Acta Oecologica 57 (2014) 97–108

Contents lists available at SciVerse ScienceDirect

Acta Oecologica

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

Original article

How to be an ant on figs

Anthony Bain [a], Rhett D. Harrison [b,*], Bertrand Schatz [c]

[a] *Institute of Ecology and Evolutionary Biology, College of Life Sciences, National Taiwan University, 1, Sec. 4, Roosevelt Rd., Taipei 10617, Taiwan*
[b] *Key Laboratory for Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China*
[c] *Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175 CNRS, 1919 route de Mende, 34293 Montpellier, France*

ARTICLE INFO

Article history:
Received 22 November 2012
Accepted 21 May 2013
Available online 1 July 2013

Keywords:
Agaonidae
Ants
Ant–plant interactions
Ficus
Fig wasp
Mutualism
Pollination
Tropical forest

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

---

* Corresponding author. Current address: World Agroforestry Center (ICRAF), East Asia Node, Heilongtan, Kunming 650210, China.
E-mail addresses: rharrison@cgiar.org, rhett_d_harrison@yahoo.co.uk (R.D. Harrison).

1146-609X/$ – see front matter © 2013 Elsevier Masson SAS. All rights reserved.
http://dx.doi.org/10.1016/j.actao.2013.05.006

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 (Jousseline 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

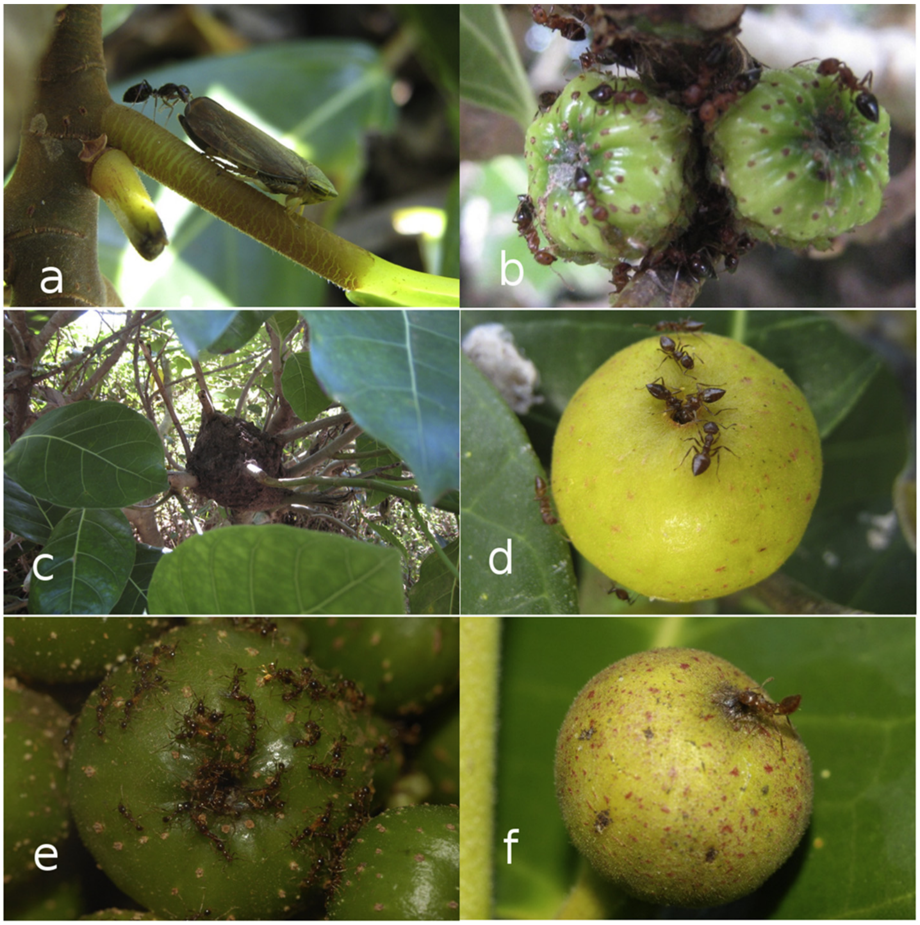

Fig. 1. Ants and figs in Taiwan. a) Dolichoderine ant tending a leafhopper on *Ficus pedunculosa* var. *mearnsii* at Kenting, South Taiwan. b) *Crematogaster* ants tending aphids and building paper protection on *Ficus septica* in North Taiwan. c) *Crematogaster* paper nest on *F. septica* in North Taiwan. d) *Crematogaster* ants searching for wasps on *F. tinctoria* subsp. *swinhoei* in Kenting, South Taiwan. e) Myrmicine ants waiting for the emergence of a *F. benguetensis* fig in North Taiwan. f) *Crematogaster* ants searching for female pollinating wasps in the ostiole of *F. tinctoria* subsp. *swinhoei* B phase fig in Kenting, South Taiwan. (Photos e and f from J.-R. Rasplus, others from A. Bain).

dominant in 12% of them (Davidson and Epstein, 1989). *Ficus trigona* has also been recorded in ant-gardens (Davidson, 1988). In addition, 15 ant species from nine genera have been recorded on *Ficus insipida* in the Dominican Republic (Weems, 2001).

About half of fig species are monoecious and the remainder are functionally dioecious (Berg and Corner, 2005). Ant species occurrence tends to be higher on monoecious (49 species, 59% of studied species) than on dioecious (34 species, 41% of studied species) figs. This situation could come from a biogeographic and researcher bias, as American *Ficus* are strictly monoecious. In dioecious figs, when ant presence was compared between male and female trees, the ants was always more abundant on male trees (Schatz et al., 2008; Harrison, *unpublished*).

By contrast, of the numerous subfamilies of ants, only five have been observed in association with the *Ficus*: Dolichoderinae, Formicinae, Myrmicinae, Ponerinae and Pseudomyrmecinae (Table 2). Nevertheless, these subfamilies represent a large proportion of the global ant diversity. Of 288 ant genera (Bolton et al., 2006), 49 have been documented on *Ficus* trees (Table 1). The genus *Crematogaster* is present on all continents and has been associated everywhere with the greatest number of *Ficus* species (Table 1). The ants from the genera *Camponotus* and *Pheidole* have also been associated with *Ficus* on all continents where ants and figs have been investigated, and *Tetraponera* was observed on *Ficus* in Africa, America and Asia–Australasia (Table 1). In the latter region, the most common ant genera on fig trees besides *Crematogaster* were *Oecophylla* (*Oecophylla smaragdina*), *Camponotus* and *Tetramorium*. On the American continent, *Atta* and *Pheidole* were the most commonly recorded on *Ficus*. In Africa, in one study, *Pheidole* ants represented 53.8%, *Anoplolepis* 6.1% and *Crematogaster* 5.3% of ant records on *Ficus* (Cushman et al., 1998), and in another study, *Pheidole megacephala* was present on 65% of fig trees, *Tetraponera* species on 40% and *Crematogaster* on 35% (Compton and Robertson, 1991).

A few studies have investigated dominance among ants on *Ficus* trees (Dejean et al., 1997; Schatz et al., 2006). From these studies, it is apparent that sometimes one species may dominate the ant assemblage to the point of excluding all other species from a tree. This may be in response to the presence of a defendable resource. For example, *Camponotus brutus* ants became aggressive if they were tending hemipterans (Dejean et al., 1997). However, most studies reviewed indicated there were multiple ant species present on individual fig trees.

4. Ants nesting in fig trees

Arboreal ants are the most abundant and diverse arthropods in the tropics (Davidson and Pattrel-Kim, 1996). About 700 fig species are mainly tropical (Berg and Corner, 2005) However, of the total of 83 *Ficus* species covered in this review, only 19 species (23%) had reports of ants nesting. Subgenus *Sycomorus* had the highest proportion of species with records of nesting ants (5 species, 26% of the trees with nesting ants), followed by *Urostigma* and *Sycidium* (4

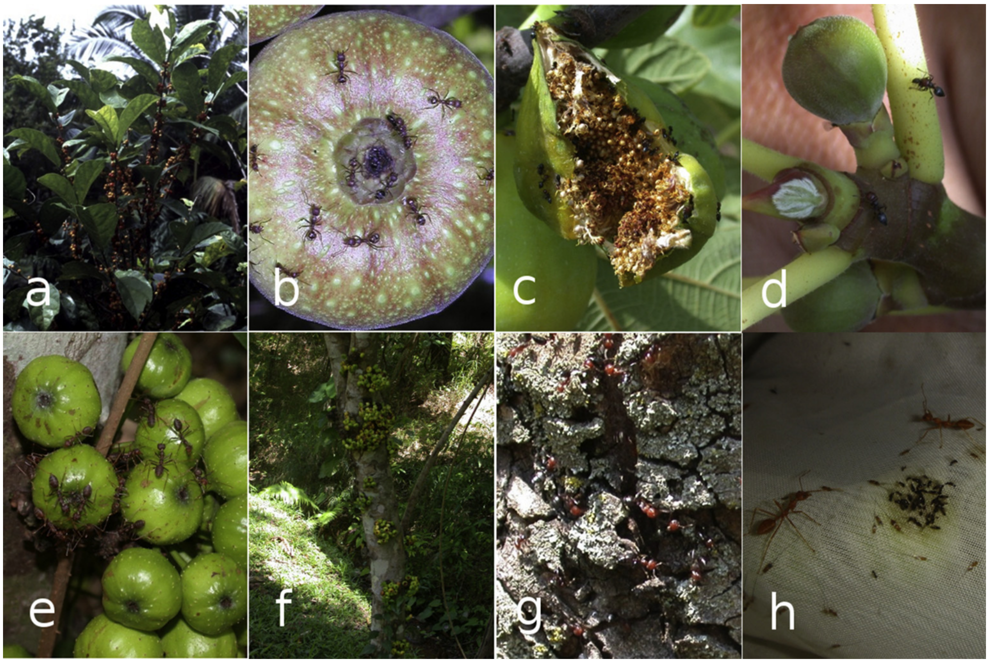

Fig. 2. a) *Ficus pisifera* on Borneo. b) Ants on syconia of *Ficus oligodon* in Thailand at the wasp emerging phase. Different behaviors of *Crematogaster scutellaris* ants on *Ficus carica* figs in France; c) workers collecting various food items in an opened syconia; d) a foraging worker and another capturing a pollinator. e) *Oecophylla* ants on a cauliflorous bunch of syconia of *Ficus fistulosa* in Brunei. f) Cauliflory on the trunk of *F. fistulosa*. g) Nest entrance of *Crematogaster scutellaris* in a dead part of the trunk. h) Bag containing receptive figs of *F. racemosa*, then attracting pollinators, NPFWs and *Oecophylla* ants as opportunistic predators during an experiment in India (Photos a–b from R.D. Harrison, c–g from B. Schatz, and h from M. Proffit).

