



Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators

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Abstract

Aim This study considered the colonization of disturbed island ecosystems by *Ficus* species (Moraceae). Specifically, we examined the extent of colonization (compared with source areas), differential roles of seed dispersing birds and mammals, and the *Ficus* fruit characters influencing mode of colonization.

Location Research was conducted on Long Island (5°20'S; 147°10'E), a volcanic island 55 km from Papua New Guinea, which erupted catastrophically in c. 1645 with probable extirpation of all life. Renewed volcanic activity in the early 1950s produced a series of temporary islands in the volcano's caldera lake. One island, Motmot, present since 1968 has persisted.

Methods Long Island and Motmot were surveyed over 15 days for *Ficus* species and their vertebrate dispersers and pollinating wasps. The *Ficus* community was compared with that of mainland sources areas and *Ficus* species present were characterised according to their figs' size, colour, crop size and height. Observations of frugivory and literature records were used to determine *Ficus* dispersal guild membership.

Results At least 31 *Ficus* species have colonized Long Island since its eruption. Evidence of pollinator wasp colonisation was found for all sixteen *Ficus* species observed fruiting. Thirty-six vertebrate species occurring on Long Island are identified as potential seed dispersers. Of these, fruit bats and pigeons are likely to have been instrumental in the island's early colonization with subsequent spread being facilitated by these frugivores as well as a number of smaller birds, and an introduced cuscus. Comparisons of fruit characters and frugivore attraction between *Ficus* species reveal two broad dispersal guilds. Members of the first guild produce relatively large, green figs in the lower strata of the forest and attract fruit bats. The second guild includes species that attract both birds and fruit bats with generally smaller, red figs produced throughout the vertical structure of the forest. Eight *Ficus* species have colonized Motmot, a 31-year-old emergent island in the volcano's crater lake. However, only one frugivore species was recorded alive on the island. Fig seeds are likely to have arrived during rare over-flights or roosting visits by frugivores, or in the bodies of prey brought to Motmot by raptors. We found no evidence of pollinator presence on Motmot. Most *Ficus* individuals on Motmot remain immature and the figs of the only three individuals observed with crops had not been pollinated.

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Main conclusions Their numerical abundance and frequency of fruiting make figs an important resource in regenerating ecosystems. *Ficus* species differ in their ability to colonise degraded habitats because of differences in the design and presentation of their figs. Fruit bats are likely to be of special importance early in succession. Once the *Ficus* species on Motmot start to produce fruit regularly we can expect a rapid increase in the numbers of fleshy-fruited plant species colonising the island.

Keywords

Figs, fruit syndromes, pollination, seed dispersal guilds, succession.

INTRODUCTION

Events that sterilize areas of tropical forests allow ecologists the opportunity to gain insights into the processes of colonization, succession and assembly of these diverse biological communities. Such knowledge is of increasing value given the extent of anthropogenic disturbance to these habitats in modern times. Natural biological extirpation events vary in scale from small fires and landslides to catastrophic volcanic eruptions. Because the former may not extinguish all life, leaving, for example, seed banks or invertebrate refugia, it is the sterilizing power of the latter, forcing the colonization to begin completely anew, that is of most interest.

Long Island (5°20'S; 147°10'E) lies 55 km off the coast of Madang province, Papua New Guinea (Fig. 1). Volcanic in origin, much of it was destroyed in a catastrophic eruption that occurred in about 1645 (Zielinski *et al.*, 1994). The volcanic activity formed a caldera 13 km in diameter where the main volcano summit had been. The eruption's pyroclastic flows and mud slides left deposits up to 30 m thick whilst layers of compacted ash up to 4 m thick covered the rest of the island (Pain *et al.*, 1981). Almost certainly Long Island's macrobiota was eradicated; the upper layers of deposits contained no plant remains (Pain *et al.*, 1981). Long Island's present land biota has, therefore, arrived since the eruption and its terrestrial ecosystem is no more than about 350 years old.

A deep freshwater lake (Lake Wisdom) formed in Long Island's caldera and renewed volcanic activity in the early 1950s built up deposits that broke the surface as a series of temporary islands in the southern part of the lake. One island, Motmot, which had emerged by 1968, persisted. Between 1969 and 1973 the island grew through further volcanic activity which included lava emissions that ensured its permanence. Motmot is now some 200–300 m in diameter and about 50 m high. It is very sparsely vegetated, its infant terrestrial ecosystem being no more than three decades old. Motmot's biota is composed of colonists that have travelled at least 4 km, presumably mostly from the ring of Long Island which surrounds the lake.

Lake Wisdom's surface is 190 m above sea level and the caldera cliff walls rise some 200–300 m above this. There

are two mountains on the caldera plateau, Mount Réaumur (1280 m) in the north and Cerisy Peak (1112 m) in the south. The plateau is now, as it was in 1925 (Evans, 1939), covered with an open forest with very little undergrowth and a scattering of large older trees. Cloud forest occurs above about 750 m on the two mountains. After Long Island's eruption people resettled in the island and a total of about 1000 people now live in five small coastal villages. In the coastal lowlands savanna woodland is mixed with rain forest and areas of secondary growth, and large areas have been cleared for gardens and coconut plantations (Ball & Hughes, 1982).

Long Island has a tropical moist climate. Mean annual rainfall has been estimated from records maintained at Umboi Island to the east and on the New Guinea coast, and comments made by administrative officers as about 2800 mm (Ball & Glucksman, 1978). Rainfall is greater on the two mountains than in the lowland forests. Seasonal variation appears to be greater than on the mainland. The dry season is longer and drier, extending from April to November. The low rainfall combined with 'over-drained' soils results in fairly frequent droughts in prolonged dry seasons, when foliage may wither and leaf fall may occur (Ball & Hughes, 1982).

Opportunities to study the colonization of tropical islands sterilized by volcanic activity are rare. The best documented of such colonization processes in the tropics is that following the eruption of Krakatau Island (Indonesia) in 1883, and subsequent emergence of Anak Krakatau in 1930 (Thornton, 1996). The importance of *Ficus* species (Moraceae), and their vertebrate seed dispersers, in the colonization of the Krakatau Islands has been described by Whittaker & Jones (1994) and Thornton *et al.* (1996). It is interesting, therefore, to see if *Ficus* species play a similar role in the regenerative process at other sites in the tropics. During 15 days on Long Island and Motmot we investigated the colonization of these islands by *Ficus* species and their associated pollinators and seed dispersers.

