

# Adaptive significance of phenological variation among monoecious hemi-epiphytic figs in Borneo

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## Abstract

Plant phenology affects reproductive success through its interaction with pollinators, seed dispersers, and seed predators. Figs are pollinated by highly specific, but short-lived (1–3 days), wasps that breed inside the inflorescence. Thus, continuous flowering at the population-level is a necessary condition for the mutualism to persist. In other respects, however, the ecology of co-occurring fig species varies greatly. Leaf and inflorescence production among 15 species of monoecious hemi-epiphytic fig (*Ficus*; section *Conosyce*) were studied over 4 years in an aseasonal lowland rainforest in Borneo. At the community-level, leaf production was significantly reduced following wetter periods. Many individuals (28%) did not flower during the entire 4 year period. Of individuals that flowered, the mean frequency of reproductive episodes was low and varied from 0.3 to 1.7 times per year. Species with smaller fruit flowered significantly more than those with large fruit, which translated into a substantial difference in fruit production (10.6 vs 1.9 kg pulp dry weight ha<sup>-1</sup> yr<sup>-1</sup>, respectively). Among species pollinated by different wasp genera, there was a significant difference in the mean densities of individuals with receptive inflorescences, and there was a substantial difference in the duration of the wasp emergence phase. The predicted mean minimum distance from a plant with wasps emerging to a receptive individual was, thus, very different between wasp genera; and varied from 3.6 km to 31.8 km across species. Management of protected areas should take into account the low levels of fruit production, especially of species with large fruit, and that fig populations must be dependent on wasps arriving from forests over a wide landscape.

**Keywords:** Agaonidae, co-evolution, *Ficus*, mutualism, fruit production, pollen

## 1. Introduction

The timing and frequency of biological activities, that is their phenology, has important consequences for organisms. In plants this is especially true for expensive activities, such as leaf renewal or flowering and fruit production (Wright and Van Schaik, 1994). Traits determining favourable phenological patterns, with respect to climate and the responses of mutualists, such as pollinators and seed dispersers, or enemies, such as herbivores and seed predators, will be selected. In strongly seasonal environments, such as occur in the temperate zone, the pattern of plant activity is obvious, as reflected in our popular notions of the seasons. However, even in less seasonal tropical environments distinct phenological patterns are evident (Borchert et al., 2005; Sakai et al., 2006), and their adaptive significance has often been

demonstrated. For example, in the Neotropical understorey shrub *Piper arielanum*, plant size, synchrony of flowering with respect to the population, and the season were all important determinants of fruit set (Marquis, 1988). In contrast, among 20 species of ginger in Borneo there was little synchrony of flowering within populations and substantial overlap among species sharing similar pollinators, reflecting their trap-lining habit (Sakai, 2000). Across seven disparate rain forests, the timing of peak leaf and flower production was shown to coincide with the period of highest irradiance, which enables the direct assimilation of the additional photosynthates by these organs (Wright and Van Schaik, 1994).

The majority of plant species in the aseasonal forests of SE Asia flower gregariously at irregular, often super-annual intervals, in response to episodic droughts (Sakai et al., 2006). In contrast, figs (*Ficus*, Moraceae) maintain

continuous population-level flowering through asynchrony among individuals, and sometimes also asynchrony at the individual-level (Harrison and Shanahan, 2005). Fig flowering is therefore not constrained by triggers (Borchert et al., 2005; Sakai et al., 2006), and the need for plant populations to flower synchronously.

Figs have a closed inflorescence lined with tiny flowers. Highly specific wasps (Agaonidae, Chalcidoidea) enter the inflorescence through the narrow neck, losing their wings and antennae in the process, and simultaneously pollinate and attempt to oviposit in some of the flowers. In a monoecious fig, ovules that receive an egg form a gall, within which the wasp larva develops, while fertilised ovules missed by the wasp develop into seeds. Approximately 4–6 weeks after oviposition, the wasp offspring emerge, mate within the inflorescence, and the females disperse with a load of pollen. Within their brief adult lifespan (1–3 days) they must locate a receptive inflorescence to breed. Shortly after the wasps disperse the inflorescences ripen and are fed on by diversity of vertebrate fruit eaters (Shanahan et al., 2001). The asynchronous production of fig fruit makes it a particularly valuable resource for wildlife and figs are often regarded as keystone species in tropical forests (Shanahan et al., 2001). In eastern Borneo unusually low levels of fruiting in hemi-epiphytic figs in Aug 1999 – Sep 2000 led to widespread famine among larger vertebrates (Wong et al., 2005).

