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HELLAS-ALIENS. The invasive alien species of Greece: time trends, origin and pathways

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Abstract

The current paper presents the first effort to organize a comprehensive review of the Invasive Alien Species (IAS) of Greece. For this purpose, a database was developed with fields of information on the taxonomy, origin, ecology and pathways of introduction of terrestrial, freshwater and marine species. Our database includes a) taxa in the Union's list that are present in Greece, b) taxa already present in Greece and considered to be invasive, and c) taxa highly likely to enter Greece in the next 10 years and become invasive. The Database served as the starting point for the compilation of the National List of Alien Invasive Species (HELLAS-ALIENS) in compliance with the EU Regulation 1143/2014. Overall, the HELLAS-ALIENS comprises 126 species, i.e. 32 terrestrial and freshwater plant species, 14 terrestrial invertebrates, 28 terrestrial vertebrates, 30 freshwater fishes and invertebrates and 22 marine species. Terrestrial invertebrates, birds and mammals are mainly of Asiatic origin. Most of the terrestrial plants have their native geographical distribution in the Americas (North and South). Most of the freshwater invertebrates and fishes are of North American origin, while the majority of the marine species are of Indo-Pacific origin. The first records of IAS concern terrestrial plant species, and date back to the 19th century, while those in freshwater and marine ecosystems seem to have been systematically recorded some decades later. Regarding the pathways of introduction, most of the taxa arrived in Greece or are expected to arrive through escape from confinement and unaided. The majority of the terrestrial, freshwater and marine species have been evaluated as of High-risk for the indigenous biodiversity and only 3% of the species listed have been evaluated of Low-risk. Our results provide an important baseline for management and action plans, as required by the priorities set by the European Union through the Biodiversity Strategy for 2030.

Keywords

European Union, Invasive Alien Species Regulation, pathways of introduction, risk assessments, temporal trends

Introduction

Biological invasions are a major threat to biodiversity, ecosystem services, the economy and human health (Millennium Ecosystem Assessment 2005; Díaz et al. 2019). Invasive alien species (IAS) pose a significant threat to the receiving environment (Simberloff et al. 2013) impacting species' habitats, synthesis of communities and ecosystem functioning (Hulme 2015; Bellard et al. 2016).

New introductions of alien species have been accelerated in recent decades by the rapid globalization, urbanization and intensification of human activities (Seebens et al. 2017). For example, at a Pan-European scale, a trends' indicator for marine alien species, based on the annual rate of introductions at 6-year cycles, has revealed an increase in new alien species from 6 in the period 1970-75 to 21 new alien species per year in the period 2012-17 (Zenetos et al. 2022). Moreover, climate change and the increase in temperature can further induce the introduction and successful establishment of marine species and fishes in particular (Karachle et al. 2022). A similar increase has been documented for groups of terrestrial species invasions. For instance, the number of terrestrial plants first recorded in the wild as alien to Europe exhibited a remarkable increase in the 20th and 21st centuries, with a constant increase between 1951 and 2010 (Arianoutsou et al. 2021). However, opposite trends have also been reported, i.e., in the new introduction events of the 16 invasive mammals of Union concern in Europe from the 1960s onwards (Tedeschi et al. 2021). In addition, the impacts of IAS may range from changes in the abiotic environment increasing the risk of disturbances, to contributing to the decline of native biodiversity (Ehrenfeld 2010; Schirmel et al. 2016; Catford et al. 2018; Essl et al. 2020; Pyšek et al. 2020) and even to extirpations, and in extreme cases to local extinctions, especially when the competition for resources is high (Gallardo et al. 2019).

