

Rapid Communication

A rather unfruitful relationship? Fig wasps (Hymenoptera: Chalcidoidea) of the alien invasive *Ficus microcarpa* in Cyprus

Jakovos Demetriou^{1,2,3}, Evangelos Koutsoukos^{1,4}, Nicole Mavrovounioti^{2,3,5}, Canella Radea¹, Margarita Arianoutsou¹, Helen E. Roy⁶, Stephen G. Compton⁷, and Angeliki F. Martinou^{2,3,8,*}

¹Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian University of Athens, 15784 Athens, Greece

²Joint Services Health Unit Cyprus, BFC RAF Akrotiri BFPO 57, Akrotiri, Cyprus

³Enalia Physis Environmental Research Centre, Acropoleos 2, Aglantzia 2101, Nicosia, Cyprus

⁴Museum of Zoology, National and Kapodistrian University of Athens, 15784 Athens, Greece

⁵Mariou Sofokleous 16, 4540 Paramytha, Limassol, Cyprus

⁶UK Centre for Ecology & Hydrology, Oxfordshire, United Kingdom

⁷School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom

⁸Climate and Atmosphere Research Centre/ Care-C, The Cyprus Institute, Athalassa Campus, 20 Konstantinou Kavafi Street, 2121 Aglantzia, Nicosia, Cyprus

*Corresponding author

E-mail: af.martinou@gmail.com

Citation: Demetriou J, Koutsoukos E, Mavrovounioti N, Radea C, Arianoutsou M, Roy HE, Compton SG, Martinou AF (2023) A rather unfruitful relationship? Fig wasps (Hymenoptera: Chalcidoidea) of the alien invasive *Ficus microcarpa* in Cyprus. *BioInvasions Records* 12(2): 573–580, <https://doi.org/10.3391/bir.2023.12.2.20>

Received: 7 February 2021

Accepted: 20 December 2022

Published: 20 March 2023

Handling editor: António Onofre Soares

Thematic editor: Tim Adriaens

Copyright: © Demetriou et al.

This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

OPEN ACCESS

Abstract

The Chinese banyan (*Ficus microcarpa*) is an Australasian fig tree commonly planted in urban and semi-urban sites throughout the warmer parts of the world. Assisted by its host-specific mutualist pollinator *Eupristina verticillata* (Agaonidae), *F. microcarpa* often manages to colonise urban areas outside its native range and can invade natural habitats. In Cyprus, the species is widely planted in city centres, town squares and parks, where seedlings have been observed. Increasing numbers of fig wasp species of Asian origin are being recorded from the Mediterranean and it appears that the pace of colonisation of *F. microcarpa* is increasing. Fig surveys in Cyprus during the last seven years have uncovered a total of 11 fig wasp species associated with *F. microcarpa*. The composition of the fig wasp fauna is described here. It includes two species previously unknown from the Western Palearctic: *Sycophila petiolata* Chen (Eurytomidae) and an undescribed species of uncertain generic affinity (Pteromalidae, Epichrysomallinae) that we refer to as “*Eufroggatisca* sp. *indesc.*”. The distribution, ecology and relationships of the Cypriot fig wasps associated with the Chinese banyan are discussed, together with their potential impacts on the spread of their host plant.

Key words: Agaonidae, alien species, biological invasions, Eurytomidae, first records, Eastern Mediterranean, Pteromalidae

