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Same but different: Larval development and gall-inducing process of a non-pollinating fig wasp compared to that of pollinating fig-wasps

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ABSTRACT

The receptacles of fig trees (*Ficus* spp.) can harbor a highly diversified and complex community of chalcid wasps. Functional groups of fig wasps (e.g. gallers, cleptoparasites and parasitoids) oviposit into the fig at different developmental stages, reflecting different feeding regimes for these insect larvae. There are few direct data available on larval feeding regimes and access to resources. We studied the gall induction and larval feeding strategy of an *Idarnes* (group *flavicollis*) species, a non-pollinating fig wasp (NPFW) associated to *Ficus citrifolia* P. Miller in Brazil. This *Idarnes* species shares with the pollinator characteristics such as time of oviposition, ovipositor insertion through flower and location of the egg inside plant ovaries. Nevertheless, we show that the gall induction differs considerably from that of the pollinating species. This *Idarnes* species relies on the induction of nucellus cell proliferation for gall formation and as the main larval resource. This strategy enables it to develop in both pollinated and unpollinated figs. The large differences between this NPFW and other fig wasps in how ovules are galled suggest that there are different ways to be a galler. A functional analysis of NPFW community structure may require descriptions of the histological processes associated with larval development.

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1. Introduction

In a synthesis on the evolution of ecological specialization, Forister et al. (2012) highlighted "the importance of interactions for understanding specialization at all levels of biological organization". The ideas were mainly drawn from systems including plants, herbivorous insects and their enemies. Open questions for future research directions included: "how does the network structure of species interactions in a community affect the distribution and evolution of specialists and generalists?" and "what are the community consequences of ecological specialization?"

Describing network structure requires a proper understanding of the biology of the individual species involved and understanding the determinants of network structure requires comparing series of similar networks. Figs and the communities of chalcid wasps colonizing figs constitute a remarkable system to investigate the determinants of community structure and the evolution of specialization. Indeed, intricate communities of chalcid wasps are harbored inside the receptacles of fig trees (*Ficus* spp.) – a genus of Moraceae with more than 700 species (Berg, 1989). Despite the constraints imposed by the morphology of the fig inflorescences and the limited number of accessible plant ovaries for wasp development, these communities can be composed of up to 30 species of fig wasps (Hawkins and Compton, 1992; Cook and Rasplus, 2003). The most singular group of fig wasps is represented by the mutualistic pollinating species. Females pollinating fig wasps enter the receptive urn-shaped *Ficus* inflorescences (hereafter referred to as figs) through a bract-lined entrance (the ostiole). They then lay eggs individually into some of the uniovulate flower ovaries (Galil and Eisikowitch, 1968) whilst simultaneously spreading the pollen they carry from their natal tree onto the stigmatic surface of the flowers (Jousselin et al., 2001, 2003). As a single egg is laid per oviposited flower, one wasp develops at the expenses of a potential seed for the plant.

Along with the pollinators, non-pollinating fig wasps (NPFW) compose most of the diversity of the fig wasp community. A majority of these species oviposit from outside of the fig and represent no benefit for the plant. It is well established that different components

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of the NPFW community oviposit at different developmental stages of the fig. Thus, feeding regime of NPFWs has been inferred from their oviposition time (Hawkins and Compton, 1992; Kerdelhué and Rasplus, 1996; Elias et al., 2008; Wang and Zheng, 2008). Moreover, it is quite intuitive to define functional groups of fig wasps according to the colonization time: 1) gallers, arriving before or during flower receptivity, 2) cleptoparasites of the gallers, arriving after fig receptivity but before fig ripening during what is called the interfloral phase of the fig, and 3) parasitoid wasps, arriving later in the interfloral phase. However, some variation for both colonization time within functional groups and feeding regime of given species has been reported (Pereira et al., 2007; Elias et al., 2008).

Further very little direct data are available on larval feeding regimes and on how the wasps access resources. Indeed, it is not trivial to elucidate feeding regimes in fig wasps, and additional information than colonization time is required. Strategies of female oviposition can be associated to how plant tissue is modified and exploited by the larvae of fig wasps (Jansen-González et al., 2012; Galil et al., 1970; Pereira et al., 2007; Elias et al., 2012). Jansen-González et al. (2012) showed that gall development in an active pollinating fig wasp, *Pegoscapus* n. sp., in *Ficus citrifolia* is partly dependent on plant embryogenesis. They also showed that the main tissue on which the larvae feed is endosperm, derived from embryo sac fertilization in the flower confirming previous observations on actively pollinating wasps (wasps presenting pollen pockets and a behavior to load and deposit pollen) (Galil and Eisikowitch, 1969; Ramírez, 1969). Similarly, in *Ficus carica* L., the pollinator larva feeds on the endosperm (Leclerc du Sablon, 1908). However in that case the initiation of endosperm development is most often parthenogenetic and does not depend on the double fertilization observed in actively pollinated *Ficus* species as the wasps colonizing the main crop of male figs emerge from figs containing little or no pollen (Neeman and Galil, 1978). Frequent development of pollinator larvae in unfertilized ovules could be generalized in passively pollinated figs (Jousselin et al., 2004). On the other hand, the parasitic species *Sycophaga sycomori* L., a NPFW galler in *Ficus sycomorus* L. oviposits from inside the fig and larvae feed on hypertrophied nucellus, a tissue independent from pollination and fertilization (Galil et al., 1970).

