

Dispersal of fig pollinators in Asian tropical rain forests

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Abstract: Fig pollinators (Agaonidae, Chalcidoidea) lay their eggs in fig inflorescences (*Ficus*, Moraceae). Reproductive success for both partners is thus largely dependent on the dispersal of these tiny wasps. Some are known to cover substantial distances (> 10 km) using wind above the canopy. However, fig ecology is extremely varied, and hence one might also expect a diversity of pollinator dispersal strategies. We studied fig pollinator dispersal in Sarawak (2001 and 2004) and Peninsular Malaysia (2003). The results indicate substantial differences in dispersal ecology between the pollinators of monoecious and dioecious figs. Monoecious-fig pollinators were common, and species composition and rank abundances were similar between years despite short sampling periods. Substantial temporal and spatial variation in their production is thus smoothed out by long-distance dispersal. Some species whose hosts do not occur at our Sarawak site and are rare throughout Borneo were caught, suggesting exceptionally long-distance dispersal in these species. Conversely, few dioecious-fig pollinators were caught and species overlap between years was low. Dispersal range in many dioecious-fig pollinators may be more restricted. At a finer scale, among genera pollinating monoecious figs we found marked differences in flight behaviour (height and time-of-dispersal). We relate these findings to the ecology of their hosts, and discuss the implications for fig–pollinator coevolution.

Key Words: Agaonidae, coevolution, *Ficus*, flight behaviour, mutualism, pollination

INTRODUCTION

Fig wasps (Chalcidoidea: Hymenoptera) lay their eggs in the inflorescence of a fig (*Ficus*, Moraceae). They are thus entirely dependent on the flowering of fig trees for reproductive opportunities. Species are highly specific, represent a range of life histories, including gallers, gall parasites, and parasitoids, and most have a negative impact on the reproductive success of their hosts. However, the species of one particular lineage of gallers (Agaoninae; Agaonidae) are the pollinators of figs. This uniquely intricate interaction is over 60 million y old (Ronsted *et al.* 2005), and the fact that *Ficus* is usually the most diverse plant genus in any particular rain forest attests to its success (Harrison 2005).

Fig flowers are enclosed within an urn-shaped inflorescence. When receptive, the stigmas release a species-specific fragrance, and the bracts in the neck of the inflorescence loosen, allowing the pollinators to enter. They lose their antennae and wings as they squeeze

through and are, therefore, prevented from flying on to a different plant, although they sometimes enter more than one inflorescence on the same plant (Moore *et al.* 2003). Inside the inflorescence, the pollinators scatter pollen, which they have carried from their natal fig, and attempt to lay eggs on some of the flowers. Ovules that receive an egg develop into a gall, and the wasp larva feeds on the gall tissue. In a monoecious fig, wasp larvae and seeds mature together in the same inflorescence. In dioecious figs, inflorescences on female plants produce seeds, while conversely male plants produce just pollinators and pollen. The wasps are deceived into pollinating the inflorescences on female plants, but fail to reproduce. Pollinator larvae take 4–8 wk to mature depending on the species. As adults, they mate within the inflorescence and the females then emerge, collecting some pollen on the way out. In many figs, high within-crown flowering synchrony means emerging wasps are forced to disperse to a different plant in order to find a receptive inflorescence in which to breed.

For female fig pollinators, reproductive success is primarily determined by whether or not they reach a receptive inflorescence. Especially among monoecious

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figs, the density of individuals with receptive inflorescences is often very low ($\approx 0.0005\text{--}0.008$ indiv. ha^{-1} in Borneo R. D. Harrison unpubl. data; Bronstein *et al.* 1990, Harrison & Shanahan 2005), and so the pollinators have to disperse substantial distances (> 10 km) (Harrison 2003, Nason *et al.* 1998). Pollination success is also likely to be an important determinant of reproductive success in their hosts. If an inflorescence is not visited neither seeds nor pollinator larvae are produced, and the inflorescence often aborts. Most studies have examined the details of the fig–fig pollinator interaction only after pollination has occurred (Corlett 1990, Herre 1989, Molbo *et al.* 2003, Weiblen *et al.* 2001), and so the importance of pollination success has probably been overlooked. Some figs suffer chronically high levels of pollination failure (Bronstein 1988). Reproductive success of both partners thus depends to a substantial degree on the process of fig wasp dispersal, about which we know relatively little.

