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Original article

How to be an ant on figs

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ABSTRACT

Mutualistic interactions are open to exploitation by one or other of the partners and a diversity of other organisms, and hence are best understood as being embedded in a complex network of biotic interactions. Figs participate in an obligate mutualism in that figs are dependent on agaonid fig wasps for pollination and the wasps are dependent on fig ovules for brood sites. Ants are common insect predators and abundant in tropical forests. Ants have been recorded on approximately 11% of fig species, including all six subgenera, and often affect the fig–fig pollinator interaction through their predation of either pollinating and parasitic wasps. On monoecious figs, ants are often associated with hemipterans, whereas in dioecious figs ants predominantly prey on fig wasps. A few fig species are true myrmecophytes, with domatia or food rewards for ants, and in at least one species this is linked to predation of parasitic fig wasps. Ants also play a role in dispersal of fig seeds and may be particularly important for hemi-epiphytic species, which require high quality establishment microsites in the canopy. The intersection between the fig–fig pollinator and ant–plant systems promises to provide fertile ground for understanding mutualistic interactions within the context of complex interaction networks.

1. Introduction

Mutualistic interactions are ubiquitous in nature, and are ecologically and evolutionarily important. However, the long-term exchange of resources between mutualistic partners attracts a large variety of other organisms that exploit the mutualism (Bronstein, 2001; Yu, 2001; Morris et al., 2003; Schatz et al., 2008). Hence, instead of isolated interactions, mutualisms are increasingly seen as being integrated within complex interaction networks (Blüthgen and Klein, 2011).

Among mutualistic interactions, the fig (*Ficus*) – fig pollinator interaction is often considered a model system (Herre and Jandér, 2010; Hossaert-McKey et al., 2010) and recent advances in the taxonomy of figs (Berg and Corner, 2005), their pollinators and non-pollinating fig wasps (NPFWs) (Cruaud et al., 2010, 2011) render easier investigations of the interactions among insect communities supported by figs. The interaction between figs and their pollinators have frequently been the subject of both evolutionary (Weiblen, 2002; Cook and Rasplus, 2003; Kjellberg et al., 2005; Dunn et al., 2008; Cruaud et al., 2010; Herre and Jandér, 2010) and ecological study (Harrison, 2005; Hossaert-McKey et al., 2010).

Figs are primarily tropical taxa and are an important component of tropical plant assemblages (Harrison, 2005). *Ficus* is also a globally diverse genus with at least 700 species (Berg, 1989; Berg and Corner, 2005). Several authors have suggested that figs are keystone resources in tropical forest because of the diversity of vertebrates that depend on their year-round production of fruits (Shanahan et al., 2001). Their ecological success is presumed to have arisen from the mutualistic association between figs and their pollinators; an interaction that is at least 60 Myrs old (Rønsted et al., 2005).

Mutualistic interactions are special cases of mutual exploitation in which both partners receive a net benefit in terms of reproductive success from the exchange (McKey and Hossaert-McKey, 2008). However, within the interacting populations, different individuals may receive net positive or negative payoffs. Moreover, the payoffs between mutualistic partners are often affected by other organisms (Yu, 2001; Bronstein, 2001, 2003; Morris et al., 2003; Ashman and King, 2005; Nahas et al., 2012).

In this review we focus on the interactions between figs and ants (Hymenoptera: Formicidae). Ants are a ubiquitous component of tropical forests and constitute a diversity of interactions with plants that range from obligate mutualism through parasitism. Ants

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occur widely on figs and are known to affect the interactions between figs and other symbionts, in particular their pollinating wasps. We explored the different types of interactions that have been studied between ants and figs, and discuss how these interactions may have affected coevolutionary processes between figs and their other symbionts.

There are over 12,000 ant species (Bolton et al., 2006) and these display an incredible range of feeding habits, associations with others species, in particular plants and other insects, and live in diverse habitats (Hölldobler and Wilson, 1990). It has been suggested that the radiation and success of ants in various ecosystems is due to the rise of the angiosperms, which released ants from a dependence on predation (Wilson and Hölldobler, 2005). In exchange for food rewards, ants often protect plants (Hölldobler and Wilson, 1990), but the interaction can be more complex when the same ants are tending sap-sucking insects (Huxley and Cutler, 1991; Moreira and Del-Claro, 2005). With respect to *Ficus*, ants are mobile actors that through their predatory behavior can alter the proportions of different wasp species that develop in fig syconia (Bronstein, 1988, 1991; Compton and Robertson, 1988, 1991; Zachariades, 1994; Cushman et al., 1998; Schatz et al., 2006; Harrison, 2014). Ants may also reduce herbivore pressure on fig leaves, act as seed dispersers or reduce seed dispersal through inhibiting feeding by vertebrate frugivores (Thomas, 1988). Ants are often observed on fig trees by researchers, but ecological studies have been limited.

