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ORIGINAL ARTICLE

Invasion and expansion of exotic whiteflies (*Hemiptera: Aleyrodidae*) in India and their economic importance

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Abstract Exotic invasive whiteflies (Hemiptera: Aleyrodidae) in India cause direct and indirect yield losses in agriculture, horticulture and forestry crop plants. Around 25 years ago, the spiralling whitefly, *Aleurodicus dispersus* Russell invaded and established on many host plants including economically important crops in India. Recently, within a span of five years, seven whiteflies invaded India viz., solanum whitefly, *Aleurothrixus trachoides* (Back) reported to breed on 37 plant species; rugose spiraling whitefly (RSW), *Aleurodicus rugioperculatus* Martin found breeding on 40 host plants; nesting whiteflies, *Paraleyrodes bondari* Peracchi on 34 host plants and *P. minei* Iaccarino infest about 25 host plants; legume feeding whitefly, *Tetraleurodes acaciae* (Quaintance) infesting 5 host plants; palm infesting whitefly, *Aleurotrachelus atratus* Hempel on 4 host plants and woolly whitefly, *Aleurothrixus floccosus* (Maskell) infesting guava. These invasive species are native to the Neotropical region, mostly from Central America and the Caribbean. Extensive spread along the coastal regions and gardens near the backwater of India is predicted owing to the favorable weather factors and availability of host plants. Species of exotic whiteflies with similar habits co-exist in more or less the same niche and have a similar pattern of growth and development. The intensity of infestation of RSW on coconut, banana and oil palm, the woolly whitefly on guava and the palm infesting whitefly and nesting whiteflies on coconut was severe. The exotic aphelinid parasitoid, *Encarsia guadeloupae* Viggiani (Hymenoptera: Aphelinidae), a predator *Pseudomallada astur* (Banks) (Neuroptera: Chrysopidae) and the entomopathogenic fungus, *Isaria fumosorosea* Wize (Hypocreales: Clavicipitaceae) play a major role in reducing the population of these invasives. The most insidious spread of these species in India is likely mediated by humans through the movement of infested seedlings and plant materials. Extensive surveys revealed that these species spread rapidly in the large geographical region of India mostly through transportation of infested seedlings. This study reports a major expansion of the geographic and host range and the patterns of co-occurrence, damage and economic impact of these exotic species in India and their natural enemies.

Keywords Co-existance · Colonization · Establishment · Host plants · Invasion · Natural enemies

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Introduction

Biological invasions are of great concern as they have a pronounced impact on the native ecosystem, biodiversity and the economy. Globally there have been frequent invasions by insects and mites, some of which are vectors of plant diseases. The enormous increase in the volume, diversity and swiftness of movement of plant products throughout the world has led to a proliferation and dissemination of invasive species, particularly ones closely associated with plants, such as scales and whiteflies (Wosula et al., 2018). So far, more than 110 exotic insect species had been reported from India, of which, whiteflies and mealybugs constitute a major part (Mandal, 2011) and represent some of the world's worst invasive pests (Naveena et al., 2020). Most alien species of whiteflies are accidentally introduced with their host plant and regularly dispersed among countries as a consequence of plant trade, the small size of whiteflies, their cryptic nature and immature stages being attached to the host-plant. Due to these characteristics they are one of the most commonly transported and most successful arthropod groups invading new geographical areas (Simala et al., 2015).

Moreover, exotic whitefly pests can multiply in large proportion in a short time, exhibit high phenotypic plasticity, and have a strong potential to compete with native species and cause damage to economically important crop plants. In India, 469 whiteflies species belonging to 71 genera are known to feed on many agricultural, horticultural and forestry crop plants which include 8 invasive species. India experienced its first invasive whitefly i.e. spiralling whitefly, *Aleurodicus dispersus* in the Western Ghat of mountain range in South India during 1995 (David & Regu, 1995). Between 2015–2019, the following seven exotic whiteflies were discovered in India: solanum whitefly, *Aleurothrixus trachoides* (Back) during 2015 (Dubey & Sundararaj, 2015); rugose spiralling whitefly, *Aleurodicus rugioperculatus* Martin during 2016 (Sundararaj & Selvaraj, 2017); legume feeding whitefly, *Tetraleurodes acaciae* (Quaintance) during 2017 (Sundararaj & Vimala, 2018); Bondar's nesting whitefly, *Paraleyrodes bondari* Peracchi during 2018 (Josephrajkumar et al., 2019); nesting whitefly, *P. minei* Iaccarino during 2018 (Mohan et al., 2019); palm infesting whitefly, *Aleurotrachelus atratus* Hempel during 2019 (Selvaraj et al., 2019) and woolly whitefly, *Aleurothrixus floccosus* (Maskell) during 2019 (Sundararaj et al., 2020a). Out of the eight invasive whiteflies of India four species: *A. dispersus, A. rugioperculatus*, *P. bondari* and *P. minei* represent the whitefly subfamily Aleurodicinae while the remaining four species, *A. trachoides*, *T. acaciae, A. atratus* and *A. floccosus* represent the subfamily Aleyrodinae.

