



The fig wasp followers and colonists of a widely introduced fig tree, *Ficus microcarpa*

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Abstract. 1. The transportation of plants and insects between countries often has negative consequences, but also provides opportunities to study community processes. Fig trees are a species-rich group of largely tropical and subtropical plants, characterised by their unusual inflorescences (figs).

2. *Ficus microcarpa* is a native of Asia and Australasia and frequently planted elsewhere. Widespread introductions of its pollinator fig wasp, *Eupristina verticillata*, have allowed the tree to reproduce and become increasingly invasive. Non-pollinating fig wasps (NPFW) are also widely introduced.

3. Here, we combine previously published records of the distributions of fig wasps associated with *F. microcarpa* with the results of our extensive surveys across much of its introduced and native ranges. At least 43 morpho-species of fig wasps are associated with figs of *F. microcarpa*, most of which have only

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been recorded from this host. Twenty-one NPFW have become established outside their native ranges, but there has been only limited colonisation by locally native fig wasps within countries of introduction.

4. Fig wasp communities in colonised areas are less species-rich and contain a lower proportion of parasitoids. The pollinator and two phytophagous NPFW are the most widely introduced species, and usually the first species to arrive in countries where the host fig has become established. The pace of colonisation appears to be accelerating.

5. The rarity of faunal acquisition on introduced *F. microcarpa* contrasts strongly with that of introduced gall wasps on oaks and chestnuts.

Key words. Agaonidae, biocontrol, community structure, dispersal, invasive species, parasitoid.

Introduction

The assembly and re-assembly of ecological communities has long been of conceptual (Drake, 1990; Luh & Pimm, 1993; Uriarte *et al.*, 2010; Weiher *et al.*, 2011); and also applied interest (Simao *et al.*, 2010; Cash *et al.*, 2012) because introductions of plants and animals have led to extinction of species in areas where they are introduced and they continue to be a major source of conservation concern (Mack *et al.*, 2000; Catford *et al.*, 2012; Simberloff *et al.*, 2013). Introductions result in novel combinations of species and novel interactions between species and consequently modify the communities where introductions take place (Richardson *et al.*, 2000; Carroll, 2011). Introduced species often also leave their natural enemies behind, resulting in relatively depauperate communities and the ‘enemy-release’ scenario that increases their invasive potential (Keane & Crawley, 2002; Pearson *et al.*, 2011).

The communities of phytophagous insects that develop on introduced plants are typically composed of local species that have switched hosts by enlarging their host ranges (Johnson & Lyon, 1976; Strong *et al.*, 1984; Keane & Crawley, 2002). In the case of figs, these ‘colonists’ are sharing figs with insects from the plant’s original range that have either also been introduced or have managed to disperse into new areas (‘followers’) (Nicholls *et al.*, 2010; van Noort *et al.*, 2013). Local colonists are likely to be generalists, already utilising a range of host taxa, or insects that were previously feeding on plants that were taxonomically or chemically related to the introduced species (Stone *et al.*, 2012). Because of their longer historical association, insect followers that were already present on the plant before it was introduced can include both specialists and generalists. Communities of parasitoids that develop around introduced hosts develop in a similar way (Cornell & Hawkins, 1993). Factors influencing the relative contributions of colonists and followers to the communities of phytophages and parasitoids that develop around introduced species are likely to include geographical elements (the proximity or isolation of native and introduced ranges), quarantine effectiveness (how fre-

quently insects are being transported into areas of plant introduction), and the taxonomic or ecological isolation of the plants and their insect followers in their new environment, which will determine how easily local species can adopt these new resources.

The introduction of the Asian fig tree *Ficus microcarpa* into Africa, Europe, and the New World and the anthropogenic expansion of its natural range in Asia, provides an opportunity to study multi-site community re-assembly among fig-feeding insects and their parasitoids. Fig trees (*Ficus*, Moraceae) belong to one of the most diverse tropical and subtropical plant genera and are of broad ecological significance because of the many vertebrates that eat their figs (Shanahan *et al.*, 2001; Harrison, 2005). Figs (syconia) are unique enclosed inflorescences. The hundreds or thousands of female flowers that line the inner surfaces of figs are only pollinated by female pollinating fig wasps (Agaonidae) that enter the figs to lay their eggs. Each fig tree species only has one or a small number of host-specific pollinator species (Molbo *et al.*, 2003; Herre *et al.*, 2008). Pollinator fig wasp larvae develop singly inside galled ovules, as do numerous species of non-pollinating fig wasps (NPFW) (Bouček, 1988) mainly belonging to families of Chalcidoidea other than Agaonidae (Heraty *et al.*, 2013; Segar *et al.*, 2013). Most NPFW may be host-specific, but there are known exceptions (Cook & Segar, 2010; Mcleish *et al.*, 2012; Zhou *et al.*, 2012). Fig wasp communities can be complex, with 30 or more fig wasp species associated with some fig trees, though only a subset of species develop inside any one fig (Bouček *et al.*, 1981; Hawkins & Compton, 1992; Compton *et al.*, 2009a, b). The communities associated with different fig trees show some convergence in ecological characters across continents, despite differences in their taxonomic composition (Segar *et al.*, 2013), but vary in species richness in response to factors such as fig size, host plant breeding system (which may be a proxy for ‘apparency’; Chen *et al.*, 2011) and latitude (Compton & Hawkins, 1992; Hawkins & Compton, 1992; Mcleish *et al.*, 2011).

Non-pollinating fig wasps can be grouped into two major trophic groups – species with larvae that feed only on plant tissue, most commonly utilising ovules that they

gall (seed predators are rare, Pereira *et al.*, 2007), and species whose offspring kill the larvae of other fig wasps (but may also feed on plant tissues). The latter include a diversity of feeding styles, including secondary galls (Chen *et al.*, 2013), parasitoids and inquilines (Segar & Cook, 2012), and obligate hyper-parasitoids (Compton *et al.*, 2009a,b). Non-pollinating fig wasps have negative impacts on their host fig trees by reducing the numbers of pollen-carrying agaonid fig wasp offspring in the figs, reducing seed production (Kerdelhué & Rasplus, 1996; Segar & Cook, 2012), or reducing both these components of plant reproductive success (Kobbi *et al.*, 1996). Parasitoids of the pollinator influence only the male component of the plant's reproductive success, but phytophages can reduce both seed and pollinator offspring numbers by competing with pollinator foundresses for oviposition sites and reducing the number of ovules that can set seed. Consequently, parasitoids that target other NPFWs, rather than pollinator offspring, indirectly benefit their host plants (Compton *et al.*, 2010).

