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Unveiling an intricate relationship: *Ficus* trees, their associated wasps (Hymenoptera, Chalcidoidea) and another story of invasion in the Iberian Peninsula and Europe

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Abstract

The plant genus *Ficus* (Moraceae) includes keystone tree species in tropical ecosystems, providing essential resources for a wide range of animals. Due to their ornamental value, fig trees have been introduced beyond their native ranges, often accompanied by their natural pollinators, which in some cases has led to ecological invasions. This study documents, for the first time, the presence of several pollinating and non-pollinating fig wasps (Chalcidoidea) on the Iberian Peninsula, focusing on three exotic *Ficus* species: *Ficus microcarpa* L.f., 1782, *F. rubiginosa* Desf. ex Vent., 1805 and *F. macrophylla* Pers., 1807. Through syconia sampling and dissection, we identified six fig wasp species: the pollinators *Eupristina* aff. *verticillata* (Waterston, 1921) and *Pleistodontes imperialis* Saunders, 1882, the gall-formers *Eufroggattisca okinavensis* Ishii, 1934, *Josephiella microcarpae* Beardsley & Rasplus, 2001, *Walkerella microcarpae* Bouček, 1993, and the parasitoid *Philotrypesis okinavensis* Ishii, 1934. Additionally, we documented several cases of non-native *Ficus* species reproducing spontaneously in urban areas, suggesting a significant ecological establishment and invasive spread through sexual reproduction. This spread poses potential risks to urban infrastructure, as the robust root systems of fig trees can damage buildings, pavements, urban trees, and heritage sites. Finally, we observed urban native and non-native bird species consuming mature fig syconia, which likely assist in the dispersal of these plants. Our findings underscore the need for further studies on the ecological impact of introduced *Ficus* species in non-native regions, their long-term economic consequences for urban heritage, and the continued monitoring of pollinator fig wasp populations.

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Keywords
Alien species, fig wasps, pollinator, parasitoid, Spain

Introduction

Ficus L. is a well-known genus of woody plants commonly known as fig trees. The genus encompasses *ca*. 880 species mainly from tropical and subtropical regions (Harrison 2005; POWO 2023) and are considered 'keystone species' in many tropical ecosystems, as it provides shelter and trophic resources for a wide variety of animals (Shanahan et al. 2001; Herre et al. 2008; Compton et al. 2010). However, due to their ease of cultivation and appealing size, many *Ficus* species have also historically been used as ornamental trees and can now be found far from their regions of origin (Aumeeruddy-Thomas and Hossaert-McKey 2024). Fig trees are characterized by their unique inflorescence, the fig, also known as syconium (Harrison 2005). For reproduction, fig trees rely on a complex and obligate relationship with fig wasps (Weiblen 2002) from the superfamily Chalcidoidea, which facilitate their pollination. For instance, the family Agaonidae, in its current circumscription, includes approximately 380 described, with an estimated 540 additional species yet to be described (Rasplus et al. 2025).

Agaonids are the main pollinators of *Ficus* species (Frodin 2004; Cardona et al. 2007; Rasplus and Soldati 2007). Female agaonids enter the fig through an aperture, the ostiole, which is closed by imbricated bracts. Once inside the receptacle, the wasps pollinate the flowers and lay their eggs in the ovules (Kjellberg et al. 2005). The larvae feed on the gall tissue induced during oviposition while the fig seeds and stamens mature. Wingless males emerge first, opening a small hole in the galled ovule containing females and mating with them while still closed in the gall. The males then dig a hole through the receptacle wall, allowing the females to emerge from the galled flowers. The females fill their pollen pockets with pollen (active pollination), or are dusted with pollen (passive pollination) and escape in search of a suitable fig tree (Kjellberg et al. 2005). Additionally, numerous Chalcidoidea wasps are gall-makers within *Ficus* ovules without fertilizing them, or act as parasitoids or inquilines of the pollinators or other non-pollinating fig wasps (van Noort 2003; Cook and Segar 2010; Cruaud et al. 2011a, 2011b; McLeish and van Noort 2012; Borges 2021). It is noteworthy that the mutualistic relationship between fig trees and their pollinators has traditionally been viewed as species-specific (Ramírez 1970; Weiblen 2002). However, several studies have shown that the one-to-one rule is often broken, with evidence of species complexes within several species (Rasplus 1996; Cook and Rasplus 2003; Molbo et al. 2003; Zhang et al. 2004; Haine et al. 2006; Jackson et al. 2008; Moe et al. 2011; Cornille et al. 2012; McLeish and van Noort 2012; Yang et al. 2012; Sutton et al. 2015). Additionally, when multiple agaonid species exist in a single fig species, they are usually sister taxa, or multiple pollinator species can develop within a single host fig species (Yu et al. 2019, 2021). While these studies mostly focused on pollinating fig wasps using

molecular markers, very few works have questioned the genetic cohesiveness of fig species as they are currently understood (but see Haisne et al. 2006).