Introduction

Increasing global trade is resulting in plants and animals being transported outside their native ranges at unprecedented rates (Hulme 2009; Seebens 2019). As a result, approximately 14,000 species are currently considered as alien to Europe, with a large proportion of them being plants (EASIN 2022). Various representatives of the genus *Ficus* L., have been introduced from their tropical and subtropical regions of origin and have been planted as

ornamental foliage in urban and semi-urban areas, mainly due to their inability to set seed without their obligate wasp-pollinators (Speciale et al. 2015; Wang et al. 2015b; Compton et al. 2020b). Among them, native to Asian and Indo-Australian regions *Ficus microcarpa* (L.), also known as the Chinese or Malayan banyan and the Cuban or Indian laurel, has been transported around the globe as an ornamental tree planted in urban habitats such as gardens, parks and town squares (Berg et al. 2005; van Noort et al. 2013). However, the extensive import and planting of *F. microcarpa* has led to the unintentional introduction and frequent establishment of fig wasps and other insects associated with the plant world wide, including its obligate pollinator, a fig wasp belonging to the *Eupristina verticillata* species complex (Hymenoptera: Agaonidae) (Wang 2014; Compton et al. 2020b).

Pollination by *E. verticillata* has allowed this invasive alien plant to reproduce, and its ripe figs are dispersed by birds and ants (Kaufmann et al. 1991; de Figueiredo et al. 1995; Shanahan et al. 2001). New plants can become established in urban settings from where they can spread into semi-natural and natural environments (Wang et al. 2015a). *Ficus microcarpa* has been reported to damage infrastructure (i.e. buildings and walls), while sidewalks made slippery by fallen figs, and clouds of wasps circling the trees, constitute a public nuisance and possible health hazard (Ramírez and Montero 1988; Starr et al. 2003; Wang et al. 2015a; Demetriou 2021). Additionally, in Hawaii, Bermuda and the Neotropics, *F. microcarpa* has been found to compete with and replace native plant species (Ramírez and Montero 1988; Starr et al. 2003; S.G. Compton *unpublished data*).

A number of fig wasp species associated with *F. microcarpa* have been recorded, and even described as new species, from areas of introduction, outside the natural range of their host plants (Wang et al. 2015a). These species form a polyphyletic assemblage representing the families Agaonidae Walker, Eurytomidae Walker, Ormyridae Förster and Pteromalidae Dalman (van Noort and Rasplus 2021). Agaonids have a coevolved mutualistic relationship with their fig tree hosts and act as their only pollinators, and in return the plants support the development of the fig wasps (Ramirez 1974). On the contrary, representatives from other families, called non-pollinating fig wasps, fall within a variety of functional groups (e.g. gall-inducers, kleptoparasites and parasitoids of pollinators or other non-pollinating fig wasps) that reduce the plant's reproductive success by reducing pollen dispersal by its mutualists or destroying ovules that could have developed seeds (Suleman et al. 2013; van Noort et al. 2013). Therefore, non-pollinating fig wasps can potentially act as biological control agents against invasive alien fig trees such as *F. microcarpa*, mitigating their adverse impacts on native biodiversity, society and human health (Wang et al. 2015b).

In Cyprus, *F. microcarpa* has been extensively planted as an ornamental in city centres, roadsides, parks and public gardens. Compton et al. (2020b)

reported on the presence of nine alien species feeding on the leaves and stems of the Chinese banyan in the Limassol district of Cyprus. Among them, only *Trioza brevigenae* Mathur, 1973 and *Josephiella microcarpae* Beardsley & Rasplus, 2001 are believed to show a specificity towards their host plant. Fig wasps tend to be much more host specific. A total of nine introduced fig wasp species were collected from *F. microcarpa* in Limassol District by Compton et al. (2020a). In addition two “accidental” captures of two fig wasps associates of *Ficus sycomorus* (L.) were recorded, namely *Sycophaga sycomori* (Linnaeus, 1758) and *Apocrypta longitarsus* Mayr, 1906, both of which were trapped on *F. microcarpa*.

Here we report on the fig wasp community of *F. microcarpa* in Cyprus. The species richness, distribution and ecology of the fig wasps as well as their impact on *F. microcarpa* in this Mediterranean island are then discussed.

