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Presence of *Aleurocanthus spiniferus* (Quaintance, 1903) haplotypes in Croatia

Prisutnost haplotipova vrste *Aleurocanthus spiniferus* (Quaintance, 1903) u Republici Hrvatskoj

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ABSTRACT

The orange spiny whitefly, *Aleurocanthus spiniferus* (Quaintance, 1903) (Hemiptera: Aleyrodidae), is a quarantine invasive pest of concern in the European Union. In Croatia, it was first detected in 2012 and afterwards reconfirmed in 2018. This study aimed to characterize the genetic variability of *A. spiniferus* in the southern coastal region of Croatia, specifically within the Dubrovnik–Neretva and Split–Dalmatia counties, using mitochondrial cytochrome c oxidase subunit I (COI) sequences from samples collected between 2019 and 2020. Two dominant haplotypes, H1 and H2, were identified in 8 samples from different host plants and locations in Dubrovnik-Neretva and Split-Dalmatia counties. Haplotype H1 was prevalent on the Hvar Island, whereas H2 was primarily detected along the mainland coastline. The coexistence of both haplotypes suggests multiple introduction pathways, likely through plant material trade and possible natural spread from Montenegro. The neighbouring obtained results provide a basis for comparison with haplotypes in countries and with those from the pest's native range, which may contribute to clarifying the origin of populations in Croatia and suggest whether they result from a single or multiple introductions.

Keywords: cytochrome c oxidase subunit I sequences, genetic variability, invasive pest, molecular diagnostic, orange spiny whitefly

SAŽETAK

Narančin trnoviti štitasti moljac *Aleurocanthus spiniferus* (Quaintance, 1903) (Hemiptera: Aleyrodidae), je invazivni karantenski štetnik, značajan za Europsku uniju. U Hrvatskoj je prvi put otkriven 2012. godine, a ponovna potvrda uslijedila je 2018. godine. Cilj ovog istraživanja bio je utvrditi genetsku varijabilnost *A. spiniferus* u južnom obalnom području Hrvatske konkretno na području Dubrovačko-neretvanske i Splitsko-dalmatinske županije, koristeći mitohondrijsku citokrom c oksidazu podjedinicu I (COI) iz uzoraka prikupljenih u razdoblju 2019.–2020. U osam uzoraka s različitih biljnih domaćina i lokacija u Dubrovačko-neretvanskoj i Splitsko-dalmatinskoj županiji identificirana su dva dominantna europska haplotipa – H1 i H2. Haplotip H1 bio je prevladavajući na otoku Hvaru, dok je H2 uglavnom zabilježen uz obalni kopneni pojas. Prisutnost dva haplotipa upućuje na višestruke putove unosa, vjerojatno putem trgovine biljnim materijalom ali i mogućim prirodnim širenjem iz Crne Gore. Dobiveni rezultati pružaju osnovu za usporedbu s haplotipovima u susjednim zemljama te s haplotipovima iz izvornog područja štetnika, što može doprinijeti boljem razumijevanju podrijetla populacije u Republici Hrvatskoj i sugerirati radi li se o jednoj ili višestrukim introdukcijama.

Ključne riječi: COI sekvence, genetska varijabilnost, invazivni štetnik, molekularna dijagnostika, narančin trnoviti štitasti moljac

INTRODUCTION

The orange spiny whitefly (OSW), *Aleurocanthus spiniferus* (Quaintance, 1903) (Hemiptera: Aleyrodidae), is a species native to Southeast Asia, and it was first described by Quaintance in 1903, based on material collected by Marlatti in 1901 on the island of Java (Cioffi et al., 2013). It belongs to the genus *Aleurocanthus* Quaintance & Baker, 1914, which comprises over 80 species worldwide (Dubey and Ko, 2012; Jansen and Porcelli, 2018). Among these, *Aleurocanthus woglumi* (Ashby, 1915) and *Aleurocanthus citriperdus* Quaintance & Baker, 1916 are also considered of significant economic importance in agriculture.

The species *A. spiniferus* poses a serious threat to European and global citrus-growing regions due to its high polyphagy. Beyond citrus crops, the pest increasingly causes problems in urban environments, affecting ornamentals, plants in private gardens and public greenery. A particularly notable example is the southern part of Hvar Island in Croatia, especially the village of Ivan Dolac, where tourism and viticulture intersect (Njavro, 2007). In such areas, *A. spiniferus* poses a dual threat. While on ornamental plants around tourist properties, this pest primarily acts as a nuisance. The real threat lies in its likely spread to nearby commercial vineyards. Infestation in grapevine can cause yellowing and leaf drop, directly affecting both yield and grape quality.