Since the pollinators can only reproduce in fig inflorescences, any cessation of flowering for a period longer than the life-cycle of the wasp will lead to its extinction. This was demonstrated in Borneo in 1998 when the pollinators of several dioecious figs were extirpated from a park during a severe drought (Harrison, 2000). Theoretical studies have indicated that fig populations must either be very large or individuals must flower frequently to maintain stable pollinator populations and high rates of pollination success (Bronstein et al., 1990; Kameyama et al., 1999). Monoecious figs tend to flower less frequently (Harrison and Shanahan, 2005; Tweheyo and Lye, 2003; Windsor et al., 1989) and the density of flowering individuals is usually low. Their pollinators must thus disperse large distances to reach a receptive inflorescence (Harrison and Rasplus, 2006). Conversely, dioecious figs tend to flower more frequently or even asynchronously at the individual level (Corlett, 1993; Harrison and Shanahan, 2005; Patel, 1996) and their pollinators probably have a more restricted dispersal (Harrison and Rasplus, 2006).

There are over 750 fig species (*Ficus*: Moraceae) globally, and many studies have now documented different aspects of the fascinating interaction between figs and their pollinators. However, few studies consider the ecological environment under which different co-evolutionary end-points have been reached. In Borneo, as elsewhere in the tropics, monoecious hemi-epiphytic figs (section *Conosycea*) form exceptionally diverse assemblages and

thus are an ideal topic for comparative study. In Sarawak it was found that species colonised different canopy strata (Harrison et al., 2003). Species on emergent hosts were larger and had higher light environments, but were rarer as a result of lower host densities. There was also a tendency for species higher in the canopy to have larger fruit that are dispersed by larger birds and mammals, especially the big hornbills (Shanahan, 2000). In addition, although closely related, these figs are host to two genera of pollinating wasps, which have substantially different dispersal behaviour (Harrison and Rasplus, 2006). *Eupristina* species fly well above the canopy and during the day when wind-speeds are higher. They are, therefore, predicted to disperse further than *Waterstoniella* species, which fly close to the canopy and at night. Here, I examine phenological variation within this same community of monoecious hemi-epiphytic figs with respect to climate, seed dispersal syndrome, and pollinator dispersal.

## 2. Materials and Methods

This study was conducted at Lambir Hills National Park (Lambir; 4°20'N 113°50'E, 150–250 m asl), Sarawak, Malaysia, which has been the site of long-term ecological study of lowland Bornean rainforest (Roubik et al., 2005). The park is approximately 6500 ha of which two thirds is primary lowland dipterocarp forest. It experiences an aseasonal climate with a mean annual precipitation of 2722 mm (1985–2003), and monthly average precipitation ranging from 168 mm in July to 328 mm in November. However, infrequent minor droughts occur, most often in February – March, and occasional severe droughts, which last for two or more months, have also been recorded particularly during El Niño events. Being only 4°N of the equator, diurnal variation in temperature is greater than seasonal variation. Mean annual temperature is 26°C. Cloud cover tends to be higher at the end of the year (November – December), when rainfall is higher, but other climatic variables show little seasonal variation. Rainfall data used in this study were obtained from the Malaysian Telecom tower approximately 3 km northwest of the study site.

Fifty-six hemi-epiphytic figs from 15 species (Table 1) were individually tagged and monitored approximately every ten days for 46 months, between October 1994 and August 1998. Three individuals died within six months of the start of observations and were discounted from the dataset. A further five individuals died during the study but were observed for over two years and hence were included in the dataset. Voucher specimens of all species were deposited in the field herbarium at Lambir Hills and at the Forest Department Herbarium Sarawak, with duplicates sent to Kew, Leiden and Harvard. Species determinations follow recent revisions (Berg and Corner, 2005), with the following exceptions. *Ficus stupenda* Miq. is regarded as a



Table 1. Species of monoecious hemi-epiphytic fig (*Ficus*, section *Conosycea*) included in this study, the number of individuals observed, and their leaf phenology over a 4 year period at Lambir Hills, Sarawak. Observations were made approximately every 10 days.