species each, 21%). No observations of nesting ants have been reported from the subgenus *Synoecia*, but this possibly reflects the fact that these are climbers and poorly studied in general. Altogether, 16 ant genera have been observed nesting in 19 fig species (Table 3). *Crematogaster*, which frequently displays an arboreal life style (Hölldobler and Wilson, 1990), was the most commonly documented and has been recorded nesting on 11 *Ficus* species (11 out of 32 ant nesting observations, 34%). *Oecophylla* ants have been observed nesting on four fig species (4 out of 32 observations, 13%), and *Camponotus* and *Cardiocondyla* ants both on two species (each 6%). As result, Myrmicinae was the most common subfamily nesting in fig trees (20 out of 32 observations, 63%), followed by Formicidae (9, 28%), Dolichoderinae (2, 6%) and Ponerinae (1, 3%).

The most common locations of ant nests on figs were in cavities occurring in dead wood in the trunk or branches. Two out of five *Sycomorus* individuals, one of four *Urostigma* individuals and two of four *Sycidium* individuals had nests on their branches. Other locations of ant nests included hollowed twigs, among leaves, roots, among cauliflorous syconia or even inside ripe syconia, and in ant gardens on figs (Table 3).

Ant nests in figs have rarely been well described. *Crematogaster* ants are known to build paper nests among branches, but they also nest in dead wood closed off by paper walls on *F. septica* (Fig. 1c, Bain, *pers. obs.*) and *F. carica* (Fig. 2g, Schatz and Hossaert-McKey, 2003; Santini et al., 2011) or in trunk cavities (Vergara Navarro et al., 2007; Santini et al., 2011). Another frequent ant nesting in figs is *Oecophylla*, which construct nests from leaves sewn together with larval silk (Crozier et al., 2010). *Pheidole* are normally considered to be leaf litter ants but they also nests on trees (Sagata et al., 2010). On *Ficus*, *Pheidole* nests have been observed both in the branches and at the base of the trunk (Table 3). Only two fig species have been described as myrmecophytic with anatomical structures specifically suited to house ants: *Ficus pisifera* (ex. *Ficus obscura* var. *borneensis*) in Borneo (Fig. 2a, Maschwitz et al., 1994) and *Ficus subpisocarpa* in Taiwan (Bain et al., 2012). Both species were occupied by *Crematogaster* colonies. It seems that the *Crematogaster* ants are inhabitants of figs whatever the conditions, and may use trunk and branch cavities or domatia.

The reports of ants nesting in fig trees are scarce considering the abundance of the two organisms in tropical forests. No study has been done comparing the density of ant nests in an area to know if the ant nests are more or less abundant on figs than on other plants. However, is seems likely that they are not more abundant, despite the fact that the fig wasps are a ready source of food.

5. Behaviour of ants on the *Ficus* trees

5.1. Insect predation

Ants are considered to be omnivorous, but the proportion of the diet that is derived from animal prey varies hugely among ant subfamilies and genera. Ponerine ants feed more on animals than Formicine ants (Lach et al., 2010). Seventeen ant genera, predominantly belonging to the Pseudomyrmecinae and Ponerinae, have been recorded preying on fig wasps (Table 4). Ants have been recorded capturing pollinators and NPFWss during the emergence phase (Fig. 1d–e, Fig. 2b–c, Table 4). These include *Tetraponera* and *Pseudomyrmex* on *Ficus aurea* and *Ficus citrifolia* in the Neotropics (Frank, 1984), *Odontomachus troglodytes* on *F. sur* in South Africa (Cushman et al., 1998), *Odontoponera transversa* on *Ficus aurata* and *F. fistulosa* in Borneo (Schatz et al., 2008), as well as *Myrmicaria* and *Philidris* on *F. schwarzii* on Borneo (Harrison, 2014). However, a combination of timing emergence to avoid periods of high ant activity, emerging rapidly, and the male wasp behavior of scattering over the syconium surface, which distracts the ants while the females pollinators disperse, often enables pollinators to escape predation even when ants are present (Ware and Compton, 1994;

Table 1
Ficus species and their associated ants arranged by biogeographic region. The species number by continent is from Berg and Corner's work (2005). The numbers between parentheses after the ant genera correspond to the number of *Ficus* species they have been observed on.

	America	Africa	Asia–Australasia	Europe
Number of *Ficus* species	120	105	367	1
Studied *Ficus* species	21	40	51	1
Associated ant genera	24	15	29	8
Ant genus	*Acromyrmex* (1)	*Anoplolepis* (31)	*Acropyga* (1)	*Camponotus* (1)
	Apterostigma (1)	*Atopomyrmex* (1)	*Anoplolepis* (5)	*Cataglyphis* (1)
	Atta (5)	*Camponotus* (30)	*Aphaenogaster* (1)	*Crematogaster* (1)
	Azteca (4)	*Cardiocondyla* (1)	*Camponotus* (22)	*Formica* (1)
	Camponotus (4)	*Cataulacus* (1)	*Cardiocondyla* (1)	*Leptothorax* (1)
	Cephalotes (1)	*Crematogaster* (32)	*Cataulacus* (1)	*Messor* (1)
	Crematogaster (6)	*Iridomyrmex* (1)	*Crematogaster* (28)	*Pheidole* (1)
	Cyphomyrmex (3)	*Lepisiota* (1)	*Diacamma* (1)	*Plagiolepis* (1)
	Mycetarotes (1)	*Melissotarsus* (1)	*Dolidocherus* (4)	
	Mycetosoritis (1)	*Odontomachus* (31)	*Iridomyrmex* (1)	
	Mycocepurus (1)	*Oecophylla* (31)	*Monomorium* (17)	
	Myrmicocrypta (1)	*Pheidole* (31)	*Myrmica* (1)	
	Odontomachus (4)	*Polyrhachis* (31)	*Myrmicaria* (2)	
	Pachycondyla (1)	*Technomyrmex* (1)	*Odontomachus* (1)	
	Paratrechina (1)	*Tetraponera* (1)	*Odontoponera* (3)	
	Pheidole (5)		*Oecophylla* (22)	
	Platythyrea (1)		*Paratrechina* (16)	
	Pseudomyrmex (2)		*Pheidole* (7)	
	Sericomyrmex (1)		*Pheidologeton* (1)	
	Solenopsis (2)		*Philidris* (2)	
	Tapinoma (1)		*Polyrhachis* (2)	
	Tetramorium (1)		*Prenolepis* (1)	
	Tetraponera (1)		*Pristomyrmex* (2)	
	Trachymyrmex (1)		*Solenopsis* (1)	
			Tapinoma (16)	
			Technomyrmex (17)	
			Tetramorium (18)	

Kjellberg et al., 2005; Zachariades et al., 2010; Harrison, 2014). Ants may also catch fig pollinators as they arrive at receptive syconia (Figs. 1d and 2d and h). This has been recorded in *Oecophylla* on *F. fistulosa* (Fig. 2e, Schatz B. *pers. obs.*), *Myrmicaria* and *Philidris* on *F. schwarzii* (Harrison, 2014), *Crematogaster* on *Ficus oligodon* in Thailand (Fig. 2d, Harrison, *per. obs.*) and in an unknown Pseudomyrmecinae species on *Ficus pertusa* (Bronstein, 1991). Capture of pollinators, but without more detailed information as to the stage at which it occurred, was observed in various ant subfamilies including Formicinae (*Polyrhachis schistacea*), Pseudomyrmecinae (*Tetraponera* sp.), and Myrmicinae (*Atopomyrmex mocquerysi* and *Myrmicaria brunnea*) (Frank, 1984; Dejean et al., 1997; Cushman et al., 1998; Ranganathan et al., 2010).

Table 2
The number and taxonomical distribution of studied *Ficus* species and the number of associated ant species.

Subgenus	*Ficus* species	Section	*Ficus* species	Ant subfamily	Ant genera
Ficus	7	*Eriosycea*	2	5	8
		Ficus	5	4	13
Pharmacosycea	4	*Oreasycea*	1	3	7
		Pharmacosycea	3	4	4
Sycidium	10	*Paleomorphe*	3	2	5
		Sycidium	7	3	10
Sycomorus	18	*Adenosperma*	1	3	9
		Dammaropsis	1	3	9
		Sycocarpus	9	5	24
		Sycomorus	7	5	21
Synoecia	3	*Rhizocladus*	2	1	2
		Kissosycea	1	1	1
Urostigma	41	*Americana*	12	5	20
		Galoglychia	19	3	7
		Urostigma	10	4	14

Predation of NPFWs by ants has also been observed, especially during oviposition in those species that oviposit through the wall of the syconium. Moreover, several studies have reported that the presence of ants prevented NPFWs from initiating oviposition, although relatively few individuals were actually caught (Compton and Robertson, 1988, 1991; Cushman et al., 1998; Schatz et al., 2006; Compton et al., 2009; Ranganathan et al., 2010; Harrison, 2014). This disproportionate effect of the presence of predators compared to the actually rate of predation is similar to the "fear of predation" effect described for large mammalian herbivores (Ripple and Beschta, 2004). Direct predation of NPFWss when they have inserted ovipositors has been recorded in *Ficus punctata*, *Ficus racemosa*, *F. fistulosa* and *F. schwarzii* (Bronstein, 1988; Chou and Yeh, 1995; Schatz et al., 2006, 2008; Ranganathan et al., 2010; Harrison, 2014). J.Y. Rasplus (*pers. com.*) reports that he has observed figs unexpectedly covered in numerous long hairs, which on closer inspection turned out to be the ovipositors of NPFWs that had been preyed upon by ants. The production of NPFWs has been negatively correlated with the presence of ants in several fig species (Compton and Robertson, 1988; Zachariades, 1994; Schatz et al., 2006; Harrison, 2014) and the abundance of NPFWss is often strongly negatively correlated with pollinator production (Kerdelhué and Rasplus, 1996; Wei et al., 2005; Tzeng et al., 2008; Ma et al., 2009; Cardona et al., 2012). Interestingly, some NPFWs, such as the *Sycophaga* species on *F. racemosa* (Bain, pers. obs.) and some *Idarnes* wasps on *Ficus obtusifolia* (Jandér, *pers. com.*), appear to escape ant predation by avoiding detection. This is presumably achieved through some form of chemical mimicry, perhaps of the ants or more likely the surface of the syconium.