Due to this obligate mutualism, fig trees cannot produce viable seeds without their specific pollinators (Cook and Rasplus 2003; Herre et al. 2008; Speciale et al. 2015). Fig trees are often planted outside their native range and have typically been propagated via cuttings. Subsequently, their pollinators have spread to areas where these trees have been planted as ornamentals (Caughlin et al. 2012). In some cases, fig species became invasive (Caughlin et al. 2012; Wang et al. 2015a) and spread into natural communities with consequences on local flora and fauna (Nadel et al. 1992; Hosking et al. 2011; Holmes et al. 2014; Riefner 2016; Demetriou et al. 2023). Beyond the impact on natural areas, the damage caused by introduced *Ficus* species in urban environments is important (Corlett 2006). These trees can make the ground slippery from fallen syconia and attract large numbers of insects (e.g., flies and wasps), leading to health issues and public nuisances (Wang et al. 2015a; Demetriou et al. 2023; Koutsoukos et al. 2025). Furthermore, fig trees develop strangler strong root systems and can grow in small cracks in buildings, walls and holes of other trees species, potentially widening them, causing significant structural damage in buildings (Wee 1992; Jim 1998; Jim 2010; Jim and Chen 2011; Morales-Gallegos et al. 2024; Koutsoukos et al. 2025), pavements (Esquivel and Quijas 2021; Demetriou et al. 2023), historical urban heritages (Caneva et al. 2009; Galanos 2015; Cozzolino et al. 2022; Metusala et al. 2023; Koutsoukos et al. 2025) or urban trees (Verloove and Reyes-Betancort 2011; Koutsoukos et al. 2025).

Therefore, it is particularly important to understand not only the actual distribution of fig wasps but also the potential impact of fig trees outside their natural range. In our study, our main goals are to a) record new species of pollinators and non-pollinator Chalcidoidea wasps for the Iberian Peninsula, b) document, for the first time, the spontaneous reproduction of exotic *Ficus* species in several areas of the Iberian Peninsula. Additionally, we discuss the potential impact of *Ficus* as invasive species and the damage they could cause to historical monuments in urban areas due to their robust root systems.

Material and methods

Syconia sampling and wasp identification

Samplings were carried out between 2019 and 2024. Several syconia from the most common ornamental *Ficus* tree species cultivated in urban parks and gardens in southwestern (Cádiz and Seville) and southeastern (Alicante) Iberian Peninsula (namely, Spain) were collected. Infrutescences were taken to the laboratory and dissected using a 20–60X stereomicroscope. All observed Hymenoptera were sorted and stored in tubes with 70° alcohol. Chalcidoidea wasps were identified following the keys and information provided in: Bouček 1988; Wiebes 1992; Rasplus et al. 1998; Chen et al. 1999; Lopez-Vaamonde et al. 2002; Cruaud et al. 2010; Feng and Huang 2010; Heraty et al. 2013; Ma et al. 2013; Burks et al. 2022. For fig trees, leaves and syconia were used for

the identification following the keys of van Noort and Rasplus (2024). Photographs of the wasps were taken using a Leica DMS1000 digital microscope. The material was conserved in the author's personal collection (AC, Spain) while some specimens were deposited at the 'Museo Nacional de Ciencias Naturales' (MNCN, Madrid, Spain). For examined material, abbreviation as follows: **ex** = specimen, **deposit** = collection of deposit and **leg** = collector.

Ficus spread

Once the pollinating wasps of various *Ficus* species were detected, special attention was given to locating seedlings, recruits, or young *Ficus* trees whose presence was compatible with sexual rather than asexual reproduction. Thus, the urban areas near the *Ficus* locations were checked. These studies were not systematic, but rather fortuitous, and the aim was only to detect presence but not to account quantitatively. In cases where *Ficus* recruits were found, photos were taken, and an attempt was made to assess the damage to the affected area in a subjective and descriptive way.

Results

Fig wasps

A total of 2 pollinating (Hymenoptera: Agaonidae) and 4 non-pollinating (Hymenoptera: Epichrysomallidae, Pteromalidae) fig wasps species (Fig. 1) were found from syconia of three species of *Ficus*: *Ficus microcarpa* L.F. (section Conosycea), *F. macrophylla* Pers., and *F. rubiginosa* Desf. ex Vent. (section Malvanthera). We provide a brief description and the main diagnostic characters to separate them from similar species and genera present in the peri-mediterranean fauna when necessary.

Order Hymenoptera Linneaus, 1758
Superfamily Chalcidoidea Latreille, 1817
Family Agaonidae Walker, 1848
Genus *Eupristina* Saunders, 1883

***Eupristina* aff. *verticillata* Waterston, 1921**

Material studied. Spain: • Cádiz: Jerez de la Frontera (Zoobotánico de Jerez): 2♂ + 2♀ ex., Í. Sánchez leg. and MNCN_Ent 235062 deposit., 7-XII-2018, 82 m a.s.l, found in dissected syconia of *Ficus microcarpa* (36.689315, -6.150638). • **Alicante**: San Vicente del Raspeig (Universidad de Alicante): 10 ♀ + 7 ♂ ex., J.M. Royo leg. and AC deposit. 5-VII-2023, 92 m a.s.l, found dissecting fallen syconia of *Ficus microcarpa*. This day, several specimens were seen flying close to the tree (38.384264, -0.512455). See in Fig. 1A.