With *c.* 750 species exhibiting a variety of growth forms that include shrubs, trees, climbers, epiphytes and hemi-epiphytic stranglers, *Ficus* is arguably the world's most diverse woody plant genus (Corner, 1988; Berg, 1990). The characteristic *Ficus* inflorescence (the fig) is remarkably uniform in structure but differences occur in the way that

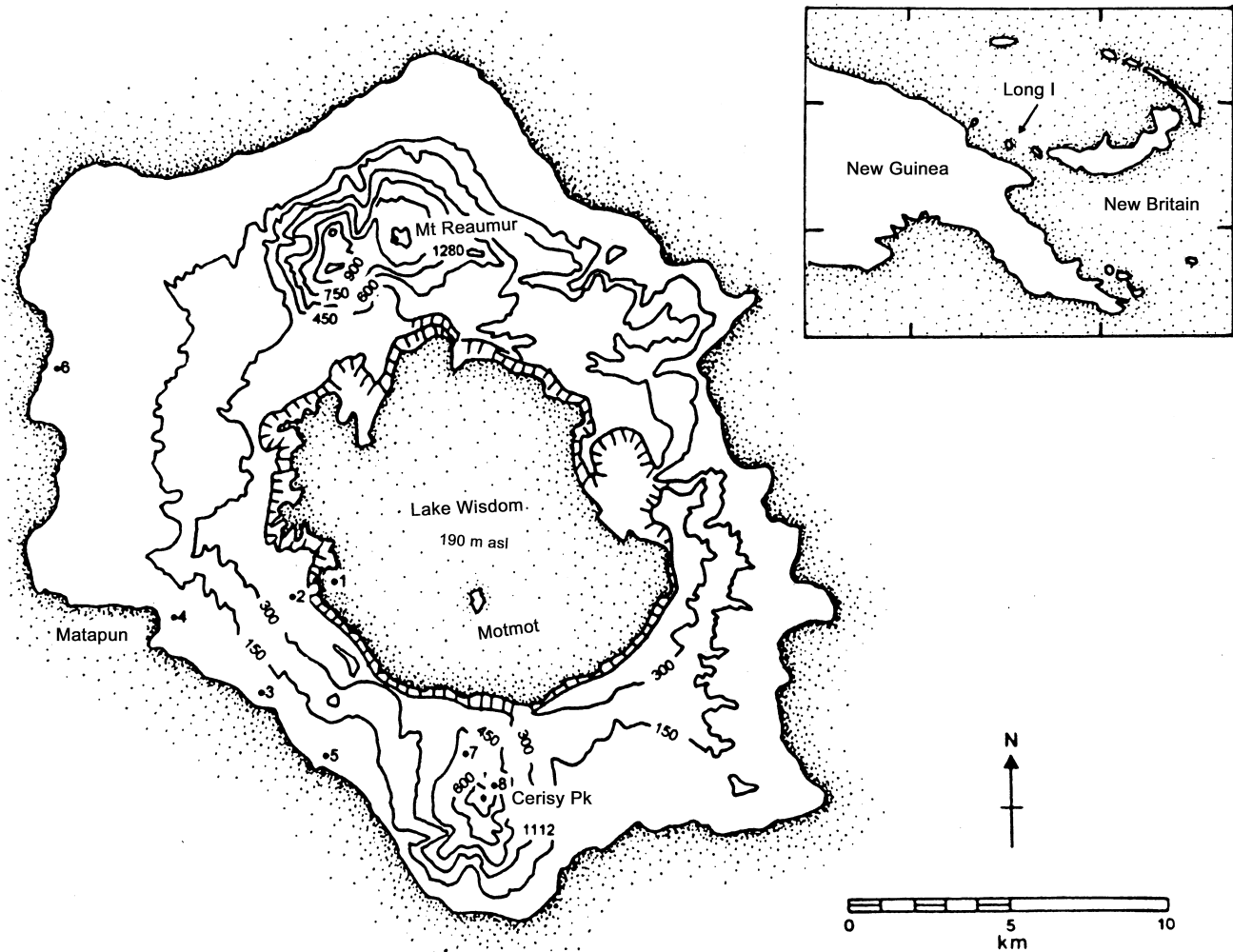


Figure 1 Long Island and Motmot. Sampling sites are numbered 1–8. 1 = main camp (short stature forest along the shore of Lake Wisdom, 200 m a.s.l.), 2 = crater rim (400 m a.s.l.), 3 = disturbed coastal habitat, 4 = cultivated land around Matapun village, 5 = small stream, 6 = dry river bed, 7 = Peak (200–600 m), 8 = Cerisy Peak (600–890 m). Redrawn from Specht *et al.* (1982).

figs are packaged and presented. Crops range from tens to millions of red, green, brown or black figs which can be geocarpic (on ground level runners), cauliflorous (growing directly from the stem or trunk) or produced in the leaf axils (Corner, 1988). Furthermore, two breeding systems, monoecy and (gyno-)dioecy occur among *Ficus* species. The diversity of *Ficus* is reflected in the fact that virtually all fruit-eating animals in the tropics include figs in their diet (Shanahan *et al.*, 2001).

The pools of potential colonists to Long Island are in New Guinea and New Britain (Fig. 1). Over 170 *Ficus* species are known from these islands (Corner, 1965), with New Guinea's *Ficus* flora being one of the world's most diverse. G. Weiblen (unpublished) has produced a list of fifty-five *Ficus* species of Madang Province, Papua New Guinea. Given its similar latitude and proximity to Madang, members of this subset of the New Guinea *Ficus* flora would be those most likely to have colonized Long Island. Potential

dispersers for *Ficus* in our study area include birds, fruit bats, the introduced Grey Cuscus [*Phalanger orientalis* (Pallas)] and feral pigs (Ball & Hughes, 1982).

In contrast to the relatively diffuse nature of relationships between fig trees and dispersers each *Ficus* species has a specific agaonid wasp (Hymenoptera; Agaonidae) pollinator (Wiebes, 1979; though see Michaloud *et al.*, 1996 for exceptions). The production of fig fruit is, therefore, dependent on the presence of pollinator wasps. Conversely, the wasp is only able to reproduce inside a fig (see Galil, 1973; Janzen, 1979). Moreover, the wasp has a very short adult life-span, usually just one day (Kjellberg *et al.*, 1988; RDH unpublished data) and is, therefore, dependent on the presence of receptive figs when it emerges. Thus, in very small fig populations, such as on islands, stochastic extinction of the pollinator wasp is possible (Bronstein *et al.*, 1990; Kameyama *et al.*, 1999). Also, even if the pollinating wasp is present, low pollination levels may be the norm if

colonization rates from mainland populations are low (Compton *et al.*, 1994). Therefore, the stability of the pollinating wasp population and pollination success of a *Ficus* species will ultimately depend on the *Ficus* species' population size, colonization rate (dispersal ability) of pollinator wasps and the frequency of fruiting by *Ficus* individuals (Kameyama *et al.*, 1999). *Ficus* species with different combinations of these characters may, therefore, differ in their ability to colonize islands.