Within the European Union, *A. spiniferus* is a quarantine pest under Regulation (EU) 2016/2031 and is listed in Annexe II, Part B, of the Commission Implementing Regulation (EU) 2019/2072, as well as on the EPPO A2 List (EPPO, 2025a; European Commission, 2016; European Commisssion, 2019). It has rapidly expanded its range and established populations in tropical and subtropical parts of Asia and Africa, as well as several European countries with favorable climatic conditions (Van den Berg and Greenland 1997; Muniappan et al., 2006; Cioffi et al., 2013; Kapantaidaki et al., 2019). In the Mediterranean region, the species was first confirmed in Italy in 2008 (Porcelli, 2008; Rapisarda and Longo, 2021), followed by subsequent reports from Croatia in 2012 (Šimala et al., 2013), Montenegro in 2013 (Radonjić et al., 2014), Greece in 2016 (Kypriotis et al., 2017), Albania in 2019 (Nugnes et al., 2020) and France in 2023 (Streito et al., 2023).

In Croatia, the pest was first intercepted in 2012 on ornamental potted *Citrus aurantium* L. seedlings in one nursery garden in Split (Šimala and Masten Milek, 2013), after which eradication measures were implemented. Although the official monitoring of this pest began in 2013, it was first identified in a natural environment in a small Satsuma mandarin (*Citrus unshiu* Marcow.) orchard in 2018 (Šimala et al., 2019a). In the following year, the pest has spread towards the northwest, with its presence confirmed in two commercial orchards (on *C. unshiu* and *Citrus sinensis* (L.) Osbeck) in the town of Ljuta and a private garden in Molunat (on *Citrus aurantium* L.) in the Dubrovnik-Neretva County (Šimala et al., 2019b) (Figure 1). In the same year, it was recorded in Ivan Dolac on the island of Hvar, not only on citrus plants, but on other hosts, such as *Hedera helix* L., *Ficus carica* L. and *Punica granatum* L. in private gardens (Šimala et al., 2019b).

Figure 1. All developmental stages of *A. spiniferus* on a satsuma mandarin (*C. unshiu*) leaf (Source: Paladin Soče I. (authors' field survey), 2020)

According to the latest data, *A. spiniferus* infests at least 104 plant species across 43 families, highlighting its extensive host adaptability (EPPO, 2025b). Among its most affected hosts are species from the genera *Citrus*, *Vitis*, and *Pyrus*, which are critical to commercial fruit production. As the geographical distribution of the species expands, the number of detections and conducted studies increases, resulting in a growing number of documented host plant species (Nugnes et al., 2020). The species has also been recorded on the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) (Bubici et al., 2020; Picciotti et al., 2023). The OSW damages host plants by feeding on plant sap. Still, it also causes indirect harm by excreting honeydew, which promotes the development of sooty mould, thereby reducing the plant's respiration and photosynthesis (Gyeltshen et al., 2005). In cases of severe infestation, defoliation, reduced shoot growth, and poor fruit set may occur (Paladin Soče et al., 2020).

A comprehensive molecular study of OSW populations from Japan and China, based on partial mtCOI sequence analysis, revealed two distinct haplogroups, designated A1 and A2 (Uesugi et al., 2016). Based on the results, the authors suggested China as the area of origin, as the mtCOI diversity there is greater than in Japan. The variability of European OSW populations from Greece, Italy and Montenegro was analysed by Kapantaidaki et al. (2019). At that time, four distinct haplotypes were observed within the Greek OSW population and designated as H1 through H4. All specimens from Montenegro and the majority of Italian specimens (80%) were found to be identical to the H2 haplotype (Kapantaidaki et al.,2019). This was further corroborated by haplotyping results of specimens collected between 2017 and 2019 in Italy and Albania, where only H1 and H2 were confirmed (Nugnes et al., 2020). All haplotypes of the European populations are clustered with the Asian mitochondrial haplogroup A2 (Uesugi et al., 2016; Nugnes et al., 2020). The objective of this study was to investigate the genetic diversity of Croatian *A. spiniferus* populations from different geographic areas and host plants, to infer possible introduction pathways.

