



## Original article

# Female figs as traps: Their impact on the dynamics of an experimental fig tree-pollinator-parasitoid community



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## ABSTRACT

Interactions between fig trees (*Ficus*) and their pollinating fig wasps (Agaonidae) result in both a highly species-specific nursery mutualism and mutual exploitation. Around half of the 800 or so fig tree species are functionally dioecious. Figs on male plants produce pollen and fig wasp offspring, whereas figs on female plants produce only seeds. Figs on female plants are traps for pollinators. The fig wasps enter the female figs to oviposit, but lose their wings on entry and are then prevented from oviposition by the long styles that characterise the flowers in female figs. Continuation of the mutualism depends on the pollinators' failure to distinguish between male and female figs before entry. Female plants may also have a negative impact on the parasitoid fig wasps that feed on pollinators, if they are also attracted to female figs. We used glasshouse populations of figs (with and without female plants), pollinators and parasitoids to infer the impact of female figs on fig wasp dynamics. Cyclic population fluctuations were present in both species. Female plants appeared to dampen the amplitudes of pollinator population cycles, and parasitoid populations may become less tightly coupled with host populations, but the presence of female figs did not reduce parasitism rates, nor parasitoid and pollinator densities, and only parasitoid sex ratios were affected. Our glasshouse experimental design was likely to favour the impact of female figs on the wasp populations, which suggests that female plants in the field are unlikely to have a major negative impact on their pollinators, despite being a major mortality factor.

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## 1. Introduction

Mutualisms are often described in terms of pairs of species interacting to their mutual benefit, but this is often just a shorthand to describe two species with individuals that interact in such a way that net benefits accrue to both species. In the case of non-symbiotic mutualisms, not all individuals of mutualistic species pairs are necessarily interacting at all, and if they are, the interactions involving some individuals may be neutral, or even to the detriment of one of the 'partners' (Stanton and Palmer, 2011; Ghoul et al., 2014). Mutualisms can therefore be viewed in terms of 'mutual exploitation' where natural selection will favour individuals that maximise their rewards and reduce the costs of interactions with the other species (Addicott, 1986; Bronstein,

2001a). Species pairs rarely interact in isolation, and the associated costs and benefits of interactions will often be modified by the mix of other species that are present locally (Bronstein, 2001b; Segreaves, 2008).

Mutualistic interactions involving figs (*Ficus* spp., Moraceae) and their pollinating fig wasps (Hymenoptera, Agaonidae) represent a classic case of species-specific obligate mutualism and co-evolution (Compton, 1993; Compton et al., 1996; Dunn et al., 2008; Herre et al., 2008). Mated adult female wasps are attracted to the volatile blends produced by young receptive figs (Proffitt et al., 2009). In monoecious *Ficus* species, seeds and the next generation of fig wasps mature from the same figs. Adult females then exit through a hole constructed by males and transport the pollen of their natal plant (Suleman et al., 2012). In figs of dioecious *Ficus*, where male and female functions are performed by separate plants, female fig wasps are only able to reproduce within male figs, whereas fig wasps entering female figs only pollinate, and die without reproducing. On female plants, the longer styles of female flowers in their figs help prevent oviposition and as a result only

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seeds are produced (Raja et al., 2008b). The pollination system of dioecious fig species is therefore an example of pollination by deceit (*sensu* Dafni, 1984) because female figs are a dead end for fig wasp reproduction.

There are conflicts of interest between dioecious figs and their pollinators (Weiblen et al., 2001), but despite this fig wasps pollinate female figs, where there is no benefit to themselves (Patel et al., 1995; Raja et al., 2008b). In some dioecious species, the short-lived adult females (that live only few hours) enter the female figs because during certain periods of the year they have no other choice available, as they are released when few receptive figs are present on male trees (Kjellberg et al., 1987; Soler et al., 2012). In others, such as *Ficus montana*, male and female figs are receptive simultaneously and selection should favour wasps that avoid female figs, leading eventually to the potential extinction of the plant and its pollinator (Patel et al., 1995; Corlett, 1987; Anstett et al., 1998; Suleman et al., 2011a). However, this selection pressure also favours female plants that mimic males, as has been described in many other plant species (Agren et al. 1986; Aronne et al., 1993; Dufaÿ and Anstett, 2004). Furthermore, male plants also need to mimic females to ensure that the next generation of wasps bearing their pollen enter female figs ('vicarious selection', Grafen and Godfray, 1991; Soler et al., 2012). The inability of fig wasps to differentiate between male and female figs means that female fig plants act as a source of mortality among adult female pollinators, and some pollinator populations pass through repeated bottlenecks as a result (Kjellberg et al., 1987). The sources of mortality among adult female fig wasps dispersing between figs are poorly known, but females will often fail to reach any receptive figs. Among those that do, the importance of losses due to entry into female figs will vary according to factors such as the relative abundance of receptive male and female figs and their distance from the male figs from which the pollinators are emerging.

