Phytoparasitica (2024) 52:39
https://doi.org/10.1007/s12600-024-01158-2

Playing both fig sides: the presence and host-switch of *Pleistodontes imperialis* (Hymenoptera: Agaonidae) is confirmed in Greece and Cyprus

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Received: 15 December 2023 / Accepted: 7 March 2024 / Published online: 15 March 2024

Abstract Several Oriental and Australian species of *Ficus* have been introduced outside their native range and planted as ornamentals in urban habitats throughout the Mediterranean. This translocation of plant species has led to the introduction of host-specific insects such as their pollinating fig wasps (Hymenoptera: Agaonidae). Here, the Australian fig wasp *Pleistodontes imperialis* Saunders, 1882 is reported for the first time from Greece. Partial COI genes were sequenced for specimens sampled in Greece and Cyprus, and they appear to share identical haplotypes. Interestingly, this species-specific wasp not only develops in figs of its usual host, *Ficus rubiginosa*, but also in figs of *Ficus watkinsiana*, another Australian species introduced in Greece, which is pollinated by a second agaonid species (*Pleistodontes nigriventris* Girault, 1915) in its native range. Although no negative economic or environmental impacts have been observed yet, monitoring of alien *Ficus* spp. in the region is encouraged to prevent their possible establishment in natural habitats.

Keywords Alien species · Biological invasions · Chalcidoidea · Cryptic species · *Ficus* · Fig-pollinating wasps

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Introduction

During recent centuries, several species of the genus *Ficus* L. (Moraceae) have been introduced as ornamentals outside their native range, where they have been extensively planted in roadsides, parks, and house gardens (Reyes-Betancort et al., 2013; Speciale et al., 2015; van Noort et al., 2013). Associated mutualist pollinators of the family Agaonidae such as *Eupristina verticillata* Waterson, 1921 and *Pleistodontes imperialis* Saunders, 1882, the pollinators of *Ficus microcarpa* L. and *F. rubiginosa* Desf. respectively, have followed their host plants and established viable populations in regions far from their native Oriental and Australian natural ranges (Speciale et al., 2015; Wang et al., 2015, b).

Eupristina verticillata, was at first detected in Tunisia (1985), followed by the Canary Islands (Spain) (1989), Italy (1990), Spain (mainland) (1994), Turkey (2011), Malta (2011), Greece (2011–2012), Libya (2011–2012) and Morocco (2010) (Lo Verde et al., 1991; Kobbi et al., 1996; Baez, 1998; Doganlar, 2012; Wang et al., 2015, b). In addition to *F. microcarpa*, the Port Jackson fig. (*F. rubiginosa*) has been also introduced and widely planted in the Mediterranean (Haine et al., 2006) and this has led to the concurrent introduction of its pollinator *P. imperialis* in various sites across the Western Palearctic such as the Canary Islands (Reyes-Betancort et al., 2013), Cyprus (Compton et al., 2020), Israel (Lopez-Vaamonde et al., 2002), Italy (Speciale et al., 2015), France (Rasplus, unpublished), Malta (Mifsud et al., 2012), Portugal (Rasplus, unpublished) and Spain (Kjellberg et al., 2001). Finally, the pollinator of *Ficus religiosa, Platyscapa quadraticeps* (Mayr, 1885) has followed its host-plant to the Middle Eastern countries of Iraq and Israel (Joseph, 1982; Chen & Chou, 1997).

The genus *Pleistodontes* Saunders (excluding *Pleistodontes claviger* which is now placed in the genus *Platyscapa* according to Harrison et al. (2017)), is composed of 25 described species which pollinate *Ficus* species belonging in the subgenus Spherosuke (=Urostigma) sect. Malvanthera and was revised by Lopez-Vaamonde et al. (2002). Analyses of cytochrome b sequences of *P. imperialis* associated with *F. rubiginosa* in Eastern Australia showed deep molecular divergences within this putative species (Haine et al., 2006). *P. imperialis* was therefore considered to be a complex of four closely related species (Haine et al., 2006). More recent analyses by Darwell et al. (2014) suggested the presence of a fifth species. However, morphological examination of these entities, showed only slight morphological differences (Rasplus, pers. obs).

Until now, there has been no report of the presence of *Pleistodontes imperialis* in Greece, although it is already widely distributed throughout the Mediterranean. Here, we present the first record of *P. imperialis* in Greece. Additionally, we provide DNA barcodes for specimens from Greece and Cyprus to facilitate and confirm their identification.