Databases are important for gathering, sharing and disseminating information on alien species, fundamental for management, scientific and educational purposes (Dyer et al. 2017). At the European level, the project Delivering Alien Species Inventories for Europe (DAISIE 2009) was a milestone in creating a European database of alien species. Similar initiatives were undertaken at a regional scale, such as the NOBANIS

European Network on Invasive Alien Species (NOBANIS 2021) for North and Central Europe, and the East and South European Network for Invasive Alien Species (ESENIAS 2020). An important step towards this goal is the European Alien Species Information Network (EASIN 2020) which has been developed by the European Commission's Joint Research Centre (https://easin.jrc.ec.europa.eu). EASIN acts as a focal point for sharing and disseminating information, where available knowledge on alien species from various data sources is standardized, harmonized and integrated (Katsanevakis et al. 2015). Global datasets, such as the Global Biodiversity Information Facility (GBIF 2020) and the CABI-Invasive Species Compendium (CABI 2020), which also include records of alien species in Europe, should be also mentioned.

At the country scale, the ELNAIS network and database (Zenetos et al. 2015) were established to record and monitor the introductions and spread of aquatic IAS (freshwater and marine species) in Greece. Concerning the alien plant species of Greece, a web-based database was created (https://www.alienplants.gr/) as a by-product of the compilation of the Flora of Greece project (Dimopoulos et al. 2020). There are other databases based mainly on information collected from citizen scientists e.g. the Alientoma database for alien insects of Greece (Kalaentzis et al. 2021).

The European Regulation 1143/2014 encompasses the list of IAS of Union Concern. The EU Regulation (hereafter referred to as the IAS Regulation) requires EU Member States to compile their national lists of IAS and carry out a comprehensive analysis and prioritization of the pathways of introduction and spread of IAS of Union concern. Greece initiated its alignment with the Regulation in February 2021 after an open call for tenders which rendered a project to the research group comprised of the authors of the current work. It was soon realized that any effort to compile a list of IAS should be supported by a database, with all important information on species origin, traits, status, habitat, pathways of introduction, potential impacts and geographical distribution.

The current work reports on the compilation of the Greek national list of IAS (HELLAS-ALIENS), along with their time trends, origin, principal pathways of introduction, and assessment of the risk they might impose.

Material and method

Compilation of the national list of IAS of Greece (hereafter HELLAS-ALIENS) was based on the following criteria:

i. Taxa already present in Greece that are included in the List of Invasive Alien Species of Union concern (hereafter mentioned as EU list) or were proposed to be included in the third update of the list entered into force on 2 August 2022.

ii. Taxa established in the wild and considered invasive (Arianoutsou et al. 2010; Barbieri et al. 2015; Zenetos et al. 2020, experts' opinion).

iii. Taxa not currently present in Greece but highly likely to be introduced within the next 10 years, assessed during a Horizon Scanning (HS) exercise that took place within this project, following the methodology suggested by Roy et al. (2014, 2015, 2019) and implemented by Peyton et al. (2019, 2020), Lucy et al. (2020) among others. For this, five groups of experts corresponding to the five groups of organisms studied were formed. Each expert scored each species based on their likelihood of i) arrival, (ii) establishment, (iii) spread, and (iv) magnitude of the potential negative impact on biodiversity within Greece for the next 10 years. Each group of experts had sequential exhaustive meetings where discussions were held on the final scoring of each species. Finally, a general workshop was held jointly with all experts where a consensus on the first 29 species that had the highest score was reached, and consequently these taxa were included in the HELLAS-ALIENS.

Taxa considered to be included in HELLAS-ALIENS were plants of the terrestrial environment (those of freshwater included), terrestrial vertebrates and invertebrates, freshwater fishes and invertebrates and marine organisms. Cryptogenic species were not considered.

For the selected taxa, contextual/relative information (available until November 2021) was collected and inserted in an exhaustive database, supporting and complementing the HELLAS-ALIENS. The structure of the database is given in Table 1.

For the classification of species with respect to their pathways of introduction into a new area, the Convention on Biological Diversity scheme (CBD 2014) was adopted, which is also used by EASIN (see for example Arianoutsou et al. 2021). This classification scheme follows the six main categories of pathways proposed by Hulme et al. (2008). In the pathways' data analysis, we included information concerning taxa that are already present in Greece, but also taxa that are very likely to arrive within the next ten years based on the HS procedure. The category "Unknown" has been excluded.