The fig story is one in which disparate taxa are inextricably linked – the population size and characteristics of the fig trees affect pollinator wasp's presence. This in turn affects seed set and fruit ripening, which then influences frugivore attraction and ultimately influences the dispersal of seeds and expansion of a fig species' range. All three groups of organisms must, therefore, be considered if the colonization of a virgin island by these fascinating plants is to be understood.

METHODS

Ad hoc searches for *Ficus* individuals were undertaken, with efforts concentrated in known habitats (forest edge, water-courses, light gaps). Species were identified by reference to Weiblen's (unpublished data) guide to the figs of Madang Province, and Corner's (1965) key. Leaf and, when possible, fig samples were collected and deposited in the Forest Research Institute, Lae, where confirmatory identifications were made by the institute staff. Sampling was conducted in eight distinct sites on Long Island (Fig. 1). In contrast to the *ad hoc* sampling employed on Long Island, Motmot was surveyed in its entirety.

The attributes of ripe figs were characterized in the following manner (with only female figs considered for dioecious species). Between ten and forty figs were collected from representative ripe crops, either directly from the plant or as freshly fallen fruit. An index of fig size was calculated as the product of fig length (basal to apical dimension) and the square of the equatorial diameter. Elsewhere, this index has been demonstrated to show a strong, significant correlation with the wet mass of figs and is of use in situations where weighing of figs is not practical (M. Shanahan, unpublished data). Crop size was either counted directly or estimated by counting the number of figs on representative branches and then extrapolating to total numbers. Fig colour and the presence or absence of a noticeable odour were noted. The placement of the figs (cauliflorous or axillary) and whether they were sessile or stalked was recorded and, in the case of the latter, stalk length was measured. Finally, estimations to the nearest metre were made of the maximum and minimum heights above ground level at which figs were presented.

Colonization by pollinating wasps was confirmed by observation of wasps inside figs or by the discovery of seeds or galls in mature figs. Placing immature figs in gauze bags (male figs only in dioecious species) allowed wasps to be collected upon emergence and later identified through reference to Boucek (1988).

Frugivorous vertebrates present on Long Island and Motmot were identified by mist-netting, live-trapping for small terrestrial mammals, and *ad hoc* search sampling (see Cook *et al.*, 2001; Schipper *et al.*, 2001). Fig-eating was confirmed by observing ripe crops and recording the identities of species seen eating figs.

The *Ficus* species recorded on Long Island and Motmot were compared with floras available for the Madang region (G. Weiblen, unpublished data) and New Guinea as a whole (Corner, 1965). Chi-squared tests with Yates' correction were used to compare the relative numbers of monoecious and dioecious fig species and of members of different sections of the genus (Corner, 1965). *Ficus* dispersal guilds were identified by comparing the proportion of New Guinea bird and fruit bat genera known to eat Long Island's figs for which fig-eating records exist for each *Ficus* species on Long Island, using data from this study or the review of Shanahan *et al.* (2001). Canonical discriminant analysis (CDA) was performed to investigate which of the fruit attributes (fruit size, stalk length, crop size and maximum and minimum crop height) were associated with the putative dispersal guilds and whether differences between guilds were significant. CDA provides multivariate axes (canonical variables) for discrimination of groups, clarifying the differences between groups by reducing the number of variables (SAS Institute Inc., 1985; procedure CANDISC). Crop size was log transformed to make it conform to an approximately normal distribution and fruit colour, as a binary variable, was not included in the analysis but its distribution amongst the groups was compared subsequently.

RESULTS

Thirty *Ficus* species were recorded on Long Island with seven of these having also colonized Motmot (Appendix 1). Additionally, *F. cf. caulocarpa* was recorded on Motmot but not observed on Long Island, although for analytical purposes we assume it is present. According to specimens in the Lae herbarium (Harrison *et al.*, 2001), one more *Ficus* species (*Ficus opposita*) was previously recorded on Mount Réaumur. We did not record this species in similar cloud forest on Mount Cerisy and we did not visit Mount Réaumur. Hence, we could not confirm the presence of *F. opposita*. Long Island's *Ficus* species exhibit much of the range of diversity of habit, breeding system and means of fruit production known from the genus. Free-standing trees (especially *F. nodosa*, *F. wassa*, and *F. septica*) were abundant around the main camp and lake shore whilst the hemi-epiphytes (notably *F. virens* and *F. virgata*) were more common in the closed forest of the caldera plateau. Climbing figs, however, were rare on Long Island. Only one individual *F. subulata* was located, despite specific searches for species with this habit.

The *Ficus* species that have succeeded in colonizing Long Island are largely a subset of those known from the Madang area of Papua New Guinea (Corner, 1965; G. Weiblen, unpublished data). The relative numbers of monoecious and dioecious species do not differ significantly from those in the

Madang area (Yates corrected $\chi^2 = 0.689$, d.f. = 1, n.s.) or in New Guinea as a whole (Yates corrected $\chi^2 = 2.97$, d.f. = 1, n.s.). Considering the taxonomy of the colonizing fig species it appears that members of each *Ficus* section are present on Long Island in proportions equivalent to those in the source areas of Madang or New Guinea (Table 1). The only statistically significant difference is that no members of section *Rhizocladus* have colonized in spite of this section accounting for over one-fifth of New Guinea's *Ficus* flora (Yates corrected $\chi^2 = 8.52$, d.f. = 1, $P < 0.005$).

Pollinator presence was confirmed for the sixteen *Ficus* species found fruiting on Long Island, either by collection of wasps or by observation of seed or galls in mature figs. Only one instance of pollinator limitation was observed. A single individual of *F. congesta* var. *chalmersii* found during the ascent of Cerisy Peak had unpollinated figs that were in the process of being aborted.

Fruit characteristics of ripe crops of the sixteen *Ficus* species observed fruiting on Long Island are presented in Appendix 1, along with supplemental data from trees on the mainland and from literature sources. Long Island's figs exhibit great diversity in terms of size (diameter ranged from 5 mm in *F. prasinicarpa* to over 40 mm in *F. sterrocarpa*), placement (cauliflorous or axillary), crop size and vertical placement. In terms of ripe fig colour, two groups of *Ficus* species can be recognized, those producing orange-red-purple figs and those producing yellow-green-brown figs. Odour was found to be an inconsistent trait as it could not be reliably assessed and is not considered further.