MATERIALS AND METHODS

Sample collection

Adults and nymphs of the orange spiny whitefly *A. spiniferus* were collected in 2019 and 2020 in locations south of Dubrovnik and on the island of Hvar, where previous infestations had been recorded. Samples were mainly collected from *Citrus* species and from ornamental hosts on Hvar Island. All sampling sites were georeferenced using precise GPS coordinates, as shown in Table 1. Adult individuals were carefully aspirated from host plants, transferred to sterile 2 mL Eppendorf tubes containing 96% ethanol, and stored at –20 °C until DNA extraction. The leaves on which the presence of the pupal stage/exuviae was detected were stored for laboratory analysis using the dry-preservation method in paper envelopes (Martin, 1987).

DNA extraction and molecular characterization

Genomic DNA extraction and all subsequent molecular analyses were performed in the Laboratory for Molecular Biology of the Centre for Plant Protection. Genomic DNA was extracted from single whitefly adults with DNeasy Blood & Tissue Kit (Qiagen®, Germany) according to the manufacturer's instructions. The extracted DNA was used for the polymerase chain reaction (PCR). Specific primers targeting *A. spiniferus* were used for the amplification of partial mtCOI (OSW-F and OSW-R), with reaction mixture and PCR conditions as described by Uesugi et al. (2016). Purified amplicons (GenElute® PCR Clean-up Kit, Sigma-Aldrich, USA) were sequenced using a commercial sequencing service (Macrogen Europe®, The Netherlands). The obtained partial mtCOI consensus sequences were compared with publicly available sequences in the NCBI GenBank database using BLAST. Sequence assembly and multiple alignment were performed using Geneious Prime 2023.1.1 software (Biomatters Ltd., New Zealand). All sequence data obtained in this study were deposited in NCBI GenBank with accession numbers.

Table 1. Samples of developmental stages of *Aleurocanthus spiniferus* collected from different plant species in the Dubrovnik–Neretva and Split–Dalmatia counties during 2019 and 2020 for molecular analysis

Sample number	Developmental stage	Sampling location	GPS position	Sampling date	Plant species
1	Adult	Vitaljina	N 42°26'8.23" E 18°28'57.50"	24.07.2019.	*Citrus unshiu*
2	Adult	Ivan Dolac, Hvar	N 43°7'38.2" E 16°38'29.5"	12.09.2019.	*Bougainvillea spectabilis*
3	Adult	Molunat	N 42°27'2.9" E 18°26'6.61"	25.09.2019.	*Citrus aurantium*
4	Adult	Ljuta 2	N 42°32'16.9" E 18°22'41.5"	25.09.2019.	*Citrus aurantium*
5	Adult	Ivan Dolac, Hvar	N 43°7'38.2" E 16°38'29.5"	12.09.2019.	*Parthenocissus quinquefolia*
6	Pupa	Ljuta 1	N 42°32'16.9" E 18°22'41.5"	25.09.2019.	*Citrus aurantium*
7	Pupa	Ivan Dolac, Hvar	N 43°7'38.2" E 16°38'29.5"	12.09.2019.	*Citrus limon*
8	Pupa	Vitaljina 3	N 42°26'8.23" E 18°28'57.50	24.07.2019.	*Citrus unshiu*
9	Pupa	Molunat	N 42°27'2.9" E 18°26'6.61"	25.09.2019.	*Citrus unshiu*
10	Adult	Vitaljina 3	N 42°26'8.23" E 18°28'57.50"	20.05.2020.	*Citrus unshiu*

Data analyses

To determine genetic diversity within Croatian populations of *A. spiniferus*, sequences were compared to European haplotype reference sequences (H1-H4), Kapantaidaki et al., 2019; Nugnes et al., 2020) alongside Asian reference sequences representing haplogroups 1 and 2 (Uesugi et al., 2016), as well as *A. camelliae* used as an outgroup. Molecular Phylogenetic was conducted using the Maximum Likelihood (ML) method based on the Hasegawa-Kishino-Yano model (Hasegawa et al., 1985). Initial tree(s) for the heuristic search were obtained automatically by applying Neighbour-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with the superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0,3187)). The analysis involved 17 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd + Noncoding. The final dataset comprised a total of 673 positions. Evolutionary analyses were conducted in MEGA7 (Kumar et al., 2016).