Early studies on the cultivated fig established that its pollinator could survive up to 3 d in the wild (Kjellberg *et al.* 1988), but longevity of fig pollinators in captivity ranges from approximately 12 h to 3 d depending on the species (R. D. Harrison, unpubl. data). Studies in a savannah environment indicated that fig pollinators dispersed by drifting downwind until they encountered the fragrance plume of a receptive tree (Ware & Compton 1994a, b). Subsequent studies in Bornean rain forests found that many fig wasps were flying above the canopy, again indicating they were using wind to disperse (Compton *et al.* 2000, 2005; Harrison 2003). However, in Sarawak the relative abundance and diversity of monoecious fig pollinators captured suggested they were dispersing much further than dioecious fig pollinators. Differences in dispersal behaviour with respect to flight height and diurnal activity patterns (night or day flying) were also revealed (Harrison 2003). Given the tremendous range of ecologies evidenced by their hosts (Harrison & Shanahan 2005), diversity in the dispersal ecology of fig pollinators is hardly surprising. However, an understanding of how pollinator dispersal constrains fig ecology, and vice versa, has the potential to elucidate the selective environment behind many aspects of the fig–fig pollinator interaction. Here, we extend the earlier findings from Sarawak with subsequent studies in both Sarawak and Peninsular Malaysia, and discuss the relevance of fig wasp dispersal to fig–fig-pollinator coevolution.

MATERIALS AND METHODS

We sampled fig wasps in August 2001 (Harrison 2003) and June/July 2004 at Lambir Hills National Park (Lambir; $40^{\circ}20'N$, $113^{\circ}50'E$, *c.* 50 m asl), Borneo and in August 2003 at Pasoh Forest Reserve (Pasoh; $2^{\circ}59'N$, $102^{\circ}18'E$), Peninsular Malaysia. Lambir supports

approximately 4500 ha of lowland dipterocarp forest, which has amongst the highest tree diversity in the world. Sampling was conducted at the site of a canopy crane located near the park headquarters. The forest is aseasonal with a mean annual rainfall of approximately 2700 mm, but short droughts are not infrequent and can last up to 3 mo in association with strong El Niño events. Pasoh also supports lowland dipterocarp forest with high tree species richness. The reserve is approximately 2000 ha, but is adjacent to the Malaysian central range, a chain of hills running most of the length of the peninsula that is still predominantly forested. The mean annual rainfall total is approximately 2000 mm, and is again aseasonal but, like Lambir, droughts are not infrequent especially in El Niño years. Trapping was conducted near the field station buildings.

We used non-attracting sticky traps suspended on light lines to capture flying insects. Traps were made from 1.5-l (surface area *c.* 0.079 m²) clear plastic bottles painted with Tanglefoot[®]. At Lambir the traps were hung from the boom of an 80-m-high canopy crane. In 2001, at each trapping point two bottles were suspended end to end, and points were set at 10-m intervals from 5–75 m on three lines spaced approximately 15 m apart (total 48 traps). Traps were checked at dawn and dusk over a 10-d period. Initial results from 2001 indicated that almost all fig wasp captures were from above the canopy (≈ 35 m) (Harrison 2003). Hence, when the exercise was repeated in 2004 we made a more intense sampling of this zone: single bottles were suspended at 2-m intervals from 28–78 m on the same three lines (total 78 traps), and checked at dawn, noon, dusk and midnight over a 6-d period. At Pasoh in 2003, three lines with two bottles at each trapping station (5-m intervals, 5–35 m, total 42 traps) were suspended from two emergent trees and a canopy tower, and checked at dawn and dusk over 5 d. At Pasoh, our inability to reach above the canopy restricted the number of fig wasps we were able to capture, and hence we use these results only to compare species overlap with Lambir. At both sites, there were no large figs within the immediate vicinity (< 200 m) of the traps, although at Lambir some small dioecious species have colonized the gap around the crane. Given these forests are aseasonal and that figs flower asynchronously at the population-level, short sampling periods can be considered representative.

All fig wasps were collected from the traps. Identifications were made using available keys (Wiebes 1994), and by comparison with reference collections held by J.-Y. Rasplus (see Appendix). Non-pollinating fig wasps were very rare and hence this paper deals only with pollinators.

The fig community at Lambir and its immediate environs has been well studied (Harrison & Shanahan 2005), and details of the Bornean figs were taken from published floras, which were recently revised (Berg & Corner 2005). The fig flora of Pasoh is incomplete. General floristic

Table 1. Composition of fig pollinators caught on sticky traps at Lambir Hills National Park (Lambir) over 10 d in August 2001 and 6 d in July 2004, and the host fig communities of Lambir and Borneo.

