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Fifty years later, figs and their associated communities

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Fifty year jubilee

Fig trees (*Ficus*, Moraceae) are a diverse genus of largely tropical and sub-tropical plants. They are of exceptional ecological and conservation importance because figs are probably eaten by more species of animals than the fruits of any other plants (Shanahan et al., 2001). Figs (syconia) are unusual protogynous inflorescences/infructescences with a structure that excludes the services of generalist pollinators. Each is formed like a hollow ball lined on the underside with tiny flowers. In order for pollen to enter a fig it must be carried through a narrow entrance (called an ostiole). Pollen transfer is achieved through the activity of small fig wasps (Agaonidae) that enter the figs to lay their eggs in the ovules, which they also gall. Ovules that receive pollen, but no egg, can develop into seeds. The morphology of adult female fig wasps reflects their need to enter through the narrow ostiole. Males are also highly modified and spend all or most of their lives inside the figs. Host specificity is high among agaonids, with most species routinely associated with a single host *Ficus*. Many host trees are also pollinated by a single recorded species of agaonid, though the list of species with two or more pollinators is increasing. In addition to agaonid pollinating fig wasps there are also numerous non-pollinating species (NPFW). Together with the pollinators they form communities of phytophages, parasitoids and secondary parasitoids inside the figs.

Fifty years ago, it was discovered that some fig-pollinating wasps collect pollen into specialised pockets before leaving their natal figs. Subsequently they deposit this pollen onto the stigmas in the receptive figs that they have entered (Ramirez 1969, Galil and Eisikowitch 1969). These original observations can be considered as representing the start of modern experimental and evolutionary studies of fig trees and their associated animals. It has often been stated that *Ficus* and fig-wasps constitute a model system to investigate the evolution of mutualisms. In fact, *Ficus* and their associated communities also provide broader insights into the structuring of ecological communities and classic organismic evolution in general, as well as into the evolution of ecological interactions. The endeavour of this special volume was to illustrate this broader view of what *Ficus* and their associated communities tell us about life.

Meetings of fig biologists have been occurring since the first “fig minisymposium” in 1983 to which participated Jacob Galil, Kees Berg and Koos Wiebes. The 9th international fig meeting was held in Montpellier, France and timed to correspond with a half century since the pioneering publications of Ramirez, Galil and Eisikowitch. It was therefore a particular pleasure to have Dan Eisikowitch present at the meeting.

Fig diversification

Ficus and their pollinating wasps have largely co-diversified (Cruaud et al. 2012). The analysis of *Ficus* phylogenies shows that they fit a "museum model" of ancient gradual diversification with a progressive accumulation of species in the context of low extinction rates (Brunn-Lund et al. 2018). Large ranges and strong gene flow, even in marginal populations (Wang et al. 2018), may explain the low extinction rates. Most probably, these two traits result from the mutualistic pollination system. Further, the analysis suggests that Neotropical rainforests are cradles of recent fig diversification within a pantropical museum model. This difference in diversification patterns, which gives a new meaning to the term ‘Neotropics’, is shown here within the context of a pantropical genus. But it could hold true for many tropical lineages. The phylogenies also suggest that the acquisition of hemi-epiphytism, and hence the colonisation of a new ecological niche, has led to increased diversification rates. Finally, phylogenetic studies confirm that active pollination favours diversification, so that, despite repeated reversals from active to passive pollination, two thirds of *Ficus* species are still actively pollinated (Kjellberg et al. 2001).

Vertebrates and figs

Given how primates relish eating figs (Shanahan et al. 2001), it is no surprise that diverse species of *Ficus* have had close associations with humans, including an important spiritual role in human societies (Shanahan 2016). They are perceived as magical by many societies since they apparently produce fruits (ripe figs) without producing flowers (their flowers being hidden within the figs). The strangling growth forms of some fig species have also helped to reinforce their supernatural powers. A case study in Madagascar demonstrates how the Merina people have used *Ficus lutea* and *Ficus polita* as symbols of power and have planted them in strategic places to assert their authority and claim territories (Aumerruddy-Thomas et al. 2018). Fig trees are often planted as ornamentals and sacred trees in tropical cities, where they are also natural colonists (Lok et al. 2013). Such trees provide welcome food for urban animals. Even better, some urban *Ficus* species provide ripe figs throughout the winter - a precious resource for urban birds (Walther et al. 2018). Monoecious *Ficus* species are known for their highly synchronised crops. But in some species that produce large crops of small, cauliflorous figs, although receptive figs are pollinated within one or two days, and the next fig wasp generation emerges synchronously, ripe figs trickle out progressively for several weeks and provide a continuous resource to local frugivores (Chiang et al. 2018). Such a fruiting phenology, as documented here for *Ficus supisocarpa* and *Ficus caulocarpa* (section *Urostigma*), is also found in the Americas within the group of *F. americana* subspecies *guianensis* (section *Americanae*) and in some African species (section *Galoglychia*). A largely understudied aspect of the interaction between *Ficus* and fruit dispersers is geographic variation in traits associated with frugivore attraction and fruit accessibility, such as for instance the presence of elongate runners bearing figs in *F. hainanensis* on the Asian continent, but on short specialised branches in Hainan Island, or geographic variation in ripe fig odor (Soler et al. 2018).