RESULTS

Molecular characterization

PCR amplification of the mitochondrial cytochrome c oxidase subunit I (mtCOI) gene confirmed the presence of *A. spiniferus* in eight of the ten analysed samples. The amplified fragments ranged in size from 586 bp to 661 bp. Haplotype H1 was detected in 62.5%, and haplotype H2 in 37.5% of the analyzed samples. On the island of Hvar (Split-Dalmatia County), only haplotype H1 was identified in OSW collected from lemon, native plants, and ornamental hosts (*Parthenocissus quinquefolia* (L.) Planch. and *Bougainvillaea spectabilis* Willd). In Dubrovnik-Neretva County, both haplotypes were present in OSW collected from different host plants. Interestingly, at the Vitaljina 3 location, haplotype H1 was recorded in 2019, whereas haplotype H2 was detected in 2020 from samples collected on the same host species (*C. unshiu*). All analysed sequences from this study, reference sequences and their respective accession numbers are listed in Table 2.

Table 2. Sampling location, county, year and host plant of *A. spiniferus* used in the mtCOI sequence analysis and their corresponding phylogenetic group

Code	Location	County*	Host Plant	Year	Haplotype	Acc. No.
2	Ivan Dolac, Hvar Island	SD	*Bougainvillaea spectabilis* Willd.	2019	H1	PV682777
3	Molunat	DN	*Citrus aurantium* L.	2019	H1	OR493434
4	Ljuta 2	DN	*C. aurantium* L.	2019	H2	OR493470
5	Ivan Dolac, Hvar Island	SD	*Parthenocissus quinquefolia* (L.) Planch.	2019	H1	OR495607
6	Ljuta 1	DN	*C. unshiu* Marcow.	2019	H2	PV682701
7	Ivan Dolac, Hvar Island	SD	*C. limon* (L.) Burm f.	2019	H1	PV682778
8	Vitaljina 3	DN	*C. unshiu* Marcow.	2019	H1	PV682702
10	Vitaljina 3	DN	*C. unshiu* Marcow.	2020	H2	OR499882
A. spiniferus haplotype reference sequences (Kapantaidaki et al., 2019**, Uesugi et al. 2016***)						
-	Greece - Corfu	-	*C. sinensis* (L.) Osbeck	-	H1**	MH700443
-	Greece, Italy, Montenegro	-	*C. limon*, *C. sinensis*, *C. reticulata* Blanco	-	H2**	MH700444
-	Greece, Italy	-	*C. limon*, *C.sinensis*, *Rosa* sp.	-	H3**	MH700445
-	Greece - Corfu	-	*C. limon*, *Rosa* sp.	-	H4**	MH700446
-	China	-	*C. unshiu* Marcow.	-	A1-2***	AB786715
-	China	-	*C. unshiu* Marcow.	-	A1-4***	AB786717
-	China	-	*C. unshiu* Marcow.	-	A2-2***	AB786719
-	China	-	*C. unshiu* Marcow.	-	A2-4***	AB786721
Aleurocanthus camelliae (Uesugi et al. 2016***)						
-	China	-	*Camellia sinensis* (L.) Kuntze		B2***	AB786712

* SD – Split–Dalmatia County; DN – Dubrovnik–Neretva County
** Haplotypes according to Kapantaidaki et al. (2019)
*** Haplotypes according to Uesugi et al. (2016)

Data analyses

According to the phylogenetic tree (Figure 2), all Croatian sequences revealed the presence of two haplotypes, H1 and H2. They clustered within haplogroup 2, together with sequences from other European populations and two sequences from China. The tree with the highest log likelihood (-1737,67) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches.