	No. of pollinator spp.					No. of <i>Ficus</i> spp.	
	2001	2004	Both years	Total spp.	Undescribed spp.	Lambir	Borneo
Monoecious-fig pollinators							
<i>Deilagaon</i>	1	0	0	1	0	1	4
<i>Dolichoris</i>	3	3	2	4	1	1	5
<i>Eupristina</i>	13	13	11	15	12	8	13
<i>Platyscapa</i>	2	2	2	2	2	2	4
<i>Waterstoniella</i>	20	18	17	21	14	17	18
All genera	39	36	32	43	30	29	44
Dioecious-fig pollinators							
<i>Blastophaga</i>	2	4	1	5	4	11	22
<i>Ceratosolen</i>	3	2	0	5	5	10	26
<i>Kradibia</i>	0	3	0	3	3	1	6
<i>Lipporhopalum</i>	3	3	1	5	5	13	15
<i>Wiebesia</i>	4	4	2	6	6	14	24
All genera	12	16	4	24	23	49	93

studies have focused on trees and thus omit many fig species. Nevertheless, a large number of species from Peninsular Malaysia are shared with Borneo, and the overall taxonomic composition is similar (Berg & Corner 2005).

We compared species abundances between years at Lambir using rank correlation (Kendall's Tau b). To compare flight heights among genera and species we used nested ANOVA (species nested within genera). Post-hoc tests were made by comparing the Least Square Mean differences using a Student's t-test (significance at $P < 0.05$ level). Flight heights from different years at Lambir were compared using non-parametric Kruskal–Wallis tests, because of unequal variances. The frequencies of captures at different times of the day were compared using χ^2 tests. Rarer species were omitted so that expected frequencies were always greater than five. All analyses were conducted using JMP[®] version 5.1.

RESULTS

Composition and abundance

At Lambir, the overall taxonomic distribution of fig pollinators was remarkably similar between 2001 and 2004. In both years monoecious-fig pollinators were over-represented relative to the number of host fig species in the park, but dioecious-fig pollinators were strongly under represented (Table 1). The pattern was similar at Pasoh (Table 2), although the total number of species collected was much lower. At Lambir among monoecious-fig pollinators there was a high degree of overlap in species composition (Table 1) and a highly significant correlation in species abundances (Figure 1; Tau b = 0.492, $P < 0.0001$) between years. In contrast, out of 24 species of dioecious-fig pollinator collected in total only four species

were recorded in both years. Comparing between sites, out of 16 species of monoecious-fig pollinator collected from Pasoh ten were also collected at Lambir, whereas only three out of six dioecious-fig-pollinating species were found at both sites (Table 2). However, there were differences among monoecious-fig-pollinating genera. Fewer than half the *Waterstoniella* species collected at Pasoh also occurred at Lambir (Table 2).

At Lambir, in both years a greater number of monoecious-fig-pollinator species were collected than there are host species in the park (Table 1). Seventy per cent of the monoecious-fig pollinators we collected were undescribed species, a much higher proportion than would be predicted (64% of Bornean monoecious figs have a described pollinator; Berg & Corner 2005, Wiebes 1994), and for both *Eupristina* and *Waterstoniella* the total number of species caught exceeded the number of host fig species known from Borneo (Table 1). These findings suggest the occurrence of multiple pollinator species on some hosts. We also identified monoecious-fig

Table 2. Composition of fig pollinators caught on sticky traps at Pasoh Forest Reserve, Peninsular Malaysia over 5 d in August 2003 and the species shared with the samples collected from Lambir in 2001 and 2004.

	Number of pollinator spp.	
	Pasoh	Shared with Lambir
Monoecious figs		
<i>Eupristina</i>	5	4
<i>Platyscapa</i>	2	2
<i>Waterstoniella</i>	9	4
All genera	16	10
Dioecious figs		
<i>Ceratosolen</i>	1	1
<i>Kradibia</i>	2	1
<i>Wiebesia</i>	3	1
All genera	6	3