Fig trees are widely grown as pot plants and are also popular amenity and street trees. They are often planted outside their native range, where any figs they produce initially fail to contain any seeds, due to the absence of their specific pollinators. Nevertheless, when suitable pollinators are introduced the trees can start to produce figs that are then attractive to a wide range of seed dispersers (McKey, 1989). Initial establishment occurs mainly in the urban environments where the trees are planted, but *F. microcarpa* L. has now also invaded natural habitats, where it is viewed as an established or potential threat to biodiversity (Stange & Knight, 1987; Caughlin *et al.*, 2012).

Here, we collate previously published information on the distribution of fig wasps associated with figs of *F. microcarpa* in its native and introduced ranges and describe the results of our recent surveys in Asia and elsewhere. We address the following questions: (i) How many fig wasp species utilise *F. microcarpa* figs within its natural range? (ii) How many of these fig wasps have become established elsewhere? (iii) How frequent is colonisation of introduced *F. microcarpa* figs by local fig wasp species? (iv) Are parasitoid fig wasps less likely to become established than phytophages because they require their insect hosts to already be present.

Materials and methods

Ficus microcarpa and its fig wasps

Ficus microcarpa is a moderate to large sized monocious fig tree with a natural distribution that extends from India to southern China and Japan and northern Australia (Berg & Corner, 2005). In natural habitats it grows on rocks or as a strangler fig. It is also widely planted within its natural range and introduced as an ornamental tree into many tropical, subtropical, and warm temperate

areas around the world. Its natural range has also been extended by deliberate planting at higher latitudes in China and Australia (Nadel *et al.*, 1992; Figueiredo *et al.*, 1995; Kobbi *et al.*, 1996; Beardsley, 1998; Burrows & Burrows, 2003; Starr *et al.*, 2003). Sexual reproduction is only possible if the tree's specific fig wasp pollinator, *Eupristina verticillata* Waterston is also present. Pollinated figs of *F. microcarpa* contain small seeds that are mainly dispersed by frugivorous birds, with ants also serving as secondary dispersal agents (Kaufmann *et al.*, 1991; Shanahan *et al.*, 2001). In urban settings its seedlings can cause damage to buildings and the tree is also increasingly reported from semi-natural vegetation, where it can become invasive (McKey, 1989; Beardsley, 1998; Starr *et al.*, 2003; Corlett, 2006; Caughlin *et al.*, 2012; Mifsud, 2014). *Ficus microcarpa* is salt tolerant and is a particular problem on islands such as Hawaii and Bermuda (Beardsley, 1998; Starr *et al.*, 2003). In warmer climates the figs on individual trees are produced in discrete synchronised crops, with different trees fruiting at different times. Fig development slows during the winter in more temperate areas, with no new crops initiated during the cold season (Yang *et al.*, 2013). Figs that are not colonised by fig wasps are retained on the trees for weeks or months and a shortage or absence of pollinators can result in a breakdown of crop synchrony.

The pollinator *Eupristina verticillata* is a taxon that molecular data suggests is a complex of several morphologically similar species, although only one of these has been introduced outside their natural range (Sun *et al.*, 2011; A. Cruaud & J.-Y. Rasplus, pers. comm.). In addition, the figs of *F. microcarpa* support a morphologically distinct 'cheater' *Eupristina* species that does not actively pollinate its host figs (J.-Y. Rasplus, unpubl. data). *Eupristina verticillata* has been recorded throughout the plant's native range (Waterston, 1921; Baltazar, 1966; Hill, 1967; Chen *et al.*, 1999; Priyadarsanan, 2000; McPherson, 2005; van Noort & Rasplus, 2010; Ramya *et al.*, 2011; Sun *et al.*, 2011), and was deliberately introduced from the Philippines to Hawaii in the 1920s (Stange & Knight, 1987) or 1930s (Pemberton, 1939; Beardsley, 1998). During the last 50 years *E. verticillata* has also been accidentally or unofficially introduced and become established in most of the areas where *F. microcarpa* is grown, including Bermuda, Brazil, California, Canary Islands, Colombia, El Salvador, Florida, Honduras, Italy, Ivory Coast, Madeira, Malta, Mexico, Morocco, Puerto Rico, Spain, Tunisia, Turkey, and United Arab Emirates (UAE) (Stange & Knight, 1987; Ramírez & Montero, 1988; Hilburn *et al.*, 1990; Lo Verde *et al.*, 1991; Bouček, 1993; Figueiredo *et al.*, 1995; Kobbi *et al.*, 1996; Baez, 1998; Koponen & Askew, 2002; Otero & Ackerman, 2002; Farache *et al.*, 2009; van Noort & Rasplus, 2010; Doğanlar, 2012; Mifsud *et al.*, 2012; J.-Y. Rasplus, pers. comm.). The pollinator has also extended its range, probably unaided, into parts of China and Australia where *F. microcarpa* is planted (R. Wang & S.G. Compton, unpubl. data).

Numerous NPFW species have been recorded from the figs of *F. microcarpa* in the plant's native range. Some of these NPFW are also widely introduced and NPFW have also colonised the extended ranges of the tree in China and Australia. *Ficus microcarpa* is the only known host plant of its pollinator and most of its associated NPFW, but there are exceptions (Zhou *et al.*, 2012). The NPFW belong to the families Pteromalidae, Eurytomidae, and Ormyridae (Grandi, 1926; Ishii, 1934; Wiebes, 1980; Bouček, 1988; Yokoyama & Iwatsuki, 1998; Chen *et al.*, 1999; Zhang & Xiao, 2008; Feng & Huang, 2010; Heraty *et al.*, 2013; Li *et al.*, 2013). Unlike the agaonids, their adult females do not enter the figs to oviposit. They utilise their long ovipositors to lay eggs through the outer walls of the figs (Galil & Copland, 1981). The larvae of all the fig wasps associated with *F. microcarpa* develop in female flowers, either as phytophages or parasitoids. Non-pollinating fig wasps belonging to the subfamilies Epichrysomallinae and Otitesellinae (Pteromalidae) may all be gallers (Bouček, 1988), whereas species in the families Eurytomidae and Ormyridae and subfamily Sycoryctinae of Pteromalidae are mainly parasitoids of gall formers (Compton, 1993; Segar & Cook, 2012; Suleman *et al.*, 2013). *Philotrypesis taiwanensis* Chen (Sycoryctinae) is exceptional because its larvae develop in seeds, not galls (Wang *et al.*, 2014). The biology of the rarely encountered pteromalid *Sirovena costallifera* Li *et al.* (2013) (Pireninae) is not known. There are no confirmed obligate hyper-parasitoids (Compton *et al.*, 2009a,b) among the NPFW associated with *F. microcarpa*, but some parasitoids mainly or entirely develop at the expense of gall-forming NPFW, rather than pollinators (R. Wang, unpubl. data).