Materials and methods

Surveys in four major districts of Cyprus were undertaken from 18th April to 15th June 2014, April to June 2015, 3rd to 24th June 2017 and from 12th September to 25th October 2018 (Compton et al. 2020a; N. Mavrovounioti *unpublished data*; Z. Deal *unpublished data*; R. Sore *unpublished data*; H. Newton *unpublished data*). More recent weekly surveys were performed in Limassol city centre from February till late May 2021, although fig wasps were only detected from 15th April to 31st May 2021 (Demetriou 2021). Mature figs at the late C or early D developmental phases were generally collected from *F. microcarpa* trees and stored in 70° ethanol (Wang 2014), but the 2018 surveys employed yellow sticky traps (H. Newton *unpublished data*; Compton et al. 2020a). In 2021 fig wasps were collected from the leaves using a beating-sheet.

The collected material was identified under a stereomicroscope using the identification keys of Ishii (1934), Beardsley (1998), Chen et al. (1999) and van Noort and Rasplus (2021). Reference material is deposited at the University of Leeds, UK, the Department of Ecology and Systematics, National and Kapodistrian University of Athens, Greece as well as the private collection of the second author.

Results

A total of 11 fig wasp species were collected (Table 1). The family Pteromalidae accounts for eight out of the 11 species. Four species, namely *E. verticillata*, *Meselatus bicolor* Chen, 1999, *Odontofroggatia galili* Wiebes, 1980 and *Sycophila maculafacies* Chen, 1999 appear widely distributed in the country and were present in all four sampled districts. Limassol district showed the highest family and species richness, but was also the most intensively sampled.

Species were provisionally assigned to functional groups corresponding to their known feeding habits or those of related species in the taxonomic

Table 1. Fig wasp species collected in Cyprus from 2014–2021, including their year of first record and distributions at district level (LA = Larnaca, LI = Limassol, NI = Nicosia, PA = Paphos).

Taxonomic affinities	Species	Year					Year of first record	Functional group	Distribution within Cyprus
		2014	2015	2017	2018	2021			
Agaonidae	<i>Eupristina verticillata</i> Waterston, 1921	X	X	X	X	X	2014	ovule galler	LA, LI, NI, PA
Eurytomidae	<i>Sycophila maculafacies</i> Chen, 1999	X	X	X	X	X	2014	parasitoid	LA, LI, NI, PA
	<i>Sycophila petiolata</i> Chen, 1999					X	2021	parasitoid	LI
Pteromalidae: Epichrysomallinae	“ <i>Eufroggattisca</i> sp. <i>indesc.</i> ”				X	X	2018	ovule galler	LI
	<i>Meselatus bicolor</i> Chen, 1999	X	X	X	X		2014	ovule galler	LA, LI, NI, PA
	<i>Odontofroggatia galili</i> Wiebes, 1980	X	X	X	X	X	2014	ovule galler	LA, LI, NI, PA
	<i>Odontofroggatia ishii</i> Wiebes, 1980	X	X				2014	ovule galler	LI, NI
Pteromalidae: Otitesellinae	<i>Micranisa degastris</i> Chen, 1999				X	X	2018	ovule galler	LI
	<i>Walkerella microcarpae</i> Boucek, 1993	X	X				2014	ovule galler	NI
Pteromalidae: Sycoryctinae: Philotrypesini	<i>Philotrypesis okinavensis</i> Ishii, 1934				X		2018	parasitoid	LI
	<i>Philotrypesis taiwanensis</i> Chen, 1999				X		2018	seed galler	LI

groups to which they belong. Eight out of the collected species are phytophagous ovule gall inducers (including the pollinator) and one species develops in seeds, *Philotrypesis taiwanensis* Chen, 1999. The remaining three species namely, *S. maculafacies* and *Sycophila petiolata* Chen, 1999 are believed to be parasitoids of *Odontofroggatia* spp. and possibly other epichrysomallines, while *Philotrypesis okinavensis* Ishii, 1934 is a parasitoid of *E. verticillata* (Wang 2014, 2015a; Wang et al. 2014).

