



Original article

Ecology of a fig ant–plant

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ABSTRACT

Mutualistic interactions are embedded in networks of interactions that affect the benefits accruing to the mutualistic partners. Figs and their pollinating wasps are engaged in an obligate mutualism in which the fig is dependent on the fig pollinator for pollination services and the pollinator is dependent on fig ovules for brood sites. This mutualism is exploited by non-pollinating fig wasps that utilise the same ovules, but do not provide a pollination service. Most non-pollinating wasps oviposit from outside the inflorescence (syconium), where they are vulnerable to ant predation. *Ficus schwarzii* is exposed to high densities of non-pollinating wasps, but *Philidris* sp. ants patrolling the syconia prevent them from ovipositing. *Philidris* rarely catch wasps, but the fig encourages the patrolling by providing a reward through extra-floral nectaries on the surface of syconia. Moreover, the reward is apparently only produced during the phase when parasitoids are ovipositing. An ant-exclusion experiment demonstrated that, in the absence of ants, syconia were heavily attacked and many aborted as a consequence. *Philidris* was normally rare on the figs during the receptive phase or at the time of day when wasp offspring are emerging, so predation on pollinators was limited. However, *Myrmecaria* sp. ants, which only occurred on three trees, preyed substantially on pollinating as well as non-pollinating wasps. *F. schwarzii* occurs in small clusters of trees and has an exceptionally rapid crop turnover. These factors appear to promote high densities of non-pollinating wasps and, as a consequence, may have led to both a high incidence of ants on trees and increased selective pressure on fig traits that increase the payoffs of the fig–ant interaction for the fig. The fig receives no direct benefit from the reward it provides, but protects pollinating wasps that will disperse its pollen.

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1. Introduction

Mutualistic interactions are a special case of mutual exploitation that results in a net reproductive benefit accruing to each species. They are open to exploitation by one or other of the partners, or other species that usurp resources without benefiting either partner. Nonetheless, mutualisms are ubiquitous in nature and understanding the factors that promote their stability is a major focus of co-evolutionary biology. Increasingly, researchers recognise the importance of factors that maintain an alignment of interests between the partners in the face of environmental variation and, in particular, variation in the network of interactions within which a mutualism is embedded (Hartley and Gange, 2009; Palmer et al., 2008; Scott et al., 2008).

Figs (*Ficus* spp.) and their pollinating wasps (Agaoninae, Chalcidoidea) are an established model mutualistic system (Cook and

Rasplus, 2003; Herre et al., 2008). Figs bear closed, urn-shaped inflorescences (syconia) that are lined on the inside by the plant's tiny flowers. The highly specific fig pollinators are able to enter the inflorescence through a narrow bract-lined passage during the phase when the fig's female flowers are receptive. Once inside, they pollinate the flowers and lay eggs in some ovules. Ovules that receive an egg develop into a gall within which the wasp larva feeds and matures. In a monoecious fig, pollinated ovules that do not receive an egg develop into a seed in the normal way. Hence, both wasp larvae and seeds develop within the same syconium. In a dioecious fig, syconia on different trees are specialised to either the female (seed production) or the male (pollinator and pollen production) roles (Galil, 1973; Harrison and Yamamura, 2003). On female trees, the pollinating wasp enters the syconium and pollinates but fails to lay any eggs and only seeds are produced. It is a form of deceit pollination. On male trees, the female flowers are modified for receiving a pollinator egg and only wasp larvae develop. Approximately one month after pollination, the male wasp offspring emerge and mate with the gall-enclosed females. The female wasps then enlarge the hole used by the male mating organ and emerge into the lumen of the syconium. Coincident with this

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phase, the syconium's male flowers bear ripe pollen. Thus, the female wasps disperse, usually exiting through a tunnel cut by the male wasps, carrying pollen from their natal fig. They have a short adult life span (<1–3 days depending on the species; Kjellberg et al., 1988; Jevanandam et al., 2013), and must find a receptive fig to reproduce. After the emergence of the wasps on a monoecious fig or at maturity on a female dioecious fig, the syconia develop into fig fruit (infructescences), which are eaten by a diversity of vertebrate frugivores (Shanahan et al., 2001).

The fig – fig pollinator interaction is at least 75 Myrs old and there are >750 extant fig species (Rønsted et al., 2005; Cruaud et al., 2012). In large part, the success of the system may be attributed to the close alignment of the reproductive interests between figs and their pollinators: the fig is entirely dependent on the wasp for pollination and the fig wasp is dependent on fig syconia for rearing its brood. Nonetheless, as with other mutualisms, the fig – fig pollinator system is exploited by a large number of other species. A diversity of non-pollinating fig wasps (Chalcidoidea: Agaonidae; Pteromalidae; Ormyridae; Eurytomidae; and Torymidae) utilise syconia for rearing brood, but do not pollinate (Al-Beidh et al., 2012; Bronstein, 1991; Compton, 1992; Compton and Hawkins, 1992; Cruaud et al., 2011; Elias et al., 2008; Joussetin et al., 2001; Kerdelhué and Rasplus, 1996; Lopez-Vaamonde et al., 2001; Marussich and Machado, 2007; McLeish et al., 2010; Munro et al., 2011; Pereira et al., 2007; Pereira and Do Prado, 2005; Proffit et al., 2007; West and Herre, 1996). Most of these species do not enter the syconium, but insert their ovipositor through the syconium wall to lay their eggs. Non-pollinators may be gallers, which may compete with the pollinator for ovules (e.g. Peng et al., 2010; Pereira et al., 2007; West and Herre, 1996), or inquiline (gall parasites) (e.g. Pereira and Do Prado, 2005) or parasitoids (Tzeng et al., 2008). An inquiline or parasitoid larva kills its host, usually a gall larva, and therefore these species can substantially impact the reproductive success of their host species. There is increasing evidence that non-pollinators may be less specific to particular fig hosts than the pollinators (Cruaud et al., 2011; Lopez-Vaamonde et al., 2001; Marussich and Machado, 2007; McLeish et al., 2010). Fig wasps, both pollinators and non-pollinators, are also preyed upon by a diversity of invertebrate and vertebrate predators. It is a common sight to see dragonflies and wasps swooping back-and-forth above a large fig tree when it is releasing wasps, and over 80% of the diet of swifts in Panama was found to be composed of fig wasps (Hespenheide, 1975). Other predators hunt fig wasps on the syconia and especially important among these are ants (Bain et al., 2014).