Thirty-one years after its appearance in Lake Wisdom, Motmot is now occupied by eight *Ficus* species, of which two are monoecious and six are dioecious (Table 1). Small expected frequencies for Motmot prevent statistical comparison with potential source areas. Despite the relatively large number of *Ficus* species for an island of its size and successional state, one species, *F. wassa*, accounts for almost two-thirds of the individuals (Table 2). Table 2 illustrates the colonization of Motmot by *Ficus* species since its emergence. Ball & Glucksman (1975) and Osborne & Murphy (1989) identified three *Ficus* species that have not been recorded since or from Long Island itself. It is likely that Ball and Glucksman's *F. ?pungens* and Osborne and Murphy's *F. opposita* were misidentified individuals of *F. nodosa*, a species on Motmot with superficially similar leaves. *F. glaberrima*, recorded on Motmot by Osborne & Murphy (1989) was not found in our survey and is not in Weiblen's (unpublished data) fig flora of Madang. We suspect that the record of *F. glaberrima* resulted from a misidentification of either *F. cf. caulocarpa* or *F. benjamina*.

Most fig individuals on Motmot are small and likely to be immature. Three small crops, two of *F. wassa* and one of *F. nodosa*, were observed but the figs were not pollinated. The large free-standing *F. benjamina* individual is the largest plant on Motmot and is of sufficient size to be producing crops of figs numbering in their thousands.

Thirty-six species of potentially or actually fig-eating vertebrates have been recorded on Long Island (Table 3). More detailed coverage of these and other colonists can be found elsewhere (Cook *et al.*, 2001; Schipper *et al.*, 2001).

Table 1 Comparison of *Ficus* breeding systems and taxonomy on Long Island, Motmot and the mainland

	New Guinea*		Madang area†		Long Island		Motmot	
	Species (<i>n</i>)	Total (%)	Species (<i>n</i>)	Total (%)	Species (<i>n</i>)	Total (%)	Species (<i>n</i>)	Total (%)
(a) Breeding system								
<i>Monoecious</i>	38	25.85	17	30.91	12	38.71	2	25
<i>Dioecious</i>	109	74.15	38	69.09	19	61.29	6	75
(b) <i>Ficus</i> section								
<i>Adenosperma</i>	17	11.56	5	9.09	2	6.45	0	0
<i>Neomorphe</i>	4	2.72	3	5.45	2	6.45	1	12.5
<i>Sycidium</i>	28	19.05	14	24.45	9	29.03	4	50
<i>Sycocarpus</i>	23	15.66	12	21.82	7	22.58	1	12.5
<i>Oreosycea</i>	11	7.48	7	12.7	2	6.45	0	0
<i>Conosycea</i>	10	6.8	5	9.09	2	6.45	1	12.5
<i>Malvanthera</i>	9	6.12	3	5.45	4	12.9	0	0
<i>Urostigma</i>	5	3.4	2	3.66	3	9.68	1	12.5
<i>Rhizocladus</i>	32	21.77	4	7.27	0	0	0	0
<i>Kalosycea</i>	2	1.36	0	0	0	0	0	0
<i>Ficus</i>	3	2.04	0	0	0	0	0	0
<i>Sycomor</i>	3	2.04	0	0	0	0	0	0
Total	147	55	31	8				

*Data from Corner (1965); †Data from G. Weiblen (unpublished data).

No significant difference exists in the relative numbers of monoecious and dioecious species between Long and Madang (χ^2 with Yates' correction = 0.689) or New Guinea (χ^2 with Yates' correction = 2.07). Regarding taxonomy, the only significant difference is the lack of *Rhizocladus* species on Long compared with New Guinea (χ^2 with Yates' correction = 8.52, $P < 0.005$). Small expected frequencies for Motmot's *Ficus* species prevent statistical comparison with potential source areas.

<i>Ficus</i> species	Year			
	1971*	1972*	1988†	1999
<i>Ficus pungens</i> Reinw. ex Bl.	?			
<i>F. benjamina</i> L.	?			* (6)
<i>F. virgata</i> Reinw. ex Bl.		?	*	* (1)
<i>F. glaberrima</i> Bl.			*	
<i>F. opposita</i> Miq.			*	
<i>F. wassa</i> Roxb.				* (21)
<i>F. septica</i> Burm. f.				* (1)
<i>F. nodosa</i> Teysm. et Binn.				* (1)
<i>F. cf. caulocarpa</i> Miq.				* (1)
<i>F. copiosa</i> Steud.				* (2)
<i>F. melinocarpa</i> Bl.				* (2)
Total <i>Ficus</i> species present	2	2	3	8

*Ball & Glucksman (1975); †Osborne & Murphy (1989).

On Motmot the only living frugivore recorded was the Melanesian Scrubfowl, *Megapodius freycinet* Gaimard. However, the skull of an *Aplonis* starling was found, indicating that it had either been killed there or brought from Long Island by a raptor. Table 3 indicates which *Ficus* species are eaten by each frugivore species or their congeners, on Long Island or elsewhere. Long Island's *Ficus* species occur in the diets of forty-four genera of volant New Guinea birds and eight genera of New Guinea bats (Shanahan *et al.*, 2001). When the proportions of these genera for which fig consumption is recorded are plotted across fig species it becomes possible to identify three putative dispersal guilds (Figs 2 and 3). The first comprises seven fig species for which very few avian genera are recorded but between one and eight fruit bat genera are recorded (i.e.; arbitrarily <10% of bird genera but >10% of bat genera) and for which we assume dispersal is primarily effected by bats. The second group includes six *Ficus* species for which both avian and fruit bat genera are well represented (>10% of both bird and bat genera recorded). Finally, for eight species only avian frugivores are known, but records for this group are too sparse for conclusions about their overall dispersal strategy to be drawn. Members of the bat-dispersed guild are all dioecious, whilst both monoecious and dioecious species are included in the other two groups.

In order to assess whether these putative dispersal guilds can be separated on the basis of the mode of fruit presentation, CDA was performed using fruit size, stalk length, crop size and maximum and minimum crop height as variables. It was possible to include only the eighteen *Ficus* species for which adequate data had been collected (data from Long Island for sixteen species, and from other localities for the remaining two; Appendix 1). For fourteen of these species identities of frugivores are known (Fig. 3). Overall, there was a highly significant difference between the putative guilds (Wilk's $\lambda = 0.0624$, $P < 0.01$). However, when Mahalanobis distances between guilds were calculated the bat-dispersed guild was significantly different from each of the other two (bat vs. bird and bat, $F = 18.8$, $P < 0.01$; bat vs. bird, $F = 12.7$, $P < 0.01$), but these were not

Table 2 *Ficus* species recorded on Motmot since its appearance in 1968. ? indicates a dubious identification. Numbers in parentheses indicate numbers of individuals recorded in 1999

significantly different from each other (bird and bat vs. bird, $F = 0.04$, $P > 0.05$). On the basis of the fruit characters considered here, the latter two putative guilds should be considered as a single group.