During the first year of surveys, non-pollinating fig wasps were more abundant than the pollinator and *M. bicolor* was found to exclude other wasps from occupied host figs (N. Mavrovounioti *unpublished data*). However, after 2017 a shift in relative abundance was observed, with *E. verticillata* being by far the most abundant species (R. Sore *unpublished data*; H. Newton *unpublished data*).

Discussion

Overall, four species of fig wasps were collected from Larnaca and Paphos, five from Nicosia and ten from Limassol. The highest fig wasp species richness was recorded from Limassol district, but this may well be attributed to the site's higher collecting effort, with Limassol being sampled during each collecting event. In addition, 2018 surveys were performed in autumn, in contrast to the others that were carried out in spring and early summer and the former provided the first records for “*Eufroggattisca* sp. *indesc.*”, *Micranisa degastris* Chen, 1999, *Ph. okinavensis* and *Ph. taiwanensis*. The use of a beating sheet may also have influenced the results, with *S. petiolata* being recorded for the first time from the Western Palearctic and outside its native range in China and Taiwan (Chen 1999; Wang et al. 2015a). Both

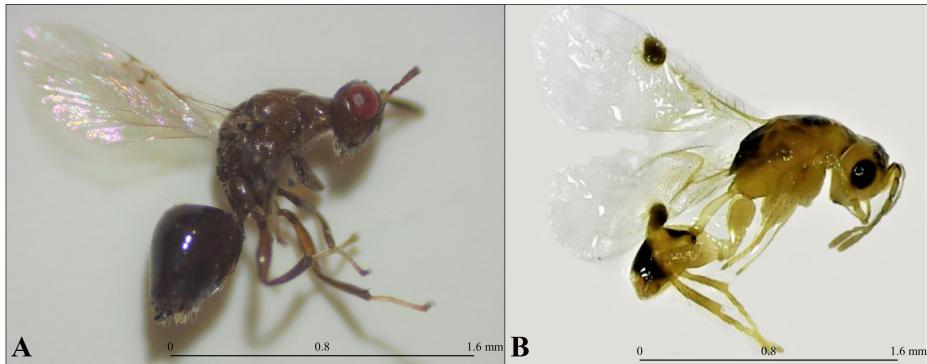


Figure 1. “*Eufroggattisca* sp. *indet.*” (A) and *Sycophila petiolata* (B), lateral view. Photographs by Jakovos Demetriou.

the use of a beating sheet and sticky traps detected fig wasps active at the time in the field rather than in figs and these methods provided additional new records. The increase in species recorded may also be attributed to the smaller number of figs collected during previous surveys and the possibility that additional species are arriving and spreading.

An undescribed species of uncertain generic affiliation “*Eufroggattisca* sp. *indesc.*” (Figure 1A) was collected from Limassol District in 2018 and 2021. It was not detected in earlier Cypriot samples and appears to represent a recent arrival on the island. There are no previously published records of this species in Europe, but it was reared from figs of *F. microcarpa* collected in Malaga, Spain in 2018, and was also present in Egypt that year (S.G. Compton *unpublished data*). Furthermore, its characteristic large galls were also present in old figs collected on the island of Ischia, Italy the same year. It therefore appears to have been a recent arrival in Europe that has spread very rapidly. The taxonomic status of this species will be treated in a later publication.

Individuals of *E. verticillata*, *S. maculafacies*, *M. bicolor* and *O. galili* are widely distributed in the island whereas *Walkerella microcarpae* Boucek, 1993 has been collected only from Nicosia. Representatives of the genera *Philotrypesis* Förster, 1878 and *M. degastris* were collected in autumn, and only from Limassol. The latter record constitutes the first confirmed representatives of subfamily Otitesellinae (Pteromalidae) for Cyprus (Noyes 2019). So far, as is known all fig wasps originate from the Chinese banyan’s native range and are therefore present as aliens to Cyprus.