2. The players

All fig species are engaged in an obligate and highly specific mutualistic interaction with agaonid wasps (Cruaud et al., 2010). Fig pollinators (Hymenoptera, Agaonidae, Agaoninae) are, with a few minor exceptions (Jousselline et al., 2001), the only pollen dispersers of the fig trees. Conversely, fig pollinators can only reproduce inside the inflorescence of their host fig (Galil and Eisikowitch, 1968; Cook and Rasplus, 2003; Harrison, 2005; Kjellberg et al., 2005). The fig has a unique closed inflorescence, or syconium, which is urn-shaped and lined with the fig's tiny flowers. When the fig's flowers are receptive, the bracts in the narrow neck (or ostiole) loosen and the pollinator is able to enter. Once inside, the pollinator pollinates the flowers and attempts to oviposit in some ovules. In a monoecious fig, ovules that receive an egg develop a gall, while those pollinated ovules missed by the wasp develop into seeds in the normal way. In dioecious fig species, on male trees the syconia produce only wasp galls and pollen, while on female trees only seeds are produced. Four to six weeks later, the wasp offspring emerge from their galls, mate inside the lumen of the syconium, and then the females collect pollen, either passively or actively, and disperse. The adult female pollinators have a short adult lifespan (1–3 days) and must find a receptive fig to reproduce.

In addition, there is a diversity of non-pollinating fig wasps (NPFWs, Hymenoptera, Chalcidoidea) (Compton and Hawkins, 1992; Kerdelhué and Rasplus, 1996; West et al., 1996; Kjellberg et al., 2005; Cruaud et al., 2011; Segar et al., 2012). These wasps include species, like the fig pollinator, that enter the fig during the receptive phase, but most NPFWs oviposit from outside the syconium by inserting their ovipositor through the syconium wall. NPFWs include gallers, cleptoparasites (inquilines) and parasites. The latter two groups may parasitize the galls of fig pollinators or other galler species (Rasplus et al., 1998; Kjellberg et al., 2005). The abundance of NPFWs varies hugely and depends on their biology and that of the fig. On some individuals of some species they may be considerably more abundant than the pollinator (Kerdelhué and Rasplus, 1996; Cook and Rasplus, 2003). For example, on *Ficus benjamina*, the NPFWs species, *Walkerella*, can be more twice more numerous than the pollinators (Wang et al., 2012).

As with other plant species, ants perform a variety of roles on figs (Fig. 1 and Fig. 2). Fig wasps, both pollinators and NPFWss, represent a huge potential food resource. A single crop on a large hemi-epiphytic fig may have as many as 1,000,000 syconia and hence may release as many 50–100 times that number of wasps. Fig wasps also arrive at syconia in smaller but still substantial numbers to oviposit. Other insects also exploit fig syconia (hemipterans, flies, nematodes, coleopterans, fruit flies, etc) and may be preyed upon by ants (Zachariades, 1994; Bronstein, 1998; Compton and Disney, 1991). As with any other trees in the forest, ants may also feed on herbivorous insects among the fig foliage, or hemipteran honey-dew, and occasionally resources provided directly by the fig in the form of pearl bodies or extrafloral nectary type structures. Some ants use ripe syconia (often partially eaten by bats or birds) as sources of carbohydrates. Moreover, mature figs may provide a source of fig seeds or elaiosomes that can also serve as ant food. In addition to food resources, ants may also use figs as nest sites, but only a few species of fig can be described as true myrmecophytes.

Hereafter, we describe factors affecting the interactions between ants and figs, and how these in turn affect the outcome of the fig–fig pollinator interaction.

3. The presence of ants on *Ficus*

Ants and angiosperms are both the ecologically and numerically dominant groups in many environments, and have evolved alongside each other for 140–168 million years (Rico-Gray and Oliveira, 2007). Thus the ancestors of modern figs were probably already interacting with ants long before the fig pollination mutualism arose.

Eighty-two publications have described 48 ant genera present on 83 *Ficus* species (Table 1). Most records of ants on fig trees have come from Asia–Australasia (28 publications, 47%), especially Borneo (8, 13%). Twenty were made from the American continent (33%), ten from Africa (17%) and two from Europe (3%). There are reports from more fig species in Asia–Australasia, but more ant genera have been recorded on figs in the Americas (Table 1). On average, African and Australasian ant species were observed on a greater number of fig species compared to those on the American continent. Eight genera and 11 species have been recorded on the European fig (*Ficus carica*) (Schatz and Hossaert-McKey, 2003; Karaman and Karaman, 2006).

The genus *Ficus* is subdivided into six subgenera: *Ficus*, *Pharmacosycea*, *Sycidium*, *Sycomorus*, *Synoecia* and *Urostigma* (Berg and Corner, 2005) and ants have been observed on all subgenera. The African *Ficus sur* (subgenus *Sycomorus*, synonym *Ficus capensis*) has the best studied ant fauna (Ben-Dov, 1978; Compton and Robertson, 1988, 1991; Zachariades, 1994; Thomas, 1988; Cushman et al., 1998; Zachariades et al., 2009, 2010). In Australasia, *Ficus fistulosa* and *Ficus schwarzii* (subgenus *Sycomorus* section *Sycocarpus*) have been well studied (Schatz et al., 2006, 2008; Schatz and Hossaert-McKey, 2010, Harrison, 2014). In addition, 13 different ant genera have been observed on *Ficus benguetensis* in Taiwan (Lin et al., *pers. comm.*) and *Ficus septica* on the Sulawesi Island in Indonesia (Floren et al., 2002). In Papua New Guinea two studies on 14 fig species showed that ants, particularly *Crematogaster* and *Camponotus* ants, were extremely abundant (Novotny et al., 1999; Janda and Konečná, 2011). In the Neotropics the ants of *Ficus paraensis* (subgenus *Urostigma*) have been well documented (Wheeler, 1921; Davidson, 1988; Davidson and Epstein, 1989; Benzing, 1990). This last species was noted for its presence in ant-gardens (Wheeler, 1921). In one study, *F. paraensis* was present in 23% of the ant-gardens and