Materials and methods

Study area, sampling and identification

Surveys took place at various urban sites in Southern Greece from April 2021 to September 2022. Mature figs of both *F. rubiginosa* and *F. watkinsiana* were collected and stored in polyethylene zip bags for rearing. Additional material was collected from *F. rubiginosa* in Cyprus for morphological and molecular comparisons. Sampling was also conducted from other fig tree species belonging to subgenus Spherosuke (=Urostigma) sect. Malvanthera (such as *F. macrophylla*), in search of the pollinator (Fig. 1a-d). Sampled localities are summarized in Table 1 and Fig. 2. Fig tree species were identified using the key of Dixon (2003). Most specimens were stored in 70% ethanol and deposited at the Museum of Zoology of the National and Kapodistrian University of Athens (ZMUA). Fig wasps that emerged were examined under a stereomicroscope following the identification key and species descriptions provided by Lopez-Vaamonde et al. (2002). Specimens were also stored in 90^{o} ethanol for further molecular treatment.

In total, ten specimens were kept in ethanol and sent to the Laboratory of Forest Entomology (Forest Research Institute, Thessaloniki) for molecular screening. DNA was extracted from each specimen individually, using the PureLink™ Genomic DNA mini kit (Invitrogen) following the manufacturers' protocol. Then, amplification of an approximately 650–700 bp locus was carried out with primers LCO2198 and HCOI1490 (Folmer et al., 1994). Each reaction contained 12.5 µl of DreamTaq DNA Polymerase™ including DreamTaq PCR Master Mix (2X) (ThermoFisher Scientific Baltics

Fig. 1 a-d Sampled trees of the subgenus Spherosuke sect. Malvanthera: a – *F. watkinsiana* (Egina town); b – *F. macrophylla* (Piraeus town); c, d – *F. rubiginosa* (Megara town)

UAB, Lithuania), 0.2 μl of each primer (20μM), 2 μl of DNA extract and finally ddH2O to the volume of 25 μl. PCR conditions included an initial denaturation step at 94 °C for 1 minutes, followed by 5 cycles at 94 °C for 60s, 45 °C for 90s and 72 °C for 75 s, and then 40 cycles at 94 °C for 60s, 51 °C for 90s and 72 °C for 75 s with a final extension step that lasted 5 minutes at 72 °C. Products were then purified with PureLink ™ PCR Purification Kit (Invitrogen) and sequenced at a commercially available service (Cemia SA, Larissa – Greece). The acquired sequences were visualized with ChromasLite® (Technelysium Pty Ltd) and aligned with CLUSTALX (Thompson et al., 1997). Finally, sequences were compared (blasted) on NCBI GenBank Fig. 2.

Table 1 Sampled localities throughout Greece and Cyprus

Country	Administrative region, locality	Date	Latitude	Longitude	Host plant	Presence of *P. imperialis*
Greece	Attica, Egina town	25.viii.2021	37.747	23.426	*F. watkinsiana*	Yes
Greece	Attica, Egina town	25.viii.2021	37.718	23.461	*F. rubiginosa*	No
Greece	Attica, Megara	iv-vi.2021	37.996	23.332	*F. rubiginosa*	Yes
Greece	Attica, Megara	20.vii.2022	37.996	23.332	*F. rubiginosa*	Yes
Greece	Attica, Piraeus	21.vi.2021; 21.viii.2021	37.946	23.649	*F. rubiginosa*	Yes
Greece	Attica, Piraeus	21.vi.2021	37.940	23.644	*F. macrophylla*	No
Greece	Cyclades, Paros, Paroikia	18.ix.2021	37.080	25.143	*F. rubiginosa*	Yes
Greece	Crete, Chania town	14.xi.2021	35.514	24.025	*F. rubiginosa*	No
Greece	Ionian islands, Zakynthos, Argasi	9.iv.2022	37.765	20.919	*F. rubiginosa*	No
Greece	Peloponnese, Argolida, Nafplio	30.xi.2021; 18.v.2022	37.565	22.802	*F. rubiginosa, F. watkinsiana*	No
Cyprus	Paphos, Konia	22.iv.2021	34.787	32.452	*F. rubiginosa*	Yes

Results and discussion

Morphological examination of the sampled specimens confirmed they belong to the *P. imperialis* species complex (Lopez-Vaamonde et al., 2002). As there is no key to species for this complex, the wasps were subsequently compared to material sequenced by Haine et al. (2006) and Darwell et al. (2014) sent to us by James Cook (Univ. Sydney). They were also compared to specimens previously compared to the

