



Original article

The non-pollinating fig wasps associated with *Ficus guianensis*: Community structure and impact of the large species on the fig/pollinator mutualism



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ABSTRACT

Understanding the ecology of non-pollinating fig-wasp communities depends on a good knowledge of larval feeding habits of the species involved, which can be gall inducers, kleptoparasites, parasitoids or seed eaters. However, larval feeding habits are poorly known and most community ecology studies on NPFW are based on hypothetical feeding habits or data analyzed independently of feeding habit. Here we take advantage of the particular situation in *Ficus guianensis* whose community is dominated by large NPFW, i.e. species that are obviously larger than pollinators, to establish the community structure and feeding habits of the most frequent wasps. We provide the first non-ambiguous negative correlation between the number of NPFW and the production of pollinators and seeds. Each developing large NPFW represents a disproportionate cost to the mutualism as it is responsible for the loss of about ten seeds plus pollinators, i.e. about 10% of the production of a fig.

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1. Introduction

1.1. Figs and fig wasps: a model system to analyze community structure

Phytophagous insects and their parasites and parasitoids may represent half of all animal species (Stone et al., 2012). They are however largely under-sampled and under-described so that even their worldwide patterns of diversity are open to discussion (Quicke, 2012). Addressing the historical and ecological determinants of their community structure is a fascinating endeavor. For instance, results on oak associated gall wasp and parasitoid communities suggest that following post glacial host expansion, recolonization by parasitoids was delayed comparatively to gall wasps resulting in frequent community under-saturation (Stone et al., 2012). Fig wasps represent a unique opportunity to investigate diversification of wasp communities involving gall inducers, kleptoparasites and parasitoids, in a tractable system allowing comparative studies. Indeed, because of the relative simplicity of these communities, because all wasps emerge at the same time from figs, and because of the high number of replicates, figs and fig

wasps are potentially a good model to investigate wasp community ecology, dynamics and evolution.

Figs are characterized by their urn-shaped inflorescence (the fig) and their highly specialized pollinators (Hymenoptera, Chalcidoidea, family Agaonidae). When receptive, the figs release an odor that attracts female pollinators. The wasps penetrate the fig through the ostiole, and pollinate female flowers and lay eggs inside some of them. Flowers that only receive pollen develop into seeds and those that receive an egg develop into galls. Both seeds and pollinator larvae develop during the post-receptive phase and, in many species, occupy all the space available within the fig. Once wasp offspring development is completed, the cavity opens again, allowing male offspring to emerge from their galls and mate female offspring before their emergence into the fig cavity. Male flowers are mature at that time and allow pollinator females to collect pollen. Male wasps then cut an exit hole through the fig wall, allowing female wasps to escape the fig. Finally the fig ripens and seed dispersion is ensured by frugivorous animals such as birds, bats or other mammals.

Beyond pollinators, most of the 750 recognized *Ficus* species host a community of non-pollinating fig wasps (NPFW) ranging from 1 to 36 species that deposit their eggs inside the figs (Cruaud et al., 2011). These NPFW can be gall inducers, kleptoparasites, or parasitoids. Some wasps may, at least facultatively, develop within a seed (Pereira et al., 2007).

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Gall inducers are assumed to lay eggs in pre-receptive to receptive figs, either very early in fig development, before the development of flowers or later in fig development, in un-galled healthy flowers. Kleptoparasites lay eggs in the same flowers as their hosts, probably shortly after gall-induction, when plant tissue is still available within the flower (Joseph, 1958). Parasitoids also oviposit in the same flower as their hosts, but feed on host larval tissues (Tzeng et al., 2008). On this basis, 5 types of NPFW can be recognized: early gallers, gallers ovipositing close to fig receptivity, fig-entering gallers (not represented in the Neotropics), kleptoparasites and parasitoids (Cruaud et al., 2011). Most of these species develop in galls of the same or similar size as pollinator galls. Some species are large and develop in galls that are obviously larger than pollinator galls.

1.2. The largely unknown biology of non-pollinating fig wasps

There is an abundant literature on community ecology of fig wasps. Even though understanding the structure of these communities requires a good knowledge of their feeding habits, these are actually known for very few NPFW species as very few studies present data on histology, larval biology or timing of oviposition. For instance, among all studies conducted on the Neotropical section *Americana*, we found only five providing data that give direct or indirect insights into larval biology. Bronstein (1991) demonstrated that among the 3 main NPFW associated with *Ficus pertusa* in Costa Rica, at least one is a galler, two species oviposit close to receptivity and one later. Bronstein (1999) documented that *Anidarnes bicolor* associated with *Ficus aurea* is a gall inducer. In *Ficus citrifolia*, a histological and experimental study showed that an *Idarnes flavicollis* group species is a gall inducer at fig receptivity while a *carme* group species is a kleptoparasite of the pollinator ovipositing shortly after pollination (Elias et al., 2012). In addition, male larvae of an *Idarnes carme* group species sometimes develop as seed eaters (Pereira et al., 2007). Finally the sequence of oviposition of the entire NPFW community associated with *F. citrifolia* has been described (Elias et al., 2008). We found no data on the biology of NPFW associated with the Neotropical section *Pharmacosyceae*.

