Acta Oecologica 57 (2014) 88–96

Contents lists available at SciVerse ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Ecology of a fig ant–plant

Rhett D. Harrison*

Key Laboratory for Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China

A R T I C L E I N F O

Article history:
Received 18 January 2013
Accepted 24 May 2013
Available online 21 June 2013

Keywords:
Agaonidae
Ant–plant
Ficus
Pollinator
Parasitoid
Trophic interactions
Tropical forest

A B S T R A C T

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, *Myrmicaria* 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.

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

---

* Current address: World Agroforestry Institute East Asia Node, Kunming 650201, China.

E-mail addresses: r.harrison@cgiar.org, rhett_d_harrison@yahoo.co.uk.

1146-609X/$ – see front matter © 2013 Elsevier Masson SAS. All rights reserved.
http://dx.doi.org/10.1016/j.actao.2013.05.008

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; Jousselin 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 inquilines (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 galler 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 swifts 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 it 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 galler 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

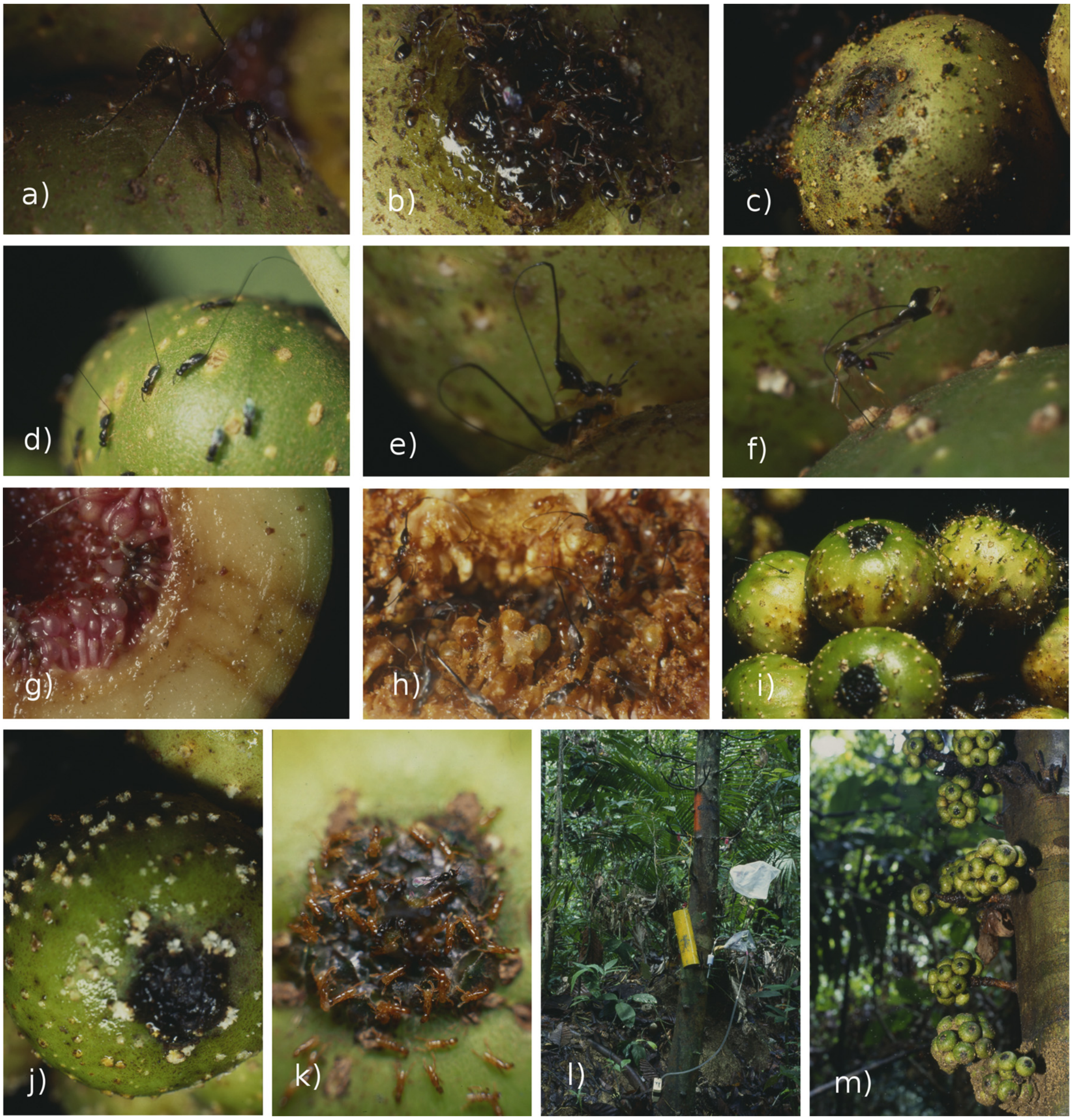

Fig. 1. Photographic illustrations of the ecology of *Ficus schwarzii*. (a) Worker individual of *Myrmicaria* sp. waiting on the surface of a syconium. (b) *Philidris* sp. workers catching non-pollinating wasps as they emerge from a mature syconium. (c) *Philidris* sp. workers on the surface of a mature syconium after the wasps have emerged. (d) *Sycophaga* sp. ovipositing. (e) *Philotrypesis* sp. ovipositing. (f) *Apocrypta* sp. ovipositing. (g) Damaged caused by ovipositor insertions of *Sycophaga* sp. in a female syconium – note that the ovules were damaged but no galls developed. (h) Non-pollinating wasps, mostly *Philotrypesis* sp., trapped in the lumen of a mature syconium, because there were insufficient pollinator males to cut an exit tunnel. (i) *Philotrypesis sp*. ovipositing – note that the ovipositing individuals are highly aggregated, while single individuals are not ovipositing. (j) Extra-floral nectaries on the surface of the syconium: This syconium was bagged to prevent ant access which resulted in the excretory cells growing out of the glands. (k) Pollinating wasps emerging from a syconium. The male wasps cut the tunnel and then spill over the surface. The female wasps follow close behind, emerging rapidly and flying directly from the tunnel exit (about four individuals can be seen emerging simultaneously in this photograph). (l) A study individual of *F. schwarzii*. The cylinder is a yellow sticky-trap. On the trunk a square is marked (the background is bright orange) for conducting 5-min ant counts. To the right is a set-up for collecting the syconium volatiles using the headspace method (not covered in this paper). (m) Pollinating wasps arriving at a tree with receptive syconia. Close inspection of the area to the left reveals reflections from the wings of the wasps as they hover in front of the syconia selecting a suitable one to enter.