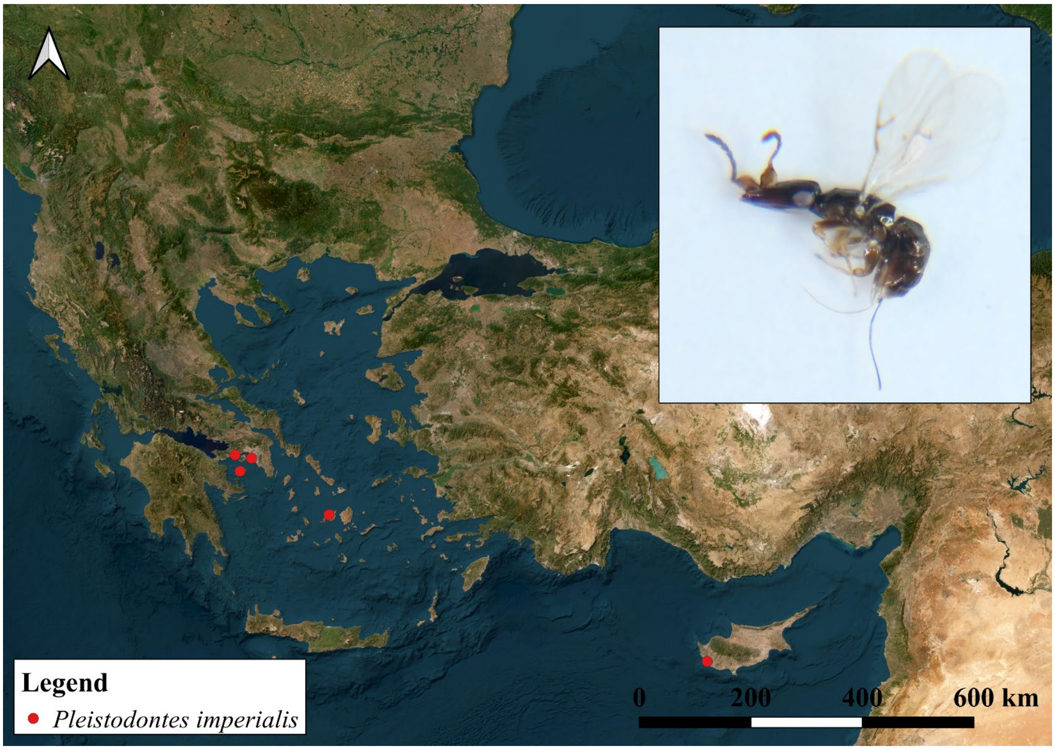

Fig. 2 Distribution of *Pleistodontes imperialis*

paralectotype specimens hosted in NHM London. These morphological analyses confirmed the specimens as belonging to *P. imperialis* sensu stricto. Blasting the sequences from the Greek specimens on GenBank (NCBI) confirmed our morphological identification of *Pleistodontes imperialis* as they were 98.9% similar to the only *P. imperialis* sequence deposited (GQ367882). The specimen from which the GenBank sequence was obtained, was sampled in Western Australia, Rottnest Island (−31.996115.541) on 5.10.2005 by Jousselin E. & Cœur d'acier A. Western Australia is also an area where *P. imperialis* have been introduced. A close examination of specimens from the same samples and hosted at CBGP, Montpellier (n° JRAS01396_01) confirmed they also belong to *P. imperialis s.s.* All other sequenced species of *Pleistodontes* were more distantly related, exhibiting 91.04% and 89.83% similarity with *P. nitens* (GQ367886) and *P. rigisamos* (AF200409), respectively.

These results confirmed the species sampled in Greece belong to *P. imperialis*. This is the first report of *P. imperialis* in this country. In Greece, the species is distributed at least throughout Attica and Cyclades, whereas material sampled from *F. rubiginosa*, and *F. watkinsiana* from Crete, the Dodecanese and the Ionian islands yielded no agaonids. Moreover, material from *F. macrophylla* throughout southern Greece, lacked pollinators as well.

Although each fig-pollinating Agaonidae species was previously considered to be an obligatory mutualist of a specific *Ficus* species, recent studies have shown that introduced fig wasps can develop in figs of new partners. This disrupts the obligate association between figs and their pollinators (Bernard et al., 2020; Yu et al., 2021). Moreover, increased sampling of fig tree species and the use of molecular tools have shown numerous *Ficus* spp. with large distribution that are pollinated by two or more agaonid species and vice versa (Bernard et al., 2020; Darwell et al., 2014; Haine et al., 2006; Machado et al., 2005; Michaloud et al., 1985; Rasplus, 1996).

