

Fig wasp dispersal and the stability of a keystone plant resource in Borneo

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Recd 31.01.03; Accptd 13.03.03; Online 15.05.03

The stability of interactions in remaining rainforest fragments is an issue of considerable concern for conservation. Figs are a pre-eminent tropical keystone resource because of their importance for wildlife, but are dependent on tiny (1–2 mm) species-specific wasps for pollination. To investigate fig wasp dispersal I trapped insects at various heights (5–75 m) in an isolated fragment (ca. 4500 ha) of Bornean rain forest. Fig wasps constituted the majority of captures above the canopy (pollinators 47%, non-pollinators 5%). However, genera were not evenly represented. There were 50% more species of monoecious fig pollinator than there were host species in the fragment, indicating some must have arrived from forests with different assemblages of figs at least 30 km away. Dioecious fig pollinators were poorly represented suggesting more limited dispersal, which could account for higher endemism and vulnerability to catastrophic disturbance in all of these figs. Diurnal activity and flight height also varied among genera. Most non-pollinating fig wasps were very rare.

Keywords: *Ficus*; Agaonidae; pollination; mutualism; pollen dispersal

1. INTRODUCTION

Small, isolated fragments of natural habitat are a significant depository of terrestrial biodiversity in the tropics. Preserving the integrity of the biotic community in such fragments is, therefore, an important component of conservation efforts. However, the stability of mutualistic interactions in these relic patches is poorly understood. Keystone plant resources are recognized for their importance in sustaining wildlife, and in tropical rainforests pre-eminent among these are the figs (Moraceae: *Ficus*), whose combined year-round production of fruit support an enormous diversity of frugivorous mammals and birds (Shanahan *et al.* 2001).

Figs are speciose and ecologically diverse in tropical lowland forests and have coevolved with their obligate species-specific pollinators, the fig wasps (Chalcidoidea: Agaoninae) in one of the most intricate interactions found in nature (Herre 1989; Kjellberg *et al.* 2001; Machado *et al.* 2001). Fig wasp larvae develop inside a fig inflorescence, and to reproduce, the short-lived adult female wasps disperse, carrying pollen from their natal fig, to a tree with receptive inflorescences. They are weak fliers and

appear to disperse using wind (Ware & Compton 1994a,b) followed by short-range attraction to receptive trees using species-specific volatile cues (Song *et al.* 2001; Grison *et al.* 2002). Asynchronous flowering among fig trees ensures year-round availability of inflorescences, but flowering individuals may be widely separated. Phenological models (Bronstein *et al.* 1990) and paternity studies of several neotropical monoecious figs (Nason *et al.* 1998) concluded that breeding populations constituted several hundred individuals, and estimated routine pollinator dispersal at 5–14 km (Nason *et al.* 1998). Therefore, given the low densities of these species, they suggested that small reserves could not support viable populations and must be dependent on a wider population of figs in the surrounding matrix (Nason *et al.* 1998).

However, these studies were conservative and did not take account of wind direction, and fig wasps have been caught at light-traps on ships up to 99 km offshore in the Pacific (Harrell & Holzapfel 1966). Moreover, the generality of predictions about fig wasp dispersal based on studies of a few similar species is questionable, given the existence of different breeding systems (monoecy and dioecy) and a tremendous diversity of life-forms among figs.

Here, I present evidence for substantial differences in pollinator dispersal among figs in Borneo.

2. MATERIAL AND METHODS

Over a 10 day period in August 2001 I used non-attracting sticky-traps (Compton *et al.* 2000) suspended from a crane and two towers at Lambir Hills National Park (LHNP) (40°20' N, 113°50' E; ca. 4500 ha lowland dipterocarp forest), Sarawak, Malaysia to catch fig wasps and other small insects. As LHNP has an aseasonal climate and figs have a year-round, asynchronous flowering phenology (Harrison 2000), this sample can be considered representative. Each sticky-trap was made from a pair of empty 1.5 l (surface area of ca. 0.079 m²) clear-plastic bottles suspended end-to-end on a string and painted with an odourless sticky coating (Tanglefoot). Traps were suspended at 10 m height intervals (crane, 5–75 m; towers, 5–45 m), and three lines of traps ca. 15 m apart were used at the crane and one each at the towers. The surface of the canopy was ca. 35 m high at the crane and 45–55 m at the towers. Traps were checked at dawn and dusk on the crane and at noon at the towers. Fig wasps and other chalcids were collected, and other insects counted. Data from the towers were used only for analyses of species abundance.

