural seed dispersal processes in forest ecosystems, further studies of the seed-dispersing role of each frugivore group in intact forests are urgently needed.

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Appendix

Characteristics of 259 vertebrate-dispersed fruits and fruit consumers in Khao Yai National Park, Thailand

FW Fruit weight (g), *FL* fruit length (mm), *FD* fruit diameter (FD), *SU* sugar concentration of fruit pulp (%), *CO* color of fruit, *NO* number of seeds per fruit, *SW* seed weight (g), *SL* seed length (mm), *SD* seed diameter (mm). *ND* no data. Fruit type: *D* dehiscent, *I* indehiscent fruit with thin husk, *T* indehiscent fruit with thick husk. Life forms: *EP* epiphyte, *HE* herbs, *LI* liana, *SH* arboreal shrub (<7 m), *ST* small tree (7–15 m), *MT* middle-sized tree (15–30 m), *TT* tall tree (>30 m). Observations: *N* not observed, *C* casually observed, *F* fairly observed (>10 h). Fruit consumers: *Bu* bulbuls, *Pi* pigeons, *Ho* hornbills, *Sq* squirrels, *Ci* civets, *Gi* gibbons, *Ma* macaques, *Be* bears, *De* deer, *El* elephants. Effects on seeds: *d* disperser, *n* neutral consumer, *p* predator, *x* unknown

Family	Species	FW	FL	FD	SU	CO	NO	SW	SL	SD	FT	LF	OB	Bu	Pi	Ho	Sq	Ci	Gi	Ma	Be	De	El
Actinidaceae	*Saurauia tristyla*	0.51	10.3	8.7	2.1	White	>100	<0.01	<0.1	<0.1	I	SH	C	d					d	d			
Alangiaceae	*Alangium chinense*	0.48	11.8	8.4	ND	Black	1.0	0.15	8.4	6.3	I	SH	C	d									
	Alangium kurzii	0.75	15.0	9.6	ND	Black	1.0	0.13	10.6	6.0	I	ST	C	d		d							
Anacardiaceae	*Buchanania arborescens*	0.56	12.3	10.0	ND	Black	1.0	0.11	9.6	6.9	I	MT	C						x				
	Choerospondias axillaris	9.19	25.7	23.3	15.4	Yellow	1.0	2.72	18.5	15.1	I	TT	F				n, p		d	n		d	d, p
	Mangifera indica	54.08	55.7	42.2	18.6	Yellow	1.0	13.16	47.8	27.7	I	MT	C				n, p			n		n	
	Rhus succedanea	0.08	7.3	6.7	ND	Brown	1.0	0.05	6.1	4.7	I	TT	C	d									
	Spondias pinnata	19.11	38.7	32.6	ND	Yellow	1.0	8.08	33.4	23.8	I	MT	C									d	
Annonaceae	*Alphonsea* cf. *cylindrica*	15.17	36.9	28.3	8.1	Yellow	4.7	0.77	16.9	10.5	T	MT	F				x	d	d	d		x	
	Artabotrys hexapetalus	11.09	35.0	26.9	ND	Yellow	1.8	1.38	18.8	12.9	I	LI	N										
	Cyathostemma micranthum	1.08	13.9	11.5	12.5	Black	4.0	0.08	7.6	5.2	I	LI	C	d	d	d	x		d	d			
	Dasymaschalon sootepense	0.60	15.5	8.2	11.1	Red	1.0	0.17	12.9	4.5	I	SH	C	d		d		x		x			
	Desmos chinensis	0.24	8.7	6.9	24.5	Black	1.0	0.09	6.7	4.8	I	LI	C	d	d	d		d	d	d			
	Fissistigma latifolium var. *ovoideum*	5.56	25.2	21.3	ND	Green	6.6	0.36	14.1	8.1	I	LI	C				p	d	d	d			
	Miliusa lineata	4.40	22.2	18.8	11.9	Red	3.9	0.25	11.4	7.7	T	MT	C				x	d	d	d		d	
	Platymitra macrocarpa	175.00	80.6	63.6	17.3	Brown	7.0	3.58	28.2	16.7	T	TT	F				n, p	d	d	d		d	d
	Polyalthia jucunda	9.38	34.2	22.0	13.9	Black	1.0	4.25	26.8	15.8	I	ST	F		d	d	n, p	d, n	d, n	d, n		x	
	Polyalthia sp. 1	0.98	12.3	11.6	7.5	Purple	1.0	0.30	8.0	7.6	I	SH	C	d				d		d, p		x	
	P. viridis	7.31	28.7	20.7	ND	Black	1.0	3.42	23.2	15.1	I	MT	F		d	d	n, p	d, n	d, n	d, n		x	