the traps were cleaned off at the start of the period. Simultaneously, the phenology of each tree was recorded, so that wasp captures and phenology could be directly correlated (these observations were in addition to the regular phenology census conducted at 10-day intervals). Traps on trees with emerging wasps were removed, since I was interested in capturing wasps arriving at trees. Adult wasp populations fluctuated within the group of trees under observation causing periods of wasp scarcity and, after January 1998, all four species became locally extinct at Lambir due to severe drought (Harrison, 2000a). Hence, I only use data from trap censuses that had >10 individuals, when summed across all species and trees (67 five-day trapping periods; total number of observations per crop stage (i.e. trees × census per crop stage), inter-crop = 62, immature = 157, receptive = 60, post-pollination = 113). Simultaneous with collections of wasps from sticky-traps, I made qualitative observations of the behaviour of wasps at the trees. Such observations usually lasted 1–5 min at each tree, but were occasionally extended (up to ~2 h) when observing interactions between wasps and ants.

Ants did not nest in the trees but patrolled them regularly. Thus, to assess ant activity on the trees I conducted 5-min direct counts of the number of individuals crossing a 10 cm wide square marked on the trunk. Tanglefoot was used to ring the remainder of the trunk so that all ant traffic up and down the trunk was forced to pass over the marked square (Fig. 1l). Counts were conducted mid-morning and repeated at 10 day intervals from November 1994 to June 1995 at the same time as the observations of fig phenology. To investigate the impact of ants on the numbers of non-pollinating fig wasps, an ant exclusion experiment was conducted on two male trees in March 1995. Tanglefoot was applied to the base of selected branchlets to prevent ants accessing the syconia. Controls had Tanglefoot applied, but bridges were built across the obstruction using bark found in the leaf litter. Control and treatment branchlets were interspersed along the length of the trunk. There were 10 and 8 treatment and control branchlets, respectively, on one tree and 8 and 4, respectively, on the other. The experiment was started immediately before the receptive period, as indicated by the initial arrival of pollinators. After approximately two weeks, syconia began rapidly aborting from treatment branches (see Results section). As I was unable to retrieve aborted syconia from the ground, I harvested the remaining syconia after 18 days (approximately 50% of their post-pollination development time) to assess the cause of their abortion. At this time, all the syconia remaining on treatment branches had bruised and shrivelled walls and would most likely have aborted within a few days. I measured the diameter of the harvested syconia and opened them to inspect the contents. The ants species were identified by S. Yamane, with vouchers held by him at Kagoshima University.

Also in March 1995, I investigated the diurnal pattern of wasp emergence at three male trees. At each tree 5–6 bunches were marked and the initial number of syconia counted. Then, the number of syconia from which wasps had emerged were counted at 06:30, 09:30, 12:30 and 18:30 every day over the emergence period (i.e. until wasps had emerged from all syconia). Counts of ants were conducted simultaneously. Dawn and dusk were approximately 07:00 and 19:00, respectively. The proportion of syconia that had emerged between each count was then calculated for each tree.

To examine the differences in phenology among sexes I used linear mixed models with tree as a random effect (function *aov*). To examine changes in the numbers of ants against crop stage, I used GLMs and set *a priori* contrasts (function *contrasts*) to compare each crop phase with the following phase. Because many data were over-dispersed, I employed both ordinary GLMs and zero-inflated GLMs (package *pscl*), which combine a count model with a binomial (link = logit) model, and used Vuong non-nested hypothesis test statistic (function *vuong*) to select the most appropriate model. Tree was included as a block factor and I examined models with both Poisson and negative-binomial error distributions. The effect of treatment on the rate of loss of syconia from branchlets during the ant-exclusion experiment was estimated using a binomial model (present, lost), with tree and branchlet entered as random effects (function *lmer*, package *ade4*). The effect of treatment on the diameter of remaining syconia in the ant exclusion experiment was investigated using a linear mixed model with tree as a random effect (function *aov*). All analyses were conducted using R v2.14.1 (R Development Core Team, 2011).

3. Results

3.1. Phenology of Ficus schwarzii

Male and female *F. schwarzii* showed strong differences in reproductive phenology (Table 1). The development time up until receptivity was similar (~1 month), but post-pollination development and ripe fruit phase (versus wasp emergence phase) were much longer on female trees. However, crops on female trees overlapped, whereas those on male trees were always separated by a short syconia-free inter-crop period. So, the turnover of crops was similar among sexes (~85 days). Trees of both sexes were essentially fruiting continuously and produced over four crops per year.

Table 1
Length of crop development phases and the inter-crop period (days, mean ± se) on male and female trees of *F. schwarzii*. Mature phase corresponds to the wasp emerging phase on male trees and the ripe fruit phase on female trees. Significance of the difference in the means between sexes was tested using a linear mixed model with tree as a random effect.

	Immature	Receptive	Inter-floral	Mature	Inter-crop period
Female	37.7 ± 1.47	6.9 ± 0.52	51.6 ± 4.23	21.2 ± 1.90	87.2 ± 5.99
Male	34.0 ± 2.14	7.0 ± 0.45	33.8 ± 1.21	10.3 ± 0.68	82.5 ± 2.69
	NS	NS	$p < 0.0001$	$p < 0.0001$	NS

Mean duration of receptivity was estimated as being approximately 1 week on both male and female trees (Table 1). However, the data on receptivity were skewed, because this phase was sometimes extended if wasps were rare (median = 5 days in both sexes). Moreover, the duration of receptivity was possibly somewhat over-estimated as the census interval (10 days) was too long to estimate this short phase accurately. From direct observation of wasps entering syconia, most crops completed their receptive period within about 3 days if pollinators were available.

3.2. Sticky-trap captures

For all wasp species, the number of wasps captured on sticky-traps varied substantially with crop stage (Fig. 2). The pollinator (*Ceratosolen vetustus*) was captured in large numbers during the receptive period, but was much rarer at other stages (Fig. 2a). *Sycophaga* were also caught in large numbers during the receptive phase and much lower numbers at other times (Fig. 2b). Overall, the captures of *Philotrypesis* and *Apocrypta* were much lower. Captures of both species initially peaked during the receptive phase. *Philotrypesis* abundance continued to be high through the first 10 days of the post-pollination period and then declined (Fig. 2c). In contrast, *Apocrypta* captures remained high throughout the entire post-pollination period (Fig. 2d).

