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

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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 monocoeious 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 keystone monoecious figs (Nason et al. 1998) 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).

<table>
<thead>
<tr>
<th>fig-pollinator genera</th>
<th>no. of fig-pollinator species</th>
<th>no. of host fig species</th>
<th>proportion of endemic figs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LHNPA</td>
<td>Borneo</td>
<td>Borneo</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>New Guinea</td>
</tr>
<tr>
<td>monoecious fig pollinators</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deilagoon</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Dolichoris</td>
<td>4</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Eupristina</td>
<td>17</td>
<td>8</td>
<td>11</td>
</tr>
<tr>
<td>Platyscapa</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Waterstoniella</td>
<td>17</td>
<td>16</td>
<td>21</td>
</tr>
<tr>
<td>all genera</td>
<td>43</td>
<td>28</td>
<td>44</td>
</tr>
<tr>
<td>dioecious fig pollinators</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blastophaga</td>
<td>1</td>
<td>11</td>
<td>19</td>
</tr>
<tr>
<td>Ceratosolen</td>
<td>2</td>
<td>13</td>
<td>28</td>
</tr>
<tr>
<td>Kradibia</td>
<td>1</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Liporrhopalum</td>
<td>3</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>Wiebesia</td>
<td>5</td>
<td>14</td>
<td>29</td>
</tr>
<tr>
<td>all genera</td>
<td>12</td>
<td>49</td>
<td>96</td>
</tr>
</tbody>
</table>

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) Diaziella; (ii) Epichrysomallinae A). Filled bar segments represent daytime captures and open bar segments represent night-time captures. There were significant differences in flight height among 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, Diaziella and Epichrysomallinae A were not significantly different but were significantly lower than the other monoecious fig-pollinating genera (ANOVA \( F_{3,376} = 55.8, \ p < 0.001 \); 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. Epichrysomallinae 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 \( F_{3,411} = 4.04, \ p < 0.05 \)).

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 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. Waterstonella flew at night and closer to the canopy than the other monocious 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 Waterstonella and also flew at night and just above the canopy. It is noteworthy that they were species that oviposited within the inflorescence. Non-pollinators of the much more species-rich assemblages that oviposited 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 monocious fig pollinators, linking fig populations between isolated forest fragments, will clearly stabilize this valuable resource. It explains the high pollination success of monocious figs and suggests that they can support diverse coteries 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. Monocious 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–fig wasp interaction will be an interesting topic for further investigation.

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