This was particularly evident in the case of *P. imperialis*, which was found developing in figs of *Ficus watkinsiana* F.M.Bailey and *Ficus rubra* Vahl (Bernard et al., 2020) on the Hawaiian island of Kauai as well as in the Moreton Bay fig *Ficus macrophylla* Desf. in Italy (Speciale et al., 2015). Interestingly, according to Rønsted et al. (2007), the closest relative of *F. rubiginosa* is *F. watkinsiana*, which may partly explain the exchange of its pollinator outside their native range. All these fig tree species have been known to be mutualistic associated with other representatives of the genus *Pleistodontes* (Lopez-Vaamonde et al., 2002). Previous records of *P. imperialis* with *Ficus obliqua* G.Forst. (Bouček, 1988) and *Ficus platypoda* (Miq.) A.Cunn. ex Miq. (Zammit & Schwarz, 2000) within the species' native range resulted in fact from misidentifications of *F. rubiginosa* and therefore were incorrect (Lopez-Vaamonde et al., 2002).

Host switches of pollinators has allowed hybridization events between closely related plant species (Wang et al., 2021). Contrastingly to fig tree hybridization between different *Ficus* species, there have been no similar signs of hybridism between their mutualistic pollinating fig wasps (Satler et al., 2023; Wang et al., 2021). Non-sympatric fig species of the same section and subgenus (i.e., Urostigma, Urostigma s.s.) have been reported to hybridize, once one of the two species is introduced within the natural distribution of the other, such as *F. aurea* with *F. religiosa* in Florida, USA (Ramírez-Benavides, 1994). Given this, the host switch of *P. imperialis* leading to the hybridization between *F. rubiginosa* and *F. watkinsiana* could be possible in areas where these two species have been introduced and co-exist, such as in Cyprus and Greece. Since the hybrid seed production and by extend the establishment of hybrid fig populations is a possible scenario, hybrid seed viability tests would be useful in the future.

The co-occurrence of another widespread fig tree species (*F. microcarpa*) with its mutualistic pollinator *E. verticillata* in their introduced areas has allowed the tree to become invasive, with well-known adverse environmental and socioeconomic impacts. Similarly, the presence of *P. imperialis* throughout the Mediterranean could assist the production of *F. rubiginosa* seedlings and facilitate its invasiveness. While seedlings of *F. microcarpa* have been detected in Southern Greece (Galanos, 2015; EK unpublished data) no similar case has been observed regarding *F. rubiginosa* or *F. watkinsiana*. Nevertheless, the discovery of seedlings of *F. macrophylla* in Italy along with the presence of *P. imperialis* in figs of a nearby older tree (Speciale et al., 2015), signifies the need of further monitoring of both host-plants and their association with *P. imperialis* in their introduced areas.

Acknowledgements We would like to thank the Hellenic Entomological Society for funding part of Mr. Evangelos Koutsoukos' MSc thesis, which indirectly contributed to the present research. Mr. Evangelos Koutsoukos acknowledges COST Action CA17122 – Alien CSI, supported by COST (European Cooperation in Science and Technology), www.cost.eu. We are also grateful to the UK Government through Darwin Plus for funding Mr. Evangelos Koutsoukos under the project DPLUS202, and Mr. Jakovos Demetriou under the project DPLUS124, which contributed to this present research. We warmly thank Dr. James Cook (Univ. Sydney) for loan of material sequenced in his studies.

Author contributions Conceptualization: Evangelos Koutsoukos, Jakovos Demetriou; Methodology: Evangelos Koutsoukos, Stephen Compton, Dimitrios Avtzis, Jean-Yves Rasplus; Formal analysis and investigation: Evangelos Koutsoukos, Jakovos Demetriou, Angeliki Martinou, Stephen Compton, Dimitrios Avtzis, Jean-Yves Rasplus; Writing - original draft preparation: Evangelos Koutsoukos, Jakovos Demetriou, Stephen Compton, Dimitrios Avtzis; Writing - review and editing: Evangelos Koutsoukos, Stephen Compton, Angeliki Martinou, Dimitrios Avtzis, Jean-Yves Rasplus; Resources: Evangelos Koutsoukos, Jakovos Demetriou, Dimitrios Avtzis, Jean-Yves Rasplus; Supervision: Stephen Compton, Jean Yves-Rasplus.

Funding Open access funding provided by HEAL-Link Greece. This article/publication is based upon work from COST Action CA17122 – Alien CSI, supported by COST (European Cooperation in Science and Technology), www.cost.eu. Jakovos Demetriou acknowledges the UK Government through Darwin Plus (DPLUS0124), for funding his material surveys. Evangelos Koutsoukos acknowledges the UK Government through Darwin Plus (DPLUS0202), for funding his material surveys.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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