The scattergram of the first (CAN 1) and second (CAN 2) canonical variables illustrates this result clearly with the putative bat-dispersed figs all positioned to the right side of the plot. CAN 1 and CAN 2 accounted for 99.8 and 0.2% of the variance between guilds, respectively. The contributions of each fig character to CAN 1 and CAN 2 are shown in terms of their standardized canonical coefficients in Fig. 3. Thus, the major determinants of guild membership are fig size and crop height. Furthermore, all members of the putative bat guild had green–yellow figs, whilst all of those in the other two putative guilds had orange–red–purple figs.

The four *Ficus* species for which frugivores are not known were classified with the bird and bird-and-bat dispersed species. However, two of these species (*F. adenosperma* and *F. mollior*) have green figs and appear to cluster away from the other species. We cannot make strong predictions about the identities of their dispersers. The outlying position of point 19 may reflect the fact that it represents a free-standing individual of *F. benjamina*, the normal habit of which is hemi-epiphytic (Corner, 1988).

DISCUSSION

In the approximately 350 years since Long Island's biota was eradicated thirty-one species of *Ficus* (a little over half of those known from the Madang area) have colonized the island. The lack of *Rhizocladus* climbers may simply reflect a west–east decline in the numbers of these species across the island of New Guinea – only four of New Guinea's thirty-two *Rhizocladus* species are known from Madang (G. Weiblen, unpublished data).

The facts that sixteen *Ficus* species were located on Long Island with ripe figs in only 15 days, and that half of the island's land-bird species eat figs or have congeners that do so support claims that figs are an exceptionally important

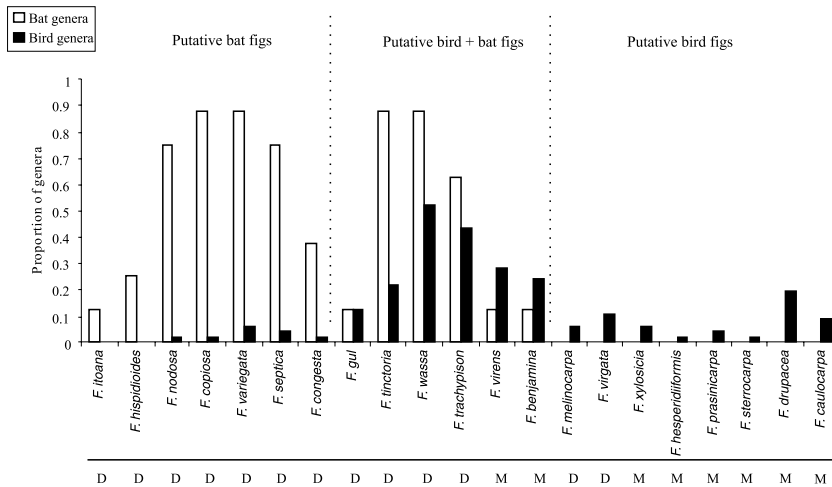


Figure 2 The proportion of New Guinea volant bird and fruit bat genera that are known to eat Long Island's figs for which frugivory has been recorded at individual *Ficus* species. Data from this study and Shanahan *et al.* (2001). M and D indicate monoecious and dioecious species, respectively.

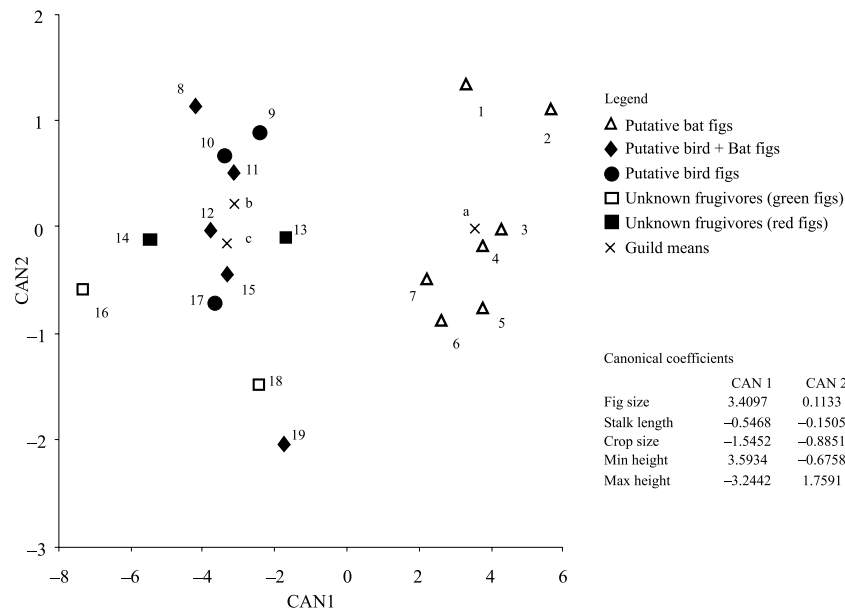


Figure 3 Scatterplot of the first (CAN1) and second (CAN2) axes of the canonical discriminant analysis (CDA) based on fruit attributes (fig size, fig stalk length, crop size and maximum and minimum crop height) of the figs of Long Island. The putative bat-dispersed species (open triangles) are significantly different from the putative bird and bat-dispersed species (black diamonds; $F = 18.8, P < 0.01$) and the putative bird-dispersed species (black circles; $F = 12.7, P < 0.01$). However, no significant difference was detected between the latter two guilds ($F = 0.04, P > 0.05$). Putative guild means are indicated by × (a = bat figs, b = bird figs, c = bird and bat figs). 1 = *Ficus septica*, 2 = *F. hispidooides*, 3 = *F. itoana*, 4 = *F. copiosa*, 5 = *F. variegata*, 6 = *F. nodosa*, 7 = *F. congesta*, 8 = *F. trachypison*, 9 = *F. xylosicia*, 10 = *F. melinocarpa*, 11 = *F. benjamina* (hemi-epiphytic), 12 = *F. virens*, 13 = *F. microdictya*, 14 = *F. subulata*, 15 = *F. wassa*, 16 = *F. adenosperma*, 17 = *F. virgata*, 18 = *F. mollior*, 19 = *F. benjamina* (free-standing tree). *F. benjamina* is represented twice because of the two different growth forms observed.

resource in regenerating tropical forests (Whittaker & Jones, 1994; Thornton *et al.*, 1996). However, fig species are not equal in terms of their suitability for particular frugivores. Our analyses suggest two distinct *Ficus* dispersal guilds: one comprising species using primarily bats for dispersal and one fed upon by a range of bird and bat species. The former present their large, dull green or yellow figs in the lower storeys of the forest whilst the latter produce bright orange

or red figs that are available throughout the vertical structure of the forest. Compared with the green/yellow figs, the red/orange figs occur across a greater size range and include smaller-sized figs.