Species	No. of individuals	Percentage of observations	
		New leaves present	New leaves occupied >20% crown
<i>F. benjamina</i> L.	5	42.6	1.2
<i>F. c.f. annulata</i>	3	7.7	1.0
<i>F. consociata</i> Bl.	1	30.0	2.0
<i>F. cucurbitina</i> King	5	13.0	1.2
<i>F. delosyce</i> Corner	2	12.0	0.0
<i>F. dubia</i> Wall ex. King	4	20.0	1.3
<i>F. kerkhovenii</i> Val.	6	19.7	1.7
<i>F. pisocarpa</i> Bl.	3	9.0	0.3
<i>F. soepadmoi</i> Kochummen	1	10.0	1.0
<i>F. stricta</i> Miq.	1	10.0	1.0
<i>F. stupenda</i> Miq.	4	7.8	1.0
<i>F. subcordata</i> Bl.	6	18.5	1.0
<i>F. subgelderi</i> Corner	4	15.8	0.5
<i>F. sundaica</i> Bl.	5	21.0	1.4
<i>F. xylophylla</i> Wall ex. Miq.	1	6.0	0.0

good species and not a subspecies of *F. crassiramea* Miq. and *F. c.f. annulata* is recognised a separate (name as yet undetermined) species from *F. annulata* Bl. It is distinguished by having larger (mean diameter  $28.3 \pm 0.50$  mm, mean length  $33.3 \pm 0.61$  mm), sessile figs (stalk sometimes to 5 mm), that are conical (not globose) in shape, and the leaf has a felt-like hairs on the underside.

At each census, the proportion of each crown with new leaves, mature leaves, senile leaves (yellowing prior to senescence), or leafless were recorded according to the following scale; 0 = 0, 1 = >0 – <5%, 2 = 5–20%, 3 = 21–50%, 4 = 51–80%, 5 = >80%. Simultaneously, the proportion of the crown with immature, developing, and mature inflorescences was recorded according to the same scale. In addition, total crop size was estimated using a logarithmic scale. Observations were conducted using binoculars from the ground, and a crown was viewed from several positions when a single position did not provide a sufficiently clear view. Estimates were derived by extrapolation from the observed crown area. In addition to the regular censuses, observations were carried out at flowering individuals on an *ad hoc* basis to determine the duration of different crop stages, in particular receptivity and wasp emergence. A large-scale survey (82 ha) of monoecious hemi-epiphytic figs, including the individuals under observation, was conducted in 1998 (Harrison et al., 2003; Harrison, unpublished data). The densities of individuals, their crown areas, liana diameter and crown

illumination were all determined. Data on fruit types and dry weight of fruit pulp were taken from Shanahan (Shanahan, 2000), who studied the seed dispersal characteristics of these same individuals. Among the fig species included here three seed-dispersal guilds can be recognised: small red (<0.3 g pulp dry weight), large red (>0.6 g pulp dry weight), and large green. The first two are dispersed by different subsets of the fruit eating canopy bird and mammal community. The last, which contained only one species, is dispersed strictly by bats.

Phenology data were sorted by individual and the start and finish dates of each leafing or reproductive episode determined. Community-level leaf and inflorescence production by month were autocorrelated to determine seasonality, and then regressed against rainfall over the previous 1–3 months, including lag relationships, to investigate associations with climate, which are primarily driven by rainfall in this region. Community-level data were used because there were insufficient observations per month at the species-level for this type of analysis. The association between leaf and inflorescence production within crowns was investigated by determining the proportion of reproductive episodes preceded by a leafing event within one month. Comparisons across species, fruit types, or species pollinated by different wasp genera were made using non-parametric tests (Wilcoxon 1-way test,  $\chi^2$  approximation), because of non-normality of data. All analyses were conducted using JMP 5.1.

### 3. Results

There was no significant time-series autocorrelation in the frequency of community-level leaf and inflorescence production by month, indicating that no seasonal effect could be detected over the four year period of observations (Fig. 1). However, there was a significant negative correlation between leaf production and rainfall over the previous 1–3 months. The strongest association was obtained for total rainfall over the previous three months ( $F_{1,42} = 5.76$ ,  $P = 0.0209$ ). Inflorescence production was not significantly associated with rainfall.