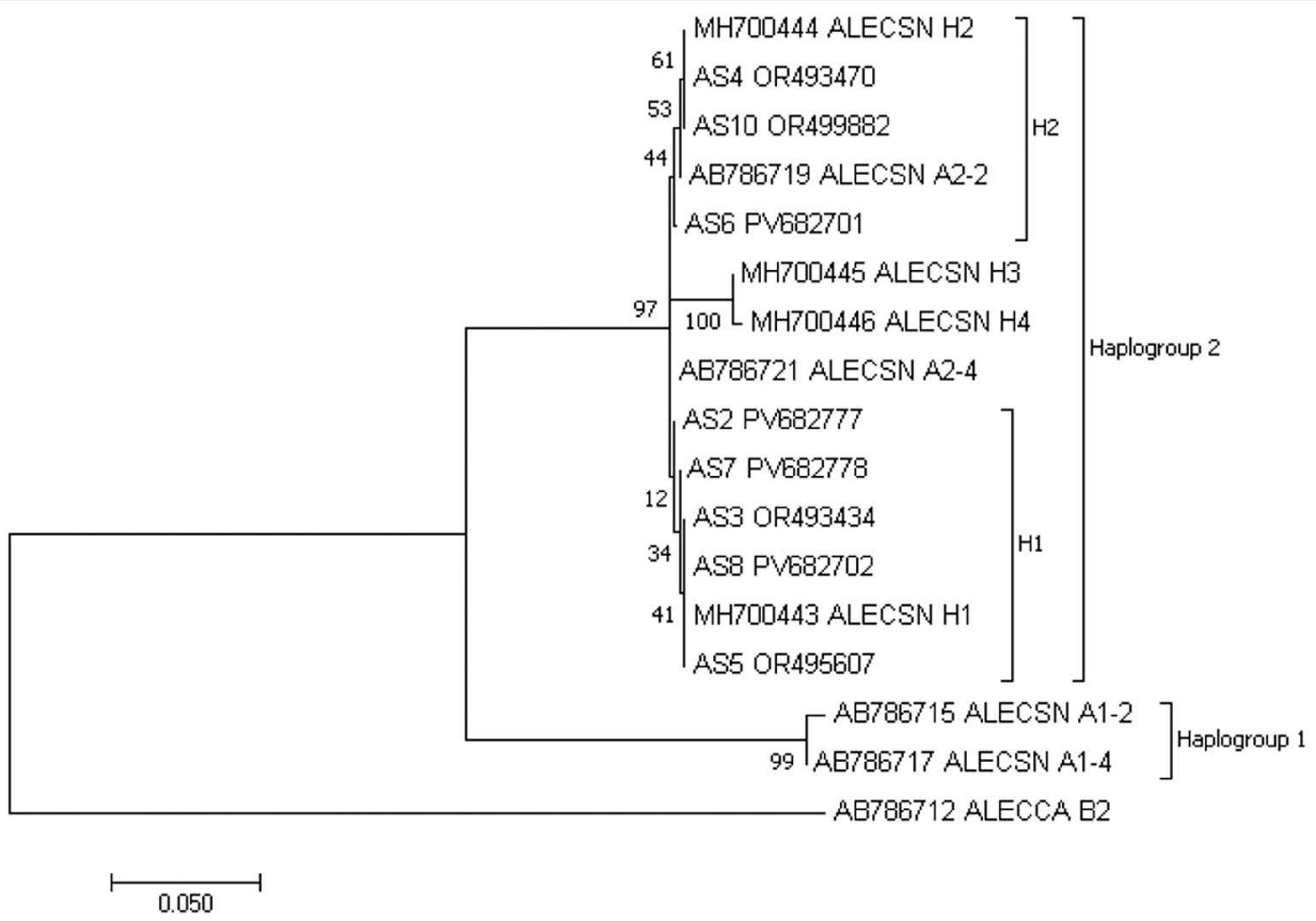

Figure 2. Molecular Phylogenetic analysis by the Maximum Likelihood method (source: Mega 7)

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DISCUSSION

Mitochondrial COI gene analysis in this study revealed two haplotypes, H1 and H2, both belonging to mitochondrial haplogroup A2, which is prevalent among European populations (Uesugi et al., 2016). This finding aligns with previous studies conducted in Greece, Italy, Montenegro, and Albania (Kapantaidaki et al., 2019; Nugnes et al., 2020), although two additional haplotypes, H3 and H4, were found in Greece, both geographically restricted (Kapantaidaki et al., 2019). Haplotype H3 was initially detected in Apulia, but subsequent surveys failed to confirm its presence, likely due to its limited distribution (Kapantaidaki et al., 2019; Nugnes et al., 2020). Presence of only H1 and H2 haplotypes in Croatian samples, indicating a more limited genetic diversity in comparison to the species' native range.