	Uvaria cordata	5.15	28.1	17.0	17.3	Black	3.8	0.32	11.1	9.1	I	LI	C			d	x	d	d	d			
	U. fauveliana	22.42	42.6	32.2	8.6	Red	8.2	2.42	13.7	8.3	T	LI	C				x	d	d	d			
	U. lurida	9.86	45.4	18.4	10.2	Red	5.4	0.50	12.2	11.2	I	LI	C			d	x	d	d	d			
Apocynaceae	*Chilocarpus denudatus*	4.66	48.0	15.4	ND	Orange	19.0	0.06	7.3	5.4	D	LI	N										
	Rauvolfia cambodiana	0.52	11.4	10.7	ND	Black	1.0	0.08	8.6	5.2	I	SH	N										
Aquifoliaceae	*Ilex* cf. *goshiensis*	0.13	6.6	5.4	18.0	Red	4.1	0.01	4.0	1.9	I	TT	F	d					d	d			
Araceae	*Amorphophallus* sp. 1	0.61	14.1	9.0	ND	Blue	1.8	0.22	11.0	6.8	I	HE	N										
	Arisaema sp. 1	0.46	9.8	9.2	ND	Red	2.2	0.12	7.1	5.9	I	HE	N										
	Pothos chinensis	0.46	13.9	7.6	ND	Red	1.0	0.31	13.0	6.3	I	EP	C	d									
Burseraceae	*Canarium euphyllum*	12.78	37.7	24.6	ND	Black	1.0	4.60	35.6	16.6	I	TT	F		d	d	n, p					d	
Caprifoliacae	*Lonicera bournei*	35.00	10.9	7.5	ND	Red	4.0	0.01	4.9	3.2	I	LI	N										
	Viburnum sp. 1	0.25	10.9	7.2	ND	Black	1.0	0.11	10.0	6.5	I	ST	C	d									
Celastraceae	*Bhesa robusta*	1.00	18.6	11.2	14.1	Yellow	1.1	0.41	15.4	8.1	D	TT	C	d		d	p						
	Celastrus paniculatus	0.33	9.0	8.1	19.0	Orange	3.6	0.05	7.0	4.4	D	LI	C	d		d	p						
	Glyptopetalum sclerocarpum	1.04	17.5	11.4	ND	Red	1.0	0.85	15.7	11.0	D	ST	N										
	Microtropis discolor	0.31	9.7	8.0	ND	Red	1.0	0.30	10.0	7.6	D	SH	N										
	Salacia sp. 1	11.30	27.5	26.6	7.9	Orange	1.5	1.13	14.8	12.3	T	LI	F				p	d	d	d		d	
Chloranthacae	*Chloranthus erectus*	0.13	6.4	5.9	ND	White	1.0	0.02	4.0	3.2	I	HE	N										
Combretaceae	*Terminalia bellirica*	9.46	29.7	23.9	ND	Brown	1.0	3.93	23.7	17.2	I	MT	C				p						
Connaraceae	*Rourea minor*	0.81	18.9	10.0	15.6	Yellow	1.0	0.41	15.2	8.1	D	LI	C	d	x	d	x		n				
	Roureopsis stenopetala	0.38	10.9	7.4	16.3	Orange	1.0	0.18	8.3	6.1	D	LI	N										
Convolvulaceae	*Erycibe* sp. 1	2.69	23.4	14.7	10.2	Orange	1.0	0.94	17.2	11.0	T	LI	F				x	d	d	d			
Cornaceae	*Mastixia pentandra*	5.14	28.2	17.9	11.2	Black	1.0	2.09	22.9	12.6	I	TT	F		d	d	p		d, n	d, n, p	x	x	
Cucurbitaceae	*Trichosanthes tricuspidata*	145.40	70.8	68.6	9.3	Red	>100	0.07	11.0	5.0	I	LI	C			d	p		d	d, p		x	
	Trichosanthes sp. 1	12.67	52.2	27.5	15.0	Red	27.8	0.13	8.0	7.5	I	LI	N										
Daphniphyllaceae	*Daphniphyllum* sp. 1	1.06	13.6	11.3		Black	1.0	0.22	10.5	6.1	I	ST	C	d	x								
Ebenaceae	*Diospyros glandulosa*	11.81	27.2	25.9	21.7	Yellow	3.6	0.20	14.8	8.4	I	ST	C				p	d	d	d	x	x	d

Family	Species	FW	FL	FD	SU	CO	NO	SW	SL	SD	FT	LF	OB	Bu	Pi	Ho	Sq	Ci	Gi	Ma	Be	De	El
Elaeagnaceae	*Elaeagnus latifolia*	15.90	41.1	25.4	11.5	Red	1.0	1.34	33.0	9.9	I	LI	F	n	x	d	p	d	d	d, n, p	d	x	
Elaeocarpaceae	*Elaeocarpus griffithii*	0.57	12.9	8.9	ND	Blue	1.0	0.15	10.8	5.2	I	MT	C				p		d	d, p			
	E. robustus	9.54	25.4	24.2	ND	Blue	1.0	3.80	18.9	18.8	I	MT	F				p		n	n		d	
	Sloanea sigun	0.98	10.3	6.3	ND	Orange	1.0	0.15	8.8	5.9	D	MT	F	d		d	p						
Euphorbiaceae	*Antidesma* cf. *burnis*	0.12	6.0	6.0	10.5	Black	1.0	0.03	4.7	3.8	I	SH	C	d									