Distinct leafing events involving >5% of the crown of an individual occurred often in all species, but the frequency varied significantly across species ( $\chi^2 = 24.6$ ,  $DF = 14$ ,  $P = 0.0391$ ; Table 1) from 6% of all observations in *F. xylophylla* to over 40% of observations in *F. benjamina*. More substantial leafing events involving >20% of the crown were relatively rare, occurring on average from 0 to 1.6 times per individual during the four year period depending on the species (Table 1). Sometimes larger leafing events were preceded by a brief leafless period, particularly in species with larger leaves, such as *F. cucurbitina* and *F. stupenda*, but the majority of species were never leafless.

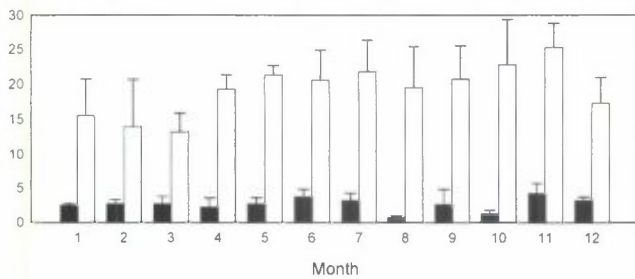


Figure 1. Mean (se) number of individuals initiating crops of new leaves (open bars) and inflorescences (filled bars) per month over a four year period by 53 monoecious hemi-epiphytic figs at Lambir, Sarawak. There was no significant time-series autocorrelation in either parameter indicating that no seasonality could be detected.

The correlation between leafing events and flowering was weak. Of species with more than five observations of flowering, the proportion of crops preceded by a leafing event within one month varied from 0.29 in *F. pisocarpa* to 0.63 in *F. benjamina*. Thus, many flowering events were not preceded by leaf renewal.

A large proportion of individuals (28%) did not flower during the entire four years of observation, and even among individuals that did flower frequencies were low. Mean individual frequencies varied from 1.7 times per year in *F. benjamina* to just 0.6 times per year in *F. pisocarpa* and *F. subcordata* for species with more than three flowering individuals, and were even lower in some species with smaller sample sizes (Table 2). Including only plants that flowered at least once, the individual-level flowering frequency was marginally significantly different across species ( $\chi^2 = 21.1$ , DF = 14,  $P = 0.0712$ ). However, figs with small-red fruit flowered significantly more frequently than those with large-red fruit ( $\chi^2 = 11.6$  DF = 1,  $P = 0.0006$ ; Table 2). As these figs also occurred at higher densities, had a higher proportion of flowering individuals (Table 2), and had larger crop sizes (Table 3), this resulted in much higher levels of fruit production in terms of pulp dry weight per hectare per year for small fruits ( $10.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ), as compared to large fruits ( $1.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) (Table 3). Among figs with large-red fruit there was a tendency for larger individuals to flower more frequently ( $F_{1,17} = 5.03$ ,  $P = 0.0385$ ), but the relationship was not significant among figs with small-red fruit ( $F_{1,23} = 3.12$ ,  $P = 0.0904$ ).

Direct observations at flowering individuals indicated that in all species the receptive phase was extremely short. Selective abortion of unpollinated inflorescences often occurred within one week. However there was a substantial difference among species in the duration of wasp emergence phases. In *Eupristina*-pollinated species (*F. benjamina*, *F. cucurbinata*, *F. dubia*, *F. kerkhovenii*, *F. stricta*, and *F. subcordata*) wasp emergence was highly

synchronous and lasted just a few days (3–5 days). This resulted in limited overlap between wasp emergence and seed dispersal phases. In contrast, in *Waterstoniella*-pollinated species (*F. c.f. annulata*, *F. consociata*, *F. delosyca*, *F. pisocarpa*, *F. stupenda*, *F. subgelderii*, *F. sundaica*, and *F. xylophylla*) the wasps emerged from inflorescences asynchronously over a period of two to three weeks, depending on the crop size. Inflorescences ripened 2–3 days following wasp emergence, so that there was almost complete overlap of wasp emergence and seed dispersal phases. From the census data, there was a highly significant difference in the duration of a reproductive episode from crop initiation to dispersal of the fruit (four weeks in *F. benjamina* and *F. stricta* to 11 weeks in *F. c.f. annulata*, *F. stupenda*, and *F. xylophylla*) among figs pollinated by different wasp genera ( $\chi^2 = 7.69$  DF = 1,  $P = 0.006$ ). This difference was clearly partly due to the staggered wasp emergence, but must also have been partly due to extended fig development.