Given the geographical proximity to the border, it was initially assumed that only a single haplotype, identical to the one present in Montenegro (haplotype H2 is prevalent), would dominate in Vitaljina. However, analysis of the obtained results revealed the presence of both haplotypes, H1 and H2. The detection of haplotype H1 in the first year and haplotype H2 in the second year of the study suggests multiple introductions in Croatia, which is consistent with patterns recorded in other European countries (Kapantaidaki et al., 2019; Nugnes et al., 2020). For definitive confirmation of this hypothesis, additional, more extensive research is required. A similar pattern was observed in Molunat, a coastal town 2 km north of Vitaljina, where only haplotype H1 was detected, and also, the exclusive presence of H1 on the island of Hvar. This observation supports the hypothesis that the occurrence of *A. spiniferus* on Hvar Island is primarily the result of introduction through imported ornamental plant material, which is highly relevant to pest spread monitoring at the regional and European levels. Consistent with Nugnes et al. (2020), our results did not confirm a strict association between specific haplotypes and host plants. Based on results from Croatia, both haplotypes (H1 and H2) were identified in samples collected from various host plants. Haplotype H1 was detected in specimens from citrus (*Citrus* spp.) as well as ornamental hosts (*Bougainvillaea spectabilis*, *Parthenocissus quinquefolia*), whereas haplotype H2 predominated in samples collected exclusively from citrus plants at multiple locations. In Italy, Nugnes et al. (2020) reported the occurrence of haplotype H2 in grapevine. Our findings corroborate previous research indicating the absence of a strict association between a specific haplotype and a particular host plant (Nugnes et al., 2020). The presence of identical or highly similar haplotypes in multiple countries raises two plausible scenarios: multiple, independent introduction events or ongoing spread facilitated by trade in plant material and the natural dispersal capacity of the insect. Long-distance dispersal of *A. spiniferus* is already recognised as a major route for the introduction of whitefly species into new regions (Kanmiya et al., 2011; Nugnes et al., 2020).

The results of this study are consistent with previous scientific findings indicating that reduced genetic diversity in Croatian populations of *A. spiniferus* is likely the result of the introduction of a limited number of individuals from the species' native range (Malacrida et al., 1998; Bonizzoni et al., 2004; Dlugosch and Parker, 2008). The observed decline in mitochondrial genetic diversity in introduced populations is considered a consequence of a gene bottleneck, during which only a limited number of genetic lineages persisted, resulting in reduced overall haplotype diversity (Guillemaud et al., 1997; Uesugi et al., 2016). Higher haplotype diversity, as seen in the native range, would be expected under scenarios involving multiple, repeated introductions (Grapputo et al., 2005).

Interestingly, all European haplotypes identified as belonging to haplogroup 2, while haplotypes of haplogroup 1, which are mostly reported from China and predominantly associated with *C. unshiu*, have not yet been detected in Europe (Uesugi et al., 2016). Moreover, the absence of haplogroup 1 in European samples may reflect either limited dispersal from its native range or ecological constraints related to host plant availability and environmental conditions. Since *A. spiniferus* is a quarantine pest in the EU, the results of this study further underscore the need to strengthen national phytosanitary measures and enhance the monitoring of plant material imports, particularly ornamental plants, which often evade strict inspection protocols. The confirmed presence of multiple haplotypes with distinct spatial distributions across Europe underscores the need for continued research. In particular, further investigation into the spread and genetic diversity of *A. spiniferus* in Croatia is essential to understand invasion pathways and enable the timely implementation of control measures.

CONCLUSIONS

Analysis of Croatian *A. spiniferus* populations revealed low mitochondrial diversity, with only haplotypes H1 and H2 detected. The spatial and temporal variability in haplotype presence suggests multiple, independent introduction events. Given that previous European studies have confirmed a widespread presence of haplotype H1 in countries where this species has been genetically analysed, these results suggest that Croatian populations originated from a limited number of source populations, with the possibility of multiple, independent introduction events linked to the trade of ornamental plants. The findings highlight the need to strengthen phytosanitary measures further and to conduct continuous genetic monitoring in order to more accurately reconstruct invasion pathways and improve management of this pest.

REFERENCES

Bonizzoni, M., Guglielmino, C.R., Smallridge, C.J., Gomulski, M., Malacrida, A.R., Gasperi, G. (2004) On the origins of medfly invasion and expansion in Australia. Molecular Ecology, 13, 3845-3855. DOI: https://doi.org/10.1111/j.1365-294X.2004.02371.x

Bubici, G., Prigigallo, M. I., Garganese, F., Nugnes, F., Jansen, M., Porcelli, F. (2020) First report of *Aleurocanthus spiniferus* on *Ailanthus altissima*: profiling of the insect microbiome and MicroRNAs. Insects, 11 (3), 161. DOI: https://doi.org/10.3390/insects11030161

Cioffi, M., Cornara, D., Corrado, I., Jansen, M.G.M., Porcelli, F. (2013) The status of *Aleurocanthus spiniferus* from its unwanted introduction in Italy to date. Bulletin of Insectology, 66 (2), 273-281.

Dlugosch, K.M., Parker, M. (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Molecular Ecology, 17, 431-449. DOI: https://doi.org/10.1111/j.1365-294X.2007.03538.x

Dubey, A.K., Ko, C.C. (2012) Sexual dimorphism among species of *Aleurocanthus* Quaintance & Baker (Hemiptera: Aleyrodidae) in Taiwan, with one new species and an identification key. Zootaxa, 3177, 1-23. DOI: https://doi.org/10.11646/zootaxa.3177.1.1

EPPO (2025a) *Aleurocanthus spiniferus*. EPPO datasheets on pests recommended for regulation. Available at: https://gd.eppo.int [Accessed 10 March 2025].