For filling the fields of the database various sources have been used: extensive literature reviews and peer-reviewed publications, existing databases [e.g. FishBase (Froese and Pauly 2022), ELNAIS], personal and citizen-scientists observations, such as iNaturalist, GBIF, or eBird (Sullivan et al. 2009), gray literature (i.e. reports, conference proceedings, theses), and occasionally personal communication with experts.

Table 1. General Structure of HELLAS-ALIENS database.

Category of information	Information
Taxonomy	Scientific name of species, genus, family, order, class
Alien status	Invasive, potentially invasive, established, casual, unknown
Origin	(non-exhaustive) Asian, American, Australian (for terrestrial and fresh water taxa), Circumtropical, Western Indo-Pacific (for marine taxa)
Year of first observation in the wild	When available
Pathway	Based on the CBD (2014) classification scheme
Impact	Health, Economy, Natural Ecosystems, other ecosystem services (e.g., fisheries, tourism)
Geolocation	Coordinates (WGS84), Region, Sea, Locality, Natura 2000 site, Island, Mountain
Taxa specific traits	(non-exhaustive) in plants: Growth form, life form, pollination mode, flowering period, fruit type, dispersal mode
	(non-exhaustive) in birds: General guilds (e.g. birds of prey, landbirds, parakeets etc.), nest type, diet
Habitat	EUNIS, when available till level 2 (Davies et al. 2004)
References	Full reference of the bibliographic sources used for the compilation of information
Comments	When applicable

For species' nomenclature, the most updated and widely accepted sources were used. In particular, the terrestrial plants' nomenclature followed mostly the World Flora Online (2022), except for *Pontederia crassipes* and *Elodea densa*, for which the names *Eichornia crassipes* and *Egeria densa*, as listed in the EU list, have been retained. The terrestrial vertebrates' nomenclature followed the IUCN Red List approach (IUCN 2022), except for two mammal species, the small Indian mongoose (treated as *Herpestes javanicus* in the EU list and as *Herpestes auropunctatus* in the IUCN Red List) and the Siberian chipmunk (treated as *Tamias sibiricus* in the EU list and as *Eutamias sibiricus* in the IUCN Red List), which have been treated according to the EU list approach. For the bird taxa, the IUCN Red List approach based on version 5 of the HandBook of the Birds of the World and BirdLife International (2020) has been followed. For terrestrial invertebrates, the CABI Compendium has been consulted regarding species nomenclature (CABI 2020). For the freshwater species, we consulted the World Register for Marine Species (WoRMS Editorial Board 2022), the National Biodiversity Atlas (NBN), FishBase and Barbieri et al. (2015). Finally, for marine species' nomenclature, we followed the World Register of Marine Species (WoRMS Editorial Board 2022).

For the risk assessments (RAs) of taxa a mixed approach, based on the EU risk assessment framework that is compiled with the EU Regulation 1143/2014 and was developed under the "Study on Invasive Alien Species – Development of risk assessments to tackle priority species and enhance prevention" (European Commission 2021), was adopted. Two different versions, adjusted to the Greek bioclimatic conditions, were built: i) an Adapted RA, for the EU list taxa that are already present in the country, which focuses mainly on the impacts of these species (19 taxa in total), and ii) a Summary RA, for the remaining IAS included in the HELLAS-ALIENS and are already present in the country or were shortlisted through the HS procedure, that focuses on impacts and their potential for introduction, entry, establishment and spread (107 taxa in total). Taxa were classified as Low, Medium or High-risk according to the likelihood and consequences of their introduction, establishment, spread, and impact potential.

Results

Overall, the HELLAS-ALIENS comprises 126 species, allocated in five general groups corresponding to terrestrial and freshwater plants (32 species), terrestrial invertebrates (14 species), terrestrial vertebrates (28 species), freshwater fishes and invertebrates (30 species) and marine species (22 species) (see Species List in Suppl. material 1).