To estimate the distances pollinating wasps would have to disperse, I calculated the mean densities of receptive trees, based on the proportion of flowering individuals and the densities of individuals in the 82 ha survey, conservatively assuming receptivity lasts one week in all species (Table 4). Among species pollinated by different wasp genera there was a significant difference in these estimates, which varied from  $0.0002 \text{ ha}^{-1}$  in *F. cucurbinata* to a maximum of  $0.0079 \text{ ha}^{-1}$  in *F. subgelderii* ( $\chi^2 = 4.1353$  DF = 1,  $P = 0.0420$ ). I then calculated the mean minimum distances between a wasp producing individual and a receptive individual, again conservatively, assuming wasp emergence lasts one week in *Eupristina*-pollinated species and two weeks in *Waterstoniella*-pollinated figs (Table 4). Distances varied from 733 m to 3972 m in *Eupristina*-pollinated figs and from 449 m to 3030 m in *Waterstoniella*-pollinated figs. Finally, as these wasps use wind-assisted flight (Harrison and Rasplus, 2006), I conservatively assumed a dispersal plume covers a  $45^\circ$  sector. Given these assumptions, *Eupristina* wasps must be dispersing mean minimum distances of 5.9–31.8 km and *Waterstoniella* 3.6–11.8 km.

#### 4. Discussion

At Lambir it was found that many trees increased leaf flushing activity following short dry periods (<14 days) (Ichie et al., 2004). Among the figs, the number of individuals producing new leaves was negatively correlated with rainfall over the preceding 30–90 day period, and the relationship was strongest over longer periods. Hence, rather than a response to short dry spells, this appears to reflect reduced photosynthetic activity during cloudier periods (Wright and Van Schaik, 1994). Nevertheless, most new leaves were produced sporadically in small quantities.

Table 2. Flowering phenology of monoecious hemi-epiphytic figs over a 4 year period at Lambir Hills, Sarawak. Results are presented by species and by fruit type.

Species	No. of individuals observed	No. of individuals flowering	Total no. reproductive events	Crop frequency (individual <sup>-1</sup> yr <sup>-1</sup> )		
				Mean	SD	Max.
<i>F. benjamina</i>	5	3	20	1.7	0.39	2.1
<i>F. c.f. annulata</i>	3	2	5	0.8	–	0.9
<i>F. consociata</i>	1	1	3	0.8	–	0.8
<i>F. cucurbitina</i>	5	2	2	0.3	–	0.3
<i>F. delosyce</i>	2	2	7	1.0	–	1.5
<i>F. dubia</i>	4	1	1	0.3	–	0.3
<i>F. kerkhovenii</i>	6	5	20	1.1	0.46	1.5
<i>F. pisocarpa</i>	3	3	7	0.6	0.39	1.0
<i>F. soepadmoi</i>	1	0	0	–	–	–
<i>F. stricta</i>	1	1	1	0.3	–	0.3
<i>F. stupenda</i>	4	2	6	0.8	–	0.8
<i>F. subcordata</i>	6	5	11	0.6	0.28	0.8
<i>F. subgelderi</i>	4	4	18	1.2	0.45	1.8
<i>F. sundaica</i>	5	5	23	1.4	0.69	2.0
<i>F. xylophylla</i>	1	1	1	0.3	–	0.3
<b>Fruit type</b>						
Small red	27	22	93	1.0	0.55	2.1
Large red	20	12	22	0.4	0.27	0.8
Large green	3	2	5	0.8	0.08	0.9

Table 3. Densities of flowering individuals (= total density of individuals in 82 ha (Harrison et al., 2003; Harrison, unpublished data) × proportion of observed individuals flowering (Table 2)), mean crop size, pulp dry weight of one inflorescence (Shanahan 2000) and fruit production for monoecious hemi-epiphytic figs at Lambir Hills National Park, Sarawak.