As a further complication, oviposition and larval feeding regimes can change according to circumstances. A cleptoparasitic wasp *Idarnes* group *carme* (on *F. citrifolia*) has been shown to use intact seeds as alternative oviposition sites when galls become scarce (Pereira et al., 2007). Studying in detail the larval biology and gall-inducing process of fig wasps, especially within lineages presenting contrasted feeding regimes, can shed light on how different feeding niches within the community are filled, how parasitic strategies evolved inside this community and how mutualism may persist despite the presence of parasitic forms.

Here we studied the gall-inducing process and larval feeding strategy of a NPFW galler associated with *F. citrifolia* in Brazil. The study species *Idarnes sp.* (group *flavicollis*) belongs to the Sycophaginae within which feeding regimes have shifted multiple times (Cruaud et al., 2011). It colonizes figs at the same time as pollinators. Even though the *Idarnes* group *flavicollis* female oviposits from outside the fig, its ovipositor is inserted in the plant ovary through the flower style, as is the case for the pollinating wasps (Elias et al., 2012). This suggests that the oviposition behavior of this *Idarnes* species and the pollinating species have in some aspects emerged by convergent evolution. Experimental data has showed that *Idarnes* group *flavicollis* can successfully gall flowers containing unfertilized embryo sacs (Elias et al., 2012). We investigated how resources are modified and exploited by the larvae, and whether gall induction and larval feeding strategies change in pollinated and unpollinated fig flowers.

2. Material and methods

2.1. Study species

F. citrifolia (subgenus *Urostigma*, section *Americana*) is a monoecious fig tree, and it is actively pollinated by an undescribed *Pegoscapus* species in São Paulo state (J.Y. Rasplus, pers. com.). *Idarnes* is a monophyletic group of NPFW (Cruaud et al., 2011). Bouček divided *Idarnes* in three morphological species groups: *incerta*, *flavicollis* and *carme*. In São Paulo state, Brazil, mainly one undescribed species belonging to the group *flavicollis* (morphospecies 3) is associated with *F. citrifolia*, and a second one is present in very low abundance. The two species are marginally larger than the pollinating wasp and produce marginally larger galls. For simplicity hereafter we refer to this first species as *Idarnes*.

2.2. Development of wasps in pollinated and unpollinated flowers

We studied *F. citrifolia* trees growing naturally on the campus of São Paulo University, Ribeirão Preto, Brazil (21°10′S; 47°48′W), between September 2010 and October 2011. We studied five cohorts of wasps, each from a different tree. We studied the development of *Idarnes* larvae in pollinated figs of three trees and unpollinated figs of two trees.

For each tree, we isolated approximately 150 figs before receptivity from 10 branches with white fabric bags to prevent natural wasp infestation. When the figs became receptive, we introduced *Idarnes* females into each bag (four wasps per fig). Receptivity was determined by the arrival of pollinating wasps and *Idarnes* females to the surrounding untreated figs. The wasps were allowed to oviposit in the bagged figs and removed after 24 h. The unpollinated treatment consisted of introducing only *Idarnes*. The pollinated treatment consisted of injecting a 2% sucrose solution containing fresh pollen of *F. citrifolia* through the ostiole. This sucrose concentration was determined based on pollen germination tests with sucrose percentages ranging from 2% to 40% (Kearns and Inouye, 1993) and has previously been successfully used in figs (Neeman and Galil, 1978). The sucrose + pollen solution was injected by syringe a few minutes before the introduction of the wasps.

We collected wasps and pollen for the experimental introductions the same day from other nearby *F. citrifolia* trees with figs at the wasp emergence phase. The development of each cohort was synchronized by performing all introductions for a particular tree on the same day.

The synchronized introductions allowed us to follow larval development by collecting the experimental figs at different times after introduction of the wasps. To do this, we collected four to five figs per tree every two days from the introduction date. After collection, the figs were fixed for 24 h in FAA 50 (formalin: acetic acid: alcohol 50%; Johansen, 1940) and then transferred to a solution of 70% ethanol. Each fig was cut open under 40× magnification stereomicroscope to sample 20 galled ovaries. Oviposited ovaries were recognized by the scar made through the style by the female ovipositor. We sampled figs until wasp pupae were detected. We measured body length and maximum width in lateral view for each larva under stereo-microscope, using IM50 Leica ™ software.

Due to the lack of evident diagnostic structures related to instar changes (e.g. remains of cephalic capsule), which is a common limitation in Microhymenoptera (Clausen, 1962; Stehr, 1987) and the absence of evident morphological differentiation between instars, larval stages were defined based on size changes throughout larval growth and events related to these changes.

For the micro-structural study (hereafter referred to as the histological study), we sub-sampled a group of 10–15 galled

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