EPPO (2025b) Global Database. *Aleurocanthus spiniferus* (ALECSN). Available at: https://gd.eppo.int/taxon/ALECSN [Accessed 22 June 2025].

European Commission. 2016. Regulation (EU) 2016/2031 of the European Parliament and of the Council on protective measures against pests of plants. Official Journal of the European Union, L 317, 4-104.

European Commission. 2016. Commission Implementing Regulation (EU) 2019/2072 establishing uniform conditions for the implementation of Regulation (EU) 2016/2031. Official Journal of the European Union, L 319, 1-279.

Grapputo, A., Boman, S., Lindstrom, L., Lyytinen, A., Mappes, J. (2005) The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. Molecular Ecology, 14, 4207-4219. DOI: https://doi.org/10.1111/j.1365-294X.2005.02740.x

Guillemaud, T., Pasteur, N., Rousset, F. (1997) Contrasting levels of variability between cytoplasmic genomes and incompatibility types in the mosquito *Culex pipiens*. Proceedings of the Royal Society of London, 264, 245-251. DOI: https://doi.org/10.1098/rspb.1997.0035

Gyeltshen, J., Hodges, A., Hodges, G.S. (2005) Orange Spiny Whitefly, *Aleurocanthus spiniferus* (Quaintance) (Insecta: Hemiptera: Aleyrodidae), Entomology and Nematology Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, 1-4.

Hasegawa M, Kishino H, Yano T. (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution, 22 (2),160-174. DOI: https://doi.org/10.1007/BF02101694

Jansen, M., Porcelli, F. (2018). *Aleurocanthus camelliae* (Hemiptera: Aleyrodidae), is a species possibly new for the European fauna of a genus in great need of revision. Tijdschrift voor Entomologie, 161 (2), 63-78. DOI: https://doi.org/10.1163/22119434-00002075

Kanmiya, K., Ueda, S., Kasai, A., Yamashita, K., Sato, Y., Yoshiyasu, Y. (2011) Proposal of new specific status for tea-infesting populations of the nominal citrus spiny whitefly *Aleurocanthus spiniferus* (Homoptera: Aleyrodidae). Zootaxa, 2797, 25-44. DOI: https://doi.org/10.11646/zootaxa.2797.1.3

Kapantaidaki, D.E., Antonatos, S., Kontodimas, D., Milonas, P., Papachristos, D.P. (2019). Presence of the invasive whitefly *Aleurocanthus spiniferus* (Hemiptera: Aleyrodidae) in Greece, Bulletin OEPP/ EPPO Bulletin, 49 (1), 127-131.

Kumar, S., Stecher, G., Tamura, K. (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular biology and evolution, 33 (7), 1870-1874. DOI: https://doi.org/10.1093/molbev/msw054

Kypriotis, A., Katerinis, S., Andreadis, S.S., Navrozidis, E. (2017) Presence, description, and developmental characteristics of the newly emerging quarantine pest *Aleurocanthus spiniferus* in Corfu. In: Abstract book of the 17th Panhellenic Entomological Congress, Athens, Greece.

Malacrida, A.R., Marinoni, F., Torti, C., Gomulski, L.M., Sebastiani, F., Bonvicini, C., Gasperi, G., Guglielmino, C.R. (1998) Genetic aspects of the worldwide colonization process of *Ceratitis capitata*. Journal of Heredity, 89, 501-507. DOI: https://doi.org/10.1093/jhered/89.6.501

Martin, J.H. (1987) An identification guide to common pest species of the world (Homoptera: Aleyrodidae). Tropical pest management, 33 (4), 298-322. DOI: https://doi.org/10.1080/09670878709371174

Muniappan, R., Purea, M.F., Sengebau, F., Reddy, G.V.P. (2006) Orange spiny whitefly, *Aleurocanthus spiniferus* (Quaintance) (Homoptera: Aleyrodidae), and its parasitoids in the Republic of Palau. Proceedings of The Hawaiian Entomological Society, 38, 21-25.

Njavro, M. (2007) Otok Hvar – turistička monografija. Zagreb: Turistička naklada. (In Croatian).