Non-pollinating wasps were only rarely captured at female trees (Table 2).

3.3. Observations of fig wasp behaviour

I made direct observations of the behaviour of *Ceratosolen vetustus* and the three species of non-pollinating fig wasp on *F. schwarzii*. These observations are based on over 100 separate visits to the site from September 1994 to January 1998.

The pollinators arrived in large numbers at receptive trees (Figs. 1m and 2a). They were rarely observed landing on non-receptive syconia. When pollinators landed on a syconium, they immediately searched for the ostiole, tapping the surface with their antennae, and then entered it rapidly. *Sycophaga* oviposited during the receptive period. *Philotrypesis* and *Apocrypta* were observed at the trees during the receptive period, but did not start ovipositing until later. *Philotrypesis* oviposited 2–10 days after pollination and *Apocrypta* oviposited 7–14 days after pollination. *Sycophaga* occasionally oviposited in the syconia of female trees (observed on <10 occasions), although these ovipositions never resulted in developing galls (Fig. 1g). *Philotrypesis* and *Apocrypta* were never observed ovipositing on female syconia.

Both *Philotrypesis* and *Apocrypta* showed highly aggregated oviposition behaviour. On a tree with several hundred syconia, they could be seen ovipositing on only a few syconia at any one time

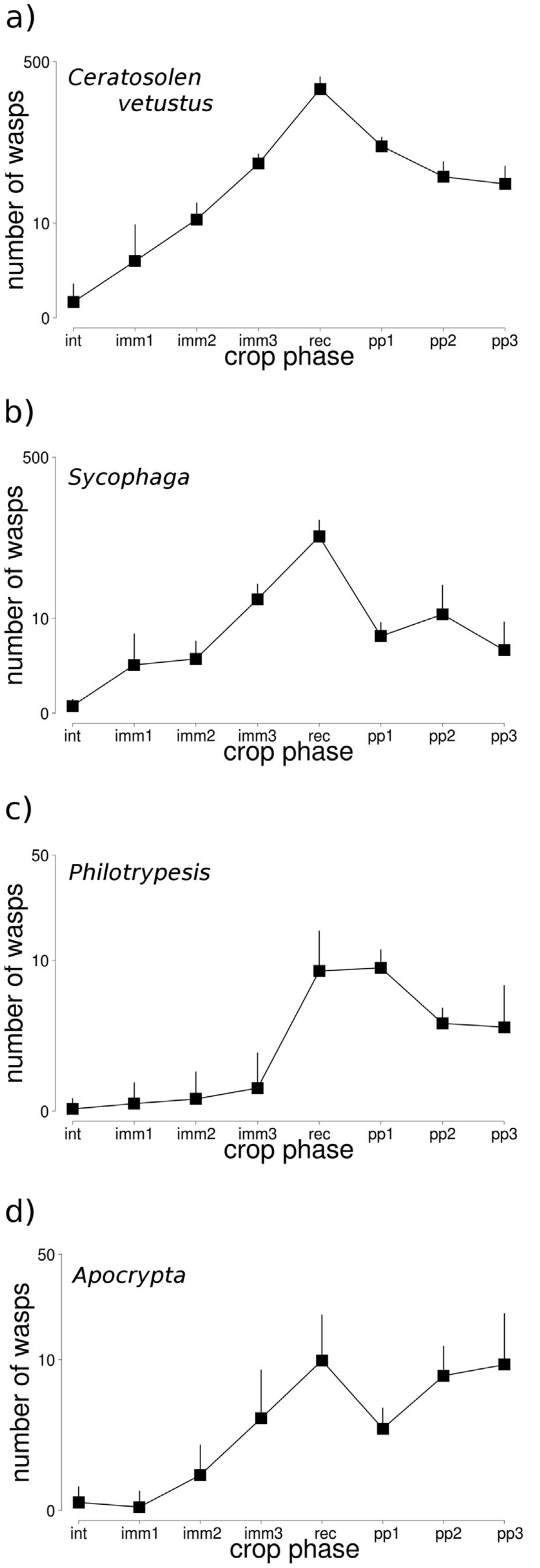

Fig. 2. Mean number of wasps (log scale, +se) caught at yellow sticky-traps with respect to crop phase at male *F. schwarzii* trees: a) *Ceratosolen vetustus*, the pollinator; b) *Sycophaga* sp., a galler; c) *Philotrypesis* sp. an inquiline of the pollinator; d) *Apocrypta* sp., a parasitoid. All the non-pollinating wasps oviposit through the syconium wall from the outside. Crop phases: int = inter-crop; imm = immature; rec = receptive; pp = post-pollination. The immature and post-pollination phases are divided into three consecutive approximately 10 day intervals. Census dates with <10 wasps total were removed from analysis.

Table 2
Total number of different species of non-pollinating fig wasps collected on yellow sticky-traps set in female and male *F. schwarzii* trees over 3 years from March 1995–February 1998. No = total number of sticky-traps censused.

	No	*Sycophaga* sp.	*Philotrypesis* sp.	*Apocrypta* sp.
Female	652	205	68	48
Male	738	8240	1748	2221

(Fig. 1i). However, over several days' observation at the same tree, the wasps were observed to select different syconia for oviposition. When wasps of either species landed on a syconium with other wasps already ovipositing, they would immediately begin to oviposit. However, if they landed on syconia without other individuals ovipositing, they would wait for long periods (>10 min). Usually this meant they were disturbed by an ant before they started ovipositing. Wasps disturbed by ants in this way were rarely caught. However, if ants encountered ovipositing wasps, they caught them easily.

Syconia that were heavily attacked by non-pollinators were often aborted and even if they completed development the wasps often failed to emerge, because they lacked sufficient male pollinating wasps to cut an exit tunnel. Such syconia could be recognised from the heavy bruising of the syconia wall caused by the wasps' ovipositors and, if I opened these during the wasp emergence phase, I would find all the wasps emerged from their galls but stuck inside the lumen (Fig. 1h, $n = \sim 30$). Such syconia usually had large numbers of *Philotrypesis. Apocrypta* and *Sycophaga* occurred in smaller numbers and there were few or no pollinators.