	Aporosa planchoniana	0.31	8.8	7.5	ND	Orange	1.0	0.05	5.9	4.4	D	SH	C	d			p						
	A. yunnanensis	0.27	8.5	7.9	9.0	Orange	1.0	0.08	6.4	5.5	D	SH	C	d			p			d, p			
	Baccaurea ramiflora	5.31	24.6	21.6	8.0	Yellow	3.3	0.18	10.4	8.2	T	ST	C				p	d	d	d		x	
	Balakata baccata	1.09	13.8	13.2	13.9	Purple	1.9	0.10	7.4	4.8	T	TT	F				p	d	d	d, p		x	
	Breynia sp. 1	0.09	6.5	5.1	ND	Red	3.5	0.01	4.6	2.8	D	SH	C	d									
	B. vitis-idaea	0.08	5.5	5.2	ND	Red	6.0	0.02	3.4	2.4	D	SH	N										
	Bridelia insulana	0.52	10.2	9.3	15.5	Purple	1.0	0.26	8.7	5.8	I	MT	F	d	x	d	p	d	d	d	d	x	
	B. stipularis	0.49	10.2	8.9	ND	Black	2.0	0.07	7.5	5.5	I	LI	N										
	B. tomentosa	0.16	6.6	6.3	ND	Black	2.0	0.03	4.6	4.1	I	SH	C	d				d					
	Claoxylon indicum	0.03	3.6	3.4	ND	Red	3.0	0.01	2.9	2.9	D	MT	C	d						p			
	Excoecaria oppositifolia	12.51	44.4	38.3	ND	Green	3.0	1.31	14.1	12.8	T	ST	C				p						
	Glochidion glomerulatum	0.24	9.9	4.7	ND	Red	9.5	0.01	3.4	3.1	D	MT	C	d									
	Glochidion sp. 1	0.04	5.7	4.4	ND	Red	9.0	0.02	4.9	3.4	D	ST	C	d									
	Macaranga denticulata	0.02	3.1	2.4	ND	Black	1.0	0.01	2.4	2.2	D	MT	F	d	x		p			p			
	M. gigantea	0.03	4.0	3.6	ND	Black	1.0	0.02	3.4	2.9	D	TT	C	d			p			p			
	Mallotus paniculatus	0.10	6.0	4.3	ND	Black	2.9	0.01	2.8	2.8	D	MT	C	d			p			p			
	M. philippensis	0.04	4.3	4.2	ND	Black	1.0	0.03	3.9	3.9	D	ST	N										
	SK233	0.32	9.2	8.0	ND	Black	2.9	0.10	6.8	6.4	D	ST	C	x			p						
Flacourtiaceae	*Casearia grewiaefolia* var. *gelonioides*	0.47	15.0	9.8	ND	Red	11.0	0.06	4.5	3.8	D	MT	F	d	x		p						
	C. grewiaefolia var. *grewiaefolia*	2.97	15.9	11.2	ND	Red	21.3	0.02	5.8	3.0	D	ST	C	d	x	d							
	Casearia sp. 1	0.09	10.1	5.0	ND	Red	3.1	0.02	4.2	3.5	D	SH	C	d									
	Casearia sp. 3	0.13	8.2	5.3	ND	Red	1.0	0.10	7.7	5.1	D	ST	C				p						
	SK563	3.25	26.4	16.9	14.2	Yellow	1.0	0.27	11.1	9.5	I	TT	C				p			p			
Flagellariaceae	*Flagellaria indica*	1.07	13.4	10.3	25.6	Red	1.6	0.40	9.6	8.0	I	LI	N										
Gentianaceae	*Fagraea ceilanica*	20.90	43.3	33.0	22.0	Green	96.5	0.07	2.8	1.5	I	EP	N										
Gnetaceae	*Gnetum montanum*	5.48	23.9	19.4	15.8	Red	1.0	2.16	20.7	12.7	I	LI	F		d	d	p	d	d	d, p			
	Gnetum sp. 1	1.61	18.4	12.3	21.2	Red	1.0	0.86	16.0	9.3	I	LI	N										
Grossulariaceae	*Polyosma* sp. 1	10.02	30.1	25.1	15.6	Green	1.0	1.59	20.3	13.3	I	SH	C				p		x	d, n			
Guttiferae	*Garcinia cowa*	68.74	55.3	49.4	12.2	Yellow	5.9	2.31	28.4	14.5	T	MT	F				p	d	d	d		d	d
	G. merguensis	34.25	43.8	39.0	ND	Yellow	7.5	0.90	21.7	11.1	T	ST	C						d	d		d	
Icacinaceae	*Gonocaryum lobbianum*	13.95	46.6	25.6	ND	Black	1.0	11.33	45.8	23.9	I	SH	C				p						
	Platea latifolia	6.60	30.0	19.5	ND	Yellow	1.0	3.63	28.7	16.4	I	MT	F		d	d	p		n	d, n, p			
Irvingaceae	*Irvingia malayana*	23.00	36.6	32.8	ND	Yellow	1.0	5.91	30.2	22.9	I	MT	C				p					x	d
Labiatae	*Callicarpa glandulosa*	0.03	4.4	3.1	6.8	White	4.0	0.03	1.6	1.2	I	LI	C	d									
	Clerodendrun paniculatum	0.23	8.8	5.8	ND	Blue	2.8	0.05	4.6	4.4	I	SH	C	d									
	C. villosum	0.24	8.2	7.0	ND	Black	2.8	0.04	6.0	4.7	I	SH	C	x									