Published records

Literature relevant to fig wasps and *F. microcarpa* was searched using electronic resources including Web of Science and Google, and from citations in other papers. Some additional records were obtained via personal communications. Together with locations, the year when each fig wasp species was first collected was noted, or if this was not provided, the year when the record was published. Synonymies were checked using the Universal Chalcidoidea Database, accessed July 2014 (<http://www.nhm.ac.uk/research-curation/research/projects/chalcidooids/database/>). Some published records do not specify the species concerned, but provide descriptions that are sufficient for provisional assignment to species. These are indicated within the tables. *Philotrypesis okinavensis* Ishii and *P. emeryi* Grandi are closely related species and their names do not appear to have been applied consistently. We have applied names to the two taxa *sensu* Chen *et al.* (1999), but not Bouček (1993), segregating the two species on the basis of lines of hairs at both sides of the head in males of *P. okinavensis* (absent in *P. emeryi*). In the absence of confirmatory specimens we retained the identifications of these taxa used in the original publications,

but these should be considered as provisional. Current higher taxonomic classifications of fig wasps are based on Rasplus *et al.* (1998), Campbell *et al.* (2000), Cruaud *et al.* (2010), and Heraty *et al.* (2013), as summarised in figweb (<http://www.figweb.org>).

Sample sites

A uniform sampling regime was adopted at sites in the introduced and native ranges of *F. microcarpa* (Table 1). Figs were sampled from native-range trees in the humid tropics (The Philippines) and areas with pronounced wet and dry seasons (China mainland, Taiwan, Thailand). The figs came mainly from planted trees, rather than natural forests. We also collected figs from 20 areas outside the plant's native range. These included areas in south-central China and eastern Australia, two countries where *F. microcarpa* grows naturally at lower latitudes than the introduced-range sample sites. Further from the native range, sample sites were located in Brazil, the Caribbean, southern USA, the Mediterranean, and South Africa. Their climates vary considerably but tend to be more seasonal than in the native range of *F. microcarpa* (<http://www.wunderground.com>).

Fig wasp faunas

Ficus microcarpa figs were sampled between December 2010 and July 2013. Each sample comprised ten or more mature figs collected haphazardly from each crop (late C or early D phase, *sensu* Galil & Eisikowitch, 1968; Table 1). Figs at this stage contain adult fig wasps that are about to emerge from the figs. Any figs found to have exit holes were rejected. The figs were stored in 70% ethanol.

The contents of each fig were recorded after they were sliced into quarters and softened by being soaked in water for more than 10 minutes. Using a binocular microscope, all fig wasps inside our sampled figs were identified using mainly Chen *et al.* (1999) and Feng and Huang (2010), with additional morpho-species coded where necessary. Note that fig wasp species were distinguished on the basis of their morphology. Molecular studies suggest that complexes of closely related fig wasp species may also be present (Li *et al.*, 2010; Sun *et al.*, 2011; Zhou *et al.*, 2012). The fig wasps were stored in 95% ethanol for long-term preservation, and are deposited at the University of Leeds, UK.

The fig wasp species were divided into two trophic groups: phytophages including the pollinator (an ovule galler), NPFW that also induce ovule galls (species in subfamilies Agaoninae, Epichrysomallinae, Otitesellinae, and (tentatively) Pireninae) and the seed predator *Philotrypesis taiwanensis*; and parasitoids with larva that develop at the expense of galler offspring (species in families Eurytomidae and Ormyridae and most species of Pteromalidae subfamily Sycoryctinae). Prevalence at each trophic level and of individual species was calculated as the proportion of

Table 1. Collections of *Ficus microcarpa* figs. Note that only figs that contained fig wasps are indicated.

Area	Site (abbreviation)	Location	Year(s)	<i>N</i> crops	<i>N</i> figs
Native range					
China mainland	Guangzhou (GZ)	N 23°11', E 113°22'	2011–2012	12	169
China mainland	Xishuangbanna (XS)	N 22°00', E 100°48'	2010–2013	17	279
Philippines	Manila (MN)	N 14°40', E 121°04'	2012	2	40
Taiwan	Taipei (TB)	N 25°01', E 121°33'	2012	11	220
Thailand	Bangkok (BK)	N 13°44', E 100°33'	2012–2013	4	39
Thailand	Chiang Mai (CM)	N 18°46', E 98°59'	2012	4	47
Thailand	Kanchanaburi (KC)	N 14°04', E 99°32'	2012–2013	6	63
Total				56	857
Introduced range					
Australia	Brisbane (BR)	S27°29', E 153°06'	2012	2	40
Brazil	Rio de Janeiro (RJ)	S22°53', W43°34'	2012	6	130
Canary Islands	Tenerife (TN)	N28°29', W16°19'	2013	1	30
China mainland	Chengdu (CD)	N 30°40', E 104°06'	2012	3	20
China mainland	Kunming (KM)	N 24°53', E 102°50'	2010–2011	6	48
China mainland	Mianyang (MY)	N 31°28', E 104°41'	2012	5	33
China mainland	Panzhihua (PZ)	N 26°35', E 101°43'	2012	10	136
China mainland	Sanming (SM)	N 26°16', E 117°38'	2013	4	71
China mainland	Xichang (XC)	N 27°53', E 102°17'	2012	12	181
Florida	Davie (DV)	N26°04', W80°14'	2012	4	100
Greece	Rhodes (RD)	N36°10', E27°58'	2011–2012	27	294
Greece	Symi (SY)	N36°35', E27°50'	2012	4	37
Italy	Sicily (SC)	N38°07', E13°22'	2012	10	99
Libya	Tripoli (TP)	N32°51', E13°12'	2011–2012	7	96
Malta	Malta (MT)	N35°56', E14°23'	2011	9	130
Puerto Rico	Puerto Rico (PR)	N18°23', W66°04'	2013	7	47
South Africa	Grahamstown (GH)	S33°19', E 26°31'	2011	7	140
South Africa	Port Elizabeth (PE)	S33°58', E 25°37'	2011	5	81
Spain	Majorca (MJ)	N39°35', E2°40'	2012	6	101
Turkey	Marmaris (MM)	N36°51', E28°15'	2012	1	10
Total				136	1824
Grand total				192	2681

figs where they were present. Any figs that contained no fig wasps were excluded from all analyses.