3.4. Fig wasp emergence

Ceratosolen vetustus is a day-flying wasp and most individuals emerged in the early morning between 06:30 and 09:30 (Fig. 3). At emergence, several male pollinators positioned back-to-back would chew their way through the ostiole, with the remaining male pollinators following close behind. This resulted in the opening of a relatively wide tunnel. When the male wasps reached the top of the ostiole, they scattered over the syconium surface (Fig. 1K, number of times observed >100). Immediately following the males, the female pollinators dispersed, emerging rapidly and flying directly from the tunnel exit (Fig. 1K). It took 2–3 min for the female pollinators in a syconium to disperse (observations of this behaviour were fewer (~20) because of the short duration). Female non-pollinating wasps emerged at the same time, but spent a few

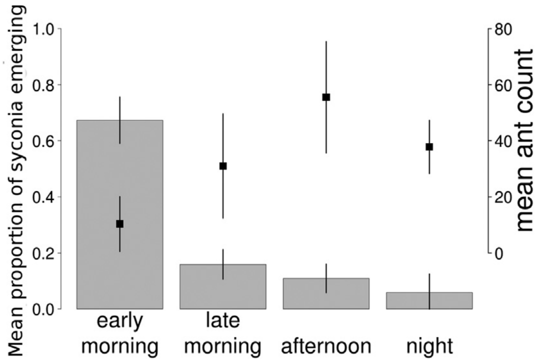

Fig. 3. Wasp emergence by time of day (bars: mean (±se) proportion of syconia; left-hand *y*-axis) for three trees in March 1995. Mean (±se) count of ant traffic up and down the trunk (see Methods for details) at the end of each phase on the same three trees (points, right-hand *y*-axis). Early morning = 06:30–09:30; Late morning = 09:30–12:30; Afternoon = 12:30–18:30; Night = 18:30–06:30.

minutes on the surface of the syconium waiting for their ovipositors to uncurl.

3.5. Observations of ants

Two ant species, *Philidris* sp. (Dolichoderinae) (Fig. 1c) and *Myrmicaria* sp. (Myrmicinae; *M. brunnea* group) (Fig. 1a), were observed on the syconia of *F. schwarzii*. *Philidris* sp. workers were small (∼3 mm, Fig. 1b), being approximately equal in size to the fig wasps (not including the ovipositor). By comparison, *Myrmicaria* sp. workers were much larger (∼8 mm, Fig. 1a). Both species were observed nesting in the ground at the site (only one nest of each species was located). Workers of both species were observed moving to and from the trees along trails through the understorey vegetation and leaf litter, on the tree trunks and branchlets supporting the syconia, and on the surface of syconia. They were not observed among the leaves, although this may in part reflect observation bias as the focus of observations was on the syconia.

Philidris occurred regularly on nine males trees and *Myrmicaria* on three male trees. Four smaller diameter male trees, which had few syconia, rarely had ants on them. Ants were also rarely observed on female trees. *Philidris* had a distinct pattern of activity that was significantly associated with the stage of crop development (Fig. 4a). With the exception of one tree, *Philidris* were rarely observed on male trees during the receptive phase. *Philidris* activity increased during the interfloral period, when *Philotrypesis* and *Apocrypta* were ovipositing, and peaked when the fig wasp offspring were emerging (Fig. 4b). However, one tree had a nest of *Philidris* at the base and ants were always abundant on this tree. At the receptive phase the ants would wait on the surface of the syconia near the ostiole and prey on wasps that landed. The receptive phase in this individual was often greatly extended and a large proportion of syconia were aborted. In contrast, the presence of *Myrmicaria* on trees was less predictable (Fig. 4b). Counts were zero on 94% of occasions across all phases, but on 3% of occasions >20 ants were counted, which is higher that the maximum count recorded for *Philidris* (Fig. 4a). There was no significant association between *Myrmicaria* abundance and crop stage (i.e. the null model was the most parsimonious). They occurred on trees during all phases in which fig wasps were present (Fig. 4b).

Philidris patrolled the syconia, moving rapidly over the surface of one syconium to the next. As a consequence of the evasive behaviour of the wasps, the ant patrolling activities disturbed a large number of non-pollinating wasps, but ants only rarely succeeded in catching any. However, ants were observed feeding on a clear exudate that was released from extra-floral nectaries on the surface of the syconia (Fig. 1j). The extra-floral nectaries were present on all syconia, but those on only few syconia appeared to produce exudate on any particular day and only during the early to mid inter-floral phase. Under a light microscope, the extra-floral nectaries were observed to comprise a small pit with the excretory cells forming an outgrowth in the middle. If syconia were bagged to exclude wasps and ants, these excretory cells grew out of the pit (Fig. 1j). *Myrmicaria* did not patrol syconia and were not observed feeding at the extra-floral nectaries. I also did not observe any other insects feeding on the exudate. *Myrmicaria* appeared to be strictly wasp predators and were most abundant and active when wasps were abundant (Fig. 4b). When non-pollinators were ovipositing I often observed them waiting on syconia for wasps to land (Fig. 1a) and they occasionally caught hovering wasps. They attacked large numbers of wasps, both pollinating and non-pollinating wasps, when the wasps were emerging.

The ant exclusion experiment was established in two male trees patrolled by *Philidris* ants and demonstrated that *Philidris* was very effective at protecting syconia from non-pollinating wasps. After approximately two weeks, syconia on ant-exclusion branchlets began rapidly aborting. After 18 days I collected the remaining syconia to examine the contents. All syconia remaining on ant-exclusion branchlets had bruised and shrivelled walls from the ovipositions of non-pollinating fig wasps and would most likely have aborted within a few more days. At collection, 83 syconia (27%) had been lost from ant-exclusions branchlets versus 7 (4%) lost from ant-access control branchlets ($est = 1.84 \pm 0.417$, $z = 4.52$, $p < 0.0001$). Moreover, syconia lost from control branchlets were most probably knocked down during handling of the ladders. Syconia from ant-exclusion branchlets were smaller ($F_{1,178} = 293$, $p < 0.0001$) and inspection of their contents revealed that, although they had been pollinated, they had few developing galls. *Philotrypesis*, in particular, were observed ovipositing in large numbers on treatment syconia, the surfaces of which were heavily bruised from the damage caused by their ovipositors.