Fig wasps were identified to genus using available keys (Boucek 1988) and species separated using a matrix of 42 morphological characters (Weiblen 2001). Details on the fig flora of LHNP are given in electronic Appendix A, available on The Royal Society's Publications Web site, and data on the regional flora were obtained from Corner (1965).

3. RESULTS

Fig wasps constituted the majority of insects caught above the canopy (≥ 45 m): fig pollinators 47% and non-pollinators 5%, diptera 19% and coleoptera 15%. They flew significantly higher than other insects (ANOVA $F_{1,1375} = 266.7$, $p < 0.001$). Out of 430 in total only 17 fig pollinators were captured on the towers.

Forty-three species of monoecious fig pollinator were caught over the 10 day period (table 1). This is 50% more species than there are host fig species occurring in the park and surrounding area. Moreover, the pattern of higher pollinator diversity than local host fig diversity was consistent across all monoecious fig-pollinating genera. In an interesting contrast, the pollinators of dioecious figs were underrepresented and less than 25% of the predicted fauna for LHNP was collected. Species abundances of dioecious fig pollinators were also very uneven (figure 1a). Out of 115 individuals 66 captures were of one species.

Table 1. The number of fig-pollinator species caught by sticky-traps over 10 days at LHNP, Sarawak, the number of host fig species in LHNP (electronic Appendix A) and Borneo (Corner 1965), and the proportion of endemic fig species in Borneo and in New Guinea (Corner 1965).

fig-pollinator genera	no. of fig-pollinator species	no. of host fig species		proportion of endemic figs	
		LHNP	Borneo	Borneo	New Guinea
monoecious fig pollinators					
<i>Deilagaon</i>	2	1	4	0.0	0.0
<i>Dolichoris</i>	4	1	5	0.0	0.3
<i>Eupristina</i>	17	8	11	0.1	0.4
<i>Platyscapa</i>	3	2	3	0.0	0.0
<i>Waterstoniella</i>	17	16	21	0.1	0.0
all genera	43	28	44	0.1	0.2
dioecious fig pollinators					
<i>Blastophaga</i>	1	11	19	0.5	0.0
<i>Ceratosolen</i>	2	13	28	0.5	0.5
<i>Kradibia</i>	1	1	6	0.3	0.2
<i>Lipporhopalum</i>	3	10	14	0.4	0.2
<i>Wiebesia</i>	5	14	29	0.4	0.9
all genera	12	49	96	0.5	0.6