Changes over time in fig wasp faunas outside the plant's native range

In the plant's introduced range, we extracted previously published distribution records of individual taxa and combined them with the results of our surveys to generate species richness estimates. We also charted the expansions in distribution of the most widely introduced phytophagous species, including the pollinator and two major NPFW (*Odontofroggata galili* Wiebes and *Walkerella microcarpae* Bouček). Records of the two most widely distributed parasitoids (*Philotrypes emeryi* and *Philotrypes okinavensis*), were combined because of issues with their identification.

Statistical analyses

The influence of sampling effort at each sample site was tested using a pooled rarefaction algorithm (Heck *et al.*,

1975) in SDR version 4.1.2 (Seaby & Henderson, 2006). This combines individual-based data (fig wasp individuals) from all samples (figs), and then scales every sample to the same number of individuals (rarefaction) when estimating species richness. Bootstrap re-sampling was carried out to calculate the standard error of species richness at each sample size.

Differences between the native and introduced ranges of *F. microcarpa* in the prevalence (the proportion of figs occupied) of the pollinator, phytophagous NPFW and parasitoids were tested using generalised linear models (GLMs) in R 3.0.0 (R Development Core Team, 2013), assuming quasi-binomial distributions of residuals because of overdispersion.

Results

Published records

Published records and personal communications provided data from 35 countries or regions (10 in the plant's native range and 25 in its introduced range) (Table 2; Tables S1 and S2). *Eupristina verticillata* was described as

Table 2. Summary of previously published records of fig wasps associated with figs of *Ficus microcarpa* (see Table S1 for full citations).

Trophic level	Wasp taxon	Native range (<i>N</i> countries/regions)	Introduced range (<i>N</i> countries/regions)
Putative phytophages			
	Agaonidae, Agaoninae		
	<i>Eupristina verticillata</i> Waterston	10	21
	Pteromalidae, Epichrysomallinae		
	<i>Acophila microcarpae</i> Chen	1	1
	<i>Acophila quinata</i> Zhang & Xiao	1	0
	<i>Epichrysomalla</i> sp.	1	0
	<i>Eufroggattisca okinavensis</i> Ishii	2	0
	<i>Meselatus bicolor</i> Chen	1	
	<i>Odontofroggattia corneri</i> Wiebes	5	1
	<i>Odontofroggattia gajimaru</i> Wiebes	4	0
	<i>Odontofroggattia galili</i> Wiebes	6	11
	<i>Odontofroggattia ishii</i> Wiebes	4	4
	<i>Odontofroggattia quinifuniculus</i> Feng & Huang	1	1
	Pteromalidae, Otitesellinae		
	<i>Micranisa degastris</i> Chen	1	1
	<i>Micranisa yashiroi</i> Ishii	1	2
	<i>Walkerella kurandensis</i> Bouček	4	0
	<i>Walkerella microcarpae</i> Bouček	4	10
	Pteromalidae, Sycoryctinae		
	<i>Philotrypesis taiwanensis</i> Chen	1	3
Putative parasitoids			
	Eurytomidae		
	<i>Bruchophagus sensoriae</i> Chen	1	0
	<i>Sycophila curta</i> Chen	1	0
	<i>Sycophila maculafacies</i> Chen	1	1
	<i>Sycophila petiolata</i> Chen	1	1
	Ormyridae		
	<i>Ormyrus lini</i> Chen	1	0
	Pteromalidae, Pireninae		
	<i>Sirovena costallifera</i> Li, Xiao & Huang	1	0
	Pteromalidae, Sycoryctinae		
	<i>Philotrypesis emeryi</i> Grandi	3	4
	<i>Philotrypesis okinavensis</i> Ishii	2	1
	<i>Sycoryctes moneres</i> Chen	1	0
	<i>Sycosapter gajimaru</i> Ishii	3	0

the pollinator of *F. microcarpa* in 1921 (Waterston, 1921) and the first of its NPFW associates were described in 1926 (Grandi, 1926). Ishii (1934) then published the first account of the tree's fig wasp fauna, from Japan. In total, 26 fig wasps have been recorded previously from the plant's native range, comprising 16 putative phytophages and 10 putative parasitoids. The highest recorded species richness was in Taiwan (20 species; Table 2; Table S1). The pollinator, *E. verticillata* was the most frequently recorded fig wasp, with *O. galili* and *W. microcarpae* the most widespread NPFW phytophages (Table 2; Table S1). Parasitoids were recorded more rarely, in both the native and introduced ranges (Table 2).

Published records from 11 of the 25 areas of introduction referred to only a single species, usually the pollinator (Table S1). The introduction of *E. verticillata* to Hawaii was recorded by Pemberton (1939), but the subsequent un-planned spread of the pollinator outside its native range was not recorded before 1986 in the New

World (Stange & Knight, 1987; Ramírez & Montero, 1988); and 1990 in Europe (Lo Verde *et al.*, 1991). Prior to that, the first NPFW colonist (*O. galili*) was recorded from Israel in 1980 (Wiebes, 1980).

The published records highlight (i) the high species richness of the fig wasp fauna associated with *F. microcarpa* in its native range; (ii) a surprisingly rich and early introduced fauna associated with the plant in Hawaii, which may indicate that not only the pollinator was introduced in the 1920s/1930s, and (iii) the spread of three species (*E. verticillata*, *W. microcarpae*, and *O. galili*) throughout most of the introduced range of the plant. Both *W. microcarpae* and *O. galili* were originally described from their introduced ranges.