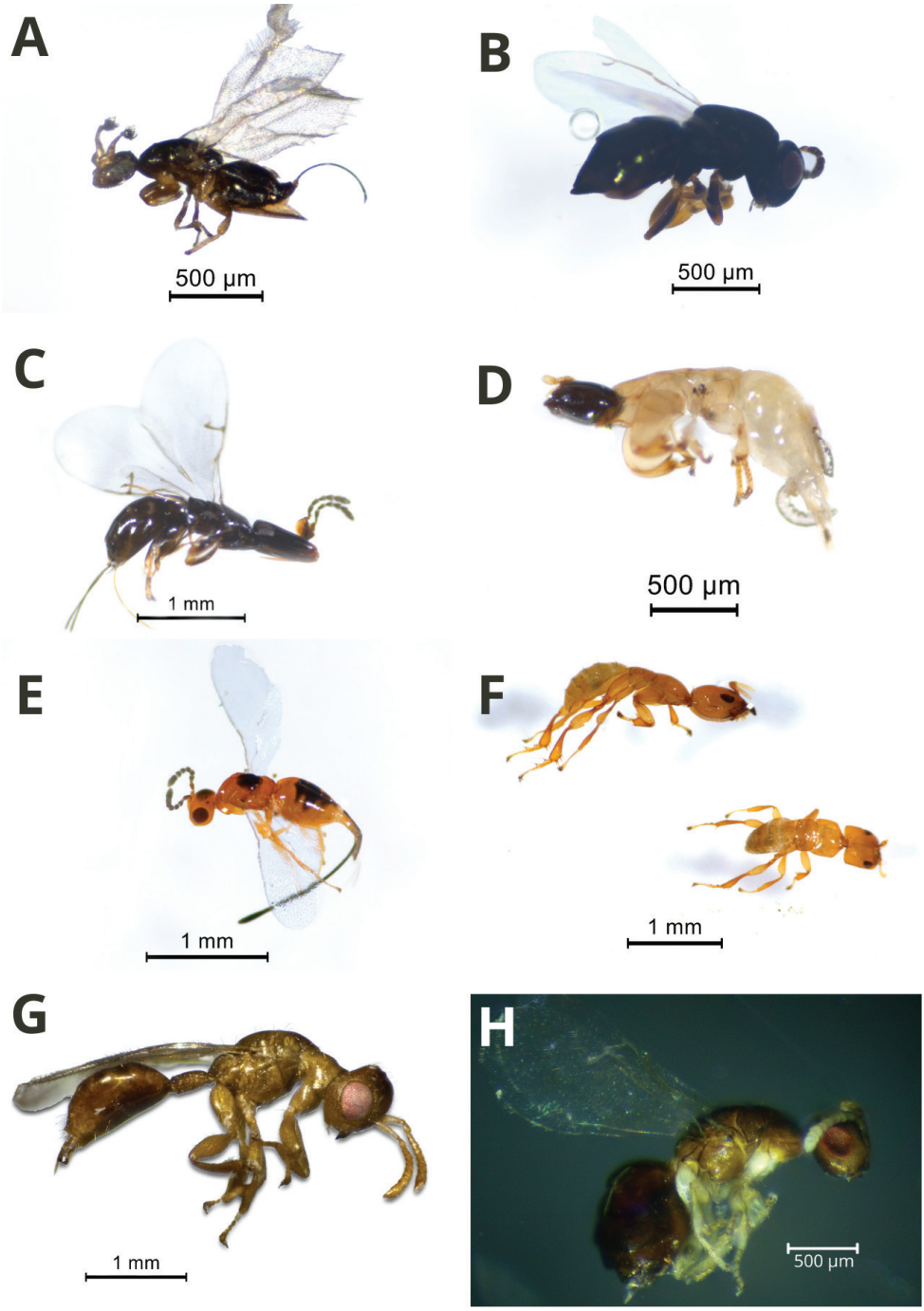


Figure 1. Wasps cited in this work **A** female of *Eupristina* aff. *verticillata* Waterston, 1921 **B** *Walkerella microcarpae* Bouček, 1993 **C** female and **D** male of *Pleistodontes imperialis* Saunders, 1883 **E** female and **F** males of *Philotrypesis okinavensis* Ishii, 1934 **G** *Eufroggattisca okinavensis* (Ishii, 1934) **H** *Josephiella microcarpae* Beardsley & Rasplus, 2001.

Ecological remarks. Pollinator of *Ficus microcarpa*. Also mentioned to be associated with *Ficus benjamina* L. but without additional data (Falcó-Garí et al. 2010), probably misidentified.

Distribution. This pollinator was described from Malaysia (Waterston 1921) and have been subsequently cited from Indonesia and Philippines (Grandi 1926), although these last records may be based on misidentification. The species is supposed to be native in China or Japan (Grandi 1927b; Ishii 1934; Corner 1965) and has been introduced in numerous countries with its host plants (van Noort and Rasplus 2024). Falcó-Garí et al. (2010) has not provided specific data for the eastern localities of Spain. Thus, we can consider this the first confirmed record for the Iberian Peninsula. Furthermore, this species was cited from continental Europe in Italy (Lo Verde et al. 2007) and Greece (Koutsoukos et al. 2025). Moreover, it was cited from several islands such as Sicily (Italy) (Lo Verde et al. 1991), Cyprus (Demetriou et al. 2023), Madeira (Koponen and Askew 2002), Canary and Balearic islands (Báez 1998; Carnero et al. 1998; Wang et al. 2015a, 2015b), and various Greek islands such as Crete, Cyclades, Dodecanese islands or Ionian islands (Wang et al. 2015a, 2015b; Koutsoukos et al. 2025) where *F. microcarpa* is a frequent ornamental tree.