The species richness of the fig wasp community associated with *F. microcarpa* in Cyprus is perhaps not unexpected; similar cases have been reported from other Mediterranean islands (Wang 2014; Wang et al. 2015a), but no other islands have been surveyed over several years. It is unknown whether the import and dispersal of alien fig wasps within Cyprus and the Mediterranean more generally is a result of multiple introduction events of their host figs, or the result of initial introductions and subsequent unaided dispersal. This could be explored with the help of molecular tools in future studies. Some species could have reached Cyprus from already invaded



Figure 2. Young *Ficus microcarpa* trees developing in the urban landscape of Limassol city, on wall (A) and pavement crevices (B). Photographs by Jakovos Demetriou.

territories such as Israel or Turkey, utilizing wind currents (van Noort and Rasplus 2010). Pollen dispersal and fig wasp air-borne movement has been observed to occur at distances of more than 160 km (Ahmed et al. 2009). This highlights not only the continuing introduction risk of alien fig wasps but also the likelihood of successful pollination of even isolated *F. microcarpa* populations and eventual range expansion of *F. microcarpa* to natural habitats.

Non-pollinating fig wasps have been identified as possible biological control agents of the invasive *F. microcarpa* that could slow its spread (Wang et al. 2015b). Reduction of pollen dispersal throughout competition and exclusion of *E. verticillata* from available figs could prevent or at least reduce seed production and therefore subsequent germination and establishment. The classification of fig wasps in functional groups based on their feeding habits suggests that only *E. verticillata* (as pollinator), *S. maculafacies* and *S. petiolata* (Figure 1B) (which attack ovule gallers) are likely be beneficial to the reproductive success of *F. microcarpa*, whereas all the remaining species will reduce the numbers of seeds or pollen-carrying agaonids produced by the tree (Wang et al. 2015b). During the initial surveys, *M. bicolor* and *Odontofroggatia* spp. were found to be the most prominent potential biological control agents due to their high abundance and demonstrated negative impacts on pollinators and seed production (N. Mavrovounioti *unpublished data*). However, the observed apparent shift in pollinator and non-pollinating fig wasps' abundances suggests that Chinese Banyan and its pollinator fig wasp will continue to be fruitful, with the risk of eventually allowing the spread of *F. microcarpa* into natural habitats. Some establishment of the Chinese banyan in Mediterranean natural habitats has been reported (Wang et al. 2015a, b) although in Cyprus such instances have not yet been observed. Nevertheless, young trees of various alien *Ficus* spp. including *F. microcarpa* have been observed in the historical centre of Limassol, where they develop on sidewalks and wall crevices (Figure 2A, B).

Sporadic records of the fig wasps associated with *F. microcarpa* around the Mediterranean have been reported since 1988 (Compton 1989). Since then, the number of recorded associates has increased rapidly; however, because surveys have been opportunistic and widely scattered, the first date that a species is recorded only provides the latest possible date when they arrived. Cyprus is perhaps unique in that surveys have been repeated for several years, but even here only the city of Limassol has repeated observations. Fig wasp communities of *F. microcarpa* in Cyprus are unquestionably in need of a thorough quantitative evaluation, with yearly monitoring. Thus, any shifts in the abundance of non-pollinating fig wasps that can act as biocontrol agents and the fig wasps that are beneficial towards the plant can be detected. The study of potentially significant biocontrol agents such as *M. bicolor* (Wang 2014; Wang et al. 2015b) is important, as is monitoring for *F. microcarpa* in natural habitats of this Mediterranean island. A risk assessment for *F. microcarpa* in Cyprus would be of value in order to inform future conservation or eradication practices and help minimize naturalization risks of *F. microcarpa* outside the urban landscape it currently occupies.