Expansion of host ranges among figs wasps that normally utilise other fig tree hosts has only been recorded in South Africa, where adult offspring of three phytophages (two of them routine pollinators of African fig trees) and two parasitoids of local fig wasps have been collected in

small numbers (Table S1). It may not be coincidental that the pollinator has not yet been introduced to South Africa, where some figs remain on the trees for long periods without being colonised by fig wasps (van Noort *et al.*, 2013).

Our fig wasp faunal surveys

We dissected 2681 figs from 192 crops (Table 1), and recorded a total of 99 038 fig wasps. Thirty-two fig wasp morpho-species were identified from the collections,

comprising 14 putative phytophages and 18 putative parasitoids (Table 3). Among these species, we recorded 12 taxa for the first time from *F. microcarpa* figs (all from the native range or adjacent to it). They belonged to the genera *Eupristina* (one species, the agaonid ‘cheater’ that fails to actively pollinate), *Sycobia* (one species), *Walkerella* (two species), *Sycophila* (two species), *Ormyrus* (one species), *Philotrypesis* (three species), *Sycoryctes* (one species), and *Sycoscapter* (one species). With the exception of the *Eupristina* sp., which was locally abundant where it occurred, each of these newly recorded species was collected from no more than two sample sites and at a low

Table 3. Fig wasps recorded from figs of *Ficus microcarpa* in this study. Prevalence = the proportion of figs occupied in the plant’s native ($N = 857$ figs) or introduced range ($N = 1824$ figs).

Trophic level	Wasp taxon	Native range		Introduced range	
		<i>N</i> sites present	Prevalence (%)	<i>N</i> sites present	Prevalence (%)
Putative phytophages					
Agaonidae					
	<i>Ev</i> <i>Eupristina verticillata</i> Waterston	7	66.6	16	41.6
	<i>Es</i> <i>Eupristina</i> sp. (‘Cheater’)	1	21.0	1	1.0
Pteromalidae, Epichrysomallinae					
	<i>Aq</i> <i>Acophila quinata</i> Zhang & Xiao	1	0.1	1	0.1
	<i>Mb</i> <i>Meselatus bicolor</i> Chen	2	1.2	7	14.6
	<i>Oc</i> <i>Odontofroggatia corneri</i> Wiebes	6	10.2	6	11.2
	<i>Og</i> <i>Odontofroggatia galili</i> Wiebes	3	24.0	15	37.8
	<i>Oi</i> <i>Odontofroggatia ishii</i> Wiebes	5	8.4	4	2.0
	<i>Oq</i> <i>Odontofroggatia quinifuniculus</i> Feng & Huang	4	2.9	1	0.4
	<i>Sbs</i> <i>Sycobia</i> sp.	0	0	2	0.8
Pteromalidae, Otitesellinae					
	<i>Md</i> <i>Micranisa degastris</i> Chen	5	6.8	6	7.5
	<i>Wm</i> <i>Walkerella microcarpa</i> Bouček	5	11.6	12	23.7
	<i>Wn</i> <i>Walkerella nigrabdomina</i> Ma & Yang	2	2.0	0	0
	<i>Ws</i> <i>Walkerella</i> sp.	1	1.5	0	0
Pteromalidae, Sycoryctinae					
	<i>Pt</i> <i>Philotrypesis taiwanensis</i> Chen	7	23.1	4	3.3
Putative parasitoids					
Eurytomidae					
	<i>Bs</i> <i>Bruchophagus sensoriae</i> Chen	0	0	2	1.2
	<i>Sc</i> <i>Sycophila curta</i> Chen	1	0.2	0	0
	<i>Sm</i> <i>Sycophila maculafacies</i> Chen	4	15.4	6	6.3
	<i>Smp</i> <i>Sycophila maculafacies</i> (‘pale’)	2	2.5	3	1.3
	<i>Sp</i> <i>Sycophila petiolata</i> Chen	3	17.0	2	0.9
	<i>Ss</i> <i>Sycophila</i> sp.	1	0.6	0	0
Ormyridae					
	<i>Ol</i> <i>Ormyrus lini</i> Chen	2	0.8	0	0
	<i>Os</i> <i>Ormyrus</i> sp.	0	0	1	0.1
Pteromalidae, Pireninae					
	<i>Sic</i> <i>Sirovena costallifera</i> Li, Xiao & Huang	1	0.1	0	0
Pteromalidae, Sycoryctinae					
	<i>Pe</i> <i>Philotrypesis emeryi</i> Grandi	5	7.7	5	0.7
	<i>Po</i> <i>Philotrypesis okinavensis</i> Ishii	5	8.3	6	6.8
	<i>Ps1</i> <i>Philotrypesis</i> sp.1	2	0.6	0	0
	<i>Ps2</i> <i>Philotrypesis</i> sp.2	1	0.1	0	0
	<i>Ps3</i> <i>Philotrypesis</i> sp.3	1	0.5	0	0
	<i>Srm</i> <i>Sycoryctes moneres</i> Chen	6	13.1	0	0
	<i>Srs</i> <i>Sycoryctes</i> sp.	1	2.8	0	0
	<i>Scg</i> <i>Sycoscapter gajimaru</i> Ishii	5	15.9	1	2.6
	<i>Scs</i> <i>Sycoscapter</i> sp.	1	0.5	0	0

prevalence in the figs at the sites where they occurred. One of the two *Walkerella* species, *W. nigrabdomina* Ma & Yang, has been recorded previously from another host tree (Ma *et al.*, 2013) and the other rarely recorded species may also be mainly associated with other *Ficus* species, rather than *F. microcarpa*. Examples include *Sycobia* sp. and *Ormyrus* sp., both of which were only recorded from trees planted north of the tree's natural distribution in China.

We failed to detect six species that have been previously recorded from *F. microcarpa* in its native range (*Acophila microcarpae* Chen, *Epichrysomalla* sp., *Eufroggattisca okinavensis* Ishii, *Odontofroggattia gajimaru* Wiebes, *Micranisa yashiroi* Ishii, and *Walkerella kurandensis* Bouček). Some of these species may again be mainly associated with other fig trees, or synonyms of other species, but it also appears that the tree supports distinct faunal elements in Japan, where we did not sample. Including the five species indigenous to African fig trees from South Africa, the total number of morphologically distinguishable fig wasp species recorded from the figs of *F. microcarpa* currently stands at 43, probably more than for any other fig tree.