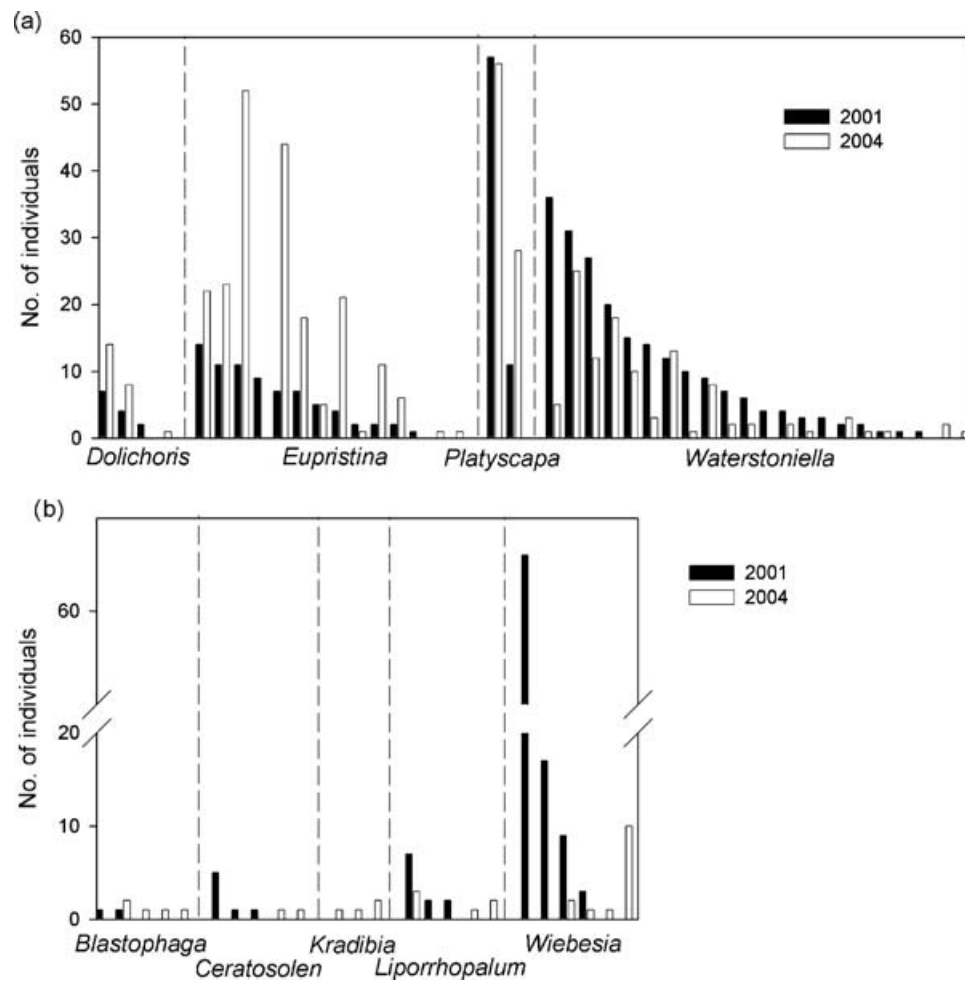


Figure 1. The species abundances of (a) monoecious-fig pollinators and (b) dioecious-fig pollinators, arranged by genera, caught on sticky traps at Lambir over 10 d in 2001 and 6 d in 2004. On average over both years, 18.1 ± 3.37 monoecious-fig-pollinating species were caught each day and the species-recruitment curve reaches an asymptote after just 3 d. By comparison, just 2.7 ± 2.46 dioecious-fig-pollinating species were caught each day, and there is no indication of a flattening out of the species-recruitment curve. There was a highly significant correlation in the abundances of monoecious-fig pollinators between years (Tau $b = 0.492$, $P < 0.0001$), but not among dioecious-fig pollinators (Tau $b = -0.180$, $P = 0.347$).

pollinator species whose hosts do not occur in Lambir or the immediate vicinity (see Appendix), indicating some species are arriving from forests with different assemblages of figs. *Dolichoris nervosa nervosa* and *D. n. philippinensis* pollinate *Ficus nervosa* subsp. *nervosa* and *F. magnoliifolia*, respectively. Both are exceedingly rare in Borneo (Kochummen & Go 2000). *Eupristina verticillata* is the pollinator of *F. microcarpa*, which is planted widely in towns and occurs naturally in freshwater swamp forests not far from Lambir (≈ 20 km, R. D. Harrison, *pers. obs.*).

Flight height and diurnal activity

As in 2001, the majority of fig wasps were captured above the canopy (≈ 35 m) at Lambir in 2004 (Figure 2). Only 6 out of the 372 captures were made beneath the surface

of the canopy, although traps extended to 8 m below this level. As a result of the low number of captures among dioecious-fig-pollinating species, subsequent analyses are confined to monoecious-fig pollinators.