In Papua New Guinea, more than 51 *Ficus* species have been investigated for their caterpillar assemblages (Novotny et al., 2005). Ant presence was not described in this study but it is highly likely that ants are preying upon caterpillars and other insect herbivores living on *Ficus*. In *F. sur*, *F. fistulosa* and *F. schwarzii*, ants captured

Table 3
Fig species with records of nesting ants, the species of ants recorded, nesting locations on the plant, and location of the observations.

Ficus subgenus (section)	*Ficus* species	Nesting ants	Nesting locations	Country	References
Ficus (*Ficus*)	*F. carica*	*Crematogaster scutellaris*, *Pheidole pallidula*, *Plagiolepis pygmaea*	Main branches, base trunk	France	Schatz and Hossaert-McKey, 2003
		Camponotus lateralis	Main branches		
		Leptothorax rabaudi, *Formica truncorum*	Dead twigs		
	F. erecta var. *beecheyana*	*Crematogaster* sp.	Main branches	Taiwan	Bain (*personal observations*)
Pharmacosycea	*F. cristobalensis*	Unknown	Leaf bases	Solomon Islands	Corner, 1967
Sycomorus (*Sycocarpus*)	*F. benguetensis*	*Crematogaster* sp.	Main branches	Taiwan	Bain (*unpublished data*)
	F. septica	*Oecophylla smaragdina*		Philippines	
Sycomorus (*Sycomorus*)	*F. botryoides*	Unknown	Fig cluster	Madagascar	Dalecky et al., 2003
	F. racemosa	*Oecophylla smaragdina*	Main branches	Thailand	Bain (Pers. Obs.)
	F. sur	*Pheidole megacephala*	Base trunk	South Africa	Zachariades et al., 2010
		Oecophylla longinoda	Tree	Ivory coast	Thomas, 1988
	F. sycomorus	*Cardiocondyla wroughtoni*	Inside ripen figs	Israel	Lupo and Galil, 1985
Sycidium (*Paleomorphe*)	*F. pisifera*	Four *Crematogaster* spp., *Cardiocondyla* sp., *Cataulacus* sp., *Tetramorium* sp., *Camponotus* sp.	Hollowed twigs	Borneo (Malaysia)	Maschwitz et al., 1994
	F. tinctoria spp. *swinhoei*	*Crematogaster* sp.	Main branches	Taiwan	Bain (Pers. Obs.)
Sycidium (*Sycidium*)	*F. virgata*	*Crematogaster* sp.	Main branches	Taiwan	Bain (Pers. Obs.)
Urostigma (*Americana*)	*F. enormis*	*Camponotus sericeiventris*	Tree	Brazil	Yamamoto and Del-Claro, 2008
	F. paraensis	*Azteca traili*, *Azteca olitrix*, *Azteca ulei*	Ant Garden	Guyana	Wheeler, 1921
Urostigma (*Galoglychia*)	*F. lyrata*	*Crematogaster* sp.	Trunk cavity	Colombia	Vergara Navarro et al., 2007
Urostigma (*Urostigma*)	*F. subpisocarpa*	*Crematogaster* sp., *Myrmica* sp., *Prenolepis* sp., *Technomyrmex* sp.	Hollowed branches	Taiwan	Bain et al., 2012
		Crematogaster sp.	Main branches		
Unknown	*Ficus* spp.	*Camponotus femoratus*, *Crematogaster limata parabiotica*.	Tree aerial roots	South America	Beattie, 1989
		Cephalotes sp.	Tree	Panama	Hespenheide, 1986
		Crematogaster sp.	Tree	Cameroon	Voglmayr et al., 2011
		Pachycondyla apicalis	"Between roots"	Mexico	Fresneau, 1985

additional prey (dead pollinators and NPFWs, in particularly the non-dispersing males, nematodes, and fruit fly larvae) by entering the syconia after the emergence of the wasps (Figs. 1d and 2c, Zachariades et al., 2010; Schatz, pers. obs.; Harrison, 2014). Finally, ant presence is known to induce some adaptive behaviors in some insects present on figs, such as a reduced period of mating in fig flies (*Lissocephala* Drosophilidae) (Lachaise and McEvey, 1990). Both pollinating fig wasps and NPFWs often search carefully for ant free syconia and may be seen hovering several centimeters above syconia clusters (Schatz et al., 2006, 2008; Harrison, 2014). In addition, NPFWs landing on syconia with other NPFWs already ovipositing will immediately start to oviposit, but those landing on syconia without other wasps will wait for several minutes to determine that the syconium is ant-free (Harrison, 2014). Ant predation on fig wasps was most frequent on species from subgenera *Sycomorus* (10 out of 23 documented species, 43%), *Urostigma* (6 out of 23, 26%) and *Ficus* (5 out of 23, 22%). Overall, ants hunted on more fig species (23 out of 83, 28%) than they nested in (19 out of 83, 23%), but this pattern was reversed in subgenus *Sycidium* (4 nest species out of 10 (40%) *vs.* 1 species with ant predation (10%)) and *Pharmacosycea* (1 nest species out of 4 (25%) *vs.* none with ant predation). Indeed, it has been suggested that cauliflory, which is especially common among *Sycomorus* species, may be an adaptive response to high NPFWs populations because it facilitates efficient patrolling of syconia by ants (Schatz et al., 2008).

5.2. Ants tending insects on Ficus

Feeding on exudates from other insects (trophobionts) is particularly widespread in ants: 41% of the ant genera interact with trophobionts belonging to Lepidoptera or Hemiptera and, for example, in the Aphididae family (Hemiptera) 40% of the species are ant-tended (Lach et al., 2010).

Sixteen ant genera have been recorded tending hemipterans on *Ficus*. *Crematogaster* and *Camponotus* ants (each 6 records out of 19, 32%) are the most common ants recorded tending insects on *Ficus* (Table 5). *Paratrechina* sp. and *Tetraponera anthracina* Santschi were observed tending scale insects (Homoptera: Coccoidea) on *Ficus vallis-choudae* in Cameroon (Dejean et al., 1997); *Acropyga acutiventris* Roger was observed tending *Xenococcus annandalei* (Hemiptera: Pseudococcidae) on *Ficus trichocarpa* (*Synoecia*) in India (Silvestri, 1924); *Dolichoderus cuspidatus* Smith was observed tending *Malaicoccus* spp. (Hemiptera: Pseudococcidae) on an unidentified *Ficus* in Peninsular Malaysia (Maschwitz and Hänel, 1985); and *Dolichoderus tuberifer* Emery was observed tending *Hippeococcus rappardi* (Hemiptera: Pseudococcidae) on an unidentified *Ficus* on Java (Reyne, 1954). Finally, a Dolichoderine ant was observed tending a leafhopper (Hemiptera: Cicadellidae) on *Ficus pedunculosa* var. *mearnsii* in Taiwan (Fig. 1a). Most records of ant-tended hemipterans on *Ficus* have been for monoecious fig species and, in contrast, among seven dioecious figs in Borneo hemipterans were either absent or rare (Schatz et al., 2008).

Across five African countries, on 38 fig species and 429 individuals, the hemipteran *Hilda patruelis* (Tettigometridae) was the most common source of attraction for ants (Cushman et al., 1998) and *Ficus* from subgenus *Sycomorus* were more frequently attacked by *H. patruelis* than figs belonging to subgenus *Urostigma* (54% and 34%, respectively; Cushman et al., 1998)). *Sycomorus* species represent 40% and *Urostigma* species 13% of host records for hemipteran insects on *Ficus* (Cushman et al., 1998). In Taiwan, the presence of *Crematogaster* ants was strongly correlated with the presence of sap-sucking insects on *F. subpisocarpa* (*Urostigma*) (Bain

Table 4
Ant genera recorded predating on fig wasps. The *Ficus* species they have been recorded on, what they were recorded predating on B, for the receptive phase (when the pollinator enters the syconia); C, for the interfloral phase (NPFWss wasps are often ovipositing from outside the syconia); and D, for the wasp emerging phase.