These invasives cause direct damage to their host by feeding and bringing the host plants under tremendous stress by removing the nutrients and water there by interfering with its normal growth, and causing premature leaf drop; they cause indirect damage by producing wax and excreting sticky honeydew which provides a substrate for the growth of black sooty mold on infested plant (Kumar et al., 2018) which reduces the photosynthetic capacity of the plant and some species; and vector plant viruses such as a begomovirus transmitted by *A. trachoides* (Chandrashekar et al., 2020). The spatial structure of invasive species populations has important implications for early warning systems and designing effective control strategies. Early detection of invasive species and immediate implementation of biological control methods could minimize the economic losses. Further, monitoring of introduced species is very important to determine the status and temporal trends, distribution over time, changes in species composition, expansion of host plants and geographical range to evaluate the invasiveness and assess the impact on crop plants. The present studies aimed to document and assess the range invasion, expansion of host plants and geographical region, patterns of co-occurrence, damage caused and the natural enemies of the species of invasive whiteflies to develop a sustainable management strategy in India.

Materials and methods

Systematic and continuous surveys were conducted from February 2015 to September, 2020 in different states viz., Karnataka, Tamil Nadu, Kerala, Andhra Pradesh, Maharastra, West Bengal, Goa, Maharastra, Telangana, Meghalaya, Gujarat and Lakshadweep of India to investigate the spatial range, host range, patterns of co-occurrence, intensity of infestation of whiteflies and their natural enemies in India. Surveys were focused on plantation crop

plants, ornamental plants, landscape plants and field crops in both rural and urban areas in various locations. The frequency of the surveys at each site varied from one to twenty six trips across the study areas.

Spatial Range: To study the distribution of these invasives at least 5–10 locations in each district and 5–12 districts in each state were chosen for sampling. Pest occurrence was recorded in each location and their damage was categorized into different grades by visual observation on all the active /live life stages. Further, host plant infested leaves with puparium were collected in paper envelopes as described by Dubey and David (2012) and adult whiteflies in 70% ethanol along with relevant collection data for further identification and documentation. Whitefly species confirmation based on morphological characteristic was achieved by preparing permanent mounts of the puparium; the best mounts were obtained from puparial cases from which adults had emerged. The generic classification was done following the key of Sundararaj et al. (2020b) and species confirmation by matching with the original and additional descriptions of respective species (Russell, 1965, Peracchi, 1971, Martin, 1987, Iaccarino, 1990, Nakahara, 1995, Martin, 2004, Dubey & Ko, 2008, Dubey & Sundararaj, 2015, Wosula et al., 2018).

Molecular characterization of the partial mitochondrial cytochrome c oxidase I (COI) (658 bp) gene was done using adult whiteflies after they morphologically identified. Genomic DNA extraction from individual adult whiteflies using DNAase Qiagen kit method (Qiagen, Germany) based on the manufacturer's protocol. Polymerase chain reaction amplification of the 5′ terminus of the COI gene was carried out following the standard protocol which involves the cocktail of reactions, using universal primers LCO 1490 5′-GGTCAACAAATCATAAAGATATTGG-3′ and HCO 2198 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′ (Folmer et al., 1994) manufactured by Bioserves, Hyderabad. The quality of the amplicons was checked using agarose gel electrophoresis and the amplified products were sequenced by Chromous Biotech, Bangalore.

Host Range: Infested host plants were collected along with whitefly adults from each study location. The infested leaves were preserved in the herbarium and the adult whiteflies in 70% ethanol for species confirmation and coexistence study. The host plants were identified with the help of plant taxonomists as well as images collected during surveys.

Patterns of Co-occurrence: To study the coexistence of these invasives with other insect species at each location and on each host plant, observations were made on the insect communities and dominant species were recorded wherever coexistence was noticed. Samples of host plant infestated with more than one species of insects were kept separately for further determination of the identity of the species and that of any natural enemies that emerged from the sample. Spatial and temporal variations of co-occuring species were also recorded during the surveys to study the pattern of coexistance. Species dominance was calculated based on the presence and number of individual of life stages of different insects in each colony.

Natural Enemies: Part of the collection of host plant leaves/parts infested with immature stages and puparium were placed in rearing jar (21 × 10 cm) for the emergence of parasitoids. The emerging parasitoids were collected using an aspirator and preserved in vials containing 70% ethanol for further identification. Identification of natural enemies was confirmed by morphological means. Assessment of parasitism (%) was determined based on the number puparium parasitized versus un-parasitized pupae on the host leaves.

Nature and Intensity of Damage: Both nymphal and adult whiteflies were usually found crowded in the abaxial surface of leaflets causing direct damage by sucking the plant sap. Adults excrete prodigious quantities of honeydew, which in turn completely darkens the adaxial surface of the leaves and also on the understory crops by the development of sooty mold. In heavily infested areas, the waxy flocculent material produced by nymphs and adults is a nuisance to human beings. The intensity of damage was assessed on randomly selected five leaf/plant and five locations at each study area on economically important host plants. An assessment of their population level was carried out using the following qualitative scale i.e. Low (= less than 10 live egg spirals or adults/leaflet), medium = (11–20 live egg spirals or

adults/leaflet) and severe = (more than 20 live egg spirals or adults/leaflet).