	Gmelina arborea	7.36	25.2	22.9	20.5	Green	1.0	0.53	15.8	8.2	I	ST	C				p			x			
	Premna sp. 1	0.20	7.2	6.8	ND	Black	1.0	0.05	5.2	4.8	I	LI	C	x	x				x	x			

Family	Species	FW	FL	FD	SU	CO	NO	SW	SL	SD	FT	LF	OB	Bu	Pi	Ho	Sq	Ci	Gi	Ma	Be	De	El
Lauraceae	*Actinodaphne* sp. 1	0.60	10.9	9.3	ND	Red	1.0	0.34	9.6	7.1	I	MT	N										
	Beilschmiedia balansae	5.71	28.0	18.2	ND	Black	1.0	3.23	25.4	14.5	I	MT	F		d	d	p		d, n	d, n		x	
	B. maingayi	6.68	35.1	17.8	ND	Black	1.0	3.48	32.2	13.9	I	MT	F		d	d	p		d, n	d, n		x	
	B. villosa	4.01	28.9	15.2	ND	Black	1.0	2.00	24.4	11.7	I	MT	F		d	d	p		d, n	d, n		x	
	Cinnamomum glaucescens	4.33	21.8	18.6	ND	Black	1.0	0.73	13.5	10.2	I	TT	F		d	d	p		d, n	d, n			
	C. iners	0.47	11.5	8.3	ND	Black	1.0	0.20	9.8	6.1	I	ST	C	d	x								
	C. subavenium	1.07	16.7	10.5	ND	Black	1.0	0.49	14.2	8.1	I	MT	F	d	d	d	n, p		d	d, n	d	x	
	Cryptocarya impressa	1.01	14.0	11.4	ND	Black	1.0	0.81	13.1	10.6	I	MT	F	d	d	d	n, p		d	d			
	C. kurzii	0.70	15.1	9.4	ND	Black	1.0	0.55	14.7	8.5	I	MT	C	d	x	d	n, p		d	d			
	Litsea glutinosa	0.35	9.1	8.2	ND	Black	1.0	0.13	7.2	5.4	I	MT	F	d	d	d	n, p			d			
	L. verticillata	0.41	10.7	8.5	ND	Black	1.0	0.20	8.9	6.6	I	ST	N										
	Neolitsea cf. *latifolia*	4.22	21.3	19.6	ND	Black	1.0	0.84	14.7	10.7	I	TT	F		d	d	p		d	d	d		
	Neolitsea sp. 2	0.57	10.1	9.5	ND	Red	1.0	0.29	8.4	7.8	I	ST	N										
	Phoebe cathia	2.18	17.7	14.7	ND	Black	1.0	1.08	14.8	10.7	I	TT	F	d	d	d	n, p		d	d, n	d	x	
	P. lanceolata	0.32	11.6	7.2	ND	Black	1.0	0.17	10.0	5.7	I	ST	C										
Leeaceae	*Leea indica*	0.67	11.2	8.5	11.6	Purple	5.1	0.03	4.5	3.7	I	SH	C	d	x					d, p			
Loranthaceae	*Helixanthera parasitica*	0.06	5.6	4.5	14.6	Red	1.0	0.01	3.0	2.2	I	EP	C	d	x			d	d	d			
	Macrosolen cochinchinensis	0.16	6.8	6.5	17.1	Black	1.0	0.04	4.4	3.7	I	EP	C	d	x					d			
Magnoliaceae	*Michelia baillonii*	0.25	9.8	7.4	ND	Red	1.0	0.07	7.6	5.8	D	TT	F	d	d	d	p			p			
	M. champaca	0.18	7.7	6.7	ND	Pink	1.0	0.08	7.0	5.5	D	MT	C	d			p						
Melastomaceae	*Diplectria divaricata*	0.36	11.9	8.1	7.3	Purple	>100	<0.01	<0.1	<0.1	I	SH	C	x					d				
	Medinilla sp. 1	0.29	9.1	7.6	ND	Purple	>100	<0.01	<0.1	<0.1	I	SH	C	x									
	Melastoma malabathricum	0.25	12.4	6.7	8.6	Purple	>100	<.01	0.7	0.5	I	SH	C	x									
	Memecylon sp. 1	1.35	13.6	12.3	25.3	Purple	1.0	0.22	7.9	6.2	I	SH	C	d									
	Memecylon sp. 2	1.50	12.6	11.0	13.3	Purple	1.0	0.21	7.4	6.3	I	SH	C	d	x								
	Memecylon sp. 3	0.40	9.3	9.0	17.8	Purple	1.0	0.10	5.7	5.4	I	SH	C	d	x	d				d, p			
Meliaceae	*Aglaia lawii*	2.65	25.2	15.7	ND	Red	1.0	1.89	21.5	13.3	D	MT	F	x	d	d	n, p						
	A. spectabilis	9.75	39.6	22.9	ND	Red	1.0	7.21	31.4	20.3	D	TT	F		x	d	n, p						
	Aphanamixis polystachya	3.58	20.2	13.0	ND	Red	1.0	0.89	14.5	11.0	D	ST	F		x	d	n, p						
	Chisocheton sp. 1	7.00	27.2	18.1	ND	Red	1.0	5.38	27.1	13.9	D	MT	N										
	Dysoxylum cyrtobotryum	1.78	18.7	15.3	ND	Black	1.1	1.21	15.5	13.0	D	MT	F		x	d	n, p						
	D. cf. *densiflorum*	2.51	18.4	17.5	ND	Orange	1.0	1.44	16.1	15.6	D	ST	C			d	n, p						