Each species of fig tree also supports a number of non-pollinating fig wasps (NPFW) (Compton and Hawkins, 1992), most or all of which are only associated with male figs of dioecious species (Wu et al., 2013). Most NPFW oviposit from the outside of the figs, but some enter the figs like pollinators. Phytophagous species tend to oviposit into younger figs than parasitoids. Regardless of when they oviposit, all NPFW usually emerge from figs at the same time as the pollinators, suggesting that larval growth rates vary between species (Bronstein, 1991; Kerdelhue and Rasplus, 1996). *Sycoscapter* species (Pteromalidae, Sycoryctinae) are NPFW with long ovipositors that lay their eggs from the outside of a fig, through the wall a few hours to several days after pollinators enter the figs, depending on the species (Kerdelhue and Rasplus, 1996). They are believed to be parasitoids of pollinators and possibly other NPFW (Tzeng et al., 2008). Correlations between fig wasp numbers can be misleading (Raja et al., 2014), but the negative, positive or absence of correlation recorded between four *Sycoscapter* species and pollinator adult offspring that were recorded in shared figs (Kerdelhue et al., 2000) suggests that they have differing relationships with the pollinators. As with other parasitoid fig wasps, a single adult offspring emerges from each ovule that had contained a pollinator.

Many pollinator fig wasps are known to adjust their adult offspring sex ratios in response to how many foundresses had entered a fig to lay their eggs (Hamilton, 1967; Frank, 1985; Herre, 1985; Pereira and Prado, 2006; Greeff and Newman, 2011). Foundresses of *Kradibia* (= *Liporrhopalum*) *tentacularis*, the pollinator of *F. montana*, contribute unequally to broods in shared figs (Zavodna, 2004). They lay mainly male offspring at the start of an oviposition sequence and competition between foundresses in figs shared with other foundresses results in smaller clutches and fewer female offspring (Raja et al., 2008a). *K. tentacularis* foundresses can re-

emerge from figs and this allows them to oviposit in several figs on the same plant. Foundresses entering their second figs lay smaller clutches, which reduces competition for oviposition sites and weakens the impact of foundress numbers on offspring sex ratios (Raja et al., 2008a; Suleman et al., 2013c).

Realized sex ratios (numbers of adult male and female offspring) do not necessarily reflect primary sex ratios, because larval mortalities can be high and not necessarily similar for male and female offspring (Ghana et al., 2012). Some parasitoid NPFW modify pollinator offspring sex ratios, because they preferentially attack more peripherally-located galls, which tend to contain female pollinator larvae (Yu and Compton, 2012).

Female dioecious figs may influence the impact of NPFW on pollinators, acting as 'ecological sinks' that reduce the search efficiency of any NPFW that fails to avoid female figs when searching for oviposition sites (Weiblen et al., 2001). This is one explanation for the observed paucity of NPFWs associated with dioecious, compared with monoecious species, though there are other explanations (Weiblen et al., 2001; Greeff and Compton, 2002). Here, we use two experimental glasshouse populations of a dioecious fig tree, one containing only male plants, the other with both sexes present, to examine the impact of female fig trees on populations of its pollinator and an associated *Sycoscapter* parasitoid. Because female plants act as traps for pollinator foundresses we hypothesised that in the presence of female plants there would be fewer foundresses entering each male fig. A single winged foundress entering her first fig is capable of utilising most of the oviposition sites within the fig, but because foundresses commonly re-emerge and then lay small clutches of eggs in second and further figs, many male figs are not fully-utilised if entered by a single foundress. As an expected consequence of fewer foundresses entering each fig in the mixed-sex glasshouse we hypothesised that (1) male figs would contain fewer fig wasp offspring and (2) pollinator offspring sex ratios would be more female-biased. We also (3) hypothesised that parasitism rates would be lower if female plants were present because searching efficiency of the parasitoids may be reduced and because parasitoids favour figs with higher densities of pollinator larvae (Suleman et al., 2013b). Further (4), we hypothesised that pollinator-parasitoid population dynamics would follow a cyclic pattern, with delayed peaks in parasitoid numbers following peaks in the numbers of their hosts, driven by seasonal patterns of resource availability (fig production) (Hunter and Price, 1998).

### 1.1. Study site and species

The study was conducted using glasshouse populations of a dioecious fig tree *F. montana* Blume, its pollinator *Kradibia* (= *Liporrhopalum*) *tentacularis* (Grandi) and the parasitoid *Sycoscapter* sp., originating from the Centre for International Forestry Research (CIFOR) plantation, West Java, Indonesia and from Rakata (Krakatau Islands), Indonesia. These populations had been maintained continuously at the Experimental Gardens, University of Leeds, UK since 1995 (Moore, 2001).

Fig of *F. montana* are small and produced in the leaf axils or from older wood. Under our experimental conditions figs are present on both sexes throughout the year and fruiting on individual plants is asynchronous, often with all developmental stages present together (Suleman et al., 2011b). Flowering phenologies of male and female plants are similar (Suleman et al., 2011b) and there are no other phenological differences between sexes as far as fig initiation and fig composition are concerned, although un-entered female figs remain attractive to pollinators for longer than male figs (Suleman et al., 2011a).

There is significant variation in flower numbers in *F. montana* figs from different individual trees grown under uniform conditions

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