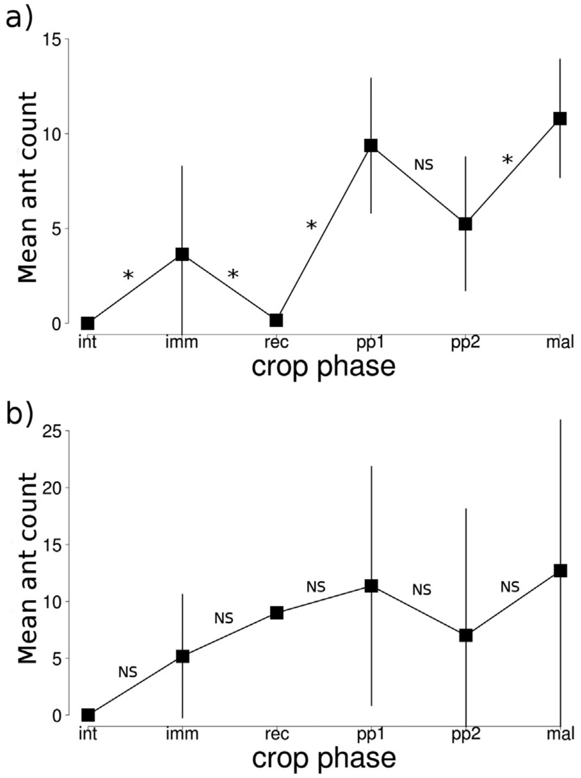

Fig. 4. Mean (±se) count of ant traffic up and down the truck (see Methods for details) by crop phase: (a) *Phildris* ants, (b) *Myrmicaria* ants. For *Philidris* crop stage had a significant effect on abundance (* indicates a significant difference ($P < 0.05$) between two observations; ns = not significant, zero-inflated negative binomial model), but for *Myrmicaria* the most parsimonious model was the null model (i.e. there was no significant effect of crop stage on the number of *Myrmicaria* counted). *Philidris* occurred on nine trees and *Myrmicaria* on three trees, out of the 16 male *F. schwarzii* trees present at the site. Crop phases: int = inter-crop; imm = immature; rec = receptive; pp = post-pollination, mal = male. The post-pollination phase was divided into two approximately 15 day intervals. The number of observations by crop phase was as follows: immature = 87; receptive = 12; post-pollination1 = 50; post-pollination2 = 28; wasp emergence = 50. One tree with a *Philidris* ant nest at the base, and as a consequence high ant activity at all times, was removed from the analysis.

At the wasp emerging phase, sometimes large numbers of ants were present (Fig. 4). However, wasp offspring emerged from the majority of syconia in the early morning before large numbers of *Philidris* ants were present (Fig. 3). Even when present, the ants succeeded in capturing relatively few emerging female pollinators (max. 15, *ca.* 150 emerge from one syconium). The scattering of the male wasps over the surface of the syconium (Fig. 1k) appeared to distract the ants from the female wasps, which escaped quickly.

Emerging female non-pollinating wasps were possibly more heavily preyed upon, because they had to wait on the surface of the syconium for their ovipositors to uncurl. After the female wasps had dispersed (as determined by opening syconia and inspecting the contents), *Philidris* ants entered syconia through the tunnel cut by the male pollinators and carried off any wasps left in the lumen. *Myrmicaria* ants were unable to enter the syconia because they were too large, but they often attacked emerging wasps.

4. Discussion

Ants are a common component of invertebrate assemblages on figs and several studies have demonstrated that ants can protect the larvae of pollinating fig wasps against non-pollinating fig wasps (Compton and Robertson, 1988; Cushman et al., 1997; Dejean et al., 1997; Schatz et al., 2006). However, in these studies, the fig appeared to be a passive partner in the interaction and did not provide any direct reward to the ants. For example, on *Ficus sur* in S. Africa ants (*Pheidole megacephala*) tending the homopteran *Hilda patruelis* were shown to reduce populations of non-pollinating fig wasps and thereby increase pollinator production (Compton and Robertson, 1988). However, ants were present on the trees at all times and also preyed upon pollinators. This type of interaction may be quite widespread and appears to be particularly prevalent among large monoecious species (Bain et al., 2014). Ants also nest in fig trees and some species of hemi-epiphytic fig have a particular branch architecture that seems to encourage ant nesting (Bain et al., 2014). Again, the continuous presence of the ants in the trees, and the diversity of different ant species involved, suggests a straightforward commensal interaction with the ants acting as an insect predator. In such situations, whether the ants have a net positive or negative outcome on fig pollinator production will depend on the specific behaviour of the ants and their abundance. Through resource consumption, a large population of sap-sucking homoptera, may also have an indirect negative impact on fig seed and pollinator production. Critically, the fig does not exert any control over the outcome of the fig–ant interaction.

In contrast, several facets of the *F. schwarzii* – *Philidris* interaction suggest that the fig exerts some control over the net outcome. (i) The secretion of exudate from the extra-floral nectaries coincided with the period during which the non-pollinators, in particular *Philotrypesis* which is probably an inquiline of the pollinator, were ovipositing. This phase coincided with a marked increase in the activity of *Philidris*. In contrast, *Philidris* ants were rare at receptive trees (with one exception) and hence presumably had a negligible impact on pollination success. (ii) The secretion of exudate from the extra-floral nectaries was restricted to 1–2 syconia on any particular day (based on observations of ant foraging behaviour) and appeared to encourage ant patrolling. This is significant in view of the fact that *Philidris* ants rarely caught non-pollinating wasps, but their patrolling activities prevented non-pollinating wasps from ovipositing on most syconia. (iii) Through the patrolling activities of the ants and the predator evasion behaviour of the non-pollinating wasps, oviposition was concentrated on a limited number of syconia missed by the patrolling ants and heavily attacked syconia were often aborted by the tree. The ant-exclusion experiment demonstrated that a large proportion of syconia were aborted in the absence of ants and *Philotrypesis* were observed ovipositing on these syconia in large numbers. The proximal cause of syconia abortion is not clear, but damage to the syconia caused by ovipositor insertions and the paucity of developing galls are possibilities.

Moreover, although *Philidris* ants were very abundant on syconia during the wasp emerging phase, the differing diurnal patterns of wasp emergence and ant activity suggest that ant predation was limited during this vulnerable phase. The behaviour of male pollinators, such as cutting a wide tunnel and scattering over the syconium surface, also appears to enhance the likelihood that female pollinators, dispersing with the fig's pollen and of course the male wasps' sperm, escape predation (Harrison and Yamamura, 2003; Zachariades et al., 2010). Because male wasps continue to search for mating opportunities while females remain in their galls, this cooperative male behaviour may be dependent on the swelling of the syconium just before wasp emergence. This enables the female wasps to emerge from their galls and empty into the lumen.

Philidris is known as a partner in other ant–myrmephyte interactions (Tresedeer et al., 1995; Chan et al., 2012). They have also been recorded as insect predators (Floren et al., 2002), as feeding on the honey-dew of lycinid caterpillers (such ants are often also recorded at extra-floral nectaries) (Fiedler, 2001), and as being aggressive against other ants (Wielgoss et al., 2010). Thus, my observations of *Philidris* on *F. schwarzii* are consistent with what is known about the biology of these ants.