Species	Fruit type <sup>1</sup>	Density of flowering individuals (ha <sup>-1</sup> )	Mean crop size (×10 <sup>3</sup> )	Pulp dry weight (g)	Fruit production (g ha <sup>-1</sup> yr <sup>-1</sup> )
<i>F. benjamina</i>	SR	0.050	59	0.065	193
<i>F. c.f. annulata</i>	LG	0.014	2	2.935	79
<i>F. consociata</i>	SR	0.057	13	0.237	175
<i>F. cucurbitina</i>	LR	0.011	14	0.694	110
<i>F. delosyce</i>	SR	0.098	10	0.065	63
<i>F. dubia</i>	LR	0.008	7	1.043	57
<i>F. kerkhovenii</i>	SR	0.231	55	0.082	1,043
<i>F. pisocarpa</i>	SR	0.051	33	0.134	227
<i>F. stupenda</i>	LR	0.038	13	1.863	915
<i>F. subcordata</i>	LR	0.017	13	1.894	426
<i>F. subgelderi</i>	SR	0.411	19	0.271	2,115
<i>F. sundaica</i>	SR	0.067	20	0.292	389
<i>F. xylophylla</i>	LR	0.072	20	1.965	2,845

<sup>1</sup>SR = Small-red, LR = Large-red, LG = Large-green. Note *F. soepadmoi* did not fruit, and fruit size data were not available for *F. stricta*.

Large leaf renewal events were relatively rare, and there was little correlation with flowering.

Fig flowering was not, unlike leaf renewal, affected by climatic variation. This may result from direct selection on figs to avoid flowering peaks. Given the highly specific pollination system, on the one hand, and the generalist fruit syndrome, on the other, figs may experience competition for pollinators and seed dispersers if individuals flower

together. Moreover, given an optimal fruiting season, optimal release of pollinators would be during the receptive phase prior to this season. Thus, conflict between the male and female reproductive effort of the fig will also tend to smooth out peaks. As previously mentioned, it is a necessary condition for the persistence of the fig-fig pollinator interaction that figs flower continuously at the population-level. Thus, some kind of counter selection to



Table 4. Estimated parameters for pollinator dispersal in monoecious hemi-epiphytic figs at Lambir Hills, Sarawak. Mean density of receptive figs (= density of flowering individuals (Table 3) x frequency of flowering (Table 2) x 1/52 (conservatively assuming receptivity lasts 7 days)), mean minimum distance between a wasp producing tree and a receptive tree (assuming wasp emergence lasts 7 days in *Eupristina*-pollinated figs and 14 days in *Waterstoniella*-pollinated figs), and the estimate mean minimum flight distance for the pollinators (assuming a dispersal plume of 45°).

Species	Pollinator genus <sup>1</sup>	Density of receptive individuals (ha <sup>-1</sup> )	Mean min. distance (m)	Min. flight distance (km)
<i>F. benjamina</i>	E	0.0003	3,030	19.8
<i>F. c.f. annulata</i>	W	0.0011	1,209	9.7
<i>F. consociata</i>	W	0.0002	3,310	26.5
<i>F. cucurbinata</i>	E	0.0019	921	7.4
<i>F. delosyce</i>	W	0.0002	3,972	31.8
<i>F. dubia</i>	E	0.0044	733	5.9
<i>F. kerkhovenii</i>	E	0.0010	1,269	10.2
<i>F. pisocarpa</i>	W	0.0003	3,030	19.8
<i>F. stricta</i>	E	0.0003	1,986	13.0
<i>F. stupenda</i>	W	0.0007	1,480	11.8
<i>F. subcordata</i>	E	0.0003	2,678	21.4
<i>F. subgelderii</i>	W	0.0079	449	3.6
<i>F. sundaica</i>	W	0.0013	1,115	8.9
<i>F. xylophylla</i>	W	0.0014	1,069	8.6

<sup>1</sup>E = *Eupristina*, W = *Waterstoniella*. Note *F. soepadmoi* was not observed flowering.

climatically induced population synchrony would appear to be essential if figs are to colonise even marginally seasonal habitats – whereas in fact figs occupy many highly seasonal environments.