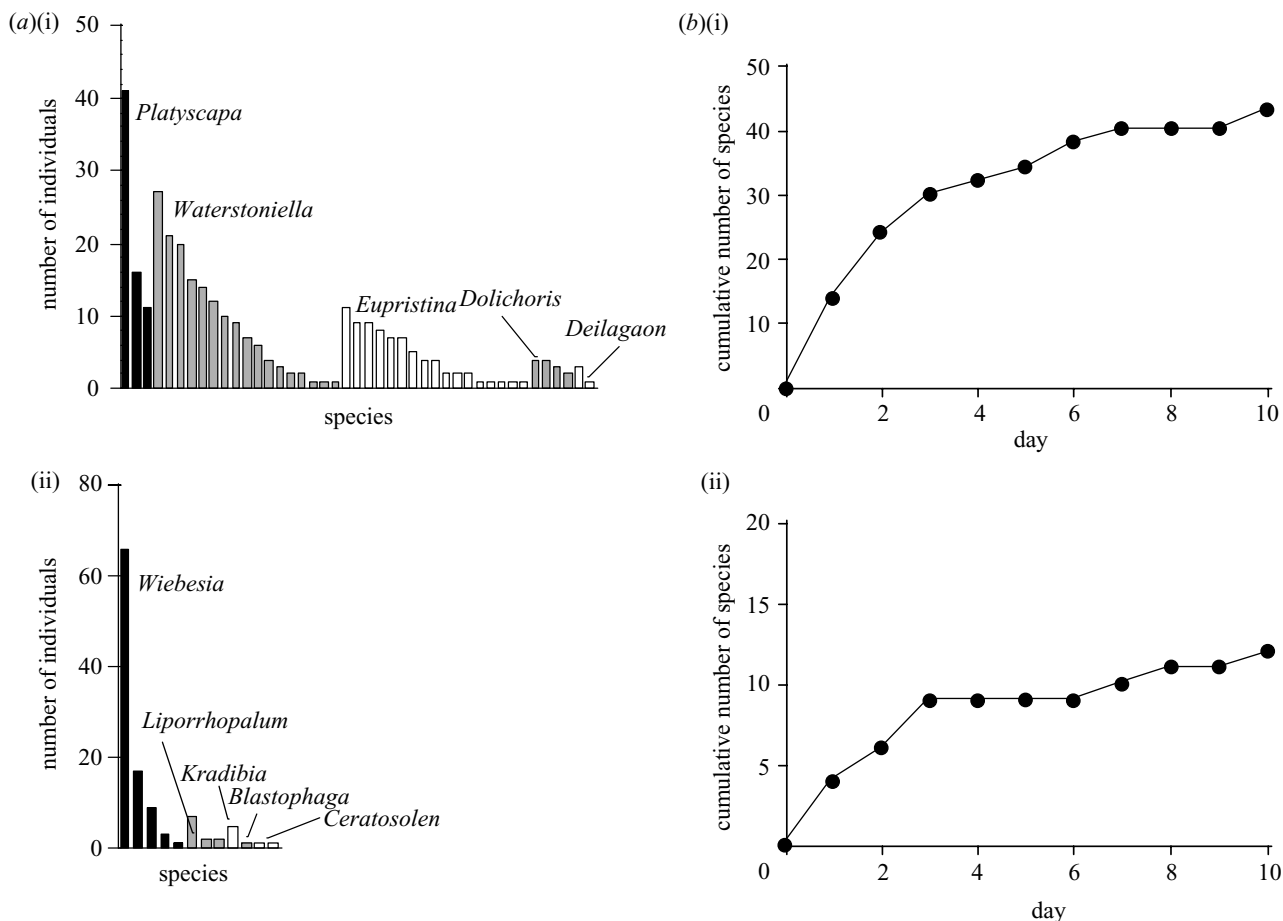


Figure 1. (a) Species abundances of fig pollinators caught on sticky-traps over a 10 day period at LHNP. (i) Monoecious fig pollinators and (ii) dioecious fig pollinators. Different shading patterns represent different genera of pollinators as indicated on the figure. (b) Cumulative number of fig-pollinator species caught on sticky-traps over a 10 day period at LHNP. (i) Monoecious fig pollinators and (ii) dioecious fig pollinators.

By comparison, out of 315 monoecious fig pollinators the most abundant species had just 41 individuals. However, both monoecious and dioecious fig pollinating species were well sampled (figure 1b).

Differences in dispersal behaviour were also evident among genera. Species within a genus were either day or night dispersing (figure 2). Day-dispersing wasps were dark brown, while night-dispersing wasps were yellowish.