Sampling intensity was variable between sites and turnover between crops meant that some species may have been missed at sites where few crops were sampled. Nevertheless, most species were detected by much smaller sub-samples at all the sample sites (Figs S1 and S2), suggesting that sampling effort was generally sufficient. As many as 18 species were recorded at single sample sites within the native range of *F. microcarpa* (in Xishuangbanna and Taibei; Table 4), though not all of the species were recorded from any one single crop. Fig wasp communities in the introduced range were generally less species-rich than in the native range, with the highest species richness (12) in Panzhihua, China (Table 4) and the lowest in Marmaris, Turkey (one species), a site where sampling was limited. Elsewhere, fig wasp communities in the introduced range always contained at least two species (Table 4). A higher proportion of phytophages, relative to parasitoids, were recorded from the plant's introduced range, and parasitoids were entirely absent from 45% of these sample sites (Tables 3 and 4).

The pollinating agaonid was numerically the most dominant fig wasp species in both the native and introduced ranges, but was present in a higher proportion of the figs in the plant's native range than elsewhere [GLM: pollinator prevalence (quasi-binomial): d.f. = 1, likelihood ratio (LR) = 148.020, $P < 0.001$; Table 3]. It was entirely absent from four sites where the tree is introduced in South Africa and China (Grahamstown and Port Elizabeth; Kunming and Mianyang; Table 4).

Fig wasps other than the pollinator were abundant throughout the native and introduced ranges of *F. microcarpa*, occupying 84% of the figs we examined. Non-pollinating fig wasps phytophages were present in a slightly higher proportion of the figs in the introduced range [82% compared with 75% in the native range; GLM: NPFW phytophages prevalence (quasi-binomial): d.f. = 1,

LR = 15.238, $P < 0.001$]. In contrast, parasitoid NPFW were far less frequent in the introduced range [in 18% of the figs, compared with 53% in the native range; GLM: parasitoids prevalence (quasi-binomial): d.f. = 1, LR = 341.180, $P < 0.001$; Tables 3 and 4].

Odontofroggattia galili and *W. microcarpae* were the most prevalent phytophagous NPFW. They were recorded from more than 40% of the sample sites and were present in more than 12% of the figs in both the native and introduced ranges (Table 3). Among the parasitoids, *Sycophila maculafacies* Chen and *Philotrypesis okinavensis*/*P. emeryi* were the most widespread. These species were recorded from more than 30% of the sites and more than 6% of the figs in both ranges (Table 3).

Fig wasp faunas outside the native range of *F. microcarpa*

Planted trees of *F. microcarpa* in China are continuous with the native range and will have allowed fig wasps to disperse northwards unaided. This is in contrast to the situation elsewhere in the plant's introduced range (probably including Australia, where *F. microcarpa* is native in parts of the country) where initial transport will have been by human agency. The relative ease of colonising the Chinese sites is likely to have been responsible for the large number of fig wasps recorded from there (17 species; Table 4; Fig. 1). This contrasts with sites elsewhere, where often just one or two species of fig wasps were present (Fig. 1).

The number of fig wasp species recorded from the introduced range of *F. microcarpa* has increased dramatically over time, but with phytophagous species consistently more numerous (Fig. 2). A total of 22 species (the pollinator and 21 NPFWs) are currently established, comprising 14 phytophages (13 NPFW phytophages) and 8 parasitoids. The dominant phytophages (*E. verticillata*, *O. galili*, and *W. microcarpae*) and the major parasitoids of the pollinators (*P. emeryi* and *P. okinavensis*) are continuing to expand their distribution outside the plant's native range (Fig. 3), suggesting that secondary dispersal is taking place within the Mediterranean, Caribbean and elsewhere, either by further human transport or natural dispersal of the fig wasps.

Discussion

We have described the fig wasp fauna associated with *F. microcarpa* within its native range in Asia and in many of the countries where the tree is grown outside its native range. A large number of taxa were recorded, probably more than for any other *Ficus* species, but the insects were identified using morphological characters, and we know that additional 'cryptic' species are likely to be detected when molecular tools are applied (Sun *et al.*, 2011; A. Cruaud & J.-Y. Rasplus, unpubl. data). Combining our survey with published accounts, this is an apparent accelerating wave of colonisations by both phytophagous

Table 4. Global distributions and prevalence (% of figs occupied) of fig wasp species recorded from figs of *Ficus microcarpa* figs in this study. Order and abbreviations of sample sites are as in Table 1; Order and abbreviations of species are as in Table 3.

Site	Putative phytophages												Putative parasitoids												S _p																											
	E _v	E _s	A _q	M _b	O _c	O _g	O _i	O _q	S _{bs}	M _d	W _m	W _n	W _s	P _t	S _g	B _s	S _c	S _m	S _{mp}	S _p	S _s	O _i	O _s	S _{ic}		P _e	P _o	P _{sl}	P _{s2}	P _{s3}	S _{rm}	S _{rs}	S _{sg}	S _{sv}	S _t																	
Native range																																																				
GZ	75				2	28	12	6		2	24			36	8							20				4	28						20			16		7	15													
XS	70	65	0.4		11	0.4	6	4		9	14	5		21	11						1	3				15	6				4			4		9		19		7	18											
MN	100													10	2																80								1	3												
TB	45				2	72	9	1		10	3			21	8							39	7	58	2	3	3				10						22		2	10	18											
BK	46			21	21		10	8		3	5		33	18	9										3	13	3	10												4	13		4									
CM	100				2							9		2	4																11								13		2	6										
KC	68			3	24		17			10	14			35	7							6	10	8		8	2	2	2	6			16							10	17											
Introduced range																																																				
BR	95					43		20			38			25	4							33	15			1	44														2	5										
RJ	78						19																																			2	6									
TN	100									37																																0	2									
CD	30			1	1	65					5				5																										0	5			4	11						
KM		38	2		8	52	31			10	33				7	6						21			2		35															4	11									
MY				94	15										2																										0	2			0	2						
PZ	12			20	29	27		7			61			1	7	14						7	4	4			25														5	12			1	7						
SM	100				6	4	4			1	6				6												1															1	7			1	7					
XC	2			2	66	62		3			27				6							30	6	6			5														3	9			3	9						
DV	75				84					91				19	4							3					2															3	7			3	7					
RD	23			60	26		3				1				4							9					8															2	6			2	6					
SY	24			65	16		3								4											8																	1	5			1	5				
SC	88				63					1					3											1																	1	4			1	4				
TP	78				76										2											1																	0	2			0	2				
MT	44				95										2																													0	2			0	2			
PR	94						17			49	11			17	5											6	2																	2	7			2	7			
GH					18						93				2																													0	2			0	2			
PE					2						100				2																														0	2			0	2		
MJ	69				40					5	10				4																													0	4			0	4			
MM	100														1																													0	1			0	1			

S_t, species richness of putative phytophages; S_p, species richness of putative parasitoids; S_i, total fig wasp species richness.