These observations mirror those made in diverse *Ficus* communities in Panamá and Sarawak (Korine *et al.*, 2000; Shanahan & Compton, 2001) and support the classical concepts of fruit syndromes and seed dispersal guilds

(e.g. van der Pijl, 1957, 1982). However, it should be noted that bats do not feed exclusively on green fruits. Rather than specifically attracting bats, it appears that the large green fruits of *F. nodosa*, *F. copiosa*, etc. are excluding birds. This contention is supported by the case of *F. wassa* which, like the primarily bat-dispersed species, is cauliflorous and produces its relatively large figs in the understorey, but has red rather than green figs and attracts a diverse range of birds (as well as bats) in New Guinea (Y. Bassett, pers. comm.; Fig. 2). All seven of Long's *Ficus* species that are primarily bat-dispersed are dioecious. The tendency for fig species that rely upon mammalian dispersers to be dioecious has also been observed in Sarawak (Shanahan, 2000).

Whilst the existence of covarying character traits may be seen as evidence of diffuse coevolution between figs and their dispersers, phylogenetic constraints should not be ignored. A comprehensive phylogeny of *Ficus* has yet to be published and, therefore, no rigorous comparative analysis can be undertaken at this stage. However, it is noteworthy that the seven members of the putative bat guild hail from three different *Ficus* sections (*Neomorphe*, *Sycidium* and *Sycocarpus*) and that red-fruited, bird-attracting species occur in two of these (*Sycidium* and *Sycocarpus*).

Against this framework of seed dispersal guilds, three distinct patterns of *Ficus* seed dispersal are occurring in the Long Island system: dispersal from the mainland to Long, dispersal within Long itself, and dispersal from Long to Motmot.

Fig seeds have been demonstrated to pass intact through the guts of *Pteropus*, *Ducula* and *Ptilinopus* species (e.g. Crome, 1975; Lambert, 1989; Utzurrum & Heideman, 1991). Based on flight capabilities and gut passage times Thornton *et al.* (1996) concluded that members of these genera and *Aplonis* starlings were the most likely agents of fig seed dispersal to the Krakatau archipelago, Indonesia. The Krakatau islands were sterilized in 1883 and lie 32–41 km from their sources of colonists (Sumatra and Java, respectively). It is probable that species in these genera are the only members of Long Island's fauna capable of retaining seeds in their guts on reaching Long Island from the mainland. The smaller fig-eating birds and bats, with shorter gut passage times and lesser flight capabilities, are more likely to defecate over the sea. Whilst Shilton *et al.* (1999) demonstrated that small *Cynopterus* fruit bats can retain *Ficus* seeds for over 12 h during daytime roosting or confinement in cages, such retention times have yet to be confirmed for bats in flight.

The potential agents of *Ficus* range expansions on Long Island comprise some thirty-five species of birds and mammals and one lizard. Although *Varanus olivaceus*, a relative of Long Island's Mangrove Monitor (*V. indicus*), has been recorded eating figs in the Philippines (Auffenberg, 1988) we do not expect these lizards to be important fig seed dispersers. Likewise, some of the bird species (e.g. *Monarcha cinerascens*, *Pitta sordida* and *Cacomantis variolosus*) are primarily insectivorous (Beehler *et al.*, 1986) and probably eat figs only rarely and contribute little to fig seed dispersal. The ground-doves in the genera *Chalcophaps* and *Macropygia* are generally considered to be seed-predatory (Corlett,

1998) and are likely to destroy a proportion of *Ficus* seeds, in spite of their small size. Although we could find no information on the fate of fig seeds ingested by Long's parrots, other members of this family are known to destroy fig seeds (Janzen, 1981; Jordano, 1983), as do passerids (Compton *et al.*, 1996), represented on Long by *Erythrura trichroa*.

Based on their propensity for fig-eating and passage of intact fig seeds we consider the most important vectors of fig seeds on Long Island to be *Ptilinopus* and *Ducula* fruit-eaters, *Aplonis* starlings, *Zosterops griseotincta*, *Eudynamis scolopacea* and *P. orientalis* and fruit bats in the genera *Pteropus*, *Nyctimene*, *Macroglossus* and *Melonycteris*.

On Long Island there was evidence of the presence of pollinators for all *Ficus* species that were found fruiting. The pollinating wasps of these species are thus capable of at least occasional long-distance dispersal enabling them to colonize Long Island. The high densities of many *Ficus* species found in our surveys of Long Island would suggest that their populations are large enough to maintain their pollinators and have high levels of pollination success. Studies from elsewhere suggest that many dioecious fig species fruit frequently (Corlett, 1987, 1993; Chou & Yeh, 1995; Harrison *et al.*, 2000) and can, therefore, support their pollinator populations with a relatively small number of trees (Kameyama *et al.*, 1999). Of the twenty dioecious *Ficus* species on Long Island, twelve were observed with pollinated figs and for a number of species (e.g. *F. nodosa*, *F. variegata*, *F. congesta*, *F. copiosa*, *F. wassa*) figs were found on several individuals. It is interesting that the crops of *F. nodosa* and *F. wassa* found on Motmot were not pollinated. In some frequently fruiting dioecious *Ficus* species pollinators apparently do not normally disperse far (Harrison, 2000). Similar dispersal behaviour of pollinators of Motmot's *Ficus* species will limit the ability of trees on Long Island to pollinate individuals on Motmot. Thus, these dioecious *Ficus* species on Motmot may be strongly pollen limited until there are sufficient mature male individuals to maintain the pollinator population continuously following a rare colonization event. Most monoecious *Ficus* species produce crops much more infrequently (Bronstein *et al.*, 1990; Harrison, 2000) and of the eleven monoecious species present on Long Island only four were found fruiting. In only one of these, *F. benjamina*, was more than one (actually two) found with figs. However, regular pollinator dispersal distances in at least some monoecious species are very long (Nason *et al.*, 1998), and frequent long-distance pollination appears to be achievable if other instances of rapid re-colonization of wasps after local extirpation events (Bronstein & Hossaert-McKey, 1995; Harrison, 2000) are indicative.