Results and discussion

Species confirmation: The identity of the whitefly species was confirmed by the senior author based on the morphological characteristics of the puparia (4th instar nymph) and comparing them with the original and additional descriptions of respective species. Further, the partial mitochondrial cytochrome c oxidase I (COI) gene of 658 bp size was amplified and sequenced. The sequences were submitted to GenBank under accession number MK421974, MF449463, MF371113, MT422352, MT422350, MT422351, MN027508, MW629855 and KY223606 for the following 8 whitefly species: *Aleurodicus dispersus, Aleurodicus rugioperculatus, Aleurothrixus trachoides, Paraleyrodes bondari, Paraleyrodes minei, Aleurotrachalus atratus, Aleurothrixus floccosus, Tetraleurodes acaciae* and a parasitoid species of the genus *Encarsia,* respectively. The COI sequences showed a 98–100% match with species reported elsewhere and submitted in National Center for Biotechnology Information database. A barcode for each species was also generated with help of the barcode of life data system.

Expansion of geographical areas:

1. *Aleurodicus dispersus* Russell, the spiralling whitefly was the first invasive whitefly recorded in India; it was first reported in the Western Ghats of south India and is now distributed throughout the country including the Andaman, Nicobar and Lakshadweep islands. Russell (1965) described this pest from specimens found on coconut (*Cocos nucifera*) in Key West, Florida, USA; however, the species is probably native to the Caribbean islands and/ or Central America
2. *Aleurodicus rugioperculatus* Martin was described from coconut in Belize and has been reported as a pest on gumbo limbo (*Bursera simaruba*) in Miami-Dade County of South Florida in 2009. This whitefly is believed to have originated from Central America and its incidence is limited to Belize, Mexico, Guatemala and Florida in Central and North America (Evans, 2008). In India, its incidence was recorded on coconut and many other crop plants during 2016 at Pollachi, Tamil Nadu (Sundararaj & Selvaraj, 2017); subsequently, it has spread to different districts of Karnataka, Kerala, Andhra Pradesh, Goa, Assam and West Bengal (Selvaraj et al., 2017 &, 2019) and was recently observed in Lakshadweep islands, coastal districts of Maharashtra, Gujarat, Telangana, Odisha, Chhattisgarh and few districts of Meghalaya.
3. *Paraleyrodes bondari* Peracchi was described on citrus (*Citrus* spp.) from Brazil in 1971 (Peracchi, 1971). This species is native to the Neotropical region and has since been reported from Belize, Honduras, Puerto Rico, Madeira, Comoros, Mauritius, Taiwan, Hawaii and Florida (USA) (Stocks, 2012). It was first reported in India on coconut palms in Kerala during 2018 (Josephrajkumar et al., 2019), Karnataka and The Andaman and Nicobar Islands (Vidya et al., 2019). Recently, its occurrence was noticed in the Lakshadweep islands and different districts of Tamil Nadu and Andhra Pradesh.
4. *Paraleyrodes minei* Iaccarino was described from Syria on citrus (*Citrus* spp.) in 1990 but is considered a native of the Neotropical region (Iaccarino, 1990). It was reported in California, USA in 1984 and has also been reported in Belize, Guatemala, Mexico, Puerto Rico, Bermuda, California, Florida, Texas, Lebanon, Morocco, Spain, Syria, Turkey and Benin (Martin, 2004). In India, it was reported on coconut in Kerala during 2018 (Mohan et al., 2019; Sujithra et al., 2019) and in the Andaman and Nicobar Islands (Dubey, 2019). Subsequently, this species rapidly spread to different districts of Karnataka and Tamil Nadu.
5. *Aleurothrixus trachoides* (Back) was described from *Solanum seaphorthianum* in Cuba. The species is native to the Neotropical Region and established in Tahiti during the 1930s (Back, 1912). The species was first found in India heavily infesting ornamental plants, *Duranta erecta* and *Capsicum annum* in South India (Karnataka) in 2015 (Dubey & Sundararaj, 2015) and has subsquently spread to Kerala, Tamil Nadu and Maharastra within a span of five years of incursion.
6. *Tetraleurodes acaciae* (Quaintance) was described from mesquite (*Acacia* sp.) from Mexico and is known from Belize, Costa Rica, Cuba, Domini-

can Republic, Guatemala, Haiti, Jamaica, Mexico, Nicaragua, Panama, Puerto Rico, Trinidad, United States and Venezuela (Nakahara, 1995) and Taiwan (Dubey & Ko, 2008). It was first recorded in India on subabul, *Leucaena leucocephala* in Bengaluru, Karnataka (Sundararaj & Vimala, 2018). Infestations of this whitefly species were observed on orchid tree, *Bauhinia variegata* in Bengaluru Urban district; tamarind, *Tamarindus indica* and rain tree, *Samanea saman* in Shivmogga district; subabul, and on an unidentified pulses crop (Fabaceae) in Udupi district of Karnataka.