General information

Terrestrial – Freshwater plants

Of the 32 plant species of the HELLAS-ALIENS, 18 are considered invasive in Greece (*Acacia saligna*, *Acer negundo*, *Ailanthus altissima*, *Azolla filiculoides*, *Bidens frondosa*, *Carpobrotus edulis*, *Cotula coronopifolia*, *Datura stramonium*, *Heliotropium curassavicum*, *Ludwigia grandiflora*, *Ludwigia peploides*, *Nicotiana glauca*, *Opuntia ficus-indica*, *Oxalis pes-caprae*, *Paspalum distichum*, *Phytolacca americana*, *Robinia pseudoacacia* and *Solanum elaeagnifolium*) (Arianoutsou et al. 2010; Dimopoulos et al. 2020) and ten were added to the list following the HS procedure. Twelve species are in the EU list. Among them, four (*Acacia saligna*, *Ailanthus altissima*, *Ludwigia grandiflora* and *L. peploides*) are already established in Greece, one (*Pennisetum setaceum*) has been observed as a casual escape from cultivation, six (*Eichhornia crassipes*, *Egeria densa*, *Elodea nuttallii*, *Hydrocotyle ranunculoides*, *Myriophyllum aquaticum* and *M. heterophyllum*) are known as either cultivated or added through the HS procedure, while the presence of *Impatiens glandulifera* in a single locality in northern Greece needs confirmation. One more species *Pistia stratiotes* (cultivated, added after the HS), has been recently included in the EU list with entry force in 2024. *Egeria densa*, *Fallopia baldschuanica*, *Reynoutria japonica* and *R.* × *bohemica* are included in the list of IAS of the European and Mediterranean Plant Protection Organization (EPPO).

Terrestrial invertebrates

Twelve out of the 14 terrestrial invertebrate species included in the HELLAS-ALIENS are present in the country. These are ten insects (*Aedes albopictus*, *Cydalima perspectalis*, *Halyomorpha halys*, *Harmonia axyridis*, *Linepithema humile*, *Paysandisia archon*, *Rhynchophorus ferrugineus*, *Solenopsis geminata*, *Xylotrechus chinensis*, *Xylotrechus stebbingi*), one acari (*Tetranychus evansi*), and one platyhelminth (*Caenoplana bicolor*). Two species considered during the HS process as highly likely to arrive in the country were also included in the list, namely *Bursaphelenchus xylophilus* (the pine wood nematode or pine wilt nematode) and *Megachile sculpturalis* (the giant resin bee). One of the terrestrial invertebrate species of the HELLAS-ALIENS, *Solenopsis geminata* (fire ant) was included in the latest version of the EU list.

Terrestrial vertebrates

Terrestrial vertebrate species of the HELLAS-ALIENS included 28 species of amphibians, reptiles, birds, and mammals.

Amphibians

Three amphibians have been included: *Lithobates catesbeianus*, (American bullfrog), included in the EU list and well established in Crete, *Xenopus laevis*, (African clawed frog), a recent addition in the EU list that has casual occurrences in urban parks and *Triturus carnifex*, (Italian crested newt), that is highly likely to invade the country within the next ten years.

Reptiles

HELLAS-ALIENS includes five reptile species. *Trachemys scripta*, (pond slider), a species of Union concern and *Podarcis siculus*, (Italian wall lizard) are already established in the country. The Italian wall lizard is native to some parts of Europe, but it is considered invasive in others, with potentially significant impacts on the native herpetofauna (Scalera 2019). The remaining three reptile species have not yet been recorded in the wild but are present in the country, in captivity, as pets. Among them, *Lampropeltis getula*, the common kingsnake, one of the most popular pets among herpers, has been recently added to the EU list.

Birds

Twelve bird taxa are included in the HELLAS-ALIENS. Three bird species with casual presence status in Greece have been included in the catalogue because they are EU-listed (*Acridotheres tristis*, *Alopochen aegyptiaca* and *Threskiornis aethiopicus*). Four bird taxa already established in Greece have been considered and included in the list, as they are threatening biodiversity (*Alectoris rufa*, *Branta canadensis*, *Phasianus colchicus* [non subsp. *colchicus*] and *Psittacula krameri*). The species *Myiopsitta monachus* (Monk Parakeet), well established in Attica, was also selected for the HELLAS-ALIENS following the recommended management approach (White et al. 2019) and as a potential disease vector (Kalodimos 2013; Postigo et al. 2019). Four bird species, selected through the HS exercise (*Corvus albus*, *Pycnonotus cafer*, *Pycnonotus jocosus* and *Pycnonotus leucotis*) were also included.