Figs are known to have reached Motmot within 3 years of its creation and now eight species are present on the island. Currently, seed-dispersing frugivores have little reason to visit Motmot as there are few mature fruit trees. Dispersal of *Ficus* seeds to the island, therefore, probably results from rare over-flights and occasional roosting by seed-bearing frugivores. Because of the threat posed by the frequently

observed diurnal raptors, birds may be less likely than fruit bats to fly over Lake Wisdom on foraging trips. The relative importance of fruit bats over birds in the very early stages of colonization is further suggested by the fact that five of Motmot's *Ficus* species (and twenty-five of the thirty-five individuals) are known from the diets of fruit bats. This pattern was also evident in the colonization of the Krakatau archipelago by fig trees (Thornton *et al.*, 1996). The discovery of skeletal remains of *Aplonis* starlings suggests that raptors may be bringing fig seeds to Long Island and Motmot in the guts of their prey items (see Zann *et al.*, 1990). Finally, some *Ficus* species may be water-borne colonists. Ball & Glucksman (1975) found *F. benjamina* seeds on the shore of Motmot in 1972 and *F. virgata* figs were observed floating in Lake Wisdom during study. However, patches of high temperature in the water around Motmot (Osborne & Murphy, 1989) may kill some of these floating seeds. Furthermore, *Ficus* plants were not observed growing as shore plants as would be expected if such dispersal were successful.

Colonization of virgin habitat requires not only that seeds arrive but that they germinate and the resulting plants survive to reach maturity. Motmot is still very sparsely vegetated, the majority of the island being covered with lava flows, ash and scoria. Most of the island is likely to be inhospitable to a *Ficus* seedling. The dioecious *Ficus* plants on Motmot are all small shrubs, generally around the fringes of the island and, therefore, presumably in the least water-stressed environment available. The craters, cliff faces and ash and scoria beds also have a scattering of individuals, again presumably because of favourable micro-climates. However, in the lava flows very few individuals have become established. With the development of better soils and more hospitable micro-climates, vegetation on Motmot will gradually cover a higher proportion of the island and more *Ficus* arrivals will become established.

Most of the monoecious *Ficus* species on Long Island are hemi-epiphytes. Their colonization of Motmot is, therefore, limited not only by seed dispersal, but also by a total lack of potential host trees. Exceptions are those species capable of adopting a free-standing habit, as represented on Motmot by *F. caulocarpa* and *F. benjamina*. Hemi-epiphytes endure extreme water stress during their seedling, epiphytic, stage (Holbrook & Putz, 1996) and this would appear to pre-adapt some species to colonizing lava or other inhospitable environments (Corner, 1988). The big *F. benjamina* individual is in the middle of a lava field near the centre of the island and yet is the largest plant on the island. Other saplings of *F. benjamina* and *F. caulocarpa* also appeared to be well-established.

Despite having arrived on Motmot, most *Ficus* species there are currently unlikely to be capable of increasing their numbers except by the arrival of further seeds from Long Island. Apart from the single large *F. benjamina*, all *Ficus* individuals on Motmot are small and probably immature. Moreover, given the small number of fruiting individuals it seems unlikely that pollinator populations on the island will become permanently established for some years. So, if

pollinator dispersal from Long Island is limiting, as suggested by the unpollinated figs of *F. nodosa* and *F. wassa*, the fig community may take some time to become established. On Anak Krakatau it took 34 years for *Ficus* species to mature (Zann *et al.*, 1990). However, the *F. benjamina* tree in the centre of Motmot is certainly big enough to produce large crops of fruit. A similar individual observed on the coast of Long Island had *c.* 6000 figs. Also, as mentioned above, the pollinators of many monoecious species appear capable of regular long-distance dispersal (Nason *et al.*, 1998). The presence on Motmot of five *F. benjamina* saplings, clearly much younger than the large tree, raises the possibility that they originated from seeds from this tree, especially as *F. benjamina* was not particularly common on Long Island itself. As the single large fruit tree on the island, this *F. benjamina* individual could play a disproportionately important role in the colonization of Motmot, not only through dispersing its own seeds but by increasing and prolonging the visits of frugivores from Long Island. Until the regular production of mature, pollinated fig crops begins on Motmot there will be little reason for volant frugivorous to visit the island. Motmot's flora remains in an early successional state (Harrison *et al.*, 2001) but following fig maturation on Motmot we can expect a rapid increase in the numbers of fleshy-fruited plant species colonizing the island.

This study suggests that *Ficus* species are not equally able to colonize virgin land. One source of variation is in the frugivores that they rely upon as seed dispersers, because of differences in fig size and presentation. Reliance on limited subsets of a frugivore community, such as fruit bats alone, for dispersal exposes plant species to risks should their narrow groups of dispersers decline in population or range, as is occurring to many fruit bat species in the Old World (Mickleburgh *et al.*, 1992). Differences in phenology, population size and fig wasp longevity and dispersal are also important factors in determining successful colonization by *Ficus*. In spite of the dispersal guild structure described here, it appears that fruit bats can eat red or green figs at various heights in the forest. This, and the fact that most *Ficus* species and individuals on Motmot are known from the diets of bats, suggest that fruit bats are of exceptional importance to seed dispersal and early rain forest regeneration in the Old World tropics. The abundance and variety of ripe figs observed during this short study suggest that *Ficus* is an important resource in regenerating forest; a resource capable of attracting a diversity of frugivores likely to disperse seeds of other plant species and, thus, encourage succession and community assembly.

ACKNOWLEDGMENTS

We wish to thank the management and staff of Jais Aben Resort for assistance before and after our time on Long and for sending emergency food supplies. Thanks are due to the Christensen Research Institute (Madang) for access to their library and the Forest Research Institute in Lae for identification of plant specimens. George Weiblen kindly provided copies of his unpublished guide to the figs of Madang.

Thanks are also due to our field assistant William Boen. RY and IWBT were supported by a grant from the National Geographic Society. MS was funded by States of Jersey, Bat Conservation International and a Water Chicken travel bursary. RDH was supported by a grant from Monbusho, Japan. Dr J.W. Grahame and Dr S.G. Compton made helpful comments on earlier versions of this paper.

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BIOSKETCHES

Mike Shanahan, a fig biologist, has examined the interaction in a Borneo forest between *Ficus* species and frugivorous animals, with particular regard to mechanisms allowing different guilds of figs to attract subsets of frugivore communities as seed dispersers.

Ruby Yamuna, field biologist, has recently completed a post-graduate course in Kenya on coral reef rehabilitation.

Rhett Harrison's interests are in insect–plant interactions, especially pollination, including fig pollination, in a Borneo forest.

William Boen is a field collector and parataxonomist now working in a research project on insect herbivory on rain forest trees in Papua New Guinea.

Ian Thornton, leader of the 1999 Long Island expedition, over the past 16 years has led research teams studying the recolonisation on Krakatau and the colonisation of the emergent island Anak Krakatau. His book, 'Krakatau: the destruction and reassembly of an island ecosystem' (Harvard University Press) was published in 1996.

