Original article

# How to be a fig wasp down under: The diversity and structure of an Australian fig wasp community

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## ABSTRACT

Endophytic insects and their parasitoids provide valuable models for community ecology. The wasp communities in inflorescences of fig trees have great potential for comparative studies, but we must first describe individual communities. Here, we add to the few detailed studies of such communities by describing the one associated with *Ficus rubiginosa* in Australia. First, we describe community composition, using two different sampling procedures. Overall, we identified 14 species of non-pollinating fig wasp (NPFW) that fall into two size classes. Small wasps, including pollinators, gallers and their parasitoids, were more abundant than large wasps (both galler and parasitoid species). We show that in figs where wasps emerge naturally, the presence of large wasps may partly explain the low emergence of small wasps. During fig development, large gallers oviposit first, before and around the time of pollination, while parasitoids lay eggs after pollination. We further show that parasitoids in the subfamily Sycoryctinae, which comprise the majority of all individual NPFWs, segregate temporally by laying eggs at different stages of fig development. We discuss our results in terms of species co-existence and community structure and compare our findings to those from fig wasp communities on other continents.

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## 1. Introduction

The insects associated with plants provide excellent opportunities to test hypotheses about patterns of species diversity and community structure (Strong et al., 1984; Lewinsohn et al., 2005). Although there has been much research since the seminal publication by Strong et al. (1984), there is still much to understand, especially in the tropics. For example, estimates of global insect diversity hinge on the host specificity of tropical insect herbivores, and vary by an order of magnitude according to the degree of specificity incorporated into calculations (Novotny and Basset, 2005). Current estimates of tropical insect diversity are also being challenged as molecular barcoding reveals cryptic species (Hebert et al., 2004; Smith et al., 2008) and previously underestimated levels of host specificity in parasitoids (Smith et al., 2007). In addition, the study of insects on plants provides important insights into species diversity on a number of scales (local to global), as well as informing debates on species co-existence, community assembly and both insect and plant diversification (Price et al., 2011; Basset et al., 2012; van der Niet and Johnson, 2012).

The insect communities associated with tropical plants can be complex, consisting of many species at different trophic levels. Some general patterns seem highly predictable, e.g. species of herbivore are likely to outnumber their predators. However, the difficulty of sampling high numbers of host-specific insects on most tropical plant species makes accurate quantification difficult or impossible. Consequently, communities that occur only within discreet plant structures are particularly convenient model systems. Moreover, because they often provide opportunities for spatial and temporal replication at a number of scales, these systems allow quantification of the insect community, making a variety of comparisons possible. For example, the temperate insect communities in oak galls have been used to study community assembly and phylogeography (Nicholls et al., 2010), host specificity and diversification (Cook et al., 2002) and patterns of regional diversity (Zargaran et al., 2011). These communities include the cynipid gall-formers and their associated inquilines (species that feed on plant tissue and may compete with the gallmakers) and parasitoids (species that feed directly on the gallmakers or other wasps).

In the tropics and sub-tropics, an analogous system is the community of chalcid wasps associated with fig trees (*Ficus* spp.). Each

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*Ficus* sp. has an obligate mutualism with one or a few species of tiny agaonid wasps (Weiblen, 2002; Cook and Rasplus, 2003). These wasps are the only pollen vectors of the trees, but they also lay their eggs individually into some of the flower ovaries within the enclosed inflorescences (or 'figs') characteristic of *Ficus*. They do this by entering a fig during a brief period of receptivity and then laying eggs in some of the flowers. The pollinator larvae develop in the galled flowers and eat the developing endosperm (Jansen-Gonzalez et al. 2012). When the wasps mature the females are released from their galls by the males and disperse to receptive figs, carrying pollen.

In addition to the pollinators, figs also host diverse communities of chalcid and a few braconid wasps, referred to collectively as non-pollinating fig wasps (NPFWs). Some of these are primary gallers, while others are kleptoparasites whose larvae take over the gall of another wasp and kill it directly or indirectly (Joseph, 1959). Others still are true parasitoids (Tzeng et al., 2008) that feed on the tissues of other wasps and kill them directly. Most NPFW species oviposit through the fig wall from outside, using their long ovipositors. They can be placed into four general categories based on adult body size and larval biology: 1) Large wasps (much bigger than pollinators) whose larvae gall flowers or wall tissue; 2) Large parasitoids/kleptoparasites of the large gallers; 3) Small wasps (of similar size to the pollinators) whose larvae gall flowers or eat seeds (Pereira et al., 2007); 4) Small parasitoids/kleptoparasites of pollinators or other small gallers.

The wasp community associated with a single *Ficus* species can be complex, containing up to 30 species (Bouček et al., 1981) at three trophic levels − herbivores, parasitoids of herbivores, and parasitoids of parasitoids (i.e. hyperparasitoids) (Compton et al., 2009). As figs are pantropical and number >750 diverse species, their wasp communities are an excellent model system for the study of community structure, host specificity, species co-existence and species richness (e.g. Compton and Hawkins, 1992; Compton et al., 1994; West et al., 1996; Kerdelhué et al., 2000; Cook and Segar, 2010; McLeish et al., 2010).