7. *Aleurotrachelus atratus* Hempel was described from coconut in Brazil (Hempel, 1922) and has spread rapidly in Antigua, Bahamas, Barbados, Bermuda, Brazil, Colombia, Guyana, Nevis, Puerto Rico, Venezuela and Florida (USA) (Howard et al., 2001). It has since been found in Africa, North and South America, Central America and the Caribbean, Europe and Oceania (Borowiec et al., 2010). This species was recorded in India on coconut and an ornamental palm in the Mandya district of Karnataka during 2019 (Selvaraj, Sundararaj, et al., 2019), and subsequently spread to Mysore, Ramanagara, Hassan, Tumkur, Kodagu, Bengaluru Rural and Bengaluru Urban districts of Karnataka and Krishnagiri and Dharmapuri districts of Tamil Nadu.
8. *Aleurothrixus floccosus* Maskell, the wooly whitefly, was described from *Citrus* sp. in Cuba (Maskell, 1896) and is native to the Neotropical region wherever citrus is grown (Malumphy et al., 2015). It was first found in India on guava (*Psidium guajava*) in the Kozhikode district of Kerala during 2019 (Sundararaj et al., 2020a). Infestation of this species have since been found on this same host in Ramanagara, Bengaluru Rural, Bengaluru Urban, Mysore, Tumkur, Udupi, Kodagu and the Mandya districts of Karnataka and in the Coimbatore, Salem, Krishnagiri, Dharmapuri, Karur, Tirupathur and Namakkal districts of Tamil Nadu. Recently, infestations of this pest were observed on guava in three islands of Lakshadweep viz., Kavaratti, Keltan and Amini.

The current rapid geographical expansion of these invasive species is likely due to favourable weather factors and availability of host plants. Dukes and Mooney (1999) commented that the global climate change favors the introduction and establishment of invasive species to new environments with a potentially devastating impact on agriculture ecosystems. Further, these changes make it easier for phytophagous insects to adapt to new environments on suitable host plants (Birke et al., 2013), as well as for polyphagous insects that have the ability to exploit new hosts.

Expansion of host range: The host range of all of the invasive whiteflies mentioned herein was found to be increasing. *Aleurodicus dispersus* has been reported on over 320 plant species belonging to 225 genera and 73 families in India (Sundararaj & Pushpa, 2012). *Aleurodicus rugioperculatus* is a highly polyphagous pest reported to feeds on about 120 plant species including economically important cultivated plants and palms. In India, it was found to feed on about 22 host plants especially coconut (*Cocos nucifera*), banana (*Musa* sp.), mango (*Mangifera indica*), sapota (*Manilkara zapota*), guava (*Psidium guajava*), cashew (*Anacardium occidentale*), ramphal (*Annona reticulata*), oil palm (*Elaeis guineensis*), maize (*Zea mays*), Indian almond (*Terminalia catappa*), water apple (*Syzygium samarangense*), jack fruit (*Artocarpus heterophyllus*) and many other ornamental plants such as bottle palm (*Hyophorbe lagenicaulis*), Indian shot (*Calophyllum inophyllum*), false bird of paradise (*Heliconia rostrata*) and butterfly palm (*Dypsis lutescens*) (Selvaraj et al., 2017; Selvaraj, Venkatesan, et al., 2019). Further, the present study revealed the expansion of its host plants (Table 1) and it was observed that they have established more on non-native plants than natives. *Aleurothrixus trachoides* was found breeding on 24 host plants representing 11 families (Sundararj et al., 2018) and the present study revealed its presence on 13 new host plants (Table 2).

Paraleyrodes bondari is a polyphagous species that has been reported to feed on more than 25 host plants including banana (*Musa* sp.), mango (*Mangifera indica*), citrus (*Citrus* spp.), cassava (*Manihot esculenta*), custard apple (*Annona squamosa*), coconut (*Cocos nucifera*), guava (*Psidium guajava*) and subabul (*Leucaena leucocephala*) in India (Vidya et al., 2019). In the present survey, the pest was found to colonize many more additional host plants in India (Table 1). Similarly, *P. minei* was found to colonize coconut (*Cocos nucifera*), banana (*Musa* sp.), guava (*Psidium guajava*), mango (*Mangifera indica*),

Table 1 Host plant distribution for the invasive whiteflies under subfamily Aleurodicinae and its occurrence