Short description. Female with head subquadrate, shorter than wide across compound eyes which are as long as the gena; with antennal scrobes separated. Antennae filiform; flagellar segments (except for the proximal two) with a whorl of long black *sensilla chaetica* (Wiebes 1992; Bouček 1993). Dorso-apical comb of fore tibia bearing two teeth; the hypopygium has a short acute spine. Body flattened. Pronotum extended laterally. Mesonotum and propodeum fused, the limit between them only marked by short lateral septa (Wiebes 1992). Fore leg with three tarsomeres; mid and hind legs with four tarsomeres. Molecular analyses have demonstrated that *E. verticillata*, as presently understood, is in fact a species complex of at least three species (Sun et al. 2011; Wang 2014; Compton et al. 2020b). This may explain the discrepancies observed in diagnostic characters used by several authors, such as the ovipositor length, which has been classified as shorter (Wiebes 1992) or longer (Bouček 1993) than the gaster.

Genus *Pleistodontes* Saunders 1882

Pleistodontes imperialis Saunders, 1883

Material studied. Spain: • Cádiz: Jerez de la Frontera (Zoobotánico de Jerez): 2♂ + 2♀ ex., Í. Sánchez leg. and AC deposit., 7-XII-2018, 82 m a.s.l., found in dissected syconia of *Ficus rubiginosa* (36.689315, -6.150638). • **Alicante:** San Vicente del Raspeig: Vicente Savall Pascual street and University area: 7 ♀ + 8 ♂ ex., J.M. Royo leg. and AC deposit., 5-VII-2023, 193 m a.s.l., found in dissecting fallen syconia of *Ficus rubiginosa* tree, excepted two females found in syconia of *Ficus macrophylla* in an urban area (38.389033, -0.518130). See in Fig. 1C, D.

Ecological remarks. Pollinator of *Ficus rubiginosa*. One specimen of *Pleistodontes* cf. *imperialis* was found inside a syconia of *Ficus macrophylla* f. *columnaris* (C. Moore) D. J. Dixon (Speciale et al. 2015). We have found two female specimens as well in

syconia of *F. macrophylla.* It has also been found in *Ficus watkinsiana* in Greece (Koutsoukos et al. 2024a) and mentioned in *Ficus elastica* Roxb. Ex Hornem. without additional data (Falcó-Garí et al. 2010).

Distribution. Native from eastern Australia (van Noort and Rasplus 2024) and already reported from Israel, New Zealand and United States (Lopez-Vaamonde et al. 2002). The species has been found from several Mediterranean islands in which it was introduced recently: Sicily in Italy (Lo Verde et al. 2007; Speciale et al. 2015), Gozo in Malta (Mitsud et al. 2012), Canary Islands (Reyes-Betancort et al. 2013) and Greece and Cyprus (Compton et al. 2020a; Koutsoukos et al. 2024a). As the reports by Falcó-Garí et al. (2010) on eastern Spanish have no localities, we consider this as a first confirmed record for the Iberian Peninsula.

Short description. Small species 1.8–1.9 mm. Female of *Pleistodontes* can easily be recognized by their elongated head, with long subparallel genae, mandibular appendage elongate, usually bearing more than 20 transverse laminae, rarely less, sometimes bearing transverse rows of small teeth (Bouček 1988). Antennal scape usually elongate, sometimes shorter, mostly bearing a dorsal lamina which can be curved outwards and downwards. Pedicel rather short without dorsal spines. Third antennal segment elongates into a triangular process, always undivided and frequently elongate. Some species have no triangular expansion on the third antennal segment. Mesosoma bears pollen pockets, sometimes reduced, or absent. The fore tibia usually bears 2–3 spines in the dorso-apical comb, rarely only one. Ovipositor sheaths about as long as or shorter than metasoma. Venation is always complete (López- Vaamonde et al. 2002). *P. imperialis* has been demonstrated to be a complex of morphologically related species (Sutton et al. 2015). The wasps discussed here share all characters of the nominal species and morphologically the species occurring in Europe belong to the nominal entity.

Family Epichrysomallidae Hill & Riek, 1967
Genus *Eufroggattisca* Ghesquière 1946

Eufroggattisca okinavensis (Ishii, 1934)

Material studied. Spain: • Cádiz: Jerez de la Frontera (Zoobotánico de Jerez): 2♂ + 3♀ ex., Í. Sánchez leg. and MNCN_Ent 235061 deposit., 7-XII-2018, 82 m a.s.l, found dissecting syconia of *Ficus microcarpa* (36.689315, -6.150638). **• Alicante:** San Vicente del Raspeig (Universidad de Alicante): 10 ♀ + 10 ♂ ex., J.M. Royo leg. and AC deposit. 19-V-2024, 92 m a.s.l, found dissecting syconia of *Ficus microcarpa* (38.384264, -0.512455). See Fig. 1G.