The interaction between *F. schwarzii* and *Myrmicaria* sp. would appear to be more similar to that situation reported from several other fig species, where the ant is simply a wasp predator (Compton and Robertson, 1988; Schatz et al., 2003). *Myrmicaria* was present on the trees whenever wasps were abundant and was observed preying on large numbers of pollinators. Significantly, it was never observed feeding at the extra-floral nectaries. The outcome of the interaction between *F. schwarzii* and ants thus clearly varies according to the ant species involved. *Myrmicaria* appeared to aggressively displace *Philidris*. After June 1996, *Myrmicaria* took over the nest-site of the *Philidris* colony at the site and from that point onwards *Philidris* were much less abundant.

Following pollination, the development time of syconia on male trees was approximately half that on female trees (Table 1), which suggests there are differing constraints on the development time of wasp larvae and seeds (Harrison and Yamamura, 2003). One possibility is that shorter development time for wasp larvae is a predator evasion strategy akin to predator satiation (Janzen, 1971). Because ovipositing through the fig wall is a relative slow process and non-pollinators have a restricted window for oviposition, rapid development of pollinator wasp larvae combined with high crop synchrony will serve to reduce oviposition opportunities. Clearly, predation by ants will only serve to enhance this effect by reducing oviposition opportunities further still. Rapid pollinator larvae development may also restrict the number of non-pollinator niches, because non-pollinator larvae have to mature at the same time as pollinators, which may contribute to the reduced diversity of non-pollinators in many dioecious figs (Kerdelhué and Rasplus, 1996).

Many fig species, in particular the canopy hemi-epiphytic species (subgenus *Urostigma*), produce crops infrequently, varying from approximately three times per year to less than once in every two years (Harrison, 2008). Combined with typically low individual densities and high within-crown crop synchrony, this means fig crops are a scarce and unpredictable resource in space and time (Harrison and Shanahan, 2005). However, pollinator production is extremely high and pollinators employ wind to achieve long-distance dispersal (Ahmed et al., 2009; Harrison and Rasplus, 2006; Nason et al., 1998; Ware and Compton, 1994). However, this type of phenology may serve to limit non-pollinator populations, as these usually have much lower reproductive capacity. In contrast, *F. schwarzii* produces over four crops per year. This high rate of crop production may be related to the fact that *F. schwarzii* occurs in clusters of individuals in a relatively rare habitat, namely stream sides with a recent history of disturbance (Berg and Corner, 2005). Several lines of evidence suggest that pollinators of these dioecious species have shorter-range dispersal (Harrison and

Rasplus, 2006; Katabuchi et al., 2008) and, because adult pollinators live less than one day (*unpublished data*; Jevanandam et al., 2013; Kjellberg et al., 1988), populations are likely to fluctuate within small groups of trees (19/86 sticky-trap censuses had <10 *Ceratosolen* across all trees). This, in turn, means there will be high temporal variance in pollination opportunities, and hence there should be selection on individuals to spread their reproductive investment more evenly over time. However, a consequence of this high rate of crop production is that it provides a relatively stable resource for non-pollinators at the scale of a cluster of trees: Within the 16 male trees under observation, pollinator larvae were present continuously from November 1994 until January 1998, when a severe drought disrupted phenology of many species (Harrison, 2000a).

Non-pollinating wasps live longer than pollinators (>10 day, *personal observations*; Jevanandam et al., 2013) and, compared to pollinators, have an extended window of opportunity for oviposition. Both *Philotrypesis* and *Apocrypta* oviposited on a crop of *F. schwarzii* for a period of over one week. Interestingly, *Philotrypesis* and *Apocrypta* also arrived at male *F. schwarzii* trees during the receptive phase. Contrary to previous reports (Proffit et al., 2007), this suggests that these non-pollinators may be using the same olfactory cues as the pollinators to locate trees and then waiting for the syconia to develop before ovipositing. As this exposes them to ant predation for longer periods, olfactory camouflage of developing syconia and ant predation may reinforce one another. Nevertheless, other things being equal, local clusters of frequently flowering figs can be expected to promote high densities of non-pollinating wasps, as higher survival during dispersal will tend to compensate for the lower reproductive capacity of these wasps. Unsurprisingly, therefore, fig species with similar types of ecology (Harrison and Shanahan, 2005) have evolved various strategies for limiting the numbers of non-pollinators. Some species have a thick or tough syconium wall and a large lumen (e.g. *Ficus cereicarpa*), which limits the number of galls a non-pollinator's ovipositor can reach from one insertion point (*personal observations*). Other species are geocarpic and bury their syconia in the leaf-litter or soil, which presumably limits access and increases predation risk from leaf-litter invertebrates to non-pollinators ovipositing from outside the syconium. *F. schwarzii* has adopted predatory ants to control non-pollinating wasp populations and, because it provides a reward for the ants, may be described as a true ant–plant.

Why the *F. schwarzii* – *Philidris* interaction appears to have evolved towards mutualism is presumably related to the very high densities of non-pollinators on *F. schwarzii* in the absence of ants. In ant-exclusion experiments on other fig species, relative to control syconia ant-free syconia suffered a higher incidence of non-pollinating wasps (Compton and Robertson, 1988; Wei et al., 2005), but not to the extent that syconia were aborted and wasp production failed entirely. Hence, high densities of non-pollinating fig wasps on *F. schwarzii* may have increased the incidence of ants on the figs, and the potential for both greater positive and negative outcomes of the fig–ant interaction for the fig.

These results demonstrate a mutualistic interaction between *F. schwarzii* and *Philidris*. The fig provided a food reward for ants at a specific stage in crop development and the patrolling activities of the *Philidris* ants substantially limited oviposition opportunities for non-pollinating fig wasps, particularly *Philotrypesis* which is an inquiline of the pollinator. Experimental ant-free syconia were heavily attacked by non-pollinators and suffered high abortion rates. This may be a unique example of a direct mutualistic interaction that bridges four tropic levels. Furthermore, although *F. schwarzii* provided a reward for the ants, it did not receive any direct benefit in return. *F. schwarzii* benefited from the patrolling activities of the ants only indirectly through the protection afforded female pollinator larvae that, when they emerge as adults, will disperse the fig's pollen. The benefits of protection against inquilines and parasitoids, also accrue to pollinator males and possibly *Sycophaga*, although these do not provide any pollination service. Clearly, such apparent altruism is evolutionarily stable only because of the close alignment of reproductive interests between the fig and its pollinator.