Acknowledgements

We are highly grateful to Zoë Deal, Rachel Sore and Holly Newton (all at the University of Leeds) for their fig wasp surveys undertaken in Cyprus as well as access to their unpublished MSc Theses. Part of this study was performed under the MSc Thesis of the first author in the program “Ecology and Biodiversity Conservation” at the Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian University of Athens, Greece under the supervision of Prof Margarita Arianoutsou. We are also thankful to the UK Government through Darwin Plus and the State Scholarship Foundation of Cyprus (IKYK) for a postgraduate scholarship awarded to Mr Jakovos Demetriou for his MSc studies and funding this project. This article/publication is based upon work from COST Action Increasing understanding of alien species through citizen science, CA17122, supported by COST (European Cooperation in Science and Technology). Finally, we would like to thank the anonymous reviewers for their comments and correction to the manuscript.

Funding declaration

This project was funded by the UK Government through Darwin Plus and the State Scholarship Foundation of Cyprus (IKYK).

Authors' contribution

Research conceptualization: JD; CR; MA; HER; SGC; AFM; sample design and methodology: JD; SGC; AFM; investigation and data collection: JD; EK; NM; SGC; AFM; data analysis and interpretation: JD; EK; NM; CR; MA; HER; SGC; AFM; ethics approval: AFM; funding provision: HER; AFM; writing – original draft: JD; writing – review & editing: JD; EK; CR; MA; HER; SGC; AFM.

Ethics and permits

Arthropod collection permits were received by the Department of Environment, Ministry of Agriculture, Rural Development and Environment of Cyprus.

References

- Ahmed S, Compton SG, Butlin RK, Gilmartin PM (2009) Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences* 106: 20342–20347, <https://doi.org/10.1073/pnas.0902213106>
- Beardsley W (1998) Chalcid Wasps (Hymenoptera: Chalcidoidea) associated with fruit of *Ficus microcarpa* in Hawaii. *Proceedings of the Hawaiian Entomological Society* 33: 19–34