Ant genus	*Ficus* species (subgenus)	Predation		Country	References
		Pollinators	NPFWs		
Crematogaster spp.	*F. aurata*, *F. deltoidea*, *F. fulva* (*Ficus*); *F. fistulosa*, *F. megaleia*, *F. uncinata* (*Sycomorus*)	X	X	Bruneï	Schatz et al., 2006, 2008
	F. carica (*Ficus*)	X (D)		France	Schatz and Hossaert-McKey, 2003
	F. tinctoria subsp. *swinhoei* (*Sycidium*); *F. benguetensis* (*Sycomorus*)	X (C,D)	X (C,D)	Taiwan	Bain (Pers. Obs.)
	F. sur, *F. sycomorus* (*Sycomorus*); *F. artocarpoides* (*Urostigma*)	X (B, D)	X (C)	Kenya; South Africa; Uganda	Compton and Robertson, 1991; Cushman et al., 1998; Compton et al., 2009
	F. vallis-choudae (*Sycomorus*)	X	X	Cameroon	Dejean et al., 1997
	F. subpisocarpa (*Urostigma*)	X	X	Taiwan	Bain et al., 2012
Camponotus spp.	*F. aurata*, *F. deltoidea*, *F. fulva* (*Ficus*); *F. fistulosa*, *F. uncinata* (*Sycomorus*)	X	X	Bruneï	Schatz et al., 2008
	F. carica (*Ficus*)	X (D)		France	Schatz and Hossaert-McKey, 2003
	F. sur (*Sycomorus*)	X	X	South Africa	Cushman et al., 1998
Tetraponera spp.	*F. aurata*, *F. deltoidea*, *F. fulva* (*Ficus*); *F. fistulosa*, *F. uncinata* (*Sycomorus*)	X	X	Bruneï	Schatz et al., 2008
	F. sur (*Sycomorus*)	X (B, D)	X (D)	South Africa	Compton and Robertson, 1991
	F. aurea, *F. citrifolia* (*Urostigma*)	X	X	USA(Florida)	Frank, 1984
Anoplolepis spp.	*F. aurata*, *F. deltoidea*, *F. fulva* (*Ficus*); *F. fistulosa*, *F. uncinata* (*Sycomorus*)	X	X	Bruneï	Schatz et al., 2008
	F. sur (*Sycomorus*)	X	X	South Africa	Cushman et al., 1998
Oecophylla spp.	*F. aurata*, *F. deltoidea*, *F. fulva* (*Ficus*); *F. fistulosa* (*Sycomorus*)	X	X	Bruneï	Schatz et al., 2006, 2008
	F. hispida (*Sycomorus*)	X (D)		Papua New Guinea	Weiblen et al., 2001
	F. racemosa (*Sycomorus*)	X	X	China, India	Wei et al., 2005; Ranganathan and Borges, 2009; Ranganathan et al., 2010
Dolichoderus spp.	*F. deltoidea* (*Ficus*); *F. fistulosa* (*Sycomorus*)	X	X	Bruneï	Schatz et al., 2008
Pheidole spp.	*F. carica* (*Ficus*)	X (D)		France	Schatz and Hossaert-McKey, 2003
	F. sur (*Sycomorus*)	X (B, C, D)	X (B, C, D)	South Africa	Compton and Robertson, 1988, 1991; Cushman et al., 1998; Zachariades et al., 2010
Tetramorium spp.	*F. deltoidea* (*Ficus*); *F. fistulosa*, *F. megaleia*, (*Sycomorus*)	X	X	Borneo (Brunei)	Schatz et al., 2008
Philidris	*F. eximia* (*Urostigma*);		X	Brazil	Pereira et al., 2000
	F. schwarzii (Sycomorus)	X	X	Borneo	Harrison and Yamamura, 2003, Harrison, 2014
Myrmicaria	*F. schwarzii* (Sycomorus)	X	X	Borneo	Harrison, 2014

et al., 2012). On figs, the vast majority of the tended insects belong to the Coccoidea and Aphidoidea superfamilies (Cryan and Urban, 2012, Table 5), but ants may also tend caterpillars (Fiedler and Maschwitz, 1989; Zachariades et al., 2009).

Ants are known to protect sap-sucking insects from parasitoids, which can lead to high levels of infestation and therefore a negative impact on the host plant (reviewed in Zachariades et al., 2009). In *Ficus* the species *P. megacephala* has been observed protecting *H. patruelis* from the parasitoid *Psyllechthrus oophagus* (Hymenoptera: Encyrtidae) and thereby increasing the level of infestation of the sap-sucking insects on figs in Africa (Zachariades et al., 2009). However, in the case of figs, hemipteran-tending ants may have a positive impact on the reproductive success of the fig if the ants also prey on NPFWs. Of the 23 ant genera that have been documented as hunting wasps and tending insects (Tables 4 and 5), 11 were doing both (48%). Not infrequently the sap-sucking insects feed directly on the syconia (Dejean et al., 1997). Compton and Robertson (1988) showed that *P. megacephala* tending *H. patruelis* on *F. sur* protected pollinator larvae against NPFWs. Ants tending insects on *Ficus* are mainly from genera for which tending behavior has already been recorded. However, the proportion of *Dolichoderus* ant records appears low, as these are considered to be specifically adapted to feeding on honeydew (Lach et al., 2010).

5.3. *Dispersal of fig seeds by ants*

The dispersal of seeds by ants (myrmecochory) has been recorded from over 3000 plant species (more than 90 genera) and includes ants from four subfamilies (Dolichoderinae, Formicinae, Myrmicinae and Ponerinae), all of which have been observed on figs (Rico-Gray and Oliveira, 2007; Lach et al., 2010). The worldwide geographical distribution of myrmecochory is heterogeneous. Myrmecochory is more prevalent in arid environments, particularly in Australia, North America, South Africa and the Mediterranean region. By comparison, only 0.2% of the known myrmecochorous species are recorded from the Neotropics (Rico-Gray and Oliveira, 2007; Lach et al., 2010).

As with other small-seeded plants, ants may disperse or prey upon fig seeds, but the action of ants on fig seeds is less well documented. Authors generally distinguish between seed dispersal and predation, even if both behaviors often co-occur (Table 6). Ant dispersal of fig seeds can occur on the ground (Roberts and Heithaus, 1986) or in the crown (Davidson, 1988). Twelve ant species have been documented dispersing or preying on fig seeds. The most frequent were *Atta* (only recorded as a herbivorous genus otherwise; Howard et al., 1996; Wirth et al., 1997; Clark, 2006), *Cyphomyrmex*, *Messor*, *Monomorium* and *Solenopsis*, but few ant genera interact only with *Ficus* via seeds (Table 6). Six other ant genera from

Table 5
Ant genera recorded tending hemiptera on *Ficus*.

Ant genus	*Ficus* species (subgenus)	Tended insects	Country	References
Crematogaster spp.	*F. aurata*, *F. fulva* (*Ficus*); *F. fistulosa* (*Sycomorus*)	Hemiptera	Borneo (Brunei)	Schatz et al., 2008
	F. carica (*Ficus*)	Hemiptera: Coccoidea	France	Schatz and Hossaert-McKey, 2003
	F. benguetensis, *F. septica* (*Sycomorus*)	Hemiptera: Aphidoidea	Taiwan	Bain (*unpublished data*)
	List out 8 *Sycomorus* species, 23 *Urostigma* species (5.3% of the trees)	*Hilda patruelis* (Hemiptera: Tettigometridae) and others Hemipterans	(list out 5 countries)	Compton and Robertson, 1991; Cushman et al., 1998
	F. subpisocarpa (*Urostigma*)	Hemiptera: Aphidoidea and Coccoidea	Taiwan	Bain et al., 2012
Camponotus spp.	*F. carica* (*Ficus*)	Hemiptera: Aphidoidea and Coccoidea	France	Schatz and Hossaert-McKey, 2003
	List out 8 *Sycomorus* species, 23 *Urostigma* species (3% of the trees)	*Hilda patruelis* (Hemiptera: Tettigometridae) and others Hemipterans	Africa (list out 5 countries)	Compton and Robertson, 1991; Cushman et al., 1998
	F. vallis-choudae (*Sycomorus*)	*Hilda undata* (Hemiptera: Tettigometridae) and Hemiptera: Coccoidea	Cameroon	Dejean et al., 1997
	F. paraensis (*Urostigma*)	Hemiptera: Auchenorrhyncha	Peru	Davidson and Epstein, 1989
Oecophylla spp.	*F. montana* (*Sycidium*)	*Anthene emolus* (Lepidoptera: Lycaenidae)	Malaysia (Peninsula)	Fiedler and Maschwitz, 1989
	F. pantoniana (*Synoecia*)	*Icerya* sp. (Hemiptera: Coccoidea)	Australia	Blüthgen and Fiedler, 2002; Blüthgen, 2003
	8 *Sycomorus* species, 23 *Urostigma* species (0.8% of the trees)	*Hilda patruelis* (Hemiptera: Tettigometridae) and others Hemipterans	Africa (list out 5 countries)	Compton and Robertson, 1991; Cushman et al., 1998
Pheidole spp.	*F. sur* (*Sycomorus*)	*Hilda patruelis* (Hemiptera: Tettigometridae), Hemiptera: Coccoidea and *Lachnocnema bibilus* (Lepidoptera: Lycaenidae)	South Africa	Compton and Robertson, 1988, 1991; Zachariades et al., 2009
	List out 8 *Sycomorus* species, 23 *Urostigma* species (53.8% of the trees)	*Hilda patruelis* (Hemiptera: Tettigometridae) and others Hemipterans	Africa (5 countries)	Cushman et al., 1998
Myrmicaria spp.	*F. racemosa* (*Urostigma*)	Hemiptera: Sternorrhyncha	India	Ranganathan and Borges, 2009
	F. vallis-choudae (*Sycomorus*)	Hemiptera: Coccoidea	Cameroon	Dejean et al., 1997
Dolichoderus spp.	Unknown	*Malaicoccus* sp. (Hemiptera: Pseudococcidae)	Malaysia	Maschwitz and Hänel, 1985
		Hypeococcus rappardi (Hemiptera: Pseudococcidae)	Java (Indonesia)	Reyne, 1954
Melissotarsus beccarii	*F. sur* (*Sycomorus*)	*Andaspis formicarum* (Hemiptera: Coccoidea)	South Africa	Ben-Dov, 1978
Melissotarsus beccarii	*F. sur* (*Sycomorus*)	*Andaspis formicarum* (Hemiptera: Coccoidea)	South Africa	Ben-Dov, 1978
Anoplolepis spp., *Odontomachus troglodytes*, *Polyrhachis schistacea*	8 *Sycomorus* species, 23 *Urostigma* species	*Hilda patruelis* (Hemiptera: Tettigometridae) and others Hemipterans	Africa (5 countries)	Compton and Robertson, 1991; Cushman et al., 1998
Paratrechina sp., *Tetraponera anthracina*	*F. vallis-choudae* (*Sycomorus*)	Hemiptera: Coccoidea	Cameroon	Dejean et al., 1997
Acropyga acutiventris	*F. trichocarpa* (*Synoecia*)	*Xenococcus annandalei* (Hemiptera: Pseudococcidae)	India	Silvestri, 1924
Lepisiota capensis	*F. sur* (*Sycomorus*)	*Hilda* sp. (Hemiptera: Tettigometridae)	South Africa	Compton and Robertson, 1991
Cataglyphis cursor	*F. carica* (*Ficus*)	Hemiptera: Aphidoidea and Coccoidea	France	Schatz and Hossaert-McKey, 2003
Dolichoderinae	*F. pedunculosa* var. *meanrsii* (*Ficus*)	Hemiptera: Cicadellinae	Taiwan	Bain, pers. obs. (Fig. 1)
Unknown	*F. erecta* (*Ficus*)	“Honeydew producers”	Japan	Tanaka et al., 2011