S.No	Plant species	Distribution (District, State)	Infestation level	Co-existence
A. Rugose spiralling whitefly, *Aleurodicus rugioperculatus* Martin				
1.	*Acacia auriculiformis* (Fabaceae)	Purba Medinipur *, West Bengal; Ramanagara district, Karnataka; Khordha, Odisha	Moderate to severe	-
2.	*Anacardium occidentale* (Anacardiaceae)	Udupi, Karnataka; West Godavari, Andhra Pradesh	Low to moderate	-
3.	*Arachis hypogaea* (Fabaceae)	Kochi, Kerala	Low	-
4.	*Bixa orellana* (Bixaceae)	Bengaluru rural, Karnataka	low	-
5.	*Canna indica* (Cannaceae)	Bengaluru rural, Udupi, Karnataka; Coimbatore, Tamil Nadu	low	*Aleurodicus dispersus* *Bemisia tabaci*
6.	*Colacasia esculenta* (Araceae)	Nadia*, West Bengal	low	-
7.	*Curcuma longa* (Zingiberaceae)	Nadia*, West Bengal	low	-
8.	*Ficus bengalensis* (Moraceae)	Nadia*, West Bengal and Goa	Low to moderate	-
9.	*Ficus microcarpa* (Moraceae)	Udupi, Karnataka	Low to moderate	-
10.	*Ficus religiosa* (Moraceae)	Udupi, Karnataka and Goa	Low to moderate	-
11.	*Magnolia champaca* (Magnoliaceae)	West Godavari, Andhra Pradesh; Bengaluru Urban, Karnataka	Low	-
12.	*Mimusops elengi* (Sapotaceae)	Purba Medinipur*, West Bengal	Low to moderate	-
13.	*Murraya koenigi* (Rutaceae)	Coimbatore, Tamil Nadu; Bengaluru Rural, Karnataka	Low to moderate	-
14.	*Palmeira ravenala* (Strelitziaceae)	West Godavari, Andhra Pradesh	Low	-
15.	*Piper nigrum* (Piperaceae)	Dakshina Kannada, Karnataka; West Godavari, Andhra Pradesh; Nadia*, West Bengal	low	-
16.	*Phyllanthus emblica* (Phyllanthaceae)	West Godavari, Andhra Pradesh	Low to moderate	-
17.	*Pimenta dioica* (Myrtaceae)	Kavaratti*, Lakshadweep	Low	-
18.	*Plumeria alba* (Apocynaceae)	Bengaluru Rural, Bengaluru Urban, Karnataka	Low	*Aleurothrixus trachoides*
19.	*Saccharum officinarum* (Poaceae)	Erode*, Tamil Nadu; Vishakhapatnam, Andhra Pradesh	Low	-
20.	*Sandallum album* (Santalaceae)	Bengaluru Rural, Karnataka	low	-
21.	*Terminalia arjuna* (Combretaceae)	Mandya, Karnataka; Kozhikode, Kerala	Moderate to severe	-
22.	*Trachycarpus fortunei* (Arecaceae)	Kottayam, Kerala; Bengaluru, Karnataka	Low	-
23.	*Zea mays* (Poaceae)	West Godavari, Andhra Pradesh; Mandya, Karnataka; Khammam*, Telangana	Moderate to severe	-
24.	*Zingiber officinale* (Zingiberaceae)	Nadia*, West Bengal	Low to moderate	-
25.	*Combretum indicum* (Combretaceae)	Kochi, Kerala; Dakshina Kannada, Karnataka*	Low	-
26.	*Gladiolus hortensis* (Iridaceae)	Pune, Maharashtra	Low to moderate	

Table 1 (continued)

S.No	Plant species	Distribution (District, State)	Infestation level	Co-existence
B. Bondar's nesting whitefly, *Paraleyrodes bondari* Peracchi				
1.	*Citrus* spp. (Rutaceae)	Coimbatore, Tamil Nadu	Low	*A. rugioperculatus*
2.	*Cocos nucifera* (Arecaceae)	West Godavari*, Andhra Pradesh; Mandya*, Karnataka; Krishnagiri, Tamil Nadu; Dakshina kannada, Karnataka	Low	*A. rugioperculatus; A.atratus*
3.	*Ficus religiosa* (Moraceae)	Bengaluru Urban, Karnataka	Low to moderate	*A. rugioperculatus*
4.	*Ficus* sp. (Moraceae)	Kavaratti*, Lakshadweep	Moderate to severe	-
5.	*Morinda citrifolia* (Rubiaceae)	Kavaratti*, Lakshadweep	Low to moderate	-
6.	*Psidium guajava* (Myrtaceae)	Coimbatore, Krishnagiri, Tamil Nadu; Kavaratti*, Lakshadweep; Bengaluru Urban, Karnataka	Low to moderate	*A. rugioperculatus, A. floccosus & A. dispersus*
7.	*Samanea saman* (Fabaceae)	Coimbatore, Tamil Nadu	Low	-
8.	*Saraca asoca* (Fabaceae)	Coimbatore, Tamil Nadu	Low	-
9.	*Syzygium cumini* (Myrtaceae)	Coimbatore, Tamil Nadu	Low	*A. dispersus*
10.	*Thespesia populnea* (Malvaceae)	Kavaratti*, Lakshadweep	Low to moderate	*A. rugioperculatus*
11.	*Gossypium hirsutum* (Malvaceae)	Bengaluru Urban*, Karnataka	Moderate	*B. tabaci*
12.	*Annona quamosa* (Annonaceae)	Mandya*, Karnataka	Low	*Paraleyrodes minei*
13.	*Phyllanthus emblica* (Phyllanthaceae)	Krishnagiri, Tamil Nadu; Bengaluru Urban, Karnataka	Low	*A. rugioperculatus*
C. Nesting whitefly, *Paraleyrodes minei* Iaccarino				
1.	*Annona quamosa* (Annonaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*Pealius nagerkoilensis*
2.	*Annona muricata* (Annonaceae)	Tumkur*, Karnataka	Low	-
3.	*Argyrea cuneata* (Convolvulaceae)	Bengaluru Rural*, Karnataka	Low	*A. trachoides*
4.	*Artabotrys odoratissimus* (Annonaceae)	Bengaluru Rural*, Karnataka	Low	-
5.	*Calophyllum inophyllum* (Calophyllaceae)	Mandya*, Karnataka	Low	*A. rugioperculatus*
6.	*Capsicum annuum* (Solanaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*A. trachoides*
7	*Cestrum diurnum* (Solanaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*A. trachoides*
8.	*Citrus* spp. (Rutaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*A. woglumi*
9.	*Dypsis lutescens* (Arecaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*A. rugioperculatus*
10.	*Elaeis guineensis* (Arecaceae)	Mandya*, Bengaluru Urban*, Karnataka	Low	*A. rugioperculatus*
11.	*Ficus religiosa* (Moraceae)	Bengaluru Rural*, Karnataka	low	*A. dispersus*
12.	*Hibiscus rosasinensis* (Malvaceae)	Bengaluru Rural*, Karnataka	Low	*A. dispersus*
13.	*Manilkara zapota* (Sapotaceae)	Bengaluru Rural*, Karnataka	Low	*A. rugioperculatus*
14.	*Mathuca longifolia* (Sapotaceae)	Bengaluru Rural*, Karnataka	Low to moderate	-
15.	*Monihot esculenta* (Euphorbiaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*A. dispersus*
16.	*Phyllanthus emblica* (Phyllanthaceae)	Bengaluru Rural*, Karnataka	Low to moderate	*Aleurocanthus* sp.
17.	*Plumeria alba* (Apocynaceae)	Bengaluru Rural*, Karnataka	Low	*A. dispersus* & *A. trachoides*
18.	*Roystonea regia* (Arecaceae)	Bengaluru Rural*, Karnataka	Low	*A. rugioperculatus*
19.	*Santalum alum* (Santalaceae)	Bengaluru Urban*, Karnataka	Low	*A. dispersus*
20.	*Strychnos nixvomica* (Loganiaceae)	Bengaluru Rural*, Karnataka	Low	-
21.	*Syzygium jambos* (Myrtaceae)	Bengaluru Rural*, Karnataka	Low	-
22.	*Thespesia populnea* (Malvaceae)	Bengaluru Rural*, Karnataka	Low	*A. dispersus*
23.	*Vitex altissima* (Lamiaceae)	Bengaluru Rural*, Karnataka	Low	