Ants have sometimes been shown to have a positive impact on the fig – fig pollinator interaction through their predation of non-pollinating wasps (Compton and Robertson, 1988; Cushman et al., 1997; Dejean et al., 1997; Schatz et al., 2006; Schatz and Hossaert-Mckey, 2010; Wei et al., 2005). Many non-pollinators are vulnerable to ant predation, because they oviposit through the wall of the syconium and therefore cannot escape if ants disturb them while ovipositing. Nevertheless, in the fig species investigated so far, there is nothing to suggest any direct interaction between the fig and the ants (Bain et al., 2014). Any net benefit that accrues to the fig – fig pollinator interaction is incidental to the fact that the ants are insect predators and that non-pollinating fig wasps tend to be more vulnerable to predation than pollinators.

A few fig species would appear to be true ant–plants in that they provide food rewards or domatia for the ants (Webber et al., 2007), but the role of the ants in these species has not yet been investigated. *Ficus schwarzii* provides a direct reward to the ants at a particular point in the crop development, when non-pollinating wasps are ovipositing, and in doing so helps protect the pollinator larvae. Here, I describe the ecology of this species and its

interactions with fig wasps and ants. Over a four year period from 1994 to 1998 I studied the reproductive phenology of a small group of 27 individuals of *F. schwarzii*. Simultaneously, I recorded the abundance of fig wasps including the pollinator and three species of non-pollinating fig wasp on sticky-traps set in each tree. In addition, upon recognising that ants were an important part of the system, I recorded the relative abundance of ants on each individual. The duration of data on fig reproductive phenology, and its integration with data on the phenology of wasp populations and ant activity is unprecedented among studies on *Ficus*, and allows insights into these relationships that would otherwise be impossible.

2. Methods

This research was conducted in a lowland tropical rain forest at Lambir Hills National Park (Lambir, 4° 20' N, 113° 50' E asl 50–450 m), Sarawak, Malaysia. The park has an aseasonal climate with over 100 mm of rainfall on average every month, and approximately 2900 mm total rainfall annually. However, short droughts are not infrequent and severe droughts, with biological consequences, may be associated with strong El Niño events. Lambir is one of the most diverse forests yet studied, with a fig flora comprising over 80 species (Harrison and Shanahan, 2005).

F. schwarzii Koord (section *Sycocarpus*) is a small (8–10 m) functionally dioecious fig tree. It is common throughout Sarawak and widely distributed in SE Asia (Berg and Corner, 2005). It often occurs in clusters of several individuals along streams, particularly in places where there has been recent disturbance (Berg and Corner, 2005). It is cauliflorous and its syconia are borne in bunches from specialised branchlets along the trunk (Fig. 1m). In 1994 to 1998 I studied a relatively isolated group of 16 male and 11 female trees. No other individuals were found within approximately 500 m of the site, although the species occurred elsewhere in the park.

I conducted phenology censuses at 10 day intervals recording the number of syconia and crop stage (inter-crop (int), immature (imm), receptive (rec), post-pollination (pp), pollen dispersal (mal) or ripe fruit; Galil and Eisikowitch, 1968; Harrison, 2005) for each individual. The short duration of receptivity meant this phase was sometimes missed. In such cases, receptivity was assumed to have occurred mid-way between consecutive observations of immature and post-pollination stages and to have lasted 5 days.

Four species of wasp have been recorded on *F. schwarzii* in Lambir (Harrison, 2000a). The pollinator (*Ceratosolen vetustus* Wiebes) and three non-pollinating species; *Sycophaga* sp., *Philotrypesis* sp. and *Apocrypta* sp. *Sycophaga* is a galller and is able to form galls in unpollinated syconia (Harrison, 2000a). Based on the timing of oviposition and its impact on the production of pollinators, *Philotrypesis* is probably an inquiline of the pollinator, and *Apocrypta* is probably a parasitoid. All three non-pollinator species oviposit through the syconium wall (Fig. 1c–e). To investigate the abundance of wasps with respect to crop phase, yellow sticky-traps were tied in the trees and censused periodically from February 1995 to October 1998 (Fig. 1l, Bronstein, 1987; Harrison, 2000a; Harrison, 2000b; Harrison and Rasplus, 2006; Ware and Compton, 1994). Yellow-traps were used to increase the short-range attraction of wasps to the traps once they had arrived at the tree, although with hind-sight this was probably not necessary. Longer range attraction of fig wasps to fig trees is effected through volatile cues (Proffit et al., 2007), hence it is unlikely that the colour distorted patterns of natural attraction at this scale. The traps were constructed from PVC pipe (30 cm long × 10 cm diameter) and spray-painted yellow. Tanglefoot was applied to them as necessary. Individual censuses comprised five-day periods and any wasps on

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