the tribe Attini (*Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex*, *Trachymyrmex* and *Acromyrmex*) have been recorded as interacting with fig seeds but without any details being provided as to their actions (Leal and Oliveira, 1998). Figs species from subgenus *Urostigma* represent 67% (eight out of 12 fig species) of these interactions (possibly due to the higher number of studies done on the American continent). These species are hemi-epiphytes and it has been suggested that ants may aid the dispersal of their seeds to suitable microsites in the canopy for germination and seedling establishment (Laman, 1996; Martínez-Mota et al., 2004). This is also suggested from the confirmation of elaiosomes in some species. Last, the aggressive ant *Oecophylla longinoda* has been recorded decreasing the fig fruit consumption by bats on *F. sur* in Ivory Coast, thereby reducing seed dispersal (Thomas, 1988).

The occurrence of myrmecochory in *Ficus* in humid tropical forests appears to go counter to the general pattern. However, the canopy of tropical rain forests is often a water-limited environment (Zotz and Hietz, 2001; Laman, 1996) and hence at micro-habitat scales similar selective factors may be favoring myrmecochory.

6. Figs as ant–plants

Myrmecophytic plants have been defined as those offering specialized domatia or direct food rewards through specialized structures to ants (Webber et al., 2007). *F. pisifera* has hollow twigs with slit-like openings that are sometimes occupied by ants and can be defined as domatia (Fig. 2a, Maschwitz et al., 1994). Other species such as *F. subpisocarpa* (Bain et al., 2012) and *F. paraensis* (Davidson and Epstein, 1989) have a particular branch morphology that appears to encourage ant nesting, but do not constitute true domatia. Some *Ficus* also provide direct food rewards: *F. septica* in Australia provides food rewards on the stem (Fig. 1b, Blüthgen, 2003); *F. aurea* in Florida (Koptur, 1992) and *F. schwarzii* in Borneo (Harrison, 2014) provide food rewards on the surface of the syconia; and on *F. vallis-choudae* in Cameroon ants have been observed feeding on exudates from buds, figs and branches (Dejean et al., 1997).

Hence, while about 100 tropical plant genera harbor specialized structures for ants to inhabit, only two species from more than 700 *Ficus* species have been discovered with such structures. Plants often

Table 6
Interactions between ant genera and fig seeds.

Ant genus	*Ficus* species (subgenus)	Seeds	Country	References
Pheidole spp.	*F. cotonifolia* (*Urostigma*)	Secondary dispersion	Costa Rica	Roberts and Heithaus, 1986
	F. americana (*Urostigma*)		Mexico	Martínez-Mota et al., 2004
	F. benjamina (*Urostigma*)		China (Yunnan)	Zhang and Chen, 2008
Atta spp.	*F. obtusifolia* (*Urostigma*); *F. yoponensis* (*Pharmacosycea*)	Seed predation	Panama	Wirth et al., 1997
	F. cotonifolia (*Urostigma*)	Secondary dispersion	Costa Rica	Roberts and Heithaus, 1986
Camponotus spp.	*F. vallis-choudae* (*Sycomorus*)	Primary dispersion	Cameroon	Dejean et al., 1997
	F. paraensis (*Urostigma*)	Secondary dispersion	Peru	Davidson, 1988; Benzing, 1990
Crematogaster spp.	*F. vallis-choudae* (*Sycomorus*)	Seed predation	Cameroon	Dejean et al., 1997
	F. paraensis (*Urostigma*)	Secondary dispersion	Peru	Davidson, 1988
Paratrechina spp.	*F. aurea*, *F. microcarpa* (*Urostigma*)	Secondary dispersion	USA (Florida)	Kaufmann et al., 1991
	F. benjamina (*Urostigma*)		China (Yunnan)	Zhang and Chen, 2008
Solenopsis invicta	*F. aurea*, *F. microcarpa* (*Urostigma*)	Secondary dispersion	USA (Florida)	Kaufmann et al., 1991
Atopomyrmex mocquerysi	*F. vallis-choudae* (*Sycomorus*)	Primary dispersion	Cameroon	Dejean et al., 1997
Messor barbarus	*F. carica* (*Ficus*)	Primary dispersion	France	Schatz (Pers. Obs.)
Polyrhachis sp.	*F. crassiramea* subsp. *stupenda*	Secondary dispersion	Borneo (Kalimantan)	Laman, 1995, 1996
Apterostigma sp., *Cyphomyrmex* sp., *Odontomachus bauri*	*F. cotonifolia* (*Urostigma*)	Secondary dispersion	Costa Rica	Roberts et al., 1983; Roberts and Heithaus, 1986
Azteca sp., *Tetramorium* sp.	*F. americana* (*Urostigma*)	Secondary dispersion	Mexico	Martínez-Mota et al., 2004
Monomorium pharaonis, *Odontoponera transversa*	*F. benjamina* (*Urostigma*)	Secondary dispersion	China (Yunnan)	Zhang and Chen, 2008
Unknown	*F. tiliifolia* (*Sycomorus*)	Seed predation	Madagascar	Dalecky et al., 2003

also offer food to attract and maintain ants on them in exchange for protection from antagonistic organisms (Rico-Gray and Oliveira, 2007; Lach et al., 2010). For these plants, the benefit is clear. However, for *Ficus*, interactions with ants may have both positive and negative outcomes on the reproductive success. In *F. subpisocarpa*, for example, figs are colonized by about 20 species of NPFWs, lepidopterans, coleopterans (from the families Curculionidae and Scarabaeidae) and hemipterans (Miridae), which combined can reduce the production of pollinating wasps to zero (Bain, *unpublished data*). In such cases, the presence of ants should be positive for the fig under most circumstances. However, on other *Ficus* species ants may prey upon large numbers of pollinating wasps (Fig. 2d) and delay or prevent pollination (Harrison, 2014).

7. How figs may influence the behavior of ants

Ants can potentially provide a number of different services to figs, including protection of fig leaves against herbivory, dispersal of fig seeds and, perhaps most significantly for figs, protection of syconia against NPFWs (Dawkins and Krebs, 1979; Bronstein, 1991; Maschwitz et al., 1994; Schatz et al., 2006, 2008; Bain et al., 2012). Fig leaves are protected by latex and herbivore pressure appears to be low on most species in most places, although exceptions are sometimes observed. No examples of ants being recruited to fig trees specifically for protection against herbivory are known. However, the unusual branch architecture that encourages ants to nest in *F. paraensis* and *F. subpisocarpa*, and the provision of food rewards on the stem in *F. septica* (Blüthgen, 2003), and from buds and branches in *F. vallis-choudae* (Dejean et al., 1997) may be examples of this type of interaction.

Ants may serve as important secondary dispersers of fig seeds. Occasionally ants are recorded removing seeds directly from fig fruit, usually from fallen fruit but sometimes from fruit that have been pecked open by birds in the canopy, but such dispersal is very short range and unlikely to result in successful recruitment. However, by actively picking fig seed from the droppings of vertebrate seed dispersers and transporting them to suitable establishment microsites, such as an ant nest, ants may greatly enhance the survival of the plant (Laman, 1996; Martínez-Mota et al., 2004). As mentioned above, this may be particularly important for hemi-epiphytes, which often have very low survivorship unless they can germinate in a knot-hole or large branch-fork with some soil. A number of plant species with small seeds attach a food reward (usually in the form of a lipid-rich coating) to the seed that can survive passage through a vertebrate gut, thereby encouraging secondary dispersal by ants (see Table 6 for references). It is no surprise to find that, although such elaiosomes have been identified in only a few *Ficus* species, these have all been hemi-epiphytic figs.

A number of studies have indicated that ants may reduce the number of NPFWs ovipositing on syconia, thereby protecting fig pollinators and perhaps also seeds. However, because ants also prey on pollinators arriving at receptive syconia or pollinator offspring emerging from mature syconia, the outcome of this interaction may not always benefit the fig (Schatz and Hossaert-McKey, 2003). However, individual ants can only capture one wasp at a time (Fig. 2d, Schatz and Hossaert-McKey, 2003; Schatz et al., 2006; Zachariades et al., 2010) and hence in a process akin to predator satiation (Janzen, 1969), large highly synchronous crops may serve to overwhelm the ants. Combined with the relatively rapid entry of fig pollinators into the syconium at receptivity and exit of pollinators at emergence, this may result in low pollinator predation rates. This possibly explains why some subgenus *Urostigma* figs apparently encourage a permanent presence of ants in the crown through the provision of nest sites (*F. paraensis* and *F. subpisocarpa*) or food rewards (*F. vallis-choudae*).

Following the same logic, it is also possible that the high prevalence of ant-tended hemiptera on *Urostigma* species is no accident. At least one study has demonstrated that ants tending hemiptera had a substantial negative impact on the abundance of NPFWs, but limited impact on pollinators (Compton and Robertson, 1988). Nevertheless, on fig species with smaller, more spatially clustered syconia, ants can have a substantial impact on pollinator arrival at receptivity or the numbers of female pollinators that disperse (Fig. 1e, Fig. 2e, f). Clearly, in this situation to maximize benefits to the fig, ants should be most abundant when NPFWs are ovipositing and least when the pollinating wasps are arriving or emerging. In *F. schwarzii* a food reward was produced on the surface of syconia in the early interfloral phase when the NPFWs started ovipositing (Harrison, 2014). The reward was present on only a small number of syconia, but appeared to be effective in encouraging the ants to patrol the syconia. It is noteworthy that, in contrast to the *Urostigma* figs, ant-tended hemiptera are apparently usually absent from cauliflorous figs (section *Sycocarpus*).