Again similar to the results obtained in 2001, there were highly significant differences in flight height among genera of monoecious-fig pollinators in 2004 (ANOVA model $F_{34,383} = 7.82$, $P < 0.0001$; effects Genus $F_3 = 27.2$, $P < 0.0001$, Species (nested within Genus) $F_{31} = 2.15$, $P = 0.0005$; post-hoc tests *Platyscapa* = *Dolichoris* > *Eupristina* > *Waterstoniella*), and the rank order of flight heights was identical between years (Figure 2). The species (nested within genus) effect was highly significant, but post-hoc tests revealed a confusing pattern of overlap, because of small sample sizes for many species. So we examined genera separately, including just common species ($N \geq 10$). There was a significant

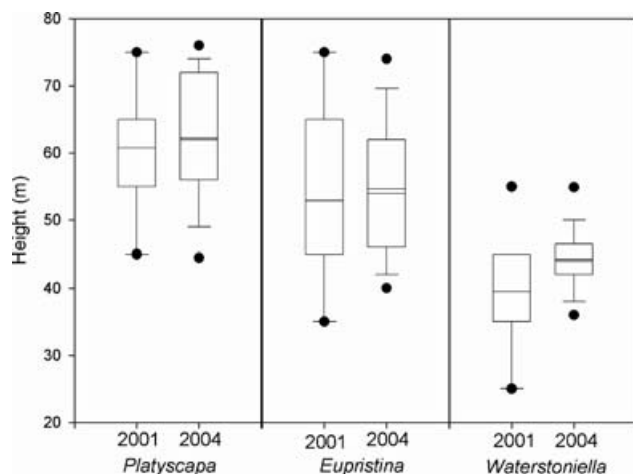


Figure 2. Box plots of the height of capture of monoecious fig pollinators at Lambir in 2001 and 2004. In 2001 traps were suspended at 10-m intervals at 5–75 m, but in 2004 they were suspended at 2-m intervals at 28–78 m. Canopy height is approximately 35 m at the site. There were highly significant differences among genera in the mean height of captures in both years (2001: ANOVA $F_{2,330} = 102$, $P < 0.0001$; 2004: ANOVA $F_{2,392} = 91.2$, $P < 0.0001$; and all pairwise comparisons were significant ($P < 0.05$) in both years). Between years there were no significant differences in the captures of *Platyscapa* or *Eupristina* (Kruskal–Wallis tests, *Platyscapa* $z = -0.779$, $P = 0.436$; *Eupristina* $z = -1.56$, $P = 0.119$), but captures of *Waterstoniella* were significantly higher in 2004 (Kruskal–Wallis test $z = 3.21$, $P < 0.01$). Note: there were insufficient captures of *Dolichoris* in 2001 and *Deilagaon* in both years for comparisons to be made.

difference in flight height among *Eupristina* species (ANOVA $F_{6,180} = 3.82$, $P = 0.0013$), but not among species of *Platyscapa* (ANOVA $F_{1,82} = 0.09$, $P = 0.763$) or *Waterstoniella* (ANOVA $F_{4,73} = 1.40$, $P = 0.239$). Even among *Eupristina* species post-hoc tests revealed substantial overlap. There were no significant differences in the height of captures between years for *Platyscapa* or *Eupristina* (Kruskal–Wallis tests, *Platyscapa* $z = -0.779$, $P = 0.436$; *Eupristina* $z = -1.56$, $P = 0.119$), but for *Waterstoniella* they were significantly higher in 2004 (Kruskal–Wallis test $z = 3.21$, $P < 0.01$) (Figure 2).

In both years, *Dolichoris*, *Eupristina* and *Platyscapa* were day flying, and *Waterstoniella* was night flying. In 2004 zero *Dolichoris* or *Platyscapa* were caught at night, and

just four *Eupristina* wasps were caught during a full moon. For *Waterstoniella* six out of 110 individuals were caught during the day. At the genus-level, frequencies of captures were very even between the dawn to midday and midday to dusk periods for day-dispersing wasps, and dusk to midnight and midnight to dawn periods for night-dispersing wasps (Table 3). However, there were significant differences among species within genera in the frequency of captures during the earlier and later parts of their activity period (*Platyscapa* $\chi^2 = 6.26$, $df = 1$, $P = 0.0124$; *Eupristina* $\chi^2 = 12.6$, $df = 6$, $P = 0.0498$; *Waterstoniella* $\chi^2 = 10.1$, $df = 4$, $P = 0.0391$).

There were no significant differences in flight height between the dawn to midday and midday to dusk periods for daytime dispersing wasps, or dusk to midnight and midnight to dawn periods for night-flying species.

DISCUSSION

Composition and abundance

The similarity in the species composition and abundances of monoecious-fig pollinators between years at Lambir was quite remarkable, when one considers the short sampling periods, the low densities of trees producing pollinators at any particular point in time, and the very short life spans of these wasps. It is another indication that these pollinators disperse substantial distances (Harrison 2003, Nason *et al.* 1998), thus smoothing out the temporal and spatial variance in their production.