Mammals

In total, eight species of mammals were included in the HELLAS-ALIENS. Of those, seven are also included in the EU list. Two of them, the coypu, *Myocastor coypus*, and the racoon, *Procyon lotor*, are already established in Greece; three species (*Ondatra zibethicus*, *Nyctereutes procyonoides*, and *Tamias sibiricus*) have casual occurrences in the country; *Herpestes javanicus* has not yet arrived in Greece but was selected through the HS exercise. The species *Callosciurus finlaysonii* is present in the country only as a pet. Finally, the American mink, *Neovison vison*, though not of Union concern, is well established in Northwest Greece with already recorded impacts on native biodiversity (Galanaki and Kominos 2022).

Freshwater species

The freshwater species of the HELLAS-ALIENS include 16 invertebrates and 14 fish species. With respect to the invertebrates, 12 species are well-established invasive or potentially invasive, while four more, i.e., *Dreissena polymorpha* (Zebra mussel), *Pomacea maculata* (Giant applesnail), *Procambarus clarkii* (the Red swamp crayfish) and *Procambarus virginalis* (Marmorkrebs) were added to the list following the HS procedure. Three freshwater invertebrate species, the established *Pacifastacus leniusculus* (American signal crayfish), and the crayfish species *P. clarkii* and *P. virginalis* currently not present in the wild, are included in the EU list.

As far as freshwater fishes are concerned, 12 species are currently present in the wild, while two more, *Perccottus glenii* (Chinese sleeper) and *Ameiurus melas* (the Black bullhead), were added to the list following the HS procedure as they are expected to invade Greek freshwater ecosystems. *Lepomis gibbosus* (Pumpkinseed) and *Pseudorasbora parva* (Stone moroko), established in Greece, are included in the EU List, while the also established and widespread Eastern mosquitofish *Gambusia holbrooki* was included in the EU list as recently as July 2022. Of the two species that are likely to arrive and invade, *P. glenii* is included in the EU list, while *A. melas* was included in the EU list in July 2022.

Marine species

With respect to the marine species of the HELLAS-ALIENS, five are plants, nine are invertebrates and eight are fishes. Currently, the only marine species in the EU list are the *Plotosus lineatus* (striped catfish) and *Rugulopteryx okamurae* (brown seaweed). Although several marine species were proposed and risk assessed, none was approved for entering the EU list. Among the proposed ones it is worth mentioning two fishes, namely the silver-cheeked toadfish *Lagocephalus sceleratus* and the lionfish *Pterois miles* as well as the blue crab *Callinectes sapidus* and the rapa whelk *Rapana venosa*. The three former species are well established, with a wide distribution in the Greek seas whereas *R. venosa* has been sporadically reported in North Greece (Zenetos et al. 2015; ELNAIS 2022).

Origin of species

The origin of all taxa is presented in Fig. 1A–C.

Most of the plants have their native range in the Americas (North and South), followed by those of Asian and African origin (Fig. 1A). The Asian origin prevails in terrestrial invertebrates, birds and mammals (Fig. 1A). Amphibians originate from one continent each: America, Africa, Europe, and most reptiles are natives of North America. Species native to Europe include one amphibian (*Triturus carnifex*), one reptile (*Podarcis siculus*) and one bird (*Alectoris rufa*).

Most of the freshwater species, both invertebrates (88%, 14 taxa) and fishes (72%, 10 taxa), are of North American and, secondarily, of Asian origin (Fig. 1B). Two invertebrate species are of South American and Oceanian origin respectively, while one fish species is of European and three of Eurasiatic origin.

As far as the marine species are concerned, the vast majority of all taxa are of Indo-Pacific origin (Fig. 1C). Fishes exclusively originate from the Indo-Pacific, whereas plants are also primarily of Indo-Pacific origin, but their introduction is not related to corridors, but to shipping. Finally, concerning the invertebrates, one species (the foraminiferan *Amphiste ginalobifera*) has a circumtropical distribution and two others (the shrimp *Penaeus aztecus* and the blue crab *Callinectes sapidus*) are native to the West Atlantic including the Tropical Atlantic.