Several studies have investigated fig wasp communities from both evolutionary (e.g. Cruaud et al., 2011a, 2012; Jousselin et al., 2006, 2008; Marussich and Machado, 2007; McLeish et al., 2010; Segar et al., 2012) and ecological (e.g. West et al., 1996; Kerdelhué et al., 2000) perspectives. These studies have focussed mainly on the wasps associated with figs in the neotropical *Americana* and the African *Galoglychia* sections (Compton, 1993a; Compton et al., 1994; West and Herre, 1994; West et al., 1996; van Noort and Compton, 1999; Kerdelhué et al., 2000; Pereira et al., 2000; van Noort, 2004; Elias et al., 2008). In contrast, there have been few studies on the wasp communities associated with Australasian figs in the *Malvanthera* section (but see Cook and Power, 1996; Al-Beidh et al., 2012; Segar and Cook, 2012).

The aim of this study is to describe the composition and structure of the NPFW community associated with *Ficus rubiginosa* (*Malvanthera*) in Australia. To do this we sampled figs from many trees across a large part of the host plant's natural range, the eastern seaboard of Australia. We compared two different methods for sampling the community of wasps from mature figs. We also recorded the co-occurrence and oviposition behaviour of different wasp species to help infer their larval ecology. For the numerically dominant NPFWs in the subfamily Sycoryctinae, we also investigated the potential for temporal niche segregation of multiple congeners on the same resource.

## 2. Materials and methods

### 2.1. Study system

*F. rubiginosa* belongs to the *Malvanthera* section of the *Urostigma* subgenus of *Ficus*. It has a large natural range along the east of

Australia from southern New South Wales to Northern Queensland (Dixon et al., 2001). *F. rubiginosa* exhibits considerable phenotypic variation and can grow as a small lithophyte approximately 1–5 m tall, a large free standing tree >15 m tall, or as a rainforest strangler >25 m tall. The mature figs are spherical and are approximately 10–15 mm in diameter. *F. rubiginosa* is pollinated by *Pleistodontes imperialis*, which is a complex of four species (Haine et al., 2006).

#### 2.1.1. Sampling and definition of wasp communities

We collected haphazardly a total of 594 figs from 54 trees from 12 *F. rubiginosa* populations in eastern Australia (Appendix A, Table A1). We selected figs that we judged to be in male phase (D stage *sensu* Galil and Eisikowitch, 1968), but which did not yet have wasp exit holes. Such figs have already turned from green to yellow (but not yet red), are relatively large, and are often slightly soft when pressed between thumb and forefinger. All figs in a crop were processed with either the "emergence" method or the "dissection" method detailed below. The emergence method is far less labour-intensive but reveals only some of the wasps from within each fig. The dissection method takes about 4 h extra per fig (for *F. rubiginosa*), but potentially reveals every single wasp.

For the emergence method, each fig was placed individually into a plastic pot (50 × 25 mm) sealed with a fine mesh lid on the day of collection. Wasps were then allowed to emerge naturally from figs for 96 h (from placement in the pot), which involved each wasp first "hatching" from its gall and then emerging from the fig. The method is based on our previous experience (e.g. Dunn et al., 2008a), which has shown that a) if no wasps emerge within 48 h of fig collection, any later wasp emergence is unlikely; b) after 96 h many fig samples rapidly become mouldy and decay; c) most wasps emerge within 24 h of the first wasp emerging. Emerged wasps were stored in 70–95% ethanol for counting and identification under 10–40× magnification with a binocular microscope.

For the dissection method, we sampled figs in the field in the same way, but on return to the laboratory each fig was placed in a plastic pot with a solid plastic lid and this was part filled with 95% ethanol. At a later date, each fig was cut open to reveal the wasps within. Wasps loose inside the fig were removed and stored and all galls were opened using fine forceps to reveal further unemerged wasps. Wasp galls can often be recognised by their dark colour relative to the pale yellowish seeds (Yao et al., 2005). All wasps were identified to morphospecies. Most of the dissection samples were processed before we had a full appreciation of the species diversity present in the system, and we were only able to identify sycoryctines to the genus level (*Sycoscapter*, *Watshamiella*), and some large wasps to the family level (Eurytomidae and Epichrysomallinae).

#### 2.1.2. Wasp behaviour and fig development

We studied wasp oviposition behaviour on *F. rubiginosa* figs around Brisbane in 2007 and 2008. In both years we captured ovipositing NPFWs (wasps with their ovipositors inserted in the fig wall) from the figs they were attacking with a pair of fine forceps, and stored them individually in tubes of 95% ethanol (Al-Beidh et al., 2012). We studied seven trees at two sites in 2007 (resulting in 169 observations) and five trees at two sites in 2008 (172 observations). After collection, wasps were returned to the laboratory for identification. For sycoryctine wasps, we also measured hind-tibia and ovipositor lengths using an eyepiece graticule mounted to a binocular microscope at 40 times magnification (see also Appendix B and Figure B.1). This was to explore absolute and relative ovipositor length differences between congeneric and non-congeneric wasp species.

In 2008 we also measured 47 figs throughout their development over time on nine trees from two sites. We haphazardly marked