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The role of non-fig-wasp insects on fig tree biology, with a proposal of the F phase (Fallen figs)

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ABSTRACT

The two seminal papers by Galil and Eisikowitch describing the development of *Ficus* flowers and their sycophilous wasps (*i.e.,* phases A-E) have been adopted in several ecological and evolutionary studies on a wide range of fig tree-insect interactions. Their classification, however, is not inclusive enough to encompass all the diversity of insects associated with the fig development, and the impact of this fauna on the fig-fig wasp mutualism is still unexplored. Here we describe the life history of the non-fig-wasp insects and propose an additional phase to fig-development classification, the F phase (Fallen figs). These figs are not consumed by frugivores while still on the parent tree, fall to the ground and turn into a resource for a diverse range of animals. To support the relevance of the F phase, we summarized a 5-years-period of field observations made on different biomes in three continents. Additionally, we compiled data from the literature of non-fig-wasp insects including only insects associated with inflorescences of wild fig tree species. We report 129 species of non-fig-wasp insects feeding on figs; they colonize the figs in different phases of development and some groups rely on the fallen figs to complete their life cycles. Their range of interaction varies from specialists – that use exclusively fig pulp or fig seeds in their diets – to generalists, opportunists and parasitoids species. The formalization of this additional phase will encourage new studies on fig tree ecology and improve our knowledge on the processes that affect the diversification of insects. It will also help us to understand the implications this fauna may have had on the origin and maintenance of mutualistic interactions.

1. Introduction

About 50 years have passed since the publication of two seminal papers by Galil and Eisikowitch (1968a, 1968b) on pollination and seed setting of *Ficus sycomorus* L. A survey on © Google Scholar (January 2017) reveals that these papers have been cited almost once a year since their publication, totaling about 360 citations. They are influential works on the fig-fig wasps ecology as they describe the development of *Ficus* L. flowers and their sycophilous wasps, introducing a developmental classification in five biologically-based phases (*i.e.* A, B, C, D and E; Fig. 1). Ever since, this classification has been adopted in several ecological and evolutionary studies in a wide range of fig tree-insect interactions (Borges and Kjellberg, 2014; Compton et al., 1996; Harrison et al., 2008). These studies, for instance, address issues involving pollination biology and the obligate mutualism (Kjellberg et al., 2005; Weiblen, 2002), the community of non-pollinating fig wasps (NPFW) (Cook and Rasplus, 2003; Kerdelhué et al., 2000) and the role of figs as resource for frugivorous vertebrates (Shanahan et al., 2001). The precise definition and succinct description of each developmental phase proposed by Galil and Eisikovitch (1968a, 1968b) has stood the test of time, not requiring any subsequent modification over the last 50 years.

The pre-female or A phase represents the initial fig development, when the pistilate and staminate flowers are in pre-anthesis stage. Later, the female or B phase is marked by the anthesis of pistilate flowers. At this phase stigmata are receptive and scents attractive to the pollinating wasps are released by osmophorus present at the ostiolar bracts and the outer layers of the fig receptacle (Grison-Pigé et al., 2002; Souza et al., 2015). During this phase, pollen-carrying wasps reach the fig cavity and then pollinate the pistilate flowers while ovipositing in the ovaries of some of them. The interfloral or C phase represents the stage during which staminate flowers, wasp larvae and fig seeds develop. Subsequently, during the male or D phase, both staminate flowers and wasp offspring are fully developed. Adult male wasps emerge from their galls and copulate with the female wasps that are still inside their galls. Shortly afterwards, female wasps emerge from their galls, load pollen (some species actively store pollen in their thoracic pockets – Galil and Eisikowitch, 1969; Ramírez, 1969) and exit the fig

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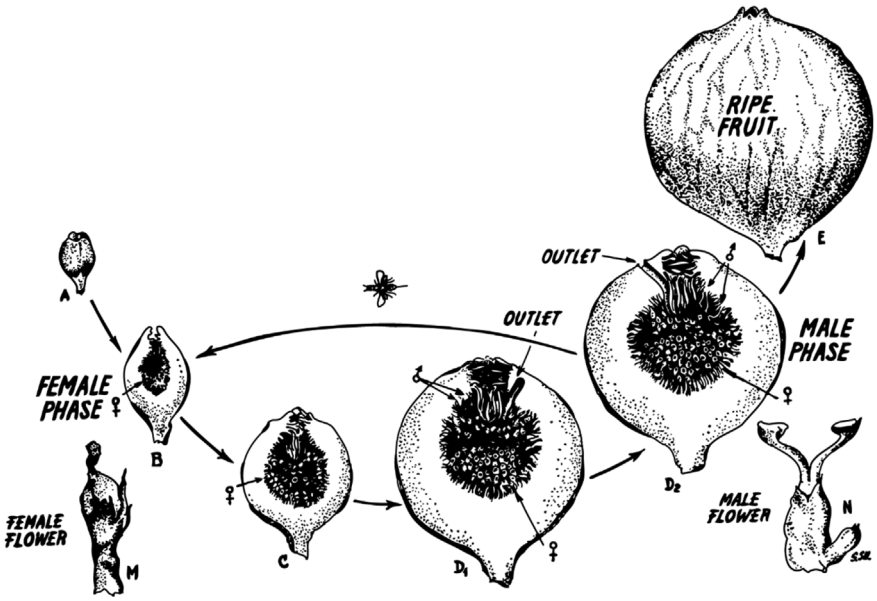

Fig. 1. Galil and Eisikovitch's original developmental cycle of the fig published in 1968b. With permission of John Wiley and Sons.

through the tunnel excavated in the fig wall by the male wasps in search of receptive figs at B phase. During the post-floral or E phase the figs ripen and become attractive to frugivorous vertebrates that can act as seed dispersers (Shanahan et al., 2001).