For Paleotropical species, most of the published information is observations that some species can prevent fig abortion and hence are gall inducers. This applies to *Sycophaga sycomori* in *Ficus sycomorus* (Galil and Eisikowitch, 1968), *Odontofroggata galili* in *Ficus microcarpa* (Galil and Copland, 1981), *Pseudidarnes minerva* in *Ficus rubiginosa* (Cook and Power, 1996), and *Otitesella sesquianellata* and *Philocaenus liodontus* in *Ficus burtt-davyi* (Compton, 1993). In addition, histological studies have demonstrated that *Phylotripes caricae* (in *Ficus carica*) is a kleptoparasite (Joseph, 1958) and that *Sycosapter* sp. (in *Ficus formosana*) is a parasitoid (Tzeng et al., 2008). Godfray (1988) inferred from relative ovipositor length that the large *Apocrypta mega* must be a parasitoid or a kleptoparasite of the large *Apocryptophagus* (= *Sycophaga*) sp. in *Ficus hispidioides*. Complete sequences of NPFW oviposition according to stage of fig development have been provided for *Ficus vallis-choudae*, *Ficus sur* (Kerdelhué and Rasplus, 1996), *Ficus racemosa* (Wang and Zheng, 2008; Ranganathan et al., 2010) and *F. burtt-davyi* (Compton, 1993). The only complete elucidation of a complex community structure has been provided for *F. racemosa* in South China and India, with two (three in India) gall inducers ovipositing sequentially, two parasitoids (or kleptoparasites) of the gall inducers and a parasitoid (or kleptoparasite) of the pollinator (Wang and Zheng, 2008; Ghara and Borges, 2010).

Because of the scarcity of data allowing inference of feeding habit of NPFW, most studies on fig wasp community structure have interpreted results without taking into account feeding habits or

using putative feeding habits based on the generalization of one or a few observations on a species to a whole genus or even a whole family. Such generalizations are questionable in the context of potential intrageneric variation as demonstrated for genera *Idarnes* and *Sycophaga* (Cruaud et al., 2011). This seems to be the case for most studies that have tried to quantify the cost NPFW may represent to the mutualism.

1.3. Impact of NPFW on pollinator and seed production

As they lay eggs inside the figs, NPFW exploit the same resources as pollinators and divert resources allocated by the fig tree to its reproduction (seed production and pollen transfer). Assessing the importance of this cost opens the question of the potential influence of NPFW on the evolution of the fig–pollinator mutualism. Several studies have analyzed correlations within figs between NPFW numbers and numbers of pollinators (pollinator reproductive success and male component of fig tree reproductive success) and numbers of seeds (fig tree female reproductive success). Often, the effect of NPFW is analyzed by pooling all NPFW species (significant effect on pollinators only: Elias et al., 2007; Wei et al., 2005; Compton and Robertson, 1988; Ma et al., 2009, no significant effect: Bronstein, 1991; Cook and Power, 1996). More detailed analyses based on putative larval biology have revealed some negative correlations (West et al., 1996; Kerdelhué and Rasplus, 1996; Kerdelhué et al., 2000). However, in both studies, confusion on feeding habits questions the results (Cruaud et al., 2011). To our knowledge, only on *F. racemosa* have correlations been analyzed for a totally resolved community structure (Wang and Zheng, 2008).

Large NPFW species are often rare in fig-wasp communities and very few studies have focused on them, as their abundance is generally too low to allow statistical analysis (e.g. Ranganathan et al., 2010). The only detailed study we are aware of on a large species demonstrated a negative impact of *A. bicolor* on pollinator production but not on seed production (Bronstein, 1999). Here we provide an analysis of a fig-wasp community dominated by large NPFW. We first established the trophic and temporal structure of the wasp community associated with *Ficus guianensis*. Taking advantage of the dominance of large NPFW in that species, we then analyzed their effect on the production of pollinators and seeds at the fig level.

2. Material and methods

2.1. Study site and species

The study trees corresponded to the nominate form of *F. guianensis* Desv. (subgenus *Urostigma* section *Americana*). In the last revision of the species complex of *Ficus americana*, Berg (2007) classified it as *F. americana* subspecies *guianensis* form *mathewsii* subform *sprucei*. It is a hemiepiphytic species, relatively dense in secondary forests and urban areas in French Guyana. In the study population each tree produced crops of figs every 2–3 months, composed of hundreds of cauliflorous figs, 4–5 mm in diameter at receptivity.

The study was conducted from January to May 2012 on an urban population located in Kourou, French Guyana, chosen for its higher than average density, easy access to the trees and high prevalence of non-pollinating fig wasps (all collected crops contained at least some NPFW).

The fig wasp fauna associated with *F. guianensis* is undescribed. Collected wasps were assigned to morphospecies, and each morphospecies was assigned to genus based on existing keys and descriptions and the assignments were confirmed by J.Y. Rasplus.

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