Of special note are the captures of *Dolichoris* and *Platyscapa*. *Dolichoris* wasps pollinate figs in section *Oreosyceae*, which are rare throughout Borneo. *Ficus vasculosa* is the only species known from Lambir, but only one mature individual has been found and it has not been recorded elsewhere in Sarawak (Harrison & Shanahan 2005, Kochummen & Go 2000). Of the other two taxa whose pollinators were identified, *F. magnoliifolia* is known from scattered collections in northern Borneo and *F. nervosa* subsp. *nervosa* has not yet been recorded in Borneo (Berg & Corner 2005). Another subspecies, *F. nervosa* subsp. *pubinervis*, is known from Mount Kinabalu, but is believed to be pollinated by a different

Table 3. Number and mean flight heights (SE) of monoecious fig pollinators caught on sticky traps over different periods of the day at Lambir during 6 days in July 2004.

	Number of pollinators		Mean flight height	
	Dawn–noon	Noon–dusk	Dawn–noon	Noon–dusk
Day-dispersing wasps				
<i>Dolichoris</i>	15	8	59.6 ± 2.86	54.8 ± 3.41
<i>Eupristina</i>	98	92	55.1 ± 1.04	55.3 ± 1.08
<i>Platyscapa</i>	35	49	62.2 ± 1.73	62.3 ± 1.45
Night-dispersing wasps	Dusk–midnight	Midnight–dawn	Dusk–midnight	Midnight–dawn
<i>Waterstoniella</i>	48	56	42.6 ± 0.73	44.9 ± 0.68

waspspecies that we did not catch (Wiebes 1994). Just two other section *Oreosycea* species are recorded from Borneo. *Ficus callosa* Willd. is widely distributed but very rare, and a single individual of one other species, *F. albipila* (Miq.) King, was recently discovered in a remote area of Sabah (Kochummen & Go 2000). Exactly how rare these *Oreosycea* figs are is, of course, impossible to say, but they are large, distinctive canopy trees and often valued timber species. So it is unlikely they have been under-collected. *Platyscapa* species are pollinators of monoecious hemi-epiphytic figs in section *Urostigma*, which are also rare in Lambir and apparently throughout Borneo (Harrison & Shanahan 2005). Two species are known from Lambir, but in a survey of approximately 120 ha only one individual of each was recorded (Harrison *et al.* 2003). Given the infrequent intervals at which their hosts flower, *Dolichoris* and *Platyscapa* wasps must be dispersing enormous distances, perhaps as far as a 100 km or more, on a regular basis to have been captured by us at all.

In contrast, few dioecious fig pollinators were caught and the turnover of species between years was substantial. It seems likely that many dioecious-fig pollinators are dispersing shorter distances. Higher densities and flowering frequencies of dioecious figs (Harrison & Shanahan 2005) negate the need for long-distance dispersal. Also, provided receptive trees are within active flight range, dispersal through the understory ought to be a more reliable strategy. In many species the inflorescences are produced near the ground. Shorter distance dispersal also relates to higher rates of endemism in these figs and vulnerability of their pollinators to local extinction (Harrison 2003).

At Pasoh, as at Lambir, the relative diversity of monoecious-fig pollinators was high compared to dioecious-fig pollinators. A similar pattern was also recorded in a separate study at Danum Valley, north-east Borneo (> 400 km from Lambir) (Compton *et al.* 2000, 2005), suggesting it is a general phenomenon. The high species overlap between Pasoh and Lambir among *Platyscapa* and *Eupristina* wasps can be explained by the high proportion of monoecious fig species that occur in both Borneo and Peninsular Malaysia (Appendix). In contrast, the comparatively low overlap in *Waterstoniella* species among sites is interesting.

Flight height and diurnal activity

At Lambir, our results from 2004 confirmed the findings from 2001 in establishing that genera of monoecious-fig pollinators fly at different heights above the canopy. Within genera, however, flight heights were not strongly differentiated among species. The fact that the captures of *Waterstoniella* were lower in 2001 simply reflects

sampling error. In 2004, 86% of captures were between 36 m and 54 m, but in 2001 only one trap was positioned in this range.

In the study at Danum Valley differences between the monoecious-fig-pollinating fauna collected in primary and logged forests led the authors to suggest that composition of samples was affected by the emergence of wasps from nearby plants (Compton *et al.* 2005). However, their traps were hung from emergent trees and hence the highest traps were just 10–20 m above the main canopy in the primary forest, but 28–38 m above surrounding vegetation in secondary forests. As one would predict from our results, a higher proportion of wasps in high-flying genera were captured in the logged forest. Thus, we suggest the shift in composition was the result of trapping bias and not the local production of pollinators.