	Melia azedarach	2.81	19.1	15.1	ND	Yellow	1.0	1.30	15.3	11.2	I	TT	N										
	Sandoricum koetjape	91.37	58.3	49.6	10.4	Yellow	4.6	2.74	25.5	15.1	T	MT	F				p	x	d	d		x	d
	Walsura robusta	0.92	13.4	11.2	9.3	Orange	1.1	0.35	10.8	8.8	T	ST	C						d	d			
	W. trichostemon	2.62	17.2	16.1	20.6	Yellow	1.1	0.70	11.5	10.3	T	MT	C						d	d			
Menispermaceae	*Anamirta cocculs*	0.84	12.3	11.2	ND	Purple	1.0	0.35	10.2	8.5	I	LI	C			d				x			
	Cyclea atjehensis	0.21	7.6	7.5	13.3	Pink	1.0	0.05	5.5	5.3	I	LI	N										
	Diploclisia glaucescens	0.87	20.0	11.1	ND	Orange	1.0	0.40	16.8	9.8	I	LI	F	d	x		n, p	d	d	d, n		d	
	Hypserpa nitida	0.45	9.4	9.3	15.4	Purple	1.0	0.19	7.7	7.4	I	LI	C	d		d							
	Stephania japonica	0.15	6.9	6.6	9.2	Red	1.0	0.03	5.6	5.0	I	LI	C							x			

Family	Species	FW	FL	FD	SU	CO	NO	SW	SL	SD	FT	LF	OB	Bu	Pi	Ho	Sq	Ci	Gi	Ma	Be	De	El
Moraceae	*Antiaris toxicaria*	5.75	26.2	21.7	ND	Red	1.0	1.93	17.7	14.9	I	TT	F		d	d	n	d	d, n	d, n		x	
	Artocarpus gomezianus	274.50	87.4	84.3	16.0	Yellow	6.0	0.70	13.2	10.9	I	MT	C						d	d, n		x	
	A. lakoocha	21.67	33.6	31.9	10.7	Yellow	8.5	0.29	9.5	7.8	I	MT	C						d	d, n		x	
	Ficus altissima	3.53	21.5	18.3	9.9	Red	18.6	0.10	1.9	1.3	I	TT	F	d	x	d	n	d	d, n	d, n	d	x	x
	F. annulata	12.00	29.4	28.3	9.2	Yellow	49.3	<0.01	6.6	1.2	I	TT	C	d	x	d	n	d	d, n	d, n		x	
	F. benjamina	3.19	18.8	18.1	13.1	Purple	>100	<0.01	1.0	1.0	I	TT	F	d	x	d	n	d	d, n	d, n	d		
	F. hirta var. *hirta*	0.65	12.7	10.0	9.0	Red	92.5	0.02	1.2	0.8	I	SH	C	d						d			
	F. hirta var. *roxburghii*	89.50	62.2	61.8	ND	Brown	>100	<0.01	1.0	1.0	I	ST	N										
	F. hispida	3.42	21.9	19.0	7.0	Yellow	>100	<0.01	1.2	0.8	I	SH	C				x						
	F. racemosa	9.97	32.9	25.7	3.1	Red	>100	<0.01	1.0	1.0	I	MT	C				n					x	
	F. subcordata	2.75	21.4	16.7	6.3	Purple	>100	<0.01	1.0	1.0	I	TT	F	d	x	d	n	d	d, n	d, n	d	x	x
	F. superba var. *japonica*	0.88	12.7	12.1	10.0	Purple	>100	<0.01	1.0	1.0	I	TT	F	d	x	d	n	x	x	x			
	F. tinctoria ssp. *gibbosa*	0.54	10.9	10.3	16.3	Orange	>100	<0.01	1.0	1.0	I	LI	N										
	Ficus sp. I no. 138	1.93	16.7	15.9	7.6	Yellow	>100	<0.01	1.0	1.0	I	TT	F	d	x	d	n	x	x	x			
	Ficus sp. II no. 460	3.54	20.6	20.6	4.5	Red	>100	<0.01	1.0	1.0	I	LI	C	d	x	d	x		x	x			
	Ficus sp. Liana	39.00	46.0	37.0	5.0	Purple	>100	<0.01	2.2	0.9	I	LI	C	d		d	n		d	d			
	Ficus sp. PH3	1.32	14.6	13.9	ND	Red	>100	<0.01	1.0	1.0	I	MT	C	d	x	d	n		d, n	d, n			
	Ficus sp. SK383	12.57	33.8	29.9	6.5	Orange	>100	<0.01	1.0	1.0	I	MT	C	d	x	d	n		d, n	d, n			
	Maclura cf. *cochinchinensis*	5.07	22.2	21.1	16.0	Yellow	24.3	0.03	4.7	4.0	I	LI	C	d	x	d	n	d	d	d			
	Morus alba	0.18	10.4	6.9	11.9	Black	9.0	0.12	1.7	1.6	I	SH	N										
	Trophis sp. 1	0.55	11.0	8.8	17.6	Yellow	4.4	0.01	2.6	2.2	I	LI	C	d	x	d	x	d	d	d			
Myricaceae	*Horsfieldia glabra*	5.00	25.9	19.2	5.1	Orange	1.0	3.23	21.2	16.7	D	MT	F		d	d	p						
	Knema elegans	4.71	25.7	17.2	10.1	Red	1.0	2.55	21.3	13.9	D	MT	F		d	d	p	d	d				
Myrsinaceae	*Ardisia colorata*	0.21	7.7	6.8	8.9	Purple	1.0	0.07	4.9	4.9	I	SH	C	d						d, p			