Fig wasps

Analysing the communities of non-pollinating fig wasps (NPFWs) and their structuring within each biogeographic region and among continents offers insights into how associated communities are structured, how they function and what drives their diversification. Generally, NPFWs are known to be specialists of a single *Ficus* species (McLeish et al. 2012). An intensive regional study in Brazil, based on 100,000 NPFW specimens assigned to morpho-species shows that while most species are specialists, few are strict specialists, and some abundant species are true generalists (Farache et al. 2018). This pattern of generalism, which has also been suggested for some American fig pollinating wasps, correlates with the recent diversification of *Ficus* in the Neotropics. Indeed examples of fig pollinating wasp species regularly pollinating several non-sister *Ficus* species are restricted to the Neotropics (Marussich and Machado 2007) and to subsection *Chlamidodorae* within section *Galoglychia*, which also diversified recently (Cornille et al. 2012, McLeish and van Noort 2012).

An important challenge will be to confirm the trophic structure and the feeding habits of the different members of NPFW communities. Some genera include fig wall gallers, flower gallers and kleptoparasites (Cruaud et al. 2011, Ghara et al. 2015). Even in a genus of parasitoids, there is room for variation, with two *Apocrypta* species, one endoparasitoid and one ectoparasitoid associated with *Ficus racemosa* (Yadav and Borges 2018). Many studies have tried to derive trophic structure from correlations between the numbers of the different wasp species and seeds. However, these correlations at best provide informed guesses and should be supplemented by experimental data or direct biological observations (Segar et al. 2018). Pollinator larval mortality in the absence of parasitism may further complicate indirect inferences. In two dioecious *Ficus* species, pollinator larval mortality has been estimated at ¼ and 1/3 of the larvae (Ghana et al. 2012, Yu et al. 2018). Such large numbers were unexpected.

Figs signal they are receptive to pollination by releasing a species-specific odour. How this odour varies along fig development, before, during and after receptivity, is understudied, but may provide a key to understanding how the suite of wasps associated with the figs of a *Ficus* species locate figs at the successive stages at which they oviposit (Proffit et al. 2018). How wasps detect fig odours may also be a dynamic process. Indeed a transcriptome analysis of genes involved in the detection of volatile organic compounds in a pollinator fig wasp recorded modifications following exposure to the odour of receptive figs (Zeng et al. 2018). In fig wasps, structures dedicated to odour perception are present as sensilla on antennae. The distribution and types of antennal sensilla seem to vary depending on wasp behaviour when searching for a fig and when probing its surface. For instance, some sensilla correlate with whether the wasps touch the surface of the fig with the whole length of the antennae or whether they just tap the fig surface with the tip of the antennae (Yang et al. 2018). Ovipositor morphology is another trait that correlates with life history in fig wasps (Ghara et al. 2011, Elias et al. 2018), and ovipositors can also act as olfactory organs (Yadav and Borges 2017).

Pollination and ovule fertilization is another facet of the fig–pollinating wasp interaction that depends on a fine match between wasp behaviour and stigma morphology. Initial descriptions of the stigmas as cohesive or non-cohesive were a caricature. New data on variation among fig species in stigma arrangement open up avenues for detailed behavioural investigations (Teixeira et al. 2018). The high larval mortalities documented in two dioecious *Ficus* species (Ghana et al. 2012, Yu et al. 2018) could be explained by imperfect correlation between oviposition into an ovule and actual pollination and fertilization of the ovule (Jousselin et al. 2001). Exploring the interaction between wasp behaviour and stigma structure is key to understanding such a mismatch.

Arthropods, other invertebrates and fig protection

Figs provide resources for a diverse array of invertebrates, not just fig wasps. The current list of non-fig wasp insects feeding on figs includes 129 species of insects, encompassing 5 orders and 24 families, and many of these are fig specialists (Palmieri et al. 2018). These insects are under-studied and their impact on fig development is little known. Figs are host to nematodes that are phoretic on pollinating fig wasps (Krishnan et al. 2010). The outcome of interactions between such invertebrates and figs may be geographically highly variable. For instance while *Parasitodiplogaster* nematode species seemed to have a strong negative effect on fig pollinating wasps in Panama (Herre, 1993), they had limited effects in Baja California (Van Goor et al., 2018).

A fascinating trait of many *Ficus* species is crop synchrony within trees, but asynchrony among trees in the same populations. Crop synchrony may be favoured by many factors such as capacity to attract pollinators from far away, or capacity to attract roaming frugivorous animals. Conversely, crop synchrony may in some cases be counter-selected by the same type of factors, such as attracting large numbers of fig-specialist lepidopterans whose larvae feed on developing figs (Piatscheck et al. 2018).

As figs are exposed to a multitude of antagonists, *Ficus* have evolved defences against them. For instance Moraceae in general, and *Ficus* in particular, produce protective latex. The distribution of laticifers in fig flowers reveals their presence in diverse parts of the flowers but they are absent from the styles, which are probed by the pollinators and where latex may interfere with pollinator reproduction (Marinho et al. 2018). Plant defences may also be indirect. In *Ficus benguetensis*, the figs have nectaries, and their sugar secretion attract ants that protect developing pollinator larvae against parasitism by non-pollinating fig wasps, and also possibly against other fig-eating insects (Lin et al. 2018).

Concluding lines

A collective property of the studies reported in this volume is how few are focused on the interactions between one species of *Ficus* and its pollinator(s). Most studies deal with interspecific interactions and interaction networks. The study of figs and their associated communities has progressively moved into a new age.

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