8. Chemical mediation of ant–fig interactions

Fig volatile signals change with syconia development and these changes are used by pollinating fig wasps and NPFWs to locate syconia at the correct phase of development for oviposition (Proffit et al., 2007, 2009; Ranganathan et al., 2010; Soler et al., 2012). This variation in odors emitted by figs can also potentially be used by ants to synchronize and enhance their predatory activity. In *F. carica*, *F. fistulosa* and *F. racemosa* ants learned to use the volatile organic compounds emitted by figs during the receptive and wasp emergence periods, which led to high predation rates on pollinating wasps (Fig. 2h, Schatz et al., 2003, 2006; 2008; Ranganathan and Borges, 2009; Schatz and Hossaert-McKey, 2010; Hossaert-McKey et al., 2010), and the volatile chemicals emitted by the pollinators and NPFWs themselves are detected by at least two species of ants on *F. fistulosa* (Schatz and Hossaert-McKey, 2010). Primary seed dispersal by birds, bats, small mammals and primates (Kalko et al., 1996; Hodgkison et al., 2007; Borges et al., 2008; Soler, 2010) and secondary dispersal by ants (Kaufmann et al., 1991) is likely to be mediated by olfactory compounds originating from the mature figs and the elaiosome of seeds, respectively. Investigations in chemical ecology promise to reveal how insect species interact in the complex communities supported by figs (Schatz et al., 2003; Ranganathan and Borges, 2009; Schatz and Hossaert-McKey, 2010; Hossaert-McKey et al., 2010).

9. Conclusions

Ants are a common component of invertebrate assemblages on fig trees in all tropical regions and across major evolutionary lineages. A broad diversity of ant subfamilies (48 genera) has been recorded on figs and at least 16 genera also nest in figs. Ants have been reported from about 11% of fig species (83 out of 735 species (Berg and Corner, 2005)) and about 3% (19 species) have records of ant nesting. However, these statistics are strongly constrained by the relative paucity of studies. At least two fig species in subgenus *Urostigma* have a special branch architecture that appears to encourage ant nesting, and one species, *F. pisifera*, has ant domatia in the twigs. At least five species of fig provide some kind of food reward for ants. On figs, the major roles of ants are as predators of fig wasps, including both pollinating and non-pollinating species, protecting and tending sap-sucking hemipterans, and as dispersers of fig seeds. The same ant species may feature in more than one of these roles, in particular ants tending hemipterans often also prey on fig wasps. In their role as predators of fig wasps, ants have the potential to affect the evolutionary dynamics of the fig–fig pollinator interaction. Because NPFWs can cause high mortality of pollinators, where ants prey predominantly on NPFWs they may be beneficial to the reproductive interests of the fig. However, ants also prey on pollinating wasps and hence the outcome for the fig is variable and will depend on the behavior of the ants involved and their abundance. Fig pollinators tend to enter receptive syconia quickly and their offspring emerge from mature syconia rapidly, limiting the opportunity for ants to prey on them. Several other factors, such as the scattering of male wasps at emergence, also contribute to limiting pollinator predation. In contrast, most NPFWs species must oviposit through the syconium wall and hence are vulnerable to ant predation. Therefore, in many cases ants appear to have a beneficial effect on fig reproductive success. However, the ant–fig interaction appears to have a different evolutionary dynamic on the large monoecious figs, especially the hemi-epiphytic figs of subgenus *Urostigma*, and on the smaller trees of subgenus *Sycomorus*, especially section *Sycocarpus*. Ant nesting and tending of hemipterans were more prevalent on subgenus *Urostigma* species. These species have infrequent large highly synchronous crops, which though predator satiation may enable most pollinators to escape predation despite the permanent presence of ants on the fig. In contrast, many section *Sycocarpus* species have frequent smaller, more asynchronous crops and, if present on the fig at receptivity or wasp emergence, ants can have a substantial impact on pollinator production. These species rarely have ant-tended hemiptera or ant-nests, and may engage in other strategies to control ant abundance in relation to crop development, such as through providing a food reward. It would be instructive to investigate the generality of this statement through a large-scale comparative study aimed at characterizing the factors that determine the nature of the fig–ant interaction across an ecologically diverse sample of figs (Schatz et al., 2008). As seed dispersers, ants often provide an essential role in removing seeds from vertebrate feces and carrying them to suitable microsites. This may be especially important for hemi-epiphytic figs, which require high quality establishment microsites to survive the arid canopy environment, and elaiosomes have been observed in several hemi-epiphytic species.

Interactions among figs and their associated insects are an established model system for investigating hypotheses concerning the evolutionary dynamics of mutualisms (Bronstein and McKey, 1989; Cook and Rasplus, 2003; Schatz et al., 2006; Herre and Jandér, 2010) and are also a useful system for studying the behavioral ecology of Hymenoptera (Kjellberg et al., 2005; Schatz et al., 2006, 2008). Meanwhile, ant–plant interactions constitute a second well-established model for understanding mutualistic interactions (Yu and Davidson, 1997; Mueller et al., 1998; Itino et al., 2001; Edwards et al., 2006; Palmer et al., 2008; Schatz et al., 2009), and can provide a powerful tool for investigating many aspects of ant biology, such as foraging behavior, interspecific competition, and predation (Heil and McKey, 2003; Debout et al., 2005; Byk and Del-Claro, 2011). Combining these two model systems to investigate how evolutionary dynamics of mutualistic interactions are constrained by the network of interactions in which they are embedded should prove a fertile field of research.

Acknowledgments

Many thanks to several collaborators who participate to discussion around this work: Lien-Siang Chou, Bruno Di Giusto Martine Hossaert-McKey, Finn Kjellberg, Shang-Yang Lin, Samhan Nyawa, Magali Proffit, Jean-Yves Rasplus, Fabien Ravary and Catherine Soler. We also acknowledge the University of Brunei Darussalam for facilities of the National Taiwan University and CNRS (PICS N°935) and the ANR-NSC (ANR-09-BLAN-0392-CSD 7, NSC 99-2923-B-002-001-MY3) for grants permitting this study. RH was supported through a National Science Foundation China grant (NSFC Grant No. 30972294) and a Foreign Young Scientists Fellowship, Chinese Academy of Sciences.

References

Ashman, T.-L., King, E.A., 2005. Are flower-visiting ants mutualists or antagonists? A study in a gynodioecious wild strawberry. American Journal of Botany 92, 891–895.

Bain, A., Chantarasuwan, B., Hossaert-McKey, M., Schatz, B., Kjellberg, F., Chou, L.S., 2012. A new case of ants nesting within branches of a fig tree: the case of *Ficus subpisocarpa* in Taiwan. Sociobiology 59, 415–434.

Beattie, A., 1989. Myrmecotrophy: plants fed by ants. Trends in Ecology and Evolution 4, 172–176.

Ben-Dov, Y., 1978. *Andaspis formicarum* n. sp. (Homoptera, Diaspididae) associated with a species of *Melissotarsus* (Hymenoptera, Formicidae) in South Africa. Insectes Sociaux 25, 315–321.

Benzing, D.H., 1990. Vascular Epiphytes. Cambridge University Press.

Berg, C.C., 1989. Classification and distribution of *Ficus*. Experientia 45, 605–611.

Berg, C.C., Corner, E.J.H., 2005. Moraceae (*Ficus*). In: Nooteboom, H.P. (Ed.), Flora Malesiana. National Herbarium Nederland, Leiden, pp. 1–730.

Blüthgen, N., 2003. How Availability and Quality of Nectar and Honeydew Shape an Australian Rainforest Ant Community. Universität Bayreuth, Bayreuth, p. 166.

Blüthgen, N., Fiedler, K., 2002. Interactions between weaver ants *Oecophylla smaragdina*, homopterans, trees and lianas in an Australian rain forest canopy. Journal of Animal Ecology 71, 793–801.

Blüthgen, N., Klein, A.-M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. Basic and Applied Ecology 12, 282–291.

Bolton, B., Alpert, G., Ward, P.S., Nasrecki, P., 2006. Bolton's Catalogue of Ants of the World. Harvard University Press.

Borges, R.M., Bessière, J.-M., Hossaert-McKey, M., 2008. The chemical ecology of seed dispersal in monoecious and dioecious figs. Functional Ecology 22, 484–493.

Bronstein, J.L., 1988. Predators of fig wasps. Biotropica 20, 215–219.

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

Bronstein, J.L., 1998. The contribution of ant–plant protection studies to our understanding of mutualism. Biotropica 30, 150–161.

Bronstein, J.L., 2001. The exploitations of mutualisms. Ecology Letters 4, 277–287.

Bronstein, J.L., 2003. The scope for exploitation within mutualistic interactions. In: Hammerstein, P. (Ed.), Genetics and Evolution of Cooperation. MIT Press, Cambridge, Massachusetts, USA, pp. 185–202.

Bronstein, J.L., McKey, D., 1989. The fig/pollinator mutualism: a model system for comparative biology. Experientia 45, 601–604.

Byk, J., Del-Claro, K., 2011. Ant–plant interaction in the Neotropical savanna: direct beneficial effects of extrafloral nectar on ant colony fitness. Population Ecology 53, 327–332.

Cardona, W., Kattan, G.H., Chacón De Ulloa, P., 2012. Non-pollinating fig wasps decrease pollinator and seed production in *Ficus andicola* (Moraceae). Biotropica 45, 203–208.

Chou, L.S., Yeh, H.M., 1995. The pollination ecology of *Ficus aurantiaca* var. *parvifolia*. Acta Zoologica Taiwanica 6, 1–12.