Table 1 (continued)

S.No	Plant species	Distribution (District, State)	Infestation level	Co-existence
24.	*Gossypium hirsutum* (Malvaceae)	Bengaluru Urban*, Karnataka	Moderate	*B. tabaci*
25.	*Punica granatum* (*Lythraceae*)	Bengaluru Urban*, Karnataka; Krishnagiri, Tamil Nadu	Low	*Siphoninus phillyreae*
26.	*Saraca asoca* (Fabaceae)	Bengaluru Urban*, Tumkur*, Karnataka	Low	*A. dispersus*
27.	*Dalbergia sissoo* (Fabaceae)	Bengaluru Urban*, Karnataka	Low	*A.dispersus*

Low less than 10 live egg spirals or adults/leaflet, *Medium* 11–20 live egg spirals or adults/leaflet), *Severe* above 20 live egg spirals or adults/leaflet)

*New distribution

jamun (*Syzygium cumini*), *Ixora* sp., and *Heliconia* (Mohan et al., 2019; Sujithra et al., 2019). The present study revealed the additional host range for this pest (Table 1). This host range expansion could be a mechanism to overcome the abiotic constraints and buffer the depletion of optimal resources. Ultimately, host range expansion leads to increases in population growth and potentially to greater geographic range expansion (Crowl et al., 2008).

Aleurothrixus trachoides was found breeding on 24 host plants representing 11 families in Karnataka, Kerala, Maharashtra and Tamil Nadu (Sundararaj et al., 2018) including several species of the family Solanaceae, Araceae, Apocynaceae and Convolvulaceae (Dubey & Sundararaj, 2015). In addition to the above reported host plants, the pest has expanded its host range in India (Table 2). In India, *Tetraleurodes acaciae* infests mainly plants of the legume family (Fabaceae) including *Leucaena leucocephala*, the host on which it was found breeding in Bangalore, Udupi districts of Karnataka. Infestations of *Aleurotrachalus atratus* were observed on coconut, arecanut, oilpalm and ornamental areca palm (Table 2). The intensity and severity of its infestation was more on coconut palm than the other host plants (Selvaraj, Sundararaj, et al., 2019; Selvaraj, Venkatesan, et al., 2019). It is known to colonize more than 110 plant species belonging to Arecaceae, Rutaceae, Solanacee, Cycadaceae and Lauraceae (Malumphy & Treseder, 2011). *Aleurothrixus floccosus* is a polyphagous species, known to feed on 20 different plant families; it exhibits a strong preference for citrus but so far in India, has been found to infest guava (Table 2).

Co-occurrence: As many as eight exotic whiteflies have been reported from different regions in India in rapid succession. All these whitefly species are highly polyphagous and have a host preference towards many economically important crop plants such as coconut, guava, banana, custard apple, oil palm. During the present study, *A. rugioperculatus*, *P. bondari*, *A. dispersus* and *P. minei* were observed to simultaneous coexistence on many of the host plants. Similar observations were made by Josephrajkumar et al. (2019) and Mohan et al. (2019). We observed *Aleurodicus rugioperculatus* co-existing with *Aleurotrachalus atratus, P. bondari*, *A. dispersus* and *P. minei* on coconut; *P. minei, P. bondari, A. rugioperculatus* and *A. dispersus* with *Aleurothrixus floccosus* on guava (Table 1 & 2); *A. trachoides* with *Bemisia tabaci* on tobacco; nesting whiteflies (*P. bondari* and *P. minei*) with *B. tabaci* on cotton (Table 1 & 2). Infestations of *A. atratus* and *A. rugioperculatus* along with *Aleurocanthus arecae,* a native whitefly species were commonly observed on coconut. *A. rugioperculatus* and *A. floccosus* were the dominant species, in their niches irrespective of the co-occurring species on the majority of host plants. In Greece, co-existence of the *P. minei* and *A. floccosus* was recorded on citrus (Kalaitzaki et al., 2016).