	A. nervosa	0.16	7.5	5.6	8.0	Black	1.0	0.05	4.7	3.9	I	SH	C	d						x			
	Ardisia sp. SK637	0.40	9.9	8.5	ND	Purple	1.0	0.17	6.8	6.3	I	SH	C	d									
	Labisia pumila	0.20	8.2	6.5	ND	Red	1.0	0.05	4.3	4.0	I	SH	C							x			
	Maesa ramentacea	0.05	4.3	4.2	ND	White	1.0	0.01	2.2	2.1	I	SH	C	d									
Myrtaceae	*Decaspermum parviflorum*	0.21	7.5	6.7	15.5	Purple	4.8	0.01	4.1	3.0	I	SH	C	d	x					d, p			
	Psidium guajava	115.50	63.7	56.8	ND	Green	>100	0.01	3.5	3.0	I	SH	C				n, p			d, p			
	Syzygium cf. *albiflorum*	7.07	25.6	22.4	ND	Green	1.0	3.12	18.7	16.9	I	MT	C				p						
	S. cumini	0.44	9.8	8.1	18.9	Purple	1.0	0.13	6.3	5.4	I	TT	F	d	x	d	p	d	d	d	d	x	
	S. siamensis	18.83	35.5	30.0	ND	Green	1.3	10.19	27.7	24.4	I	ST	N										
	Syzygium sp. 1	1.07	16.9	10.7	14.5	Black	1.0	0.21	10.8	5.5	I	MT	N										
	Syzygium sp. SK441	1.13	15.1	13.1	9.3	White	1.0	0.21	7.6	6.4	I	MT	C	d	x								
Olacaceae	*Schoepfia fragrans*	0.48	10.7	8.9	ND	Green	1.0	0.26	9.8	7.0	I	SH	N										
Oleaceae	*Chionanthus ramiflorus*	3.16	23.0	15.3	26.1	Black	1.0	1.07	19.7	9.8	I	ST	F			d	x		n				
	Jasminum elongatum	0.47	10.3	8.5	18.0	Black	1.0	0.20	9.2	5.9	I	LI	C	x		d		d					
	Ligustrum confusum	0.25	8.1	7.5	ND	Black	1.4	0.07	7.2	5.0	I	SH	C	d						x			
Palmae	*Areca triandra*	4.60	27.1	16.9	6.1	Red	1.0	1.99	27.2	11.0	I	SH	C			d	p	d		n		x	
	Calamus sp. 1	2.47	18.0	15.5	ND	Brown	1.0	0.32	11.1	9.3	T	LI	C					d		d, p			
	Livistona speciosa	9.37	26.6	23.9	ND	Purple	1.0	4.63	21.8	18.9	I	MT	F		x	d				p			
Piperaceae	*Piper ribesioides*	0.14	6.6	5.4	22.5	Orange	1.0	0.04	3.9	3.8	I	EP	C	d		d				p			
	Piper sp. 1	0.13	5.9	5.9	9.0	Orange	1.0	0.03	3.3	3.2	I	HE	N										
Podocarpaceae	*Podocarpus neriifolius*	1.63	21.3	11.8	15.6	Red	1.1	0.61	11.0	9.6	I	MT	F		d	d	n	n	n	n			
Proteaceae	*Helicia formosana* var. *oblanceolata*	31.80	45.6	36.5	ND	Green	1.0	21.00	37.9	27.2	I	MT	C				p						
Rhamnaceae	*Zizyphus oenoplia*	0.20	8.5	6.9	ND	Black	1.0	0.08	7.1	5.2	I	SH	C	d	x								
	Zizyphus sp. 1	2.34	17.3	16.3	20.6	Orange	1.0	0.65	15.0	10.2	T	LI	C					x	d	d			

Family	Species	FW	FL	FD	SU	CO	NO	SW	SL	SD	FT	LF	OB	Bu	Pi	Ho	Sq	Ci	Gi	Ma	Be	De	El
Rosaceae	*Prunus arborea* var. *montana*	0.34	8.6	8.5	ND	Black	1.0	0.19	7.3	7.0	I	ST	C	d	x			d	d				
	Prunus sp. 1	2.92	21.5	16.9	18.0	Yellow	1.0	1.54	17.3	13.6	I	MT	C			d							
	Rubus alceaefolius	0.35	10.0	7.1	6.7	Red	14.1	0.00	2.3	1.8	I	LI	C	x				d		d			
	R. kerrii	0.61	12.4	8.9	7.4	Red	42.1	0.00	2.2	1.5	I	LI	C	x									
Rubiceae	*Anthocephalus chinensis*	76.31	55.9	50.8	ND	Orange	>100	<0.01	<0.1	<0.1	I	TT	C				n, p	d	d, n	d, n		x	
	Canthium coffieoides	11.72	28.0	27.8	11.5	Yellow	1.5	0.61	15.8	8.5	I	SH	C							x		x	
	C. glabrum	4.62	20.0	19.2	ND	Yellow	3.0	0.31	16.4	8.4	I	MT	C			d			d				
	Chassalia sp. 1	0.48	9.7	9.0	7.0	Black	1.8	0.05	6.9	5.3	I	SH	N										
	Geophila sp. 1	0.53	9.6	9.1	6.3	Red	2.0	0.02	4.3	3.7	I	HE	N										
	Ixora ebarbata	0.21	8.1	7.3	ND	Red	1.0	0.08	6.0	5.2	I	SH	N										
	Lasianthus fordii	0.35	10.2	8.9	4.4	Blue	4.9	0.01	3.6	2.1	I	SH	C	d						p			