Galil and Eisikovitch's developmental classification, although accurate to describe the fig-fig wasp mutualism, is not inclusive enough to encompass all the diversity of interactions that are associated with the fig development. A diversity of flies and curculionid beetles lay their eggs during C, D or E phased figs, but their last larval instar rely on fallen figs to complete their development (Table 1). Additionally, the figs that are not consumed by frugivores and drop under the tree crown create a short-duration niche for a large community of generalist insects as well as for some specialized species (Paarmann et al., 2001). Moreover, much attention has been drawn to the multifaceted mutualism between fig and fig wasps, but the other insect groups and their relationship with fig trees have been neglected. Although several non-fig wasp species related to figs have been described as closely associated to fallen figs, this fauna is reported in relatively few studies, generally in a preliminary treatment. Ground beetles (Borcherding et al., 2000; Paarmann et al., 2001; Rasplus et al., 2003), drosophilid flies (Harry et al., 1996; Lachaise et al., 1982; Rasplus et al., 2003) and lygaeid bugs (Slater, 1972) are examples that can be listed among them, participating in a vast range of ecological interactions such as herbivory, seed predation, parasitism and secondary seed dispersion. Nevertheless, their impact on the fig-fig wasp mutualism is still unexplored. Hence here we (1) summarize all non-fig-wasp insects associated with figs reported in the literature (with some exceptions), as well as the author's own observations, and (2) provide the life history of some insects, in particular those interacting with fallen figs (F phase, see below).

We summarized field observations made from October 2010 to February 2015. For each crop, 200 to 1000 figs, depending on the fig size, were collected during C – E phases. The sampled figs were put into a 3 L glass jar containing a 5 cm substrate of a 1:2 mix of soil and vermiculite. The substrate had been previously sterilized at 100 °C for 2 h. The glass jars were covered with a voile cloth and kept in laboratory conditions up to adult insect emergence (aprox. 30 days). Observations of the life history of insects were made in the field and also in laboratory during the fig incubations.

Data were collected on several occasions in different biomes in three continents, *i.e.* Tropical Rainforests (Brazilian Atlantic and Amazonian Forests, Philippine Dipterocarp Forest and Costa Rican Rainforest and Cloud Forest), Seasonal Rainforests (Brazilian Semidecidual Forest and Costa Rican Dry Pacific Forest) and Subtropical Forest (South Africa). A detailed list of the *Ficus* species studied in each locality is supplied (Supplementary S1). Additionally we compiled data from the literature of non-fig-wasp insects, excluding insects associated with inflorescences of the cultivated fig *Ficus carica* L, as they generally correspond to applied studies on pests of commercial cultivation, often introduced, and do not represent natural associations. Other herbivorous insects such as sap suckers and leaf chewing insects (Basset and Novotny, 1999) were not considered as they are not directly associated with fallen figs. Ants were not extensively discussed; although they present a complex network of biotic interactions with figs, their role on fig tree ecology was recently reviewed by (Bain et al., 2014).

2. Non-fig-wasp insects

A diversity of 129 non-fig-wasp insects, encompassing 5 orders and 24 families, is reported feeding on figs (Table 1). These insects can colonize the figs in different phases of development and some groups rely on the fallen figs to complete their life cycles. According to their role on fig tree ecology and their potential impact on fig tree reproduction, we divided these insects into two groups: early fig interloper (EFI) and fallen fig fauna (FFF). Their range of interaction varies from specialized – species that use exclusively fig pulp or fig seeds on their diets – to generalist, opportunist and parasitoid species. Information about insect life histories comes from our unpublished observations or from literature, when properly referenced. On the last topic we discuss the evolutionary implications of the non-wasp insects on fig trees, especially those occurring in the fallen figs.

3. Why an F phase?

The close association between some groups of insects and fallen figs indicates that they are not “occasional pests” (Galil and Eisikowitch, 1968b). In fact, they might exert a significant selective pressure on fig tree reproduction (Bronstein, 1988; Janzen, 1979). Thus, we propose here an additional phase to the Galil and Eisikovitch fig-development classification: the F phase (fallen figs). Figs not consumed by vertebrate frugivores while still hanging on the parent tree fall to the ground, becoming essential for several groups of insects to complete their life cycle and turning into a resource for an additional diverse range of animals (see references in Table 1). Formalizing this phase and discerning it from the E phase reveals a set of particular ecological