Nugnes, F., Laudonia, S., Jesu, G., Jansen, M.G.M, Bernardo, U., Porcelli, F. (2020) *Aleurocanthus spiniferus* (Hemiptera: Aleyrodidae) in some European countries: diffusion, hosts, molecular characterization, and natural enemies. Insects, 11 (1), 42, 1-14.
DOI: https://doi.org/10.3390/insects11010042

Paladin Soče, I., Šimala, M., Gotlin Čuljak, T. (2020) Trnoviti štitasti moljac agruma *Aleurocanthus spiniferus* (Quaintance, 1903) u Dubrovačko-neretvanskoj županiji. Glasilo biljne zaštite, 20 (4), 441-448. (In Croatian).

Picciotti, U., Araujo-Dalbon, V., Ciancio, A., Colagiero, M., Cozzi, G., De Bellis, L., Finetti-Sialer, M. M., Greco, D., Ippolito, A., Lahbib, N., Logrieco, A. F., López-Llorca, L. V., Lopez-Moya, F., Luvisi, A., Mincuzzi, A., Molina-Acevedo, J. P., Pazzani, C., Scortichini, M., Scrascia, M., ... Porcelli, F. (2023) "Ectomosphere": Insects and Microorganism Interactions. Microorganisms, 11 (2), 440.
DOI: https://doi.org/10.3390/microorganisms11020440

Porcelli, F. (2008) The first record of *Aleurocanthus spiniferus* (Homoptera: Aleyrodidae) was in Apulia, Southern Italy. Bulletin OEPP/EPPO Bulletin, 38, 516-518.

Radonjić, S., Hrnčić, S., Malumphy, C. (2014) First record of *Aleurocanthus spiniferus* (Quaintance) (Hemiptera: Aleyrodidae) in Montenegro. Redia, XCVII, 141-145.

Rapisarda, C., Longo, S. (2021) First report from Sicily (Italy) of the Orange spiny whitefly, *Aleurocanthus spiniferus* (Quaintance) (Hemiptera: Aleyrodidae), and its potential risk for the Italian citrus industry. Bulletin OEPP/EPPO Bulletin, 51 (2), 1–4.

Šimala, M., Masten Milek, T. (2013) First record of whitefly quarantine species *Aleurocanthus spiniferus* Quaintance, 1903 (Hemiptera: Aleyrodidae) in Croatia. Glasilo biljne zaštite, 13 (6), 425-433.

Šimala, M., Masten Milek, T., Pintar, M. (2013) Narančin trnoviti štitasti moljac *Aleurocanthus spiniferus* (Quaintance, 1903) (Hemiptera, Aleyrodidae, Aleyrodinae). Hrvatski centar za poljoprivredu hranu i selo. Zagreb. Available at: https://www.hapih.hr/wp-content/uploads/2021/07/narancin-trnoviti-stitasti-moljac.pdf [Accessed 23 June 2025]. (In Croatian).

Šimala, M., Pintar, M., Kajić, Z., Masten Milek, T. (2019a) Prvi nalaz narančinog trnovitog štitastog moljca u proizvodnom nasadu agruma u RH. In: Proceedings of the 63rd Seminar of Plant Protection, Opatija, 5-8 February 2019, 64-65. (In Croatian).

Šimala, M., Pintar, M., Masten Milek, T., Markotić, V., Kajić, Z., Kotlar, A., Paladin, I. (2019b) Narančin trnoviti štitasti moljac – opasan invazivni štetnik. Glasilo biljne zaštite, 6 (19), 640-648. (In Croatian).

Streito, J. C., Mendes, E., Sanquer, E., Strugarek, M., Ouvrard, D., Robin-Havret, V., Poncet, L., Lannou, C., Rossi, J. P. (2023) Incursion preparedness, citizen science and early detection of invasive insects: The case of *Aleurocanthus spiniferus* (Hemiptera, Aleyrodidae) in France. Insects, 14 (12), 916.
DOI: https://doi.org/10.3390/insects14120916

Uesugi, R., Sato, Y., Han, B. Y., Huang, Z. D., Yara, K., Furuhashi, K. (2016) Molecular evidence for multiple phylogenetic groups within two species of invasive spiny whiteflies and their parasitoid wasp. Bulletin of Entomological Research, 106 (3), 328-340.
DOI: https://doi.org/10.1017/S0007485315001030

Van den Berg, M.A., Greenland, J. (1997) Classical biological control of *Aleurocanthus spiniferus* (Hemiptera: Aleyrodidae), on citrus in Southern Africa. Entomophaga, 42 (4), 459-465.