	L. hirsutus	0.67	21.4	13.3	3.0	Blue	5.0	0.01	5.0	2.5	I	SH	N										
	L. hookeri	0.17	7.6	7.1	6.9	Blue	5.4	0.00	3.7	1.8	I	SH	N										
	L. kurzii	0.38	11.2	9.2	5.3	White	5.7	0.01	3.5	1.9	I	SH	C	d						p			
	L. cf. *lancifolius*	0.62	11.6	11.1	ND	Blue	4.8	0.01	4.0	2.6	I	SH	N										
	L. cf. *longifolius*	0.56	11.5	9.5	6.3	Blue	3.0	0.04	7.7	3.3	I	SH	N										
	L. verticillatus	0.36	11.8	9.0	6.7	Black	4.3	0.01	4.4	2.4	I	SH	C	d						p			
	L. wallichii	0.45	12.0	9.9	ND	Blue	5.0	0.01	4.0	2.2	I	SH	N										
	Lasianthus sp. SBF	0.26	9.6	8.8	ND	Black	3.9	0.01	4.4	2.9	I	SH	C	d						p			
	Lasianthus sp. SK119	0.28	9.2	8.0	ND	Orange	4.9	0.01	4.0	1.9	I	SH	C	d						p			
	Lasianthus sp. SK150	0.15	7.8	7.4	ND	Blue	2.4	0.01	4.3	2.9	I	SH	C	d						p			
	Lasianthus sp. SK531	0.84	12.9	10.8	4.1	Blue	1.3	0.03	6.4	3.2	I	SH	C	d						p			
	Mitragyna sp. 1	3.98	21.0	18.2	9.3	Brown	>100	<0.01	1.2	0.8	I	MT	C				p		d, p	d, p		x	
	Morinda sp. SK042	2.20	17.3	13.2	23.0	Orange	16.7	0.08	6.1	4.4	I	LI	C	x	x	d				x			
	Mussaenda sanderiana	1.01	15.8	12.1	24.7	Black	>100	<0.01	0.8	0.6	I	LI	C	x									
	Prismatomeris sessiliflora	0.54	11.5	9.8	ND	Black	1.0	0.09	7.8	4.7	I	SH	C	d						p			
	Psychotria adenophylla	0.15	6.8	6.5	ND	Black	1.7	0.05	5.1	4.7	I	SH	N										
	P. ophioxyloides	0.36	8.8	8.2	ND	Black	2.0	0.05	5.5	4.9	I	SH	N										
	P. rubra	0.26	7.6	7.1	9.2	Red	2.0	0.05	5.4	4.9	I	SH	C	x									
	Randia cochinchinensis	0.30	10.4	7.3	ND	Black	46.7	0.00	1.7	1.1	I	MT	N										
Rutaceae	*Acronychia pedunculata*	0.13	6.4	5.9	ND	White	1.0	0.02	4.0	3.2	I	SH	C				p	d					
	Citrus sp. 1	148.00	70.1	61.2	7.4	Yellow	22.9	0.18	12.4	6.9	T	SH	C									x	x
	Clausena excavata	0.47	10.9	8.3	ND	Pink	1.1	0.14	8.5	5.8	I	SH	C	d						p			
	C. harmandiana	0.72	10.5	9.5	17.0	Pink	1.1	0.19	6.7	6.6	I	SH	C	d						p			
	Evodia meliaefolia	0.02	3.4	3.2	ND	Black	1.1	0.01	2.7	2.4	D	MT	C	d	x								
	Glycosmis craibii	0.48	9.8	7.9	13.8	Pink	1.1	0.16	6.9	5.4	I	SH	C	d						x			
	G. pentaphylla	0.51	10.3	7.9	11.6	Pink	1.0	0.21	7.6	6.2	I	SH	N										
	Glycosmis sp. 1	0.55	10.5	8.6	8.9	Pink	1.1	0.21	7.5	6.3	I	SH	N										
	Melicope pteleifolia	0.05	6.0	4.8	ND	Black	1.3	0.02	3.7	3.0	D	SH	N										
	Micromelum minutum	0.42	12.0	7.8	19.5	Red	1.5	0.12	9.7	5.1	I	SH	C	d									
	Toddalia asiatica	0.55	10.0	9.8	17.1	Yellow	2.7	0.02	4.7	3.1	T	LI	C					d	d	d			
Sabiaceae	*Sabia limoniacea*	1.00	13.6	12.6	10.3	Blue	1.0	0.21	11.3	9.6	I	LI	C				p	d					
Sapindaceae	*Allophylus cobbe*	0.57	10.1	9.8	ND	Red	1.0	0.20	8.4	7.2	I	SH	N										
	Dimocarpus longan	2.03	15.5	15.1	9.2	Brown	1.0	0.91	12.1	11.4	T	MT	C				p	d	d, n	d, n			
	Harpullia arborea	2.59	21.6	14.5	ND	Black	1.0	2.38	20.2	14.2	D	ST	N										
	Lepisanthes rubiginosa	1.16	17.3	10.3	25.3	Black	1.0	0.43	15.2	6.9	I	SH	C	x									
	Mischocarpus pentapetalus	0.55	20.7	8.9	ND	Red	1.0	0.41	9.5	8.3	D	ST	C	d				x				x	
	Nephelium melliferum	18.18	33.9	26.4	13.0	Red	1.0	2.01	22.4	12.7	T	MT	F				n, p		d	d, n		x	