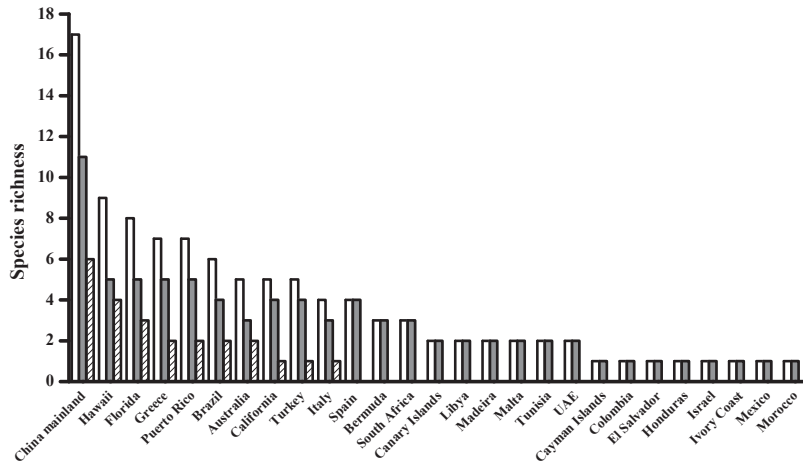


Fig. 1. Species richness of fig wasps where *Ficus microcarpa* has been introduced. Open, filled, and hatched bars represent total, phytophagous, and parasitoid species richness respectively. Data were extracted from both previous publications and this study. Note that local colonists in South Africa are not included.

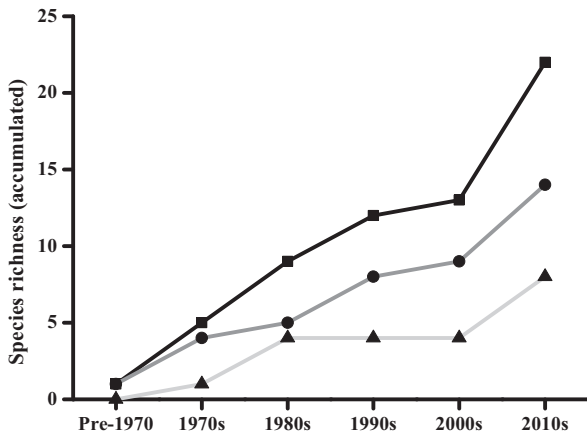


Fig. 2. The numbers of fig wasp species of Asian origin recorded from the introduced range of *Ficus microcarpa*. Squares, circles and triangles represent total, phytophagous, and parasitoid species richness respectively. Data were extracted from both previous publications and this study.

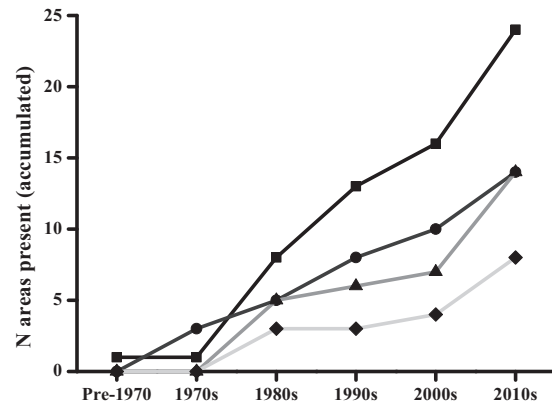


Fig. 3. Changes over time in the number of countries/regions where *Eupristina verticillata*, *Odontofroggattia galili*, *Walkerella microcarpae*, and *Philotrypesis emeryi*/*P. okinavensis* have been recorded in the introduced range of *Ficus microcarpa*. *E. verticillata* (Squares), *O. galili* (circles), *W. microcarpae* (triangles), and *Philotrypesis* spp. (diamonds). Data were extracted from both previous publications and this study.

and parasitoid fig wasps, but piecemeal sampling in the past makes detailed assessments difficult. As an example of apparent recent colonisations, only one species (*O. galili*) was recorded on the Greek island of Symi in the late 1980s (Compton, 1989), whereas five additional species were present 25 years later, including the pollinator, two other gall formers and two parasitoids. Increasing recent migration would be consistent with the generally increasing number of exotic species being introduced around the world, linked to globalisation and the increasing volume of international trade (Mack *et al.*, 2000).

Fig wasp faunas in the plant's native range were generally more species-rich than elsewhere, and supported a

higher proportion of parasitoids. Most of the fig wasps are likely to have *F. microcarpa* as their main or only host plant, but some of the NPFW are known to also be associated with other fig trees, and species that were recorded from few sites, in low numbers, may be mainly associated with other hosts. Some species in China were only recorded in our survey from planted trees north of the tree's native range. They included species recorded in large numbers that had previously been described from within the native range. Seasonal climates may favour these species, as it appears they were sufficiently rare further south in the plant's native range for our surveys to fail to detect them.

Almost all the fig wasps collected outside the native range were species routinely associated with *F. microcarpa* in Asia and South Africa was the only country outside Asia where native species associated with other trees were found to have colonised the figs (van Noort *et al.*, 2013). Three species of fig wasps have been particularly widely distributed, the pollinator and two phytophagous NPFW (*O. galili* and *W. microcarpae*). These are also often the first species to be recorded from a new location. The widespread introduction of these three species mirrors their wide distribution within the native range of *F. microcarpa* and wide environmental tolerances may have facilitated their colonisation of new areas, which often have relatively seasonal climates, rather than tropical ones. In addition, with these species being widespread in their native range it predisposes their presence in the first figs that were translocated overseas. If most current human international transportation involves the moving of figs from one area where the insects have been introduced to another, then the first species to become established will again also have become the most widely distributed. Several factors may explain the small numbers of parasitoid NPFW that have become established. Within the native range they are present at lower densities than their hosts and occupy a smaller proportion of the figs, so the chance of them being occasionally transferred by humans will be reduced, and of course they also require their particular hosts to already be established when they arrive in a new area, so must follow colonisation by phytophagous NPFW.