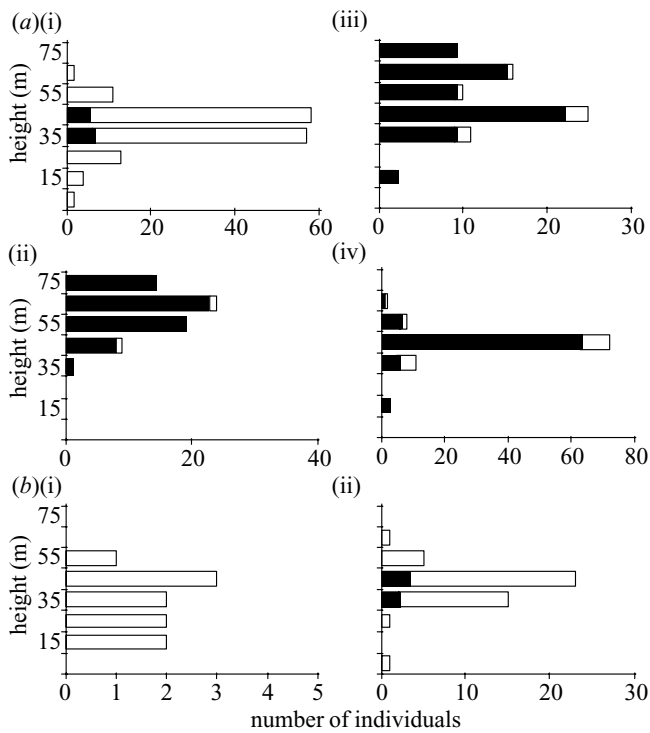


Figure 2. Diurnal activity and flight heights among common genera of fig wasps. (a) Pollinators (monoecious fig pollinators: (i) *Waterstoniella*, (ii) *Platyscapa*, (iii) *Eupristina*; and dioecious fig pollinators: (iv) *Wiebesia*). (b) Non-pollinators ((i) *Dziatiella*; (ii) *Epichrysmallinae* A). Filled bar segments represent daytime captures and open bar segments represent night-time captures. There were significant differences in flight height among all pollinator genera (ANOVA $F_{3,378} = 78.9$, $p < 0.001$; *post hoc* comparisons with Bonferroni correction, $p < 0.001$). *Platyscapa* flew highest, followed by *Eupristina*, *Wiebesia* and *Waterstoniella*. Flight heights among *Waterstoniella*, *Dziatiella* and *Epichrysmallinae* A were not significantly different but were significantly lower than the other monoecious fig-pollinating genera (ANOVA $F_{4,338} = 55.8$, $p < 0.001$; *post hoc* comparisons with Bonferroni correction, significance at $p = 0.05$ level). Both non-pollinating genera are associated with *Waterstoniella* pollinated figs and thus, flight heights among fig wasp genera associated with the same figs were not significantly different. *Epichrysmallinae* A is an undescribed genus that has been previously collected and studied by J.-Y. Rasplus (personal communication).

There were also significant differences in flight height among genera (figure 2; ANOVA $F_{3,378} = 78.9$, $p < 0.001$). Considering genera together, monoecious fig pollinators flew significantly higher than dioecious fig pollinators (ANOVA $F_{1,411} = 4.04$, $p < 0.05$).

Non-pollinating fig wasps were rare. Only two genera had more than five individuals (figure 2). Both are associated with monoecious figs pollinated by *Waterstoniella* and morphological convergence with pollinators indicates that they enter the inflorescences to oviposit. Like *Waterstoniella*, both genera were night dispersing and yellowish in colour, and flew just above the canopy (figure 2).

4. DISCUSSION

Fig wasps clearly appear to be using wind-assisted dispersal (Ware & Compton 1994a,b). They were found

predominantly above the canopy and flew significantly higher than other insects (Compton *et al.* 2000). There may be some trap bias in these results, as capture rates may be lower beneath the canopy owing to reduced wind speeds. However, such bias is unlikely to explain the differences among insect groups. Moreover, birds feeding above the canopy in a neotropical rainforest were found to have a high proportion of fig wasps in their crops (Hespenheide 1975). Nevertheless, the abundance of fig wasps above the canopy is remarkable. Fig trees often produce very large crops (104–106 inflorescences) and several tens to hundreds of wasps may emerge from a single inflorescence. Hence, the production of fig wasps in tropical forests may be very high. Poorer captures of fig wasps on the towers in this study and in a previous study in Sabah (Compton *et al.* 2000) are most probably explained by the fact that traps did not reach above the canopy.

A greater number of monoecious fig-pollinator species than there are host species in LHNP can have two possible explanations. Either there is a breakdown in the specificity of the fig–fig wasp interaction such that there are multiple wasp species per host, or fig wasps are arriving from areas with different assemblages of figs. Breakdown in specificity is rare and usually allopatric (Rasplus 1994), although recently in Panama, pairs of morphologically similar pollinator species coexisting on the same fig were identified genetically (Molbo *et al.* 2003). However, in this study only morphological characters were used, hence such cryptic species if they exist in Borneo are unlikely to have been detected. Moreover, low densities and infrequent flowering (Harrison 2000) make it improbable that in a single 10 day period pollinators could have emerged from every monoecious fig species at LHNP. Therefore, monoecious fig pollinators must have been arriving from forests with different assemblages of figs. The nearest potential source areas lie 30 km from LHNP, but the diversity of the fauna suggests they may have been arriving from much further away.