	Sapindus rarak	3.80	23.4	21.5	ND	Black	1.0	1.95	15.7	15.3	I	TT	N										

Family	Species	FW	FL	FD	SU	CO	NO	SW	SL	SD	FT	LF	OB	Bu	Pi	Ho	Sq	Ci	Gi	Ma	Be	De	El
Sapotaceae	*Chrysophyllum lanceolatum*	8.50	28.1	21.2	ND	Yellow	5.0	0.51	14.2	10.4	I	TT	C				p	x	d, n	d, n		x	
	Palaquium garrettii	14.17	26.7	26.0	13.0	Yellow	3.8	0.57	18.8	10.1	I	TT	C				p	x	d, n	d, n	x	x	
Simaroubaceae	*Picrasma javanica*	0.69	11.3	10.6	ND	Blue	1.4	0.40	10.4	9.1	D	ST	N										
Smilacee	*Smilax glabra*	0.18	6.9	6.8	ND	Red	1.8	0.02	3.5	3.4	I	LI	C	x						d, p			
Solaanacee	*Solanum* sp. 1	0.72	11.7	9.4	ND	Red	>100	<0.01	1.9	1.6	I	HE	C	x									
	Solanum sp. 2	10.62	26.8	26.5	ND	Yellow	>100	<0.01	2.4	2.1	I	SH	N										
Staphyleaceae	*Turpinia cochinchinensis*	0.30	8.4	7.2	ND	Black	1.7	0.04	4.6	4.6	I	ST	C	d									
Sterculaceae	*Sterculia balanghas*	1.47	17.2	12.0	ND	Black	1.0	1.17	16.3	10.4	D	MT	F			d	p						
	S. pexa	0.41	12.9	8.1	ND	Black	1.0	0.34	11.9	7.4	D	MT	C			d	p						
Symplocosiaceae	*Symplocos cochinchinensis* ssp. *laurina*	0.30	7.7	7.6	12.3	Black	1.0	0.08	5.3	5.2	I	MT	F	d	x	d	x	d	d	d			
Theaceae	*Eurya acuminata* var. *acuminata*	0.19	6.9	6.5	15.2	Black	3.8	<0.01	2.1	1.6	I	ST	C	x									
	Sladenia celastrifolia	0.16	9.9	6.0	ND	Blue	1.0	0.06	8.0	4.2	I	ST	C	d									
	Ternstroemia wallichiana	1.33	19.1	14.3	ND	Red	1.0	1.11	18.6	13.5	D	MT	C			d							
Tiliaceae	*Muntingia calabura*	1.34	13.4	12.2	8.0	Red	>100	<0.01	0.5	0.3	I	SH	F	d		d	p	d		d	d		
Ulmaceae	*Celtis tetrandra*	0.37	9.2	7.8	ND	Orange	1.0	0.11	6.5	4.8	I	TT	C	d			p						
	Gironniera nervosa	0.21	8.8	7.7	7.2	Orange	1.1	0.03	5.3	4.8	I	TT	F	d			p		x	p			
	Trema orientalis	0.06	4.6	4.6	10.1	Black	1.0	0.01	2.6	2.5	I	MT	C	d									
Vitacee	*Ampelocissus* cf. *martinii*	0.84	14.7	9.8	14.3	Black	1.0	0.20	10.7	6.0	I	LI	C			d		x	d	d, n			
	Ampelopsis cantoniensis	0.25	7.7	7.1	13.7	Black	2.0	0.03	5.2	4.5	I	LI	C	d									
	Cayratia sp. 1	0.46	9.6	8.4	10.0	White	3.9	0.03	5.5	4.2	I	LI	C	x									
	Cissus convolvulacea	1.36	13.9	13.6	9.3	Black	1.0	0.35	10.7	8.7	I	LI	C	d					d	d, n			
	C. javanica	0.38	8.6	7.4	9.6	Purple	1.1	0.13	7.1	5.2	I	LI	N										
	Tetrastigma cruciatum	0.80	11.9	10.2	ND	Red	1.0	0.34	9.9	7.8	I	LI	C	d					d	d, n			
	Tetrastigma sp. 1	0.88	12.0	11.1	25.0	Orange	1.0	0.29	7.9	7.5	I	LI	C	x		d		d	d				
	Tetrastigma sp. 2	0.80	10.9	10.2	ND	White	1.5	0.14	7.8	6.2	I	LI	N										
	Vitis sp. 1	0.19	6.8	6.7	ND	Purple	1.0	0.04	5.1	3.7	I	LI	N										
Zingiberaceae	*Alpinia oxymitra*	4.70	41.9	15.7	ND	Orange	17.9	0.08	6.6	5.4	T	HE	C							d			
	Hedychium speciosum	7.41	26.2	24.6	ND	Orange	42.6	0.07	5.7	4.4	T	HE	C							d			
Miscellaneous	*Ficus* like	25.30	67.0	33.2	ND	Yellow	1.0	3.51	22.3	17.5	I	ST	N										
	Sd.Ref. no. 131	2.92	19.4	15.9	14.2	Yellow	1.3	0.42	11.1	9.1	T	LI	C				p	d	d	d			
	SK690	2.15	18.7	17.6	ND	Orange	2.0	0.28	15.0	14.2	T	ST	N										
	SK707	0.70	12.6	9.3	ND	Yellow	1.0	0.32	11.0	7.1	I	SH	N										

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