Establishment of fig wasp communities on *F. microcarpa* growing outside its native range has followed a very different pattern to that provided by an analogous system, that involving oak trees (*Quercus* spp. Fagaceae), gall wasps (Cynipidae) and their numerous parasitoids and inquiline (Askew *et al.*, 2013). Planting of exotic oaks has helped facilitate the establishment of eight European oak gall wasps that have arrived in the UK during the last 180 years (Schönrogge *et al.*, 2012), producing an expansion at the western edge of their natural range similar to the northern extension of *F. microcarpa* in China. The gall wasps have recruited numerous parasitoids and inquilines associated with other galling cynipids on oaks in the UK, and there has also been some 'pursuit' by additional species from the native ranges of the gall wasps (Nicholls *et al.*, 2010; Schönrogge *et al.*, 2012; Stone *et al.*, 2012). This is similar to *F. microcarpa* in China, where several parasitoid and phytophagous NPFW recorded from its native range have extended their distributions northwards and the more successful species, such as the galler *M. degastriis*, are more prominent there than in the native range. The major difference is that there is very limited evidence for recruitment of novel species from the locally resident fig wasps. The contrast is likely to reflect differences in the pools of potential recruits for local colonisation in combination with differing levels of host specificity, and possibly differences in the dispersal behaviour of the insects. Numerous chalcids are associated with oak galls in the UK, compared with relatively few fig wasps in the

extended range of *F. microcarpa* and oak associates often have quite broad host ranges, attacking a range of cynipid species, whereas most NPFW, so far as is known, are restricted to figs produced by a single species of fig tree. Fig wasps include species with extreme dispersal abilities (Ahmed *et al.*, 2009) and in combination with the large numbers of planted *F. microcarpa* this may have facilitated expansion of the fig wasp ranges in China that was not possible for the oak gall associates in Europe.

Cynipid gall wasps have also been introduced far away from their native ranges, where unaided dispersal of their parasitoids was highly unlikely. *Dryocosmus kuriphilus* Yasumatsu forms galls on sweet chestnut (*Castanea* spp. Fagaceae), and has spread from its native China into Japan, Europe, and North America (Aebi *et al.*, 2007). One parasitoid has been widely introduced as a biocontrol agent against *D. kuriphilus* and in addition, like the introduced cynipids in the UK, the galler has accumulated parasitoids from within the pools of locally available species in different parts of its introduced range (Quacchia *et al.*, 2013). This again contrasts with the insects associated with *F. microcarpa*, where despite the tree being introduced across several continents and the establishment of numerous fig wasps that provide potential hosts for parasitoids, recruitment of native species has been very rare and has only been detected in South Africa (van Noort *et al.*, 2013). A combination of two factors may have facilitated this limited local recruitment in South Africa: some local fig trees belong to the same subgenus of *Ficus* as *F. microcarpa* and the pollinator has not yet arrived. Two Asian NPFW are present, but in parts of the range they are present only at low densities and the lack of fig wasps results in figs remaining unutilised, where they may be retained on the trees for long periods. Accidental contacts between native fig wasps and suitable figs are thereby increased, and some of the African species, including parasitoids, are clearly capable of developing in the figs.

The lack of concordance in the patterns of colonisation of introduced *Ficus* and *Quercus* suggests that each insect-plant system may display unique features. Most obviously these are linked to the extent of host specificity among the insects and the extent to which the insects are able to switch to novel hosts when they become available. The communities of insects associated with oak galls and figs may never become 'saturated' with species (Hawkins & Compton, 1992; Stone *et al.*, 2012), so climatic tolerances, time, and opportunities for transport and colonisation appear to be the only other factors limiting the numbers of species they contain. Fig wasps seem to be easily transported between countries, presumably in the figs that provide a source of seed for nurseries, implying that a lack of economic value of oak galls is another reason that the two systems differ.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12111:

Figure S1. Estimated *Ficus microcarpa* fig wasp regional species richness in relation to increasing sample size (fig wasp abundance – the total number of fig wasps sampled and identified) at sites in the plant's native range using a pooled rarefaction algorithm. Standard errors were calculated by bootstrap resampling. The variation in *X* axis scales reflects the different numbers of individuals sampled at different sites.

Figure S2. Estimated *Ficus microcarpa* fig wasp regional species richness in relation to increasing sample size (fig wasp abundance – the total number of fig wasps sampled and identified) at sites outside the plant's native range using a pooled rarefaction algorithm. Standard errors were calculated by bootstrap resampling. The variation in *X* axis scales reflects the different numbers of individuals sampled at different sites.

Table S1. Published records of the distributions of fig wasps associated with *Ficus microcarpa* in its native range. Note that *Eupristina verticillata* Waterston in its native range is a complex of 'cryptic' species and that the name *Parapristina verticillata* (Waterston), used in older literature, is a synonym. Names follow Noyes, J.S. 2014 in Universal Chalcidoidea Database. World Wide Web electronic publication. <http://www.nhm.ac.uk/chalcidoids> the Universal Chalcidoidea Database, accessed July 2014.

Table S2. Published records of the distributions of fig wasps associated with *Ficus microcarpa* outside its native range, as summarised in previous publications. The latest possible date of colonisation of a fig wasp species in each area is given as either the year specimens were first collected (where collection dates are provided) or as the year before publication if collection dates were not provided. Note that the study site in Australia (Brisbane) is to the south of the plant's native range, and we therefore included it in the introduced areas of the plant. We have tentatively re-identified several species in Beardsley (1998) and Otero and Ackerman (2002) based on descriptions and photographs. The original identifications are given in parentheses. The native African fig tree hosts of colonists of *F. microcarpa* in South Africa are also given in parentheses. Names follow Noyes, J.S. 2014. Universal Chalcidoidea Database. World Wide Web electronic publication. <http://www.nhm.ac.uk/chalcidoids> the Universal Chalcidoidea Database, accessed July 2014.

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