As a result of turbulence and drag from tree crowns, wind-speeds increase with height above the canopy for the first few tens of metres (Kumagai *et al.* 2001). Therefore, one would predict that the potential dispersal range of fig pollinators increases with the height they fly above the canopy. It is therefore interesting that *Platyscapa* and *Dolichoris* wasps, which flew the highest, are the pollinators of figs that are so rare. Conversely, the low proportion of *Waterstoniella* species from Pasoh that were also recorded at Lambir may reflect the fact that they fly close to the canopy and at night, when wind speeds are lower (Kumagai *et al.* 2001), and thus have a more limited dispersal range, leading to greater geographic isolation and higher rates of allopatric speciation.

Fig pollinators may be limited in how high they fly above the canopy by their ability to detect and respond to the volatile attractants released by receptive trees. Other things being equal, a larger crop will produce a bigger volatile plume. Thus, one would predict that rarer fig species, whose pollinators have to fly higher in order to disperse farther, should produce larger crops. Although there is substantial variation in crop sizes even within species, the overall trend is clearly in the predicted direction: *Platyscapa*-pollinated figs produce crops with several hundred thousand to over a million inflorescences; *Eupristina*-pollinated figs produce crops of several thousand to several hundred thousand inflorescences, but species with smaller crops have very large inflorescences that presumably have a greater volatile output; and *Waterstoniella* pollinate figs that normally produce crops of a few tens to a few thousand inflorescences (occasionally \approx 50 000 in the largest individuals) (Lambert & Marshall 1991, Shanahan & Compton 2001, data are lacking for *Dolichoris*-pollinated figs). Moreover, *Waterstoniella*-pollinated figs are predominantly subcanopy hemi-epiphytes, while *Eupristina*- and *Platyscapa*-pollinated figs are either large canopy or emergent hemi-epiphytes and stranglers, or banyans of open habitats (Harrison *et al.* 2003).

Captures in 2004 confirmed that *Platyscapa*, *Dolichoris* and *Eupristina* are day flying, and *Waterstoniella* night flying. The short life spans of these wasps and their vulnerability to predation by ants or other arthropods if they rest on vegetation suggest that, despite the distances moved, most dispersal may be limited to the first 12-h period following emergence. Further studies on the longevity of fig pollinators would be instructional.

Segregation into day- and night-dispersing pollinators may permit a degree of temporal partitioning in the release of attractant volatiles. Figs form diverse assemblages of species throughout the tropics (Harrison 2005), and so may need to employ various mechanisms, in addition to the release of a specific bouquet of volatiles (Grison *et al.* 2002), to attract the appropriate pollinator. Interestingly, while pollinators of a particular genus dispersed throughout either the day or night, there was variation among species in the frequency of capture in the first or second half of their activity periods. If corresponding variation in the production of volatile attractants is found, it would be strong evidence for this type of temporal partitioning.

Fig-fig wasp co-evolution

Studies of fig-fig-pollinator coevolution have to date focused on traits related to interactions that occur within the fig inflorescence (Herre 1989, Kjellberg *et al.* 2001, Molbo *et al.* 2003, Weiblen 2004). The role of the broader ecology of figs or fig wasps in determining evolutionary trajectories has been largely ignored. However, breeding system, growth form, density of reproductive individuals, and crop size are important niche parameters in figs, as in other plants, that correspond to other fundamental traits, such as physiology, habitat preferences and interactions with seed dispersers (Harrison 2005, Jusselin *et al.* 2003, Shanahan & Compton 2001). Our results indicate that the dispersal ecology of fig pollinators is also related to host niche. The paucity of dioecious-fig pollinators in our samples and the high turnover of species between years at Lambir indicate a major difference in their ecology compared to that of monoecious-fig pollinators. At a finer scale, among monoecious-fig-pollinating genera we found differences in flight behaviour that are consistent with differences in host ecology. These results thus extend our appreciation of the fig-fig-pollinator interaction beyond the confines of the fig inflorescence, and open a new perspective on the coevolutionary process.