Ecological remarks. Large galler in syconium of *Ficus microcarpa*. In Greece, *Eufroggattisca okinavensis* was repeatedly recorded from the same syconia as *Meselatus bicolor*, whose large galls suggest a possible host-parasitoid or inquiline relationship (Wang et al. 2015b; Koutsoukos et al. 2024b). This association raises the possibility that *M. bicolor* is also present in Spain, although its presence remains unconfirmed.

Distribution. Originally from eastern Asia (China, Japan and Taiwan) and Australia (van Noort and Rasplus 2024). It was reared from figs of *F. microcarpa* collected in Málaga (Spain) in 2018 and cited from Spain as *Eufroggattisca* sp. (Demetriou et al. 2023).

Short description. The species exhibits the following combination of characters: Head with occipital carina. In male petiole distinct, only slightly transverse, and pronotum long, much narrower than mesoscutum. Scutellum with two pairs of bristles (Bouček 1988). Female with gaster petiolated, either broadly convex or even slightly compressed from side-to-side. Body yellowish or brownish. This species present head and thorax mainly smooth, with sparse long setae, only rarely with some punctures sublaterally on thoracic dorsum. Notauli, usually formed by a line of punctures (Feng and Huang 2010). Both sexes winged, this is true for this species and also for many species in Epichrysomallidae, but not in general Epichrysomallidae because of the fact that several species have apterous males.

Genus *Josephiella* Narendran 1994

Josephiella microcarpae Beardsley & Rasplus, 2001

Material studied. Spain: • Alicante: San Vicente del Raspeig: Vicente Savall Pascual Street: 4 ♀ ex., J.M. Royo leg. and AC deposit., 02-II-2021, 193 m a.s.l, found in dissecting leaf galls of *Ficus microcarpa* (38.389033, -0.518130). **• Cádiz:** Algeciras: Barriada El Cobre: 8 ♀+ 1 ♂ ex., I. Sánchez and Á. Pérez leg and AC deposit. 15-VIII-2019, 84 m a.s.l, found in dissecting leaf galls of *F. microcarpa* (36.118236, -5.479646). See Fig. 1H.

Ecological remarks. Leaf galler of *Ficus microcarpa*.

Distribution. The exact origin of the wasp is unknown but could be Southeast Asia as its host plant originates from there. The species was first reported in Hawaii, California (USA) and the Canary Islands (Spain) (Beardsley and Rasplus 2001; Rodríguez and Rodríguez 2006). Subsequently it was recorded from several European areas like Sicily (Italy), Balearic Islands (Spain), Malta, Portugal, Greece, and Cyprus (Lo Verde et al. 2007; Caldwell 2008; Rasplus et al. 2010; Mifsud et al. 2012; Wang et al. 2015a; Kalaentzis et al. 2023). The species was recently reported in the Spanish peninsular area, namely Valencia (Rodrigo et al. 2017), Alicante (Hernández Martínez and Marcos García 2019) and Catalonia (Riba-Flinch and Pujade-Villar 2022).

Short description. The female has a body uniformly dark brown except antennal and legs pale yellow, wings hyaline. Head reticulate in dorsal occipital area behind ocelli. Pronotum reticulate without carinae, mesoscutum smooth centrally, scutellum smooth with weak, longitudinally oriented reticulation. Hind coxae reticulate. Gaster smooth and shiny (Beardsley and Rasplus 2001). This species is recognized also by the spherical swellings or warty blisters that develop on the lower and upper surfaces of the leaves of *Ficus microcarpae*.

Family Pteromalidae Dalman, 1820
Subfamily Pteromalinae Dalman, 1820
Tribe Otitesellini (see Burks et al. 2022)
Genus *Walkerella* Westwood 1883

***Walkerella microcarpae* Bouček, 1993**

Material studied. Spain: • Cádiz: Jerez de la Frontera (Zoobotánico de Jerez): 3♂ + 3♀ ex., Í. Sánchez leg. and MNCN_Ent 235063 deposit., 7-XII-2018, 82 m a.s.l., found in dissected syconia of *Ficus microcarpa* (36.689315, -6.150638). • **Alicante:** San Vicente del Raspeig (Universidad de Alicante): 11 ♀ + 5 ♂ ex., J.M. Royo leg. and AC deposit., 5-VII-2023, 92 m a.s.l., found dissecting fallen syconia of *Ficus microcarpa* and some flying specimens close to the tree (38.384264, -0.512455). See in Fig. 1B.

Ecological remarks. Gall-forming wasp in figs of *Ficus microcarpa*.

Distribution. This species probably originates from the Oriental region and was introduced to the Palearctic and the Nearctic (Ma et al. 2013). In Europe, it is only known from the Canary Islands (Tenerife) (Carnero Hernandez et al. 1998), Majorca (Wang et al. 2015a), as well as Cyprus (Demetriou et al. 2023) and Greece (Koutsoukos et al. 2025). As the reports by Falcó-Garí et al. (2010) from eastern Iberian Peninsula have no localities, we consider this as a first confirmed record for the Iberian Peninsula.