The synchrony of coexistence and mutual survival of these competing insect species could be due to the marked time partitioning of the resource use among the species except that they are demographically nearly equivalent and need detailed study. Such co-occurrence has been observed among these invasive species, in which one species occupies the breeding and feeding niche of another species under optimum weather parameters and attempts to displace one or more of its competitors gradually which leads to temporal variation. Venner et al. (2011) reported the communities of consumers of limited resources offer a promising avenue for developing a unifying theory of biodiversity in fluctuating environments which might predict the

Table 2 Host plant distribution for the invasive whiteflies under subfamily Aleyrodinae and its occurrence

S.No	Plant species	Distribution (District, State)	Intensity of infestation	Co-existence
A. Solanum whitefly, *Aleurothrixus trachoides* (Back)				
1.	*Argyrea cuneata* (Convolvulaceae)	Bengaluru Rural*, Karnataka	Low	*P. minei*
2.	*Cestrum diurnum* (Solanaceae)	Bengaluru Rural *, Karnataka	Low	*P. minei*
3.	*Cestrum nocturnum* (Solanaceae)	Bengaluru Rural *, Karnataka	Low to moderate	*P. minei*
4.	*Cleodendrum inerme* (Lamiaceae)	Bengaluru Rural *, Karnataka	Low to moderate	-
5.	*Ipomoea batatas* (Convolvulaceae)	Bengaluru Rural *, Karnataka	Low to moderate	-
6.	*Ipomoea purpurea* (Convolvulaceae)	Bengaluru Rural *, Karnataka	Low to moderate	-
7.	*Nicotiana tabacum* (Solanaceae)	Bengaluru Rural *, Karnataka	Moderate to severe	*Bemisia tabaci*
8.	*Plumeria alba* (Apocynaceae)	Bengaluru Rural *, Karnataka	Low to moderate	*A. dispersus*
9.	*Solanum lycopersicum* (Solanaceae)	Bengaluru Rural *, Karnataka	Moderate to severe	-
10.	*Solanum nigrum* (Solanaceae)	Bengaluru Rural *, Karnataka	Low	-
11.	*Tabebuia avellanedae* (Bignoniaceae)	Bengaluru Rural *, Karnataka	Moderate to severe	-
12.	*Tectona grandis* (Verbenaceae)	Bengaluru Rural *, Karnataka	Moderate to severe	-
13.	*Withania somnifera* (Solanaceae)	Bengaluru Rural *, Karnataka	Moderate to severe	-
B. Legume feeding whitefly *Tetraleurodes acaciae* (Quaintance)				
1.	*Bauhinia variegata* (Fabaceae)	Bengaluru Rural *, Bengaluru Urban, Karnataka	Moderate to severe	*A.dispersus*
2.	*Leucaena leucocephala* (Fabaceae)	Bengaluru Rural *, Bengaluru Urban, Karnataka	Moderate to severe	*P. bondari*
3.	*Tamarindus indica* (Fabaceae)	Shivmogga, Karnataka	Low	-
4.	*Samanea saman* (Fabaceae)	Shivmogga, Karnataka	Low	-
5.	Pulses (unidentified) (Fabaceae)	Udupi, Karnataka	low	-
C. Palm infesting whitefly, *Aleurotrachelus atratus* Hempel				
1.	*Cocos nucifera* (Arecaceae)	Mandya, Mysore*, Tumkur*, Hassan*, Kodagu*, Ramanagara*, Bengaluru Rural*, Bengakuru Urban*, Karnataka; Krishnagiri, Dharmapuri, Tamil Nadu	Moderate to severe	*A. rugioperculatus, P. minei, Aleurocanthus arecae, A. atratus*
2.	*Areca catchu* (Arecaceae)	Ramanagara*, Mandya*, Karnataka	Low to moderate	*P. minei, A. rugioperculatus, Aleurocanthus arecae*
3.	*Dypsea lutescens* (Arecaceae)	Mandya*, Mysore*, Ramanagara*, Karnataka	Low to moderate	*P. minei, A. rugioperculatus, Aleurocanthus arecae*
4.	*Elaeis guineensis* (Arecaceae)	Bengaluru Urban*, Karnataka	Low	*A. rugioperculatus, P. minei*

Table 2 (continued)

S.No	Plant species	Distribution (District, State)	Intensity of infestation	Co-existence
Woolly whitefly, *Aleurothrixus floccosus* (Maskell)				
1.	*Psidium guajava* (Myrtaceae)	Mandya*, Ramanagara*, Tumkur*, Bengaluru Rural, Bengaluru Urban*, Mysore*, Udupi*, Karnataka; Kozhikode, Manapuram*, Kerala; Coimbatore*, Krishnagiri*, Salem*, Dharmapuri*, Namakkal*, Karur*, Tirupathur*, Tamil Nadu; Kavaratti*, Keltan*, Lakshadweep	Moderate to severe	*Aleurodicus dispersus, P. bondari; P. minei, A. rugioperculatus*

Low less than 10 live egg spirals or adults/leaflet, *Medium* 11–20 live egg spirals or adults/leaflet), *Severe* above 20 live egg spirals or adults/leaflet)

*New distribution

co-occurrence, within the same community, of species that are ecologically either very similar, or very different. Further, this mutual survival of more than one species indicates deferred its existing pest management options in various crop plants.