Clark, E., 2006. Dynamic matching of forager size to resources in the continuously polymorphic leaf-cutter ant, *Atta colombica* (Hymenoptera, Formicidae). Ecological Entomology 31, 629–635.

Compton, S.G., Disney, R.H.L., 1991. New species of *Megaselia* (Diptera: Phoridae) whose larvae live in fig syconia (Urticales: Moraceae), and adults prey on fig wasps (Hymenoptera: Agaonidae). Journal of Natural History 25, 203–219.

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.

Compton, S.G., Robertson, H.G., 1991. Effects of ant–homopteran systems on fig-fig wasp interactions. In: Huxley, C.R., Cutler, D.F. (Eds.), Ant–Plant Interactions. Oxford University Press, Oxford, pp. 120–130.

Compton, S.G., Van Noort, S., Mcleish, M., Deeble, M., Stone, V., 2009. Sneaky African fig wasps that oviposit through holes drilled by other species. African Natural History 5, 9–15.

Cook, J.M., Rasplus, J.Y., 2003. Mutualists with attitude: coevolving fig wasps and figs. Trends in Ecology and Evolution 18, 241–248.

Corner, E.J.H., 1967. *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. Philosophical Transactions of the Royal Society B 253, 23–159.

Crozier, R.H., Newey, P.S., Schlüns, E.A., Robson, S.K.A., 2010. A masterpiece of evolution – *Oecophylla* weaver ants (Hymenoptera: Formicidae). Myrmecological News 13, 57–71.

Cruaud, A., Jabbour-Zahab, R., Genson, G., Cruaud, C., Couloux, A., Kjellberg, F., Van Noort, S., Rasplus, J.Y., 2010. Laying the foundations for a new classification of Agaonidae (Hymenoptera: Chalcidoidea), a multilocus phylogenetic approach. Cladistics 26, 359–387.

Cruaud, A., Jabbour-Zahab, R., Genson, G., Kjellberg, F., Kobmoo, N., Van Noort, S., Yang, D.-R., Peng, Y.-Q., Ubaidillah, R., Hanson, P.E., Santos-Mattos, O., Farache, F.H.A., Pereira, R.A.S., Kerdelhué, C., Rasplus, J.-Y., 2011. Phylogeny and evolution of life-history strategies in the Sycophaginae non-pollinating fig wasps (Hymenoptera, Chalcidoidea). BMC Evolutionary Biology 11, 178–192.

Cryan, J.R., Urban, J.M., 2012. Higher-level phylogeny of the insect order hemiptera: is *Auchenorrhyncha* really paraphyletic? Systematic Entomology 37, 7–21.

Cushman, J.H., Compton, S.G., Zachariades, C., Ware, A.B., Nefdt, R.J.C., Rashbrook, V.K., 1998. Geographic and taxonomic distribution of a positive interaction: ant-tended homopterans indirectly benefit figs across southern Africa. Oecologia 116, 373–380.

Dalecky, A., Kerdelhué, C., Johnson, S., Razafindratsita, V.R., Grassi, C., Razafiarimalala, A.C., Overdorff, D.J., Rasplus, J.Y., 2003. Moraceae, *Ficus* and associated fauna. In: Goodman, S.M., Benstead, J.P. (Eds.), The Natural History of Madagascar. University of Chicago Press.

Davidson, D.W., 1988. Studies of Neotropical ant gardens. Ecology 69, 1138–1152.

Davidson, D.W., Epstein, W.W., 1989. Epiphytic associations with ants. In: Luttge, U. (Ed.), Vascular Plants as Epiphytes – Evolution and Ecophysiology. Springer-Verlag, New York, pp. 200–233.

Davidson, D.W., Pattrel-Kim, L., 1996. Tropical arboreal ants: why so abundant? In: Gibson, A.C. (Ed.), Neotropical Biodiversity and Conservation. University of California, Los Angeles, pp. 127–140.

Dawkins, R., Krebs, J.R., 1979. Arms race between and within species. Proceedings of the Royal Society of London B 205, 489–511.

Debout, G., Schatz, B., McKey, D., 2005. Comparison of foraging behavior in two plant–ants, the mutualist *P. phylax* and the *C. mckeyi* mutualism parasite. Insectes Sociaux 43, 111–118.

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.

Dunn, D.W., Segar, S.T., Ridley, J., Chan, R., Crozier, R.H., Yu, D.W., Cook, J.M., 2008. A role for parasites in stabilising the fig-pollinator mutualism. PLoS Biology 6, e59.

Edwards, D.P., Hassall, M., Sutherland, W.J., Yu, D.W., 2006. Selection for protection in an ant–plant mutualism: host sanctions, host modularity, and the principal-agent game. Proceedings of the Royal Society of London B 273, 595–602.

Fiedler, K., Maschwitz, U., 1989. The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. Journal of Natural History 23, 833–846.

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

Frank, S.A., 1984. The behavior and morphology of the fig wasps *Pegoscapus assuetus* and *P. jimenezi*: descriptions and suggested behavioral characters for phylogenetic studies. Psyche 91, 289–308.

Fresneau, D., 1985. Individual foraging and path fidelity in a ponerine ant. Insectes Sociaux 32, 109–116.

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

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

Harrison, R.D., 2014. Ecology of a fig ant–plant. Acta Oecologia 57, 88–96.

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

Heil, M., McKey, D., 2003. Protective ant–plant interactions as model systems in ecological and evolutionary research. Annual Review of Ecology and Systematic 34, 425–553.

Herre, E.A., Jandér, K.C., 2010. Host sanctions and pollinator cheating in the fig tree–fig wasp mutualism. Proceedings of the Royal Society of London B 227, 1481–1488.

Hespenheide, H.A., 1986. Mimicry of ants of the genus *Zacryptocerus* (Hymenoptera: Formicidae). Journal of the New York Entomological Society 94, 394–408.

Hodgkison, R., Ayasse, M., Kalko, E.K.V., Haeberlein, C., Schulz, S., Mustapha, W.A.W., Zubaid, A., Kunz, T.H., 2007. Chemical ecology of fruit bat foraging behavior in relation to the fruit odors of two species of paleotropical bat-dispersed figs (*Ficus hispida* and *Ficus scortechinii*). Journal of Chemical Ecology 33, 2097–2110.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Harvard University Press.

Hossaert-McKey, M., Soler, C., Schatz, B., Proffit, M., 2010. Floral scents: their role in nursery pollination mutualism. Chemoecology 20, 75–88.

Howard, J.J., Henneman, M.L., Cronin, G., Fox, J.A., Hormiga, G., 1996. Conditioning of scouts and recruits during foraging by a leaf-cutting ant, *Atta colombica*. Animal Behaviour 52, 299–306.

Huxley, C.R., Cutler, D.F., 1991. Ant–Plant Interactions. Oxford University Press, Oxford.

Itino, T., Davies, S.J., Tada, H., Hieda, Y., Inoguchi, M., Itioka, T., Yamane, S., et al., 2001. Cospeciation of ants and plants. Ecological Research 16, 787–793.

Janda, M., Konečná, M., 2011. Canopy assemblages of ants in a New Guinea rain forest. Journal of Tropical Ecology 27, 83–91.

Janzen, D.H., 1969. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology 50, 147–153.

Jouselline, E., Rasplus, J.-E., Kjellberg, F., 2001. Shift to mutualism in parasitic lineages of the fig/fig wasp interaction. Oikos 94, 278–294.

Kalko, E.K.V., Herre, E.A., Handley, C.O., 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography 23, 565–576.

Karaman, G.S., Karaman, M.G., 2006. Contribution to the knowledge of the ants (Hymenoptera: Formicidae) of Crna Gora (Montenegro). Natura Montenegrina 5, 91–108.

Kaufmann, S., McKey, D., Hossaert-McKey, M., Horvitz, C.C., 1991. Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). American Journal of Botany 78, 971–977.

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.

Kjellberg, F., Jousselin, E., Hossaert-McKey, M., Rasplus, J.Y., 2005. Biology, ecology, and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae). In: Raman, A., Schaefer, W., Withers, T.M. (Eds.), Biology, Ecology and Evolution of Gall-inducing Arthropods. Science Publishers, Inc., Enfield (NH), USA Plymouth (UK), pp. 539–572.

Koptur, S., 1992. Plants with extrafloral nectaries and ants in Everglades habitats. The Florida Entomologist 75, 38–50.

Lach, L., Parr, C., Abbott, K., 2010. Ant Ecology. Oxford University Press, Oxford.

Lachaise, D., McEvey, S.F., 1990. Independent evolution of the same set of characters in fig flies (*Lissocephala*, Drosophilidae). Evolutionary Ecology 4, 358–364.

Laman, T.G., 1995. *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. Ecology 76, 2617–2626.

Laman, T.G., 1996. The impact of seed harvesting ants (*Pheidole* sp. nov.) on *Ficus* establishment in the canopy. Biotropica 28, 777–781.

Leal, I.R., Oliveira, P.S., 1998. Interactions between fungus-growing ants (Attini), fruits and seeds in Cerrado vegetation in southeast Brazil. Biotropica 30, 170–178.

Lupo, A., Galil, J., 1985. Nesting habits of *Cardiocondyla wroughtoni* Forel (1890) (Hymenoptera: Formicidae). Israel Journal of Entomology 19, 119–125.

Ma, W.J., Yang, D.R., Peng, Y.Q., 2009. Disturbance effects on community structure of *Ficus tinctoria* fig wasps in Xishuangbanna, China: implications for the fig/fig wasp mutualism. Insect Science 16, 417–424.

Martínez-Mota, R., Serio-Silva, J.C., Rico-Gray, V., 2004. The role of canopy ants in removing *Ficus perforata* seeds from howler monkey (*Alouatta palliata mexicana*) feces at Los Tuxtlas, México. Biotropica 36, 429–432.

Maschwitz, U., Hänel, H., 1985. The migrating herdsman *Dolichoderus (Diabolus) cuspidatus*: an ant with a novel mode of life. Behavioral Ecology and Sociobiology 17, 171–184.

