IL205 Enclosed worlds: the evolutionary ecology of fig wasps

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Trees from the large (over 700 species) pantropical terrestrial plant genus *Ficus* form a vital part of many rainforest habitats. Populations of fig trees must fruit all year round to sustain viable populations of their small, often species specific, obligate pollinating wasps. This constant production of fruit provides a valuable resource for vertebrates and as such fig trees are considered key stone resources. Pollinating fig wasps (Chalcidoidea: Agaonidae) can home in on species-specific volatile blends released by receptive fig 'fruit' (actually enclosed inflorescences referred to as syconia). Laden with pollen from their natal syconium they proceed to burrow into a small bract lined tract (the ostiole) at the base of the syconium. Once inside, they pollinate a proportion of female flowers within before laying their eggs in the remainder. Female fig wasps rarely re-emerge and are highly adapted to life within the syconium. After a period ranging from four weeks to six months the female's offspring will emerge. Male pollinating fig wasps are blind, pale and wingless: their sole functions being to mate females within the syconium and dig an exit hole from which females can escape. Mated females gather pollen (either actively or passively) before emerging and starting the cycle anew.

A conflict between mutualists occurs because wasps can only reproduce by galling flowers that otherwise could become seeds; selection should favour wasps that exploit all of the flowers within the inflorescence at the expense of the fig trees' female function. However, this clearly does not happen as seeds are always produced. Female flowers are also stratified, and generally seeds are produced in a layer of flowers closer to the fig wall, whereas wasps are produced in the outer layer, closer to the cavity. Various sanctions may help to achieve the more even seed to wasp ratio likely to maximise host fitness and resulting in long-term mutualism stability.

Alongside pollinating fig wasps fig syconia host an array of other chalcid wasps from eight subfamilies/families, many of these lay their eggs externally and are therefore not restricted to single syconia. Often referred to as the 'non pollinating fig wasps' (NPFWs) these wasps usually provide no pollination service but consume resources that would otherwise be used to produce seeds or pollinators. They are therefore often considered as parasites of the mutualism. All fig wasps develop alongside each other in individual syconia and develop at the cost of one seed or pollinator. Therefore the impact of wasps in these complex multitrophic communities should be relatively straightforward to assess by counting all seeds and wasps. Previous studies have elucidated the impact of numerous genera of NPFW on different *Ficus* sections on different continents. We have investigated the impact of NPFWs on mutualism stability in the Australasian section *Malvanthera* both in Australia and Indonesia. This research has demonstrated that putative parasitoid fig wasps do indeed have a negative relationship with pollinating wasps (but not seeds). However, they are more likely to target pollinator offspring in the outer 'seed layer' of the syconium. Therefore they reduce the fitness of pollinating wasp females who exploit their *Ficus* partner, potentially contributing to mutualism stability. In contrast herbivorous galling wasps have a detrimental impact on seed number (each one consumes one seed) as well as pollinator output (these galling NPFWs may usurp a proportion of oviposition sites). Previous projects in this area have involved the collection and dissection of syconia to count their contents, using multiple regression to untangle the relationships between pollinating and non-pollinating fig wasps as well as the impact of NPFWs on mutualism stability. This type of project would involve a larger proportion of laboratory dissection work than fieldwork.

These complicated communities also provide fascinating systems in which to study community ecology. Communities of fig wasps can be complex (containing up to 30 species) and con-generic species, or morphologically similar genera can co-exist, seemingly without large ecological niche divergence. Yet little is known about basic NPFW life history and behaviour. By conducting field surveys on ovipositing wasps we can investigate the existence of differentiation through behaviour (at which stage in syconial development wasps lay their eggs, how long they take, the number of egg laying attempts per syconium, the level of ant predation and diurnal/nocturnal activity levels etc). By combining this with ecological data collected in the laboratory such as longevity, desiccation tolerance, emergence time and mean egg count we can begin to establish the intensity of competition between closely related NPFWs. This type of project would involve equal parts laboratory and fieldwork. Data collection methods in the field would involve behavioural observations and sticky traps whilst lab work could potentially involve egg counts, wasp longevity and emergence experiments. An additional project could involve the impact of ants on fig wasps. Ants have been shown to be an important factor contributing to fig wasp mortality. Time limitations would prevent manipulation experiments but surveys of ant diversity on different species of *Ficus* species, for example, would be possible, alongside more behaviourally orientated projects.

Furthermore it was once thought that figs and their pollinating wasps had co-speciated in a strict 1:1 manner, but it is becoming widely accepted that individual *Ficus* species often host multiple species of pollinator. Sometimes these co-pollinators differ in cuticle colour, one being black and the other yellow. Previous studies in Africa have shown that black wasps are diurnal and that yellow wasps tend to be nocturnal. Dispersing at night may help wasps to avoid desiccation. On Buton the rainforest strangler, *Ficus glandifera* var *brachyscye* hosts two co-pollinators differing in cuticle colour (these may well be sister species). We have established morphological and behavioural differences that suggest differences in dispersal period. However, it would be interesting to establish other ecological differences such as if cuticle colour relates to desiccation tolerance or body size. This project would rely on canopy access to some extent and involve equal parts laboratory (wasp longevity trials, timed wasp emergence observations) and fieldwork (collecting syconia, setting up and analysing sticky traps).

Figs and fig wasps have been used to answer questions in a wide range of areas. Topics range from empirically testing sex ratio theory, investigating the co-existence of cryptic species and the maintenance of mutualism stability through to predicting vertebrate diversity and studying long distance insect dispersal. The projects listed above represent a selection of those that would be possible, I am more than happy to discuss other suggestions that may arise through consultation of the primary literature.

Suggested reading

General:

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

Cook, J.M. & Segar, S.T. (2010). Speciation in fig wasps. *Ecological Entomology*, 35, 54–66.

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

Herre, E.A., Jander, K.C. & Machado, C.A. (2008). Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annual Review of Ecology Evolution and Systematics*, 39, 439-458.

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Mutualism stability and parasites:

Dunn, D.W., Segar, S.T., Ridley, J., Chan, R., Crozier, R.H., Yu, D.W., et al. (2008a). A role for parasites in stabilising the fig-pollinator mutualism. *PLoS Biology*, 6, 490-496.

Kerdelhue, 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.

West, S.A. & Herre, E.A. (1994). The ecology of the New World fig-parasitizing wasps Idarnes and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 258, 67-72.

Commuity ecology:

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Ghara, M. & Borges, R.M. (2010). Comparative life-history traits in a fig wasp community: implications for community structure. *Ecological Entomology*, 35, 139–148.

Kerdelhue, C., Rossi, J.P. & Rasplus, J.-Y. (2000). Comparative community ecology studies on old world figs and fig wasps. *Ecology*, 81, 2832-2849.

Ants and fig wasps:

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.

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., Proffit M., Rakhi, B.V., Borges, R.M. & and 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.

Co-pollinating wasps:

Warren, M., Robertson, M.P. & Greeff, J.M. (2010). A comparative approach to understanding factors limiting abundance patterns and distributions in a fig tree-fig wasp mutualism. *Ecography*, 33, 148-158.