Trends of "introductions" in time

The year of the first record in the wild has been detected for all 100 taxa currently present in the country. Data is available for 54 terrestrial species, 24 freshwater spe-

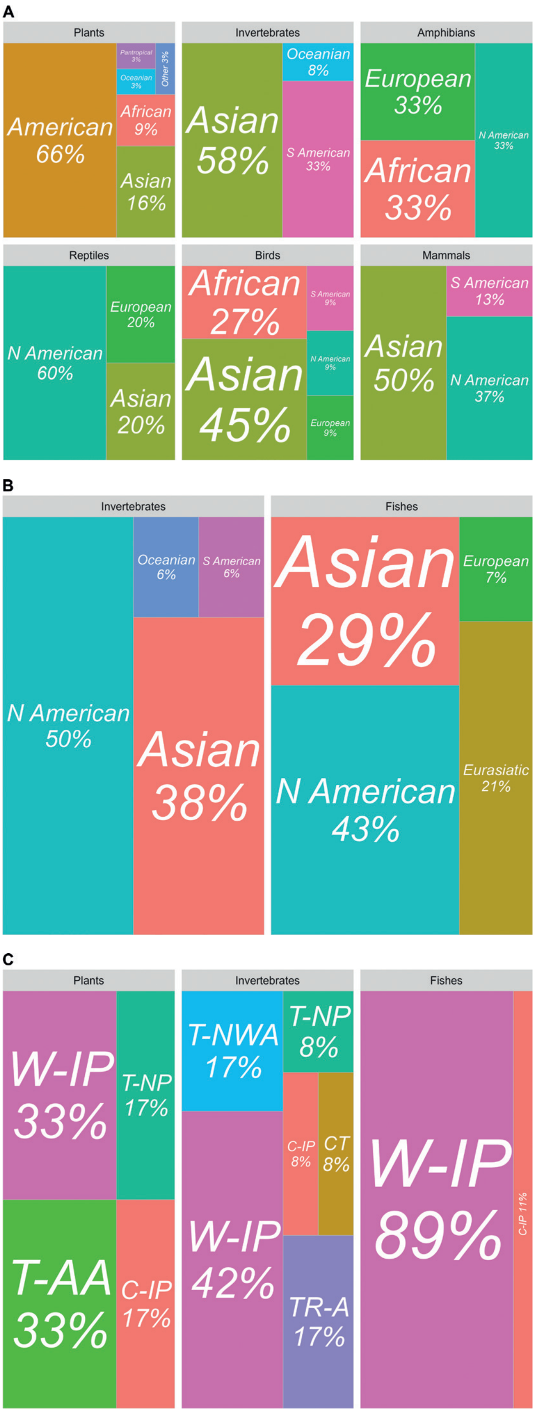

Figure 1. Treemap graphical representation of HELLAS-ALIENS taxa origin. Colours of tiles are consistent within each group of organisms. **A** terrestrial taxa **B** freshwater taxa **C** marine taxa. C-IP: Central Indo-Pacific; W-IP: Western Indo-Pacific; CT: Circumtropical; T-NP: Temperate Northern Pacific; T-NWP: Temperate Northern Western Atlantic; TR-A: Tropical Atlantic; T-AA: Temperate Australo-Asia.

cies and 22 marine species. The rate of introduction of new IAS records shows a rapid increase during the last two decades (Fig. 2), with the highest number of new records originating from terrestrial environments (Fig. 3). The first records of IAS in the country concerned terrestrial plant species and date back to the 19th century while IAS in freshwater and marine ecosystems seem to have been systematically recorded some decades later (Fig. 3).

Pathways

The pathways followed by the IAS of the HELLAS-ALIENS per environment are shown in Fig. 4. Several taxa were linked to more than one introduction pathway. Pathways are given both for species already present in the country, but also for species that are likely to arrive within the next ten years based on the HS procedure followed. The majority of the taxa arrived in Greece or are expected to arrive through escape from confinement, and unaided.