Maschwitz, U., Fiala, B., Saw, L.G., Yusoff, N.R., Idris, A.H., 1994. *Ficus obscura* var. *borneensis* (Moraceae), a new non-specific ant–plant from Malaysia. Malayan Nature Journal 47, 409–416.

McKey, D., Hossaert-McKey, M., 2008. La coévolution entre les plantes et les animaux. In: Hallé, F. (Ed.), Aux origines des Plantes. Fayard, Paris, pp. 482–505.

Moreira, V.S.S., Del-Claro, K., 2005. The outcomes of an ant–treehopper association on *Solanum lycocarpum* St. Hil: increased membracid fecundity and reduced damage by chewing herbivores. Neotropical Entomology 34, 881–887.

Morris, W.F., Bronstein, J.L., Wilson, W.G., 2003. Three-way coexistence in obligate mutualist–exploiter interaction: the potential role of competition. American Naturalists 161, 860–875.

Mueller, U.G., Rehner, S.A., Schultz, T.R., 1998. The evolution of agriculture in ants. Science 281, 2034–2038.

Nahas, L., Gonzaga, M.O., Del-Claro, K., 2012. Emergent impacts of ant and spider interactions: herbivory reduction in a tropical savanna tree. Biotropica 44, 498–505.

Novotny, V., Basset, Y., Auga, J., Boen, W., Dal, C., Drozd, P., Kasbal, M., Isua, B., Kutil, R., Manumbor, M., Molem, K., 1999. Predation risk for herbivorous insects on tropical vegetation: a search for enemy-free space and time. Australian Journal of Ecology 24, 477–483.

Novotny, V., Miller, S.E., Basset, Y., Cizek, L., Darrow, K., Kaupa, B., Kua, J., Weiblen, G.D., 2005. An altitudinal comparison of caterpillar (Lepidoptera) assemblages on *Ficus* trees in Papua New Guinea. Journal of Biogeography 32, 1303–1314.

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.

Pereira, R.A.S., Semir, J., De Oliveira Menezes, A.J., 2000. Pollination and other biotic interactions in figs of *Ficus eximia* Schott (Moraceae). Revista Brasileira de Botânica 23, 217–224.

Proffit, M., Schatz, B., Borges, R.M., Hossaert-McKey, M., 2007. Chemical mediation and niche partitioning in non-pollinating fig-wasp communities. Journal of Animal Ecology 76, 296–303.

Proffit, M., Chen, C., Soler, C., Bessière, J.M., Schatz, B., Hossaert-McKey, M., 2009. Can chemical signals, responsible for mutualistic partner encounter, promote the specific exploitation of nursery pollination mutualisms? The case of figs and fig wasps. Entomologia Experimentalis et Applicata 131, 46–57.

Ranganathan, Y., Borges, R.M., 2009. Predatory and trophobiont-tending ants respond differently to fig and fig wasp volatiles. Animal Behaviour 77, 1539–1545.

Ranganathan, Y., Ghara, M., Borges, R.M., 2010. Temporal associations in fig-wasp-ant interactions: diel and phenological patterns. Entomologia Experimentalis et Applicata 137, 50–61.

Rasplus, J.-Y., kerdelhué, C., Clainche, lL., Mondor, G., 1998. Molecular phylogeny of fig wasps Agaonidae are not monophyletic. Comptes Rendus de l'Académie des Sciences Paris, Sciences de la vie/Life Sciences 321, 517–527.

Reyne, A., 1954. *Hippeococcus*: a new genus of Pseudococcidae from Java with peculiar habits. Zoologische Mededelingen 32, 233–257.

Rico-Gray, V., Oliveira, P.S., 2007. The Ecology and Evolution of Ant–Plant Interactions. The University of Chicago Press, Chicago.

Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54, 755–766.

Roberts, J.T., Heithaus, E.R., 1986. Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. Ecology 67, 1046–1051.

Roberts, J.T., Heithaus, E.R., Chaverri, A., 1983. Post dispersal movements by ants of seeds from a neotropical fig, *Ficus hondurensis* (Moraceae). Ohio Journal of Science 83, 88–89.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, V., 2005. 60 million years of co-divergence in the fig–wasp symbiosis. Proceedings of the Royal Society of London B 272, 2593–2599.

Sagata, K., Mack, A.L., Wright, D.D., Lester, P.J., 2010. The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. Insectes Sociaux 57, 333–341.

Santini, G., Ramsay, P.M., Tucci, L., Ottonetti, L., Frizzi, F., 2011. Spatial patterns of the ant *Crematogaster scutellaris* in a model ecosystem. Ecological Entomology 36, 625–634.

Schatz, B., Hossaert-McKey, M., 2003. Interactions of the ant *Crematogaster scutellaris* with the fig/fig wasp mutualism. Ecological Entomology 28, 359–368.

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

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

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., Kjellberg, F., Nyawa, S., Hossaert-McKey, M., 2008. Fig wasps: a staple food for ants on *Ficus*. Biotropica 40, 190–195.

Schatz, B., Djieto-Lordon, C., Dormont, L., Bessière, J.M., McKey, D., Blatrix, R., 2009. A simple, non-specific chemical signal mediates defence behaviour in a specialised ant–plant mutualism. Current Biology 19, 361–362.

Segar, S.T., Lopez-Vaamonde, C., Rasplus, J.Y., Cook, J.M., 2012. The global phylogeny of the subfamily Sycoryctinae (Pteromalidae): parasites of an obligate mutualism. Molecular Phylogeny and Evolution 65, 116–125.

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

Silvestri, F., 1924. A new myrmecophilous genus of Coccidae from India. Records of the Indian Museum 26, 311–315.

Soler, C., 2010. Parfum de figues: Approche évolutive de la communication entre une plante, ses insectes pollinisateurs et ses vertébrés disperseurs. PhD. University of Montpellier, p. 248.

Soler, C., Proffit, M., Bessiere, J.M., Hossaert-McKey, M., Schatz, B., 2012. Evidence for intersexual chemical mimicry in a dioecious plant. Ecology Letters 15, 978–985.

Tanaka, H., Ohnishi, H., Tatsuta, H., Tsuji, K., 2011. An analysis of mutualistic interactions between exotic ants and honeydew producers in the Yanbaru district of Okinawa Island, Japan. Ecological Research 26, 931–941.

Thomas, D.W., 1988. The influence of aggressive ants on fruit removal in the tropical tree, *Ficus capensis* (Moraceae). Biotropica 20, 49–53.

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

Vergara Navarro, E.V., Echavarría Sánchez, H., Serna Cardona, F.J., 2007. Ants (Hymenoptera Formicidae) associated with the arboretum of the Universidad Nacional de Colombia, Medellín. Boletín Sociedad Entomológica Aragonesa 40, 497–505.

Voglmayr, H., Mayer, V., Maschwitz, U., Moog, J., Djiéto-Lordon, C., Blatrix, R., 2011. The diversity of ant-associated black yeasts: insights into a newly discovered world of symbiotic interactions. Fungal Biology 115, 1077–1091.

Wang, Z.J., Li, G.C., Peng, Y.Q., Yang, D.R., 2012. Spatial distribution of fig wasps in syconia of two monoecious *Ficus* sp. Zoological Research 33, 182–186.

Ware, A.B., Compton, S.G., 1994. Dispersal of adult female fig wasps. 1. Arrivals and departures. Entomologia Experimentalis et Applicata 73, 221–229.

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. Botanical Journal of the Linnean Society 154, 353–371.

Weems, J.R., 2001. Ant Species Diversity at Different Heights along the *F. insipida*. T. Lacher and B. Wharton, Dominica. Texas A&M University, College Station, Texas.

Wei, Z.D., Peng, Y.Q., Xu, L., Yang, D.R., 2005. Impact of *Oecophylla smaragdina* on the percentage number of offspring of pollinator and non-pollinating wasps on *Ficus racemosa*. Zoological Research 26, 386–390.

Weiblen, G.D., 2002. How to be a fig wasp. Annual Review of Entomology 47, 299–330.

Weiblen, G.D., Yu, D.W., West, S.A., 2001. Pollination and parasitism in functionally dioecious figs. Proceedings of the Royal Society of London B 268, 651–659.

West, S.A., Herre, E.A., Windsor, D.M., Green, P.R.S., 1996. The ecology and evolution of the New World non-pollinating fig wasp communities. Journal of Biogeography 23, 447–458.

Wheeler, W.M., 1921. A new case of parabiosis and the "Ant Gardens" of British Guiana. Ecology 2, 89–103.

Wilson, E.O., Hölldobler, B., 2005. The rise of the ants: a phylogenetic and ecological explanation. PNAS 105, 7411–7414.

Wirth, R., Beyschlag, W., Ryel, R.J., Holldobler, B., 1997. Annual foraging of the leaf-cutting ant *Atta colombica* in a semideciduous rain forest in Panama. Journal of Tropical Ecology 13, 741–757.

Yamamoto, M., Del-Claro, K., 2008. Natural history and foraging behavior of the carpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Campotonini) in the Brazilian tropical savanna. Acta Ethologica 11, 55–65.

Yu, D.W., 2001. Parasites of mutualisms. Biological Journal of Linnean Society 72, 529–546.

Yu, D.W., Davidson, D.W., 1997. Experimental studies of species-specificity in Cecropia–ant relationships. Ecological Monographs 67, 273–294.

Zachariades, C., 1994. Complex interactions involving the Cape fig, Ficus sur Forsskål, and its associated insects. Rhodes University, South Africa. thesis.

Zachariades, C., Compton, S.G., Schatz, B., 2009. Honeydew as Danegeld? Ants (Hymenoptera: Formicidae) tending a honeydew-producing homopteran do not offer protection from its main natural enemies. Sociobiology 54, 471–488.

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

Zhang, S., Chen, J., 2008. Secondary seed dispersal of *Ficus benjamina*: new evidence for ant-non myrmecochorous mutualism. Chinese Journal of Ecology 27, 1913–1919.

Zotz, G., Hietz, P., 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. Journal of Experimental Biology 52, 2067–2078.