Acknowledgements

I wish to thank the late Tamiji Inoue for advice and the Forest Department Sarawak for supporting the research activities at Lambir. I would like to thank the two anonymous reviewers for their efforts to improve the manuscript. Funding for this research came in part from a National Science Foundation of China grant (NSFC #30972294) and a Young Foreign Scientist Fellowship, Chinese Academy of Sciences..

References

Ahmed, S., Compton, S.G., Butlin, R.K., Gilmartin, P.M., 2009. Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. PNAS 106, 20342.

Al-Beidh, S., Dunn, D.W., Power, S.A., Cook, J.M., 2012. Parasites and mutualism function: measuring enemy-free space in a fig-pollinator symbiosis. Oikos 121, 1833–1839.

Bain, A., Harrison, R.D., Schatz, B., 2014. How to be an ant on figs. Acta Oecol. 57, 97–108.

Berg, C.C., Corner, E.J.H., 2005. Moraceae (*Ficus*). In: Noteboom, H.P. (Ed.), 2005. Flora Malesianaser. Ser 1, vol. 17. National Herbarium of Nederland, Leiden, The Netherlands, pp. 1–730.

Bronstein, J.L., 1987. Maintenance of species-specificity in an neotropical fig – pollinator wasp mutualism. Oikos 48, 39–46.

Bronstein, J.L., 1991. The nonpollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? Oikos 61, 175–186.

Chan, C.S., Cheng, J., Loh, J.Y.Q., Tan, E., Loo, A.H.B., Tang, J., 2012. Observations of ants and aphids in the rattan species *Korthalsia echinometra* becc. and *Korthalsia rostrata* blume. Raffles Bull. Zoo. (Supplement), 133–139.

Compton, S.G., 1992. Southern African fig wasps (Hymenoptera: Chalcidoidea): resource utilisation and host relationships. Proc. K Ned Akad Wet C 95, 423–435.

Compton, S.G., Hawkins, B.A., 1992. Determinants of species richness in southern African fig wasp assemblages. Oecologia 91, 68–74.

Compton, S.G., Robertson, H.G., 1988. Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. Ecology 69, 1302–1305.

Cook, J.M., Rasplus, J., 2003. Mutualists with attitude: coevolving fig wasps and figs. TREE 18, 241–248.

Cruaud, A., Jabbour-Zahab, R., Genson, G., Kjellberg, F., Kobmoo, N., Noort van, S., Da-Rong, Y., Yan-Qiong, P., Ubaidillia, R., Hanson, P.E., Santos-Mattos, O., Farache, F.H.A., Periera, R.A.S., Kerdelhué, C., Rasplus, J.-V., 2011. Phylogeny and evolution of life-history strategies in the Sycophaginae non-pollinating fig wasps (Hymenoptera, Chalcidoidea). BMC Evol. Biol. 11, 178.

Cruaud, A., Rønsted, N., Chantarasuwan, B., Chou, L.S., Clement, W.L., Couloux, A., Cousins, B., Genson, G., Harrison, R.D., Hanson, P.E., Hossert-McKey, M., Jabbour-Zahab, R., Jousellin, E., Kerdelhué, C., Kjellberg, F., Lopez-Vaamonde, C., Peebles, J., Peng, Y.-Q., Periera, R.A.S., Schramm, T., Ubaidillia, R., van Noort, S., Weiblen, G., Yang, D.-R., Yodpinyanee, A., Libeskind-Hadras, R., Cook, J.M., Rasplus, J.-V., Savolainen, V., 2012. An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. Syst. Biol. 61, 1029–1047.

Cushman, J.H., Compton, S.G., Zachariades, C., Ware, A.B., Nefdt, J.C., Rashbrook, V.K., Nefdt, R.J.C., 1997. Geographic and taxonomic distribution of a positive interaction: ant-tended homopterans benefit figs across southern Africa indirectly. Oecologia 116, 373–380.

Dejean, A., Bourgoin, T., Gibernau, M., 1997. Ant species that protect figs against other ants: result of territoriality induced by a mutualistic homopteran. Ecoscience 4, 446–453.

Elias, L.G., Menezes Jr., A.O.M., Pereira, R.A.S., 2008. Colonization sequence of non-pollinating fig wasps associated with *Ficus citrifolia* in Brazil. Symbiosis 45, 107–111.

Fiedler, K., 2001. Ants that associate with Lycaeninae butterfly larvae: diversity, ecology and biogeography. Divers. Distributions 7, 45–60.

Floren, A., Biun, A., Linsenmair, K.E., 2002. Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia 131, 137–144.

Galil, J., 1973. Pollination in dioecious figs: pollination of *Ficus fistulosa* by *Ceratosolen hewitti*. Gdn. Bull. Singapore 26, 303–311.

Galil, J., Eisikowitch, D., 1968. Flowering cycles and fruit types in *Ficus sycomorus* in East Africa. New Phytol. 67, 745–758.

Harrison, R.D., 2000a. Phenology and Wasp Population Dynamics of Several Species of Dioecious Fig in a Lowland Tropical Rain Forest in Sarawak, Malaysia. Kyoto University, Japan. (PhD thesis).

Harrison, R.D., 2000b. Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. Proc. R Soc. Lond B Biol. Sci. 267, 911–915.

Harrison, R.D., 2005. Figs and the diversity of tropical rainforests. Bioscience 55, 1053–1064.

Harrison, R.D., 2008. Adaptive significance of phenological variation among monoecious hemi-epiphytic figs in Borneo. Symbiosis 45, 83–90.

Harrison, R.D., Rasplus, J.-Y., 2006. Dispersal of fig wasps in Asian rain forests. J. Trop. Ecol. 22, 631–639.

Harrison, R.D., Shanahan, M., 2005. Seventy-seven ways to be a fig: an overview of a diverse assemblage of figs in Borneo. In: Roubik, D.W., Sakai, S., Hamid Karim, A.A. (Eds.), Pollination Ecology and the Rain Forest. Springer, New York, pp. 111–127. Appendix B 246–249.

Harrison, R.D., Yamamura, N., 2003. A few more hypotheses for the evolution of dioecy in figs (*Ficus*, Moraceae). Oikos 100, 628–635.

Hartley, S.E., Gange, A.C., 2009. Impacts of plant symbiotic fungi on insect herbivores: mutualism in a multitrophic context. Annu. Rev. Entomol. 54, 323–342.