- Berg CC, Corner EJH, Nooteboom HP (2005) Flora Malesiana Series I (Seed Plants) Vol. 17, part 2. National Herbarium of the Netherlands, Leiden, the Netherlands, 730 pp
- Chen Y, Chuang W, Wu W (1999) Chalcid wasps on *Ficus microcarpa* L. in Taiwan (Hymenoptera: Chalcidoidea). *Journal of the Taiwan Museum* 52: 39–79
- Compton SG (1989) The fig wasp *Odontofroggatia galili* in the Greek Isles. *Entomologist's Gazette* 40: 183–184
- Compton SG, Newton H, Stavrinides M, Kaponas C (2020a) First confirmed records of fig wasps (Hymenoptera: Chalcidoidea) associated with the Sycamore Fig *Ficus sycomorus* on a Mediterranean Island. *Entomologist's Gazette* 71: 121–124, <https://doi.org/10.31184/G00138894.712.1735>
- Compton SG, Stavrinides M, Kaponas C, Thomas PJ (2020b) No escape: most insect colonisers of an introduced fig tree in Cyprus come from the plant's native range. *Biological Invasions* 22: 211–216, <https://doi.org/10.1007/s10530-019-02132-4>
- de Figueiredo RA, Motta Jr. JC, Vasconcellos LADS (1995) Pollination, seed dispersal, seed germination and establishment of seedlings of *Ficus microcarpa*, Moraceae, in southeastern Brazil. *Revista Brasileira de Biologia* 55: 233–239
- Demetriou J (2021) Alien insects in protected and urbanised areas in Cyprus. MSc Thesis, Department of Ecology and Systematics, Faculty of Biology, School of Science, National and Kapodistrian University of Athens, Anthes, Greece, 101 pp
- Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Ishii T (1934) Fig chalcidooids of Japan. *Kontyū* 8: 84–100
- Kaufmann S, McKey DB, Hossaert-McKey M, Horvitz CC (1991) Adaptations for a two phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). *American Journal of Botany* 78: 971–977, <https://doi.org/10.1002/j.1537-2197.1991.tb14501.x>
- Ramirez WB (1974) Coevolution of *Ficus* and Agaonidae. *Annals of the Missouri Botanical Garden* 61: 770–780, <https://doi.org/10.2307/2395028>
- Ramírez WB, Montero JS (1988) *Ficus microcarpa* L., *F. benjamina* L. and other species introduced in the New World, their pollinators (Agaonidae) and other fig wasps. *Revista de Biología Tropical* 36(2B): 441–446
- Seebens H (2019) Invasion Ecology: Expanding trade and the dispersal of alien species. *Current Biology* 29: 120–122, <https://doi.org/10.1016/j.cub.2018.12.047>
- Shanahan M, So S, Compton SG, Corlett R (2001) Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76: 529–572, <https://doi.org/10.1017/S1464793101005760>
- Speciale M, Cerasa G, Lo Verde G (2015) First record in Europe of seedling of *Ficus macrophylla* f. *columellaris* (Moraceae) and of its pollinating wasps *Pleistodontes* cf. *imperialis* (Chalcidoidea: Agaonidae). *Il Naturalista siciliano* 39(2): 399–406
- Suleman N, Raja S, Compton SG (2013) Parasitism of a pollinator fig wasp: mortalities are higher in figs with more pollinators, but are not related to local densities of figs. *Ecological Entomology* 38: 478–484, <https://doi.org/10.1111/een.12041>
- van Noort S, Rasplus JY (2010) Order Hymenoptera, Chalcidoidea associated with figs (families Agaonidae and Pteromalidae). *Arthropod fauna of the UAE* 3: 325–355
- van Noort S, Wang R, Compton SG (2013) Fig wasps (Hymenoptera: Chalcidoidea: Agaonidae, Pteromalidae) associated with Asian fig trees (Ficus, Moraceae) in southern Africa: Asian followers and African colonists. *African Invertebrates* 54: 381–400, <https://doi.org/10.5733/afin.054.0208>
- Wang R (2014) The fig wasps associated with *Ficus microcarpa*, an invasive fig tree. PhD Thesis, University of Leeds, Leeds, United Kingdom, 300 pp
- Wang R, Matthews A, Ratcliffe J, Barwell L, Peng Y-Q, Chou L-S, Yu H, Yang H-W, Compton SG (2014) First record of an apparently rare fig wasp feeding strategy: obligate seed predation. *Ecological Entomology* 39: 492–500, <https://doi.org/10.1111/een.12122>
- Wang R, Aylwin R, Barwell L, Chen XY, Chen Y, Chou LS, Cobb J, Collette D, Craine L, Giblin-Davis RM, Ghana S, Harper M, Harrison RD, McPherson JR, Peng YY, Pereira RAS, Reyes-Betancort A, Rodriguez LJV, Strange E, van Noort S, Yang HW, Yu H, Compton SG (2015a) The fig wasp followers and colonists of a widely introduced fig tree, *Ficus microcarpa*. *Insect Conservation and Diversity* 8: 322–336, <https://doi.org/10.1111/icad.12111>
- Wang R, Aylwin R, Cobb J, Craine L, Ghana S, Reyes-Betancort J, Quinnell R, Compton SG (2015b) The impact of fig wasps (Chalcidoidea), new to the Mediterranean, on reproduction of an invasive fig tree *Ficus microcarpa* (Moraceae) and their potential for its biological control. *Biological Control* 81: 21–30, <https://doi.org/10.1016/j.biocontrol.2014.11.004>

Web sites and online databases

- EASIN (2022) European Alien Species Information Network (EASIN). <https://easin.jrc.ec.europa.eu/easin> (accessed 19 December 2022)
- Noyes JS (2019) Universal Chalcidoidea Database. <http://www.nhm.ac.uk/chalcidooids> (accessed 28 May 2021)
- Starr F, Starr K, Loope L (2003) *Ficus microcarpa* Chinese banyan Moraceae. http://www.hear.org/starr/hiplants/reports/pdf/ficus_microcarpa.pdf (accessed 28 May 2021)
- van Noort S, Rasplus JY (2021) Figweb: figs and fig wasps of the world. www.figweb.org (accessed 28 May 2021)