Short description. Difficult to separate morphologically from other genera of European Pteromalidae. *Walkerella* is recognized by the following characters: body blackish, without conspicuous external ovipositor and apterous males with long mandibles. The genus *Otitesella* is also present in the Palearctic region (associated with *Platyscapa*). Also, the genus *Micranisa* from Greece and Cyprus (Demetriou et al. 2023; Koutsoukos et al. 2025), which is quite close to *Walkerella*, although is easily separated by its ovipositor which is extended and curved downwards.

Genus *Philotrypesis* Förster, 1878

***Philotrypesis okinavensis* Ishii, 1934**

Material studied. Spain: • Cádiz: Puerto Real: 2 ♂ + 1 ♀ ex., A. Pérez-Gómez leg. and AC. deposit., 10-XI-2020, 316 m a.s.l., found dissecting fallen syconia of *Ficus microcarpa* (36.530600, -6.211997). See in Fig. 1E, F.

Ecological remarks. Parasitoid of *Eupristina verticillata* and *W. microcarpae* (see Compton et al. 2018).

Distribution. This species originates from eastern Asia, namely China, Hong Kong, Japan and Taiwan (van Noort and Rasplus 2024). This is the first record from Spain and the Iberian Peninsula.

Short description. Female yellowish red brown in general. Antennae brown except the scape which is yellowish red brown; abdominal segments 5–6 with transverse brown

band at the base; segments 7–9 with a median longitudinal brown band; ovipositor black. Mandible tridentate the lower tooth largest. Mesoscutum and scutellum with a shallow median longitudinal furrow; propodeum with three longitudinal keels, the median one only indicated in the anterior half; Wings hyaline, the veins pale brown. Legs yellowish red-brown. Abdomen almost as long as the head and thorax combined, long ovate; stalk very short; ovipositor if the abdomen, dilated in the middle.

Ficus spread

Regeneration cases of various *Ficus* species have been documented across the three study areas in this research. Seedlings and saplings of different sizes are abundant near adult fig trees planted for ornamental purposes in urban areas (e.g., close Guadalquivir river in Seville; 37.404262, -5.998787; or the city centre of Seville, 37.377322, -5.991610; or in Jerez de la Frontera, 36.688914, -6.150606). These young plants have been found in diverse environments, contributing to different types of damage. Common sites for these regrowths include small cracks or gaps in pavements (Fig. 2A), walls (Fig. 2B), balconies (Fig. 2C) sewer systems (Fig. 3C), stairways (Fig. 2D), sidewalks (Fig. 2E), and other vertical urban surfaces (Fig. 2F) (e.g., in Cádiz, 36.535678, -6.305543). Observations reveal the presence of small seedlings, less than one to two years old, in locations such as Figs 2A, 3D, E. In contrast, larger plants, which suggest older ages, have been identified in Figs 2B, 3C, F, often associated with a lack of urban management. This type of *Ficus* regrowth is also found on historic and culturally significant structures, such as on moats (Fig. 3A), castle towers (Fig. 3B), and ancient wall systems (Fig. 3D), among others (Fig. 2C) (e.g., in Seville, 37.380059, -5.992258; or in Jerez de la Frontera, 36.689976, -6.150292). Additionally, these trees grow on urban ornamental vegetation, starting as numerous seedlings (Fig. 3E) and potentially covering the trunks of certain tree species entirely over time (Fig. 3F) (e.g., in Alicante, 38.384264, -0.512455). Notably, in some cases, the root systems are causing visible damage, including the cracking of walls and pavement (Fig. 2B, D), damage to balcony structures through slab lifting (Fig. 2C), as well as harm to historic architecture (Fig. 3B), or could even be causing crowding and collapse of urban tree individuals (Fig. 3F).

Particularly interesting are the occasional observations we have made while searching for *Ficus* seedlings and saplings, in which certain urban bird species were seen feeding on the mature syconia of these trees. These species include the common wood pigeon *Columba palumbus* L., the house sparrow *Passer domesticus* L., and, the invasive rose-ringed parakeet *Psittacula krameri* Scopoli, both in the María Luisa's urban park in Seville (37.378662, -5.988352) or in the ZooBotánico Jerez (36.689533, -6.150595).

Discussion

Biological invasions are of global concern with significant ecological, health, and socioeconomic impacts (Crystal-Ornelas and Lockwood 2020). New invasions are still being reported, especially by plants, underscoring the need for stronger prevention, monitoring,