Several instances of two or more sympatric pollinators on the same host have been reported (Kerdelhué *et al.* 1999, Lopez-Vaamonde *et al.* 2002, Molbo *et al.* 2003). In Panama, a detailed study examining multiple-pollinator coexistence did not detect any differences in post-dispersal measures of reproductive success (Molbo *et al.* 2003). However, in Africa it was found that two closely related,

sympatric pollinators on *F. sur* were adapted to dispersal in savannah and forest habitats, respectively (Kerdelhué *et al.* 1999). Cases of host switching may also be explained by dispersal ecology. In our study, the consistent differences in flight behaviour among monoecious-fig pollinators from different genera suggest niche conservatism. Hence, through a change of habitat or growth-form, a fig could potentially evolve into a new niche that was unsuitable to its pollinator, and thereby induce colonization by an alternative species. Interestingly in this respect, section *Urostigma* species resemble ecologically other monoecious hemi-epiphytic figs (Berg & Corner 2005, Harrison & Shanahan 2005), but are nested within a separate clade of mostly dioecious figs (Jusselin *et al.* 2003). However, their *Platyscapa* pollinators are more closely related to the other monoecious-fig-pollinating genera (Weiblen 2001). To understand the role of pollinator dispersal on the fig-fig-pollinator coevolutionary process will ultimately require more detailed phylogenies and further ecological information. In combination with the type of study presented here, seed paternity studies would be very instructional. We also suggest that people collecting fig wasps, in addition to noting the host species, make more effort to record habitat information.

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Appendix. Fig pollinator species (Agaoninae: Chalcidoidea) collected using sticky-traps suspended above the canopy at Lambir in 2001 (10 d) and 2004 (6 d), and Pasoh in 2003 (5 d) (+: indicates collection) that could be identified from keys and reference collections; their host *Ficus* species (? : presumed host because of morphological similarity to described pollinator); and the fig's presence or absence at Lambir, Borneo, and Peninsular Malaysia (+: indicates presence) (note: the fig flora of Pasoh is not known).

Pollinator species	Lambir		Pasoh		Host species		
	Lambir	Pasoh	Ficus	Lambir	Borneo	PM	
Monoecious fig pollinators							
<i>Deilagaon megorhopalum</i> Grandi	+		<i>F. cf. annulata</i>	+	+	+	
<i>Dolichoris cf. valentinae</i>	+		<i>F. pubinervis</i> Bl. (?)		+		
<i>Dolichoris n. nervosae</i> Hill	+		<i>F. nervosa</i> Heyne ex. Roth				
<i>Dolichoris n. philippinensis</i> Wiebes	+		<i>F. magnoliifolia</i> Bl.		+	+	
<i>Dolichoris vasculosa</i> Hill	+		<i>F. vasculosa</i> Wall	+	+	+	
<i>Eupristina verticillata</i> Waterston	+		<i>F. microcarpa</i> L.		+	+	
<i>Eupristina koningsbergii</i> Grandi	+		<i>F. benjamina</i> L.	+	+	+	
<i>Eupristina leightoni</i> Wiebes	+	+	<i>F. kerkhovenii</i> Val.	+	+	+	
<i>Eupristiina sp. nov.</i>	+		<i>F. spathulifolia</i> Corner	+	+	+	
<i>Platyscapa cf. fisheri</i>	+	+	<i>F. caulocarpa</i> Miq. (?)	+	+	+	
<i>Waterstoniella sp. nov.</i>	+	+	<i>F. xylophylla</i> (Miq.) Wall ex Miq.	+	+	+	
<i>Waterstoniella cuspidis</i>	+		<i>F. crassiramea</i> Miq.	+	+	+	
<i>Waterstoniella sp. nov.</i>	+		<i>F. subsecta</i> Corner	+	+	+	
<i>Waterstoniella javana</i> Wiebes	+		<i>F. retusa</i> L.	+	+		
<i>Waterstoniella malayana</i> Wiebes	+		<i>F. consociata</i> Bl.	+	+	+	
<i>Waterstoniella masii</i> Grandi	+	+	<i>F. stupenda</i> Miq.	+	+		
<i>Waterstoniella borneana</i> Wiebes	+	+	<i>F. binnendykii</i> Miq.	+	+	+	
<i>Waterstoniella brevigena</i> Wiebes	+		<i>F. pellucido-punctata</i> Griff.	+	+	+	
<i>Waterstoniella sp. nov.</i>	+		<i>F. soepadnoi</i> Kochummen	+	+	+	
<i>Waterstoniella sp. nov.</i>	+		<i>F. paracamptophylla</i> Corner	+	+		
<i>Waterstoniella calcaria</i> Wiebes	+		<i>F. sumatrana</i> var. <i>microsyce</i> Corner	+	+	+	
Dioecious fig pollinators							
<i>Blastophaga auratae</i> Wiebes	+		<i>F. aurata</i> Miq.	+	+	+	
<i>Lipporrhopalum cf. mindanaensis</i>	+		<i>F. heteropleura</i> Bl.	+	+	+	