Herre, E.A., Jandér, K.C., Machado, C.A., 2008. Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. Ann. Rev. Ecol. Evol. Syst. 39, 439–458.

Hespenheide, H.A., 1975. Selective predation by two swifts and a swallow in Central America. Ibis 117, 82–99.

Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. 2, 465–492.

Jevanandam, N., Goh, A.G.R., Corlett, R.T., 2013. Climate warming and the potential extinction of fig wasps, the obligate pollinators of figs. Biol. Lett. 9, 20130041.

Jousselin, E., Rasplus, J.Y., Kjellberg, F., 2001. Shift to mutualism in parasitic lineages of the fig/fig wasp interaction. Oikos 94, 287–294.

Katabuchi, M., Harrison, R.D., Nakashizuka, T., 2008. Documenting the effect of foundress number in a dioecious fig, *Ficus fistulosa*, in Malaysia. Biotropica 40, 457–461.

Kerdelhué, C., Rasplus, J.-Y., 1996. Non-pollinating afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. Oikos 75, 3–14.

Kerdelhué, C., Rasplus, J.-Y., 1996. The evolution of dioecy among *Ficus* (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure on the fig-pollinator mutualism. Oikos 77, 163–166.

Kjellberg, F., Doumesche, B., Bronstein, J.L., 1988. Longevity of a fig wasp (*Blastophaga psenes*). Proc. K Ned Akad Wet C 91, 117–122.

Lopez-Vaamonde, C., Rasplus, J.Y., Weiblen, G.D., Cook, J.M., 2001. Molecular phylogenies of fig wasps: Partial cocladogenesis of pollinators and parasites. Mol. Phylogenet. Evol. 21, 55–71.

Marussich, W.A., Machado, C.A., 2007. Host-specificity and coevolution among pollinating and nonpollinating new world fig wasps. Mol. Ecol. 16, 1925–1946.

McLeish, M.J., Van Noort, S., Tolley, K. a, 2010. African parasitoid fig wasp diversification is a function of *Ficus* species ranges. Mol. Phylogenet. Evol. 57, 122–134.

Munro, J.B., Heraty, J.M., Burks, R.A., Hawks, D., Mottern, J., Cruaud, A., Rasplus, J.-Y., Jansta, P., 2011. A molecular phylogeny of the Chalcidoidea (Hymenoptera). PLoS ONE 6, e27023.

Nason, J.D., Herre, E.A., Hamrick, J.L., 1998. The breeding structure of a tropical keystone plant resource. Nature 391, 685–687.

Palmer, T.M., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M., Karban, R., 2008. Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. Science 319, 192–195.

Peng, Y.Q., Zhao, J.B., Harrison, R.D., Yang, D.R., 2010. Ecology of parasite *Sycophilomorpha* sp. on *Ficus altissima* and its effect on the fig-fig wasp mutualism. Parasitology 137, 1913–1919.

Pereira, R.A.S., Do Prado, A.P., 2005. Non-pollinating wasps distort the sex ratio of pollinating fig wasps. Oikos 110, 613–619.

Pereira, R.S.A., De Pádua Teixeira, S., Kjellberg, F., 2007. An inquiline fig wasp using seeds as a resource for small male production: a potential first step for the evolution of new feeding habits? Biol. J. Linn Soc. 92, 9–17.

Proffit, M., Schatz, B., Borges, R.M., Hossaert-McKey, M., 2007. Chemical mediation and niche partitioning in non-pollinating fig-wasp communities. J. Anim. Ecol. 76, 296–303.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, P., 2005. 60 million years of co-divergence in the fig-wasp symbiosis. Proc. R Soc. Lond B Biol. Sci. 272, 2593–2599.

Schatz, B., Proffit, M., Rakhi, B.V., Borges, R.M., Hossaert-McKey, M., 2006. Complex interactions on fig trees: ants capturing parasitic wasps as possible indirect mutualists of the fig-fig wasp interaction. Oikos 113, 344–352.

Schatz, B., Anstett, M.C., Out, W., Hossaert McKey, M., 2003. Olfactive detection of fig wasps as prey by the ant *Crematogaster scutellaris* (Formicidae; Myrmicinae). Naturwissenschaften 90, 456–459.

Schatz, B., Hossaert-Mckey, M., 2010. Ants use odour cues to exploit fig-fig wasp interactions. Acta Oecol. 36, 107–113.

Scott, J.J., Oh, D., Yuceer, M.C., Klepzig, K.D., Clardy, J., Currie, C.R., 2008. Bacterial protection of beetle-fungus mutualism. Science 322. http://dx.doi.org/10.1126/science.1160423.

Shanahan, M., Compton, S.G., So, S., Corlett, R., 2001. Fig-eating by vertebrate frugivores: a global review. Biol. Rev. 76, 529–572.

Tresedeer, K.K., Davidson, D.W., Ehleringer, J.R., 1995. Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. Nature 375, 137–139.

Tzeng, H., Tseng, L., Ou, C., Lu, K., Lu, F., Chou, L., 2008. Confirmation of the parasitoid feeding habit in *Sycoscapter*, and their impact on pollinator abundance in *Ficus formosana*. Symbiosis 45, 129–134.

Ware, A.B., Compton, S.G., 1994. Dispersal of adult female fig wasps: 2. Movements between trees. Entomol. Exp. Appl. 73, 231–238.

Webber, B.L., Moog, J., Curtis, A.S.O., Woodrow, I.E., 2007. The diversity of ant–plant interactions in the rainforest understorey tree, *Ryparosa* (Achariaceae): food bodies, domatia, prostomata, and hemipteran trophobionts. Bot. J. Linn Soc. 154, 353–371.

Wei, Z., Peng, Y.Q., Lei, X., Yang, D.-R., 2005. Impact of *Oecophylla smaragina* on the percentage number of offspring of pollinator and non-pollinating wasps on *Ficus racemosa*. Zoo Res. 26, 386–390.

West, S.A., Herre, E.A., 1996. The ecology and evolution of the new world non-pollinating fig communities. J. Biogeo. 23, 447–458.

Wielgoss, A., Tscharntke, T., Buchori, D., Fiala, B., Clough, Y., 2010. Temperature and a dominant dolichoderine ant species affect ant diversity in Indonesian *Cacao* plantations. Agri, Eco Environ. 135, 253–259.

Zachariades, C., Schatz, B., Compton, S.G., 2010. Wasp emergence from the figs of *Ficus sur*: characteristics and predation by ants. Trop. Zool. 23, 121–138.