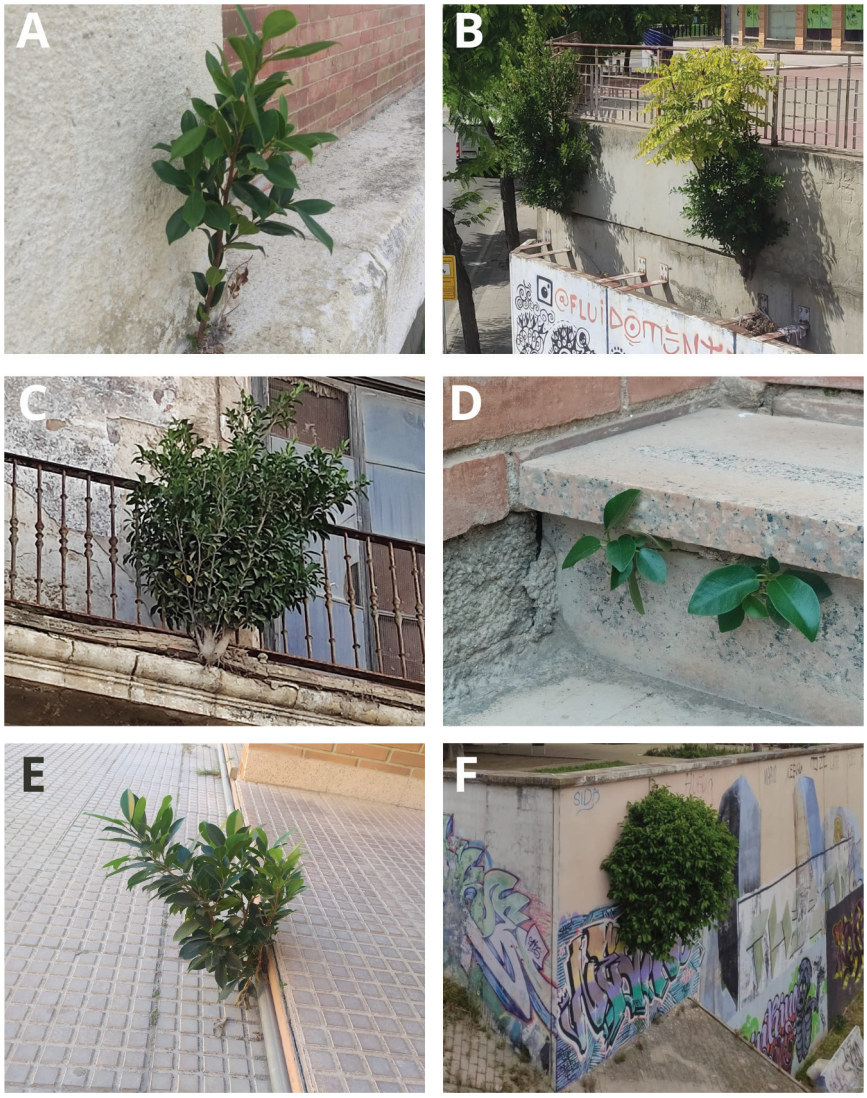


Figure 2. *Ficus microcarpa* affecting urban buildings and structures **A** train station building in Jerez de la Frontera **B** wall in Jerez de la Frontera **C** historic palace in Cádiz **D, E** University of Alicante building **F** urban wall in Seville.

and eradication programs (Vantarová et al. 2023). One noteworthy case is that of *Ficus* species (Wang et al. 2015a). Although widely used for ornamental purposes worldwide due to their resistance and form (Goor 1965), it is only recently that certain *Ficus* species have begun to show invasive tendencies (e.g., Caughlin et al. 2012). The specific mutualistic relationship between fig trees and their pollinating wasps has typically restricted *Ficus* reproduction to asexual means outside their native range, limiting their spread and their potential as invasive species (Herre et al. 2008; Speciale et al. 2015). However, the