Appendix 1 Fig species recorded on Long Island (L) and Mormot (M). Nomenclature follows Corner (1965). Growth form: T = tree, HE = hemi-epiphyte, C = climber. Breeding system: D = dioecious, M = monoecious. Fig placement: A = axillary, C = cauliflorous. Data from this study unless otherwise noted. Fig size index calculated as (length × diameter²)/100

Subgenus	Section	Species name and authority	Growth form	Locality	Breeding system	Ripe fig colour	Placement	Diameter mm (mean ± SD)	Length mm (mean ± SD)	Peduncle	Fig size index	Crop size	Crop height
<i>Ficus</i>	<i>Adenosperma</i>	<i>Ficus adenosperma</i> Miq.	T	L	D	Green [†]	A [§]	10.24 ± 0.932 [†]	8.8 ± 0.92 [†]	5.74 ± 1.11 [†]	9.23	15,000 [†]	2–12 m [†]
<i>Ficus</i>	<i>Adenosperma</i>	<i>F. mollis</i> Benth.	T	L	D	Green	A/C	16.34 ± 1.103	16.16 ± 0.994	6.86 ± 0.581	43.15	5000	1–5 m
<i>Ficus</i>	<i>Neomorphe</i>	<i>F. nodosa</i> Teyss. et Binn.	T	L, M	D	Green	C	27.91 ± 3.48	26.44 ± 3.64	9.83 ± 1.87	205.96	2500	1–5 m
<i>Ficus</i>	<i>Neomorphe</i>	<i>F. variegata</i> Bl.	T	L	D	Green/dark red	C	27.31 ± 1.41	24.66 ± 1.33	22.47 ± 1.47	183.90	1000	2–4 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. copiosa</i> Steud.	T	L, M	D	Yellow	C	29.07 ± 4.31	28.25 ± 4.11	20.1 ± 2.02	245.64	1200	1–6 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. gul</i> Laut. et K. Schumm.	T	L	D	Orange [§]	A [§]	6–9 [§]	No data	3–18 [§]	No data	No data	No data
<i>Ficus</i>	<i>Sycidium</i>	<i>F. melinocarpa</i> Bl.	T	L, M	D	Orange–red	A	8.21 ± 0.57	8.17 ± 0.55	4.95 ± 1.15	5.51	4000	10–16 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. porphyrochaete</i> Corner	T	L	D	No data	C [§]	5–12 [§]	No data	0–2 [§]	No data	No data	No data
<i>Ficus</i>	<i>Sycidium</i>	<i>F. subulata</i> Bl.	C	L	D	Orange [§]	A [§]	8.12 ± 1.304 [‡]	8.65 ± 1.56 [‡]	2.73 ± 0.647 [‡]	5.70	4500 [‡]	1–10 m [‡]
<i>Ficus</i>	<i>Sycidium</i>	<i>F. tinctoria</i> Forst.f.	HE	L	D	Orange–red	A	10–17 [†]	No data	Present	no data	12,000	10–20 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. trachypison</i> K. Schum.	T	L	D	Orange–red	A	7.23 ± 0.56	7.15 ± 0.599	Sessile	3.74	5500	12–20 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. virgata</i> Reinw. ex Bl.	HE	L, M	D	Orange–red	A	8.44 ± 0.95	8.15 ± 1.11	Sessile	5.81	18,000	12–16 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. uassa</i> Roxb.	T	L, M	D	Pink	C	11.01 ± 1.34	10.89 ± 1.18	14.11 ± 3.6	13.20	2000	1–7 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. botryocarpa</i> Miq.	T	L	D	Yellow–green [§]	C	20–50 [†]	No data	Present [§]	No data	No data	No data
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. congesta</i> Roxb.	T	L	D	Yellow [§]	C	25.82 ± 3.16	24.9 ± 1.97	17.75 ± 0.979	166.00	1200	1–5 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. itoana</i> Diels	T	L	D	Yellow–green	C	34.28 ± 1.69	32.08 ± 2.05	57.8 ± 6.54	376.98	2500	3–10 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. microdicya</i> Diels	T	L	M	Red	A	9.48 ± 1.20	8.57 ± 1.07	3.38 ± 0.95	7.70	2000	6–10 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. papuana</i> Corner	T	L	M	No data	C [†]	20–30 [†]	No data	No data	No data	No data	No data
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. septica</i> Burm. f.	T	L, M	D	Green	C	29.96 ± 5.82	20.67 ± 2.98	8.53 ± 3.87	185.53	300	1–8 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. cf. hispidioides</i> S. Moore	T	L	D	Green–brown	C	34.55 ± 2.19	25.06 ± 1.4	14.66 ± 2.3	299.14	450	1–8 m
<i>Pharmacosycea</i>	<i>Oreosycea</i>	<i>F. pachystemon</i> Warb.	T	L	M	No data	A/C	no data	No data	No data	No data	No data	No data
<i>Pharmacosycea</i>	<i>Oreosycea</i>	<i>F. polyantha</i> Warb.	T	L	M	No data	A	18–30 [†]	No data	No data	No data	No data	No data
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. benjamina</i> L.	T, HE	L, M	M	Red–purple	A	9.28 ± 1.09	9.64 ± 1.19	Sessile	8.30	*	*
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. drupacea</i> Thunb.	HE	L	M	Orange–red [§]	A [§]	15–25 [†]	12–20 [†]	Sessile [§]	No data	No data	–30 m
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. glandifera</i> Summerh.	HE	L	M	No data	A	10–35 [†]	10–18 [†]	Sessile	No data	No data	No data
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. hesperidiiformis</i> King	HE	L	M	No data	A	>35 [†]	No data	10–50 [†]	No data	No data	No data
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. sterrocarpa</i> Diels	HE	L	M	No data	A	40–50 [†]	70–110 [†]	Present [§]	No data	No data	No data
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. xylosicta</i> Diels.	HE	L	M	Red	A	13.13 ± 0.91	25.78 ± 1.81	4.43 ± 0.74	44.44	3500	10–17 m
<i>Urostigma</i>	<i>Urostigma</i>	<i>F. prasinicarpa</i> Elm.	HE	L	M	Red	A	5–8 [†]	No data	1–2.5 [†]	No data	No data	No data
<i>Urostigma</i>	<i>Urostigma</i>	<i>F. virens</i> Ait.	HE	L	M	Orange–red	A	10.3 ± 1.11	9.43 ± 0.99	1.55 ± 0.53	10.00	18,000	15–20 m
<i>Urostigma</i>	<i>Urostigma</i>	<i>F. cf. caulocarpa</i> Miq.	T	M	M	No data	A	5–8 [†]	No data	1–4 [†]	No data	No data	No data

*One individual was a free standing tree with 6000 figs presented between 2.5 and 3.5 m, another was a hemi-epiphyte with figs presented between 20 and 25 m and a crop of 20,000 figs. [†]Data from Madiang (MS); [‡]data from Sarawak (MS); [§]data from Weiblen's unpublished flora, [¶]data from Corner (1965).