Natural enemies of the invasive whiteflies: Explorative surveys were carried out for the biological control of these invasive pests through naturally occurring insect predators and parasitoids which are economically feasible, ecologically compatible and environmentally benign. Two parasitoids, *Encarsia guadeloupae* Viggiani and *E. dispersa* Polaszek (Hymenoptera: Aphelinidae) were found to colonize *A. dispersus* and *A. rugioperculatus* (Mani, 2010; Selvaraj et al., 2017). *Encarsia guadeloupae* was the dominant parasitoid which parasitized 62–95% and 56–82% of *A. dispersus* and *A. rugioperculatus*, respectively (Mani, 2010; Selvaraj et al., 2016, 2017) whereas *E. dispersa* parasitized 28 -92% and 5–10% of *A. dispersus* and *A. rugioperculatus,* respectively (Mani, 2010; Selvaraj et al., 2017). Predators such as *Pseudomallada astur* (Neuroptera: Chrysopidae), *Jauravia pallidula, Cheilomenes sexmaculata* (Coleoptera: Coccinellidae) and *Cybocephalus indicus* (Coleoptera: Nitidulidae) were also observed to be feeding on *A. rugioperculatus* and *A. dispersus* (Mani, 2010; Selvaraj et al., 2017). In addition, three species of entomopathogenic fungi, *Lecanicillium lecani, Simplicillium cylindrosorum* (Hypocreales: Cordycipitaceae) and *Isaria fumosorosea* (Hypocreales: Clavicipitaceae) were found to be effective against all the life stages of *A. rugioperculatus* and *A. dispersus* (Boopathi et al., 2013; Sumalatha et al., 2020; Sujithra et al., 2020). *Isaria fumosorosea* was highly pathogenic to the egg and early nymphal instar stage with mortality up to 91% in these stages and up to 80% mortality in the late nymphal instar stages. *Simplicillium cylindrosporum* caused about 21.8 to 52.80% mortality in *A. rugioperculatus*. Neither parasitoids nor native predators such as *Pseudomallada astur*, *Cybocephalus indicus, Axinoscymnus puttarudriahi* (Coleoptera: Coccinellidae)*, Cryptolaemus montrouzieri* (Coleoptera: Coccinellidae) and *Acletoxenus indicus* (Diptera: Drosophilidae) were recorded for the other invasive whitefly species (Selvaraj, Sundararaj, et al., 2019; Selvaraj, Venkatesan, et al., 2019; Sundararaj et al., 2020a).

Economic importance of invasive whiteflies: Invasive whiteflies pose a challenge to the Indian economy as biologists and the public worldwide increasingly recognize the damage caused by invasive non-indigenous species. Normally, the introduction of an invasive species is through single or multiple interceptions at the border or port of entry; successful invasion and establishment of the species often occurs if its new environment is favourable and it is able to find suitable hosts. Despite the severe ecological damage and economic loss caused by the invasive species, the factors contributing to successful invasion remain elusive. Non-native species can achieve major pest status when they are accidentally introduced to new locations and are separated from their natural enemy complexes (Duan et al., 2015). Further, the invasive process from the initial introduction through establishment and spread under extreme climatic conditions (Diez et al., 2012) and the ongoing dispersal of exotic is one of the most striking biological outcomes of global climatic changes (Gao & Reitz, 2017). Bellard et al. (2013) predicted an increase in the number of invasive alien species for northwestern Europe and northeastern United States, India and eastern China under all future scenarios, as opposed to a decrease in the number of invasive alien species that was projected for Central and South America, southwestern Europe, central Africa, eastern Australia and the Indonesian and Pacific islands regions.

Coconut and guava are important crops grown mainly in the tropical and subtropical regions of the world. Host preference of these invasive whiteflies towards coconut and guava in the country of their origin leads to quicker establishment on these host plants in the newly introduced regions. Out of the eight invasive species new to India, *A. dispersus, A. rugioperculatus, A. floccosus, P. bondari* and *P. minei* were found to infest guava and coconut. The global invasive species program proposes three major management options: prevention, early detection, and eradication for the management of alien species (Wittenberg & Cock, 2001). Prevention of an invasion is the most economical option as it contains pest to spread to neo geographical regions. Post incursion management mostly through timely implementation of classical biocontrol programme using potential natural enemies by importation. Fortunately, most of such invasions, especially those of hemipteran species of the suborder Sternorrhyncha, which includes whiteflies, scale insects, aphids, psyllids and some smaller families are amenable for classical biological control. Effective biological control programme has been implemented for *A. rugioperculatus* and *A. dispersus* resulting in the saving millions of rupees by mitigating their adverse impacts on agriculture. Moreover, it is imperative that identification of these species be accurate and timely so that further studies on their bioecology, population dynamics on different environments and development of management especially biocontrol strategies can be carried out. There is urgent need to survey and document the natural enemies of *P. bondari*, *P. minei*, *A. floccosus* and *A. atratus,* and evaluate potential candidates for their introduction from their native countries to India for the development of efficient biocontrol management strategies. The impact of the incursion of insect pests can be minimized by international exchange of information on potential invasive pests and by interdisciplinary coordinated investigations. Further, a nation-wide surveillance programme is required to determine the potential geographic and host range of the species to prevent its expansion by restricting the movement of planting materials.

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Declarations

Conflict of Interest No conflict of interest among authors.

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