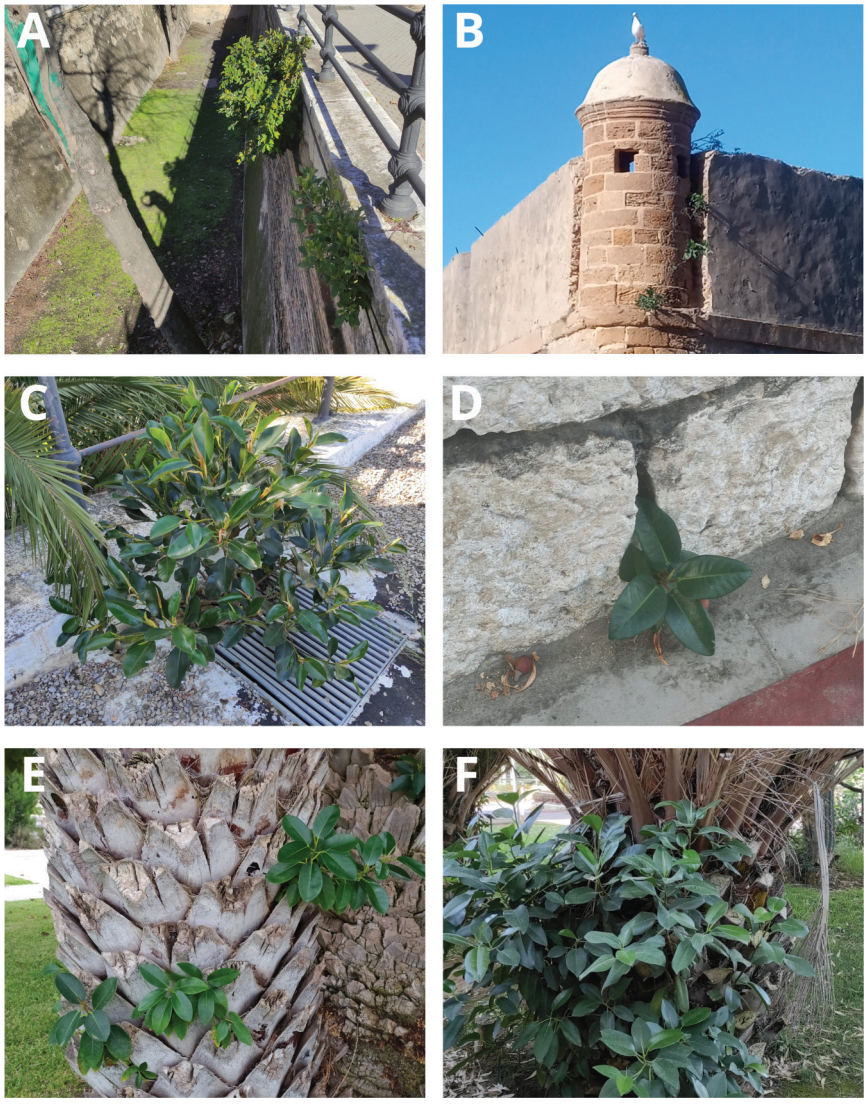


Figure 3. *Ficus* species impacting urban monuments and structures **A** *Ficus microcarpa* in the moat of the Rectorate in Seville and **B** on a watchtower of the Cádiz city wall **C** *Ficus macrophylla* emerging from a drainage outlet on the roof of the Tempul water reservoir (Jerez de la Frontera) **D** on a wall in Jerez de la Frontera, and **E, F** on ornamental palm trees in Alicante.

reports of these wasps beyond their native habitats are increasingly common (see, for example, Koutsoukous et al. 2025 and references included), potentially enabling *Ficus* to cause invasions and have potential ecological and economic consequences (Caughlin et al. 2012; Rasplus et al. 2024; Koutsoukous et al. 2025). Many of these wasps may have been established in new regions for some time, yet due to their morphological and sometimes genetic similarities, their spread may have gone unnoticed due to misidentification

or lack of detailed studies (Yu et al. 2019; 2021). Notably, this is the first report of some of these wasp species in the Iberian Peninsula, and the second of continental Europe (Koutsoukos et al. 2025), despite the prevalence of exotic plans in urban green spaces across Europe (e.g., DAISIE 2009; Čeplová et al. 2017). While pollinator wasps are the primary facilitators of invasions, other wasp species associated with *Ficus* also play significant roles. Non-pollinator wasps include gall-formers, seed predators, and parasitoids (Kong et al. 2016), which can negatively impact the reproductive success of fig trees by reducing both pollinator numbers and viable seed production (Kerdelhué and Rasplus 1996; Wang et al. 2015b). Thus, the potential role of these wasps as biological control agents cannot be ruled out, although their impact appears to be less significant than previously thought (Kong et al. 2016; Demetriou et al. 2023).

Our detection of sexual reproduction in *Ficus* species in Spain (and in mainland Europe), and outside their native ranges signals a new biological invasion case with potentially severe future impacts. Curiously, there are very few cases reporting the spontaneous sprouting of fig trees in Europe, most of them from island areas (e.g., Demetriou et al. 2023) or recently in continental areas (Koutsoukous et al. 2025). However, this problem could be greater than expected given the actual extent of cultivation of non-native *Ficus* in Europe. Urban trees, especially exotic species, have been shown to significantly damage infrastructure (Lee 2022), leading to costly repairs in the medium to long term. In several works, *Ficus* trees have already been identified as damaging pavements, urban infrastructure, sewage systems, historical sites, and local urban trees (e.g., Corlett 2006; Verloove and Reyes-Betancort 2011; Esquivel and Quijas 2021; Demetriou et al. 2023; Metusala et al. 2023; Morales-Gallegos et al. 2024; Koutsoukous et al. 2025). Thus, it is crucial to assess the impact of these newly observed *Ficus* seedlings and saplings on local infrastructure. Notably, many of these trees are already over 2–3 years old, indicating limited intervention on this issue by the administrators. As *Ficus* trees grow, their root systems expand, worsening cracks and causing progressively more difficult-to-repair damage (Morales-Gallegos et al. 2024). Additionally, these trees have a history of invading natural ecosystems, impacting ecosystem functions, and competing with native species, often spreading from urban areas (Nadel et al. 1992; Hosking et al. 2011; Holmes et al. 2014; Riefner 2016). Therefore, sexual reproduction in urban environments cannot be ignored as a future source of problems for seminatural and natural ecosystems (Wang et al. 2015a). The natural zoochorous (animal-assisted) dispersal of mature fig syconia by ants, birds and other vertebrates (Kaufmann et al. 1991; Starr et al. 2003) may further facilitate *Ficus* spread. We observed several cases of birds feeding on mature syconia, a behaviour previously documented in *F. macrophylla* and other *Ficus* species, like *F. rubiginosa*, by several non-native parrot birds in the Iberian Peninsula (Hernández-Brito et al. 2021). This reflects how the synergistic effect between fig wasp pollinators and potential dispersers (especially non-native ones) can promote the invasion of these plants and facilitate their spread from urban areas into the closest natural habitats.

With this new case of a biological invasion in the Iberian Peninsula, many questions remain. First, we need to refine our understanding of the distribution of these fig wasps and identify areas where they may promote the natural reproduction and spread

of *Ficus* trees. Second, it is essential to assess the damage that *Ficus* can cause in urban and natural settings. Finally, it is important to investigate potential synergies with other species that may act as dispersers and amplify the invasive impact of these trees.

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