Perhaps the most extraordinary finding in this study was the very low frequency of individual-level flowering. Twenty-eight percent of individuals did not flower once in the four year period, although all individuals were apparently mature and many have subsequently flowered. Even among those that did flower the maximum individual flowering frequency was just twice per year, and mean individual flowering frequencies varied from just 0.6 to 1.7 across species with over three flowering individuals (Table 2). Such low levels of flowering are in stark contrast to the situation in Panama where in most species individuals flower 2–3 times per year (Korine et al., unpublished data). The comparison suggests the figs at Lambir may be energy limited as a result of the year-round rainy and therefore commonly cloudy conditions (both sites have relatively infertile soils).

Figs with small-red fruit flowered significant more frequently than those with large-red fruit. Larger fruit will require a greater investment of energy and nutritional resources, although smaller crops sizes may partially compensate. Species with larger fruit also occurred at lower densities (Harrison et al., 2003), and so the fruit production per hectare of large fruit was less than one fifth that of small fruit (Table 3). The frugivores that feed on these larger fruit must, therefore, range over a proportionally greater area. In Panama larger figs were also shown to require evaporative cooling to avoid reaching temperatures that would be lethal to the pollinator larvae, whereas

convective cooling was sufficient for smaller figs (Patino et al., 1994). Selection for larger inflorescences, whether driven by interactions with fig wasps or fruit eaters, thus entails a suite of simultaneous changes in the ecology of a fig.

The tendency for larger individuals to flower more frequently among species with large-red fruit likely reflects the better light environment bigger individuals enjoy (Harrison et al., 2003). The lack of a relationship among species with small-red fruit may reflect the fact that these species usually occupy subcanopy strata and thus do not markedly improve their light environment as they grow. Or it may simply be an artefact of averaging across species.

Both the census data and direct observations at flowering trees indicate that there are substantial differences in phenology between species pollinated by different wasp genera. The two critical phases for pollinating wasps are the emergence and receptive phases. Female wasps must disperse from the former to the latter, which they enter to lay their eggs, during a very brief lifespan (1–3 days). The density of individuals with receptive phase inflorescences is therefore of critical importance to the pollinators. On average *Eupristina*-pollinating species had significantly lower densities of receptive individuals than *Waterstoniella*-pollinated species. Moreover, the phenology of the wasp emergence phase exacerbated this difference. In *Eupristina*-pollinated figs wasp emergence was highly synchronous and completed within 3–5 days, whereas in *Waterstoniella*-pollinated figs it was staggered over a 2–3 week period. Using figures that are conservative with respect to these differences, the estimated mean minimum wasp dispersal distances were

over twice as far for *Eupristina* (Table 4). Studies of fig wasp dispersal in Lambir found that *Eupristina* flew higher above the canopy than *Waterstoniella* and during the day, when windspeeds are higher (Harrison and Rasplus, 2006), suggesting they disperse further. Thus, similar predictions result from these two very different approaches. It should be noted that these are mean minimum estimates. Due to the stochastic nature of flowering in these figs, these distances will sometimes be greatly increased. It is also worth noting that paternity studies in Panamian figs found pollen from 6–17 different individuals, depending on the species, siring a single crop of inflorescences (Nason et al., 1998). If the situation is similar in Borneo, this would mean some wasps disperse up to at least 30 km in *Waterstoniella* and 70 km in *Eupristina*. As was also suggested from the studies of wasp dispersal (Harrison and Rasplus, 2006), the figs at Lambir must be dependent on the arrival of pollinators from forests outside the park. Given the keystone role of these figs for wildlife, the effects of fragmentation and isolation should be investigated.

This study has demonstrated that there is a wide variation in phenological strategies among monoecious hemi-epiphytic figs in Borneo, and differences in flowering phenology were shown to have consequences for both seed dispersers and pollinators. In particular, species with larger fruit have much lower fruit production on a per area basis. Wildlife dependent on these large figs, such as the bigger hornbills, must range over big areas to obtain sufficient food. These factors should be taken into account in the planning and management of protected areas. Fruit production in smaller protected areas could perhaps be enhanced through artificial planting of large-fruited fig species. The predictions of wasp dispersal distances indicate that even in large parks some figs may be dependent on the arrival of wasps from outside the protected area. The sustainability of fig populations in protected areas therefore needs to be investigated, and appropriate management of matrix habitats implemented.

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