Dioecious fig pollinators were underrepresented and only 25% of the predicted fauna of LHNP was collected. Poor captures cannot be explained by a low abundance of flowering figs because many are common pioneer species (electronic Appendix A) with high flowering frequencies (Patel 1996; Harrison 2000). Smaller crop sizes could account for low capture rates of some species. However, the high density of receptive trees nullifies the need for long-distance pollinator dispersal. In these figs, short-distance active dispersal is probably more common and would explain why the sticky-traps intercepted so few species. Nevertheless, of the species caught, most individuals were found above the canopy. Thus, the relative importance of active and passive dispersal probably varies among species, and may be related to the density of host figs and their canopy position. For example, *Wiebesia*, which was the only common dioecious fig-pollinating genus, is associated with climbing figs.

Compared with dioecious figs, monoecious figs have very low rates of endemism (table 1): a full 23% of the Bornean monoecious fig flora is shared with New Guinea (Corner 1965). Also, following a catastrophic El Niño drought in 1998 when dioecious fig pollinators were extirpated from LHNP and took from one month to 3 years to return, monoecious fig-pollinator populations

recovered immediately (Harrison 2001). A difference in the range of pollinator dispersal that is correlated to fig breeding system would explain these observations.

Differences in diurnal activity and flight height among genera suggest a further correlation between fig wasp dispersal and fig biology. The diurnal cycle of pollinator dispersal could be related to the release of volatiles from receptive figs, the activity of predators (Hespenheide 1975) or wasp physiology. Wind speeds above the canopy are also higher during the day and increase with distance above the canopy. Hence, day flying and flying higher may be associated with increased dispersal range. *Waterstoniella* flew at night and closer to the canopy than the other monoecious fig-pollinating genera (figure 2). Hence, it is interesting that it had fewer 'extra' species (table 1). Moreover, common non-pollinators were associated with figs pollinated by *Waterstoniella* and also flew at night and just above the canopy. It is noteworthy that they were species that oviposit within the inflorescence. Non-pollinators of the much more species-rich assemblages that oviposit through the inflorescence wall (Boucek 1988) were very rare: whether this reflects lower abundance or different dispersal behaviour is unknown.

In tropical forests fig fruit are a renowned keystone resource. Long-distance dispersal of monoecious fig pollinators, linking fig populations between isolated forest fragments, will clearly stabilize this valuable resource. It explains the high pollination success of monoecious figs and suggests that they can support diverse coterie of frugivores even in small forest patches. In the case of dioecious figs, high densities and flowering frequencies will normally stabilize pollinator populations and, thereby, fruit production for many species. However, the slow recovery of dioecious fig-pollinator populations following the 1998 El Niño drought illustrates how they may be more vulnerable to isolation or climate change (Harrison 2000). The ecological diversity among figs questions the validity of the keystone epithet. Species vary in their importance to frugivores (Shanahan *et al.* 2001), but pioneer species with smaller frugivore assemblages are important in forest succession, and variation in pollinator dispersal suggest species will respond differently to disturbance and isolation.

The results presented here indicate that there is substantial variation in fig wasp dispersal. Monoecious fig pollinators clearly disperse substantial distances (more than 30 km), even further than previously reported (Nason *et al.* 1998). However, many dioecious fig pollinators appear to have a more restricted dispersal. Fig wasp genera also differed in diurnal activity and flight height. How differences in pollinator dispersal relate to the balance of fig-wasp interaction will be an interesting topic for further investigation.

Acknowledgements

I am grateful to the Forest Department Sarawak and the Canopy Biology Programme for use of the facilities at LHNP, to George

Weiblen, Finn Kjellberg and Jean-Yves Rasplus for advice on fig wasp identification, and to Allen Herre, Drude Molbo and two anonymous reviewers for comments on earlier drafts of this manuscript. The Japanese Society for the Promotion of Science funded this study.

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