Most of the terrestrial and freshwater plant taxa (27 taxa) have entered, or are expected to enter, Greece through escape from confinement (See Suppl. material 2: fig. S1). Nine taxa were released in the wild for human-use purposes, and eight taxa contaminated unintentionally transferred commodities. Seven taxa have dispersed unaided from adjacent areas where they were already present, and six taxa moved through artificial corridors (mainly canals) and enter the country. Four plant taxa (*Amorpha fruticosa*, *Impatiens glandulifera*, *Ludwigia grandiflora* and *Ludwigia peploides*) use only one main pathway. *Solanum elaeagnifolium* used two principal pathways related to commodities or vectors and in total six sub-categories as a contaminant or stowaway. *Robinia pseudoacacia* also used multiple pathways (two principal), mostly connected to its utilization in forestry, horticulture and erosion control, as well as for ornamental and landscape “improvement” purposes.

Most of the invasive terrestrial vertebrates in Greece have escaped from confinement and this pathway seems to apply also to the species that are expected to enter the country in the next 10 years. Only 17% of the vertebrates enter the country through natural dispersal across borders (Suppl. material 2: fig. S1). *Phasianus colchicus* [non subsp. *colchicus*] (Ring-necked Pheasant) and *Alectoris rufa* (Red-legged Partridge) are the animals released in nature on purpose, as game.

The majority of the terrestrial invertebrates (67%) have arrived as contaminants in transport pathways such as *Xylotrechus chinensis*, followed by transport-stowaway (17%) e.g., *Aedes albopictus* (Suppl. material 2: fig. S1).

Six freshwater invasive invertebrates out of the 16 included in the HELLAS-ALIENS have been introduced through the transport – contaminant pathway (37.5%), six species (37.5%) have entered or are expected to enter unaided, while four species (25%) have escaped or are expected to escape from confinement. Seven freshwater invasive fishes (50%) have entered or are expected to enter the inland water ecosystems of the country unaided. Three species (21.4%) have been un-

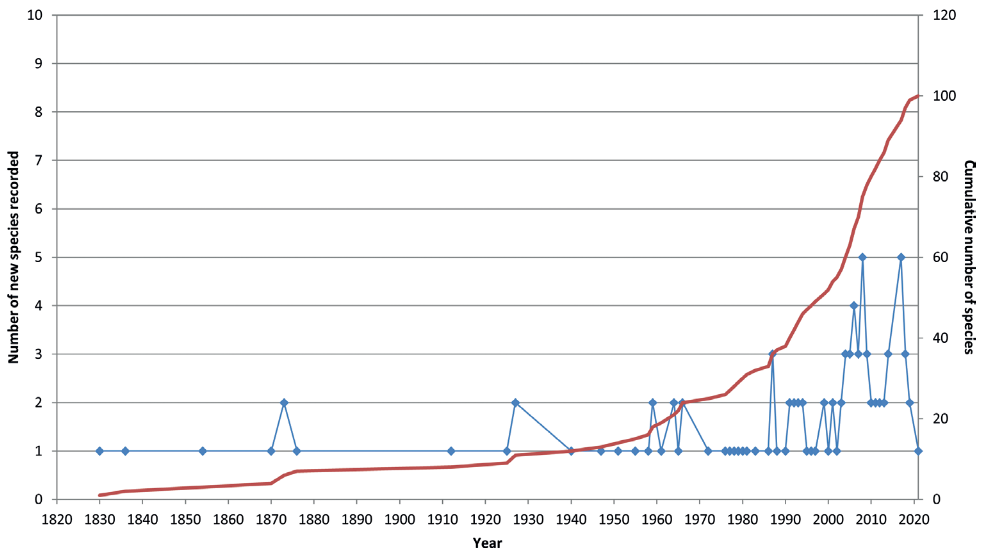

Figure 2. Number of new invasive alien species reported during the 1830–2021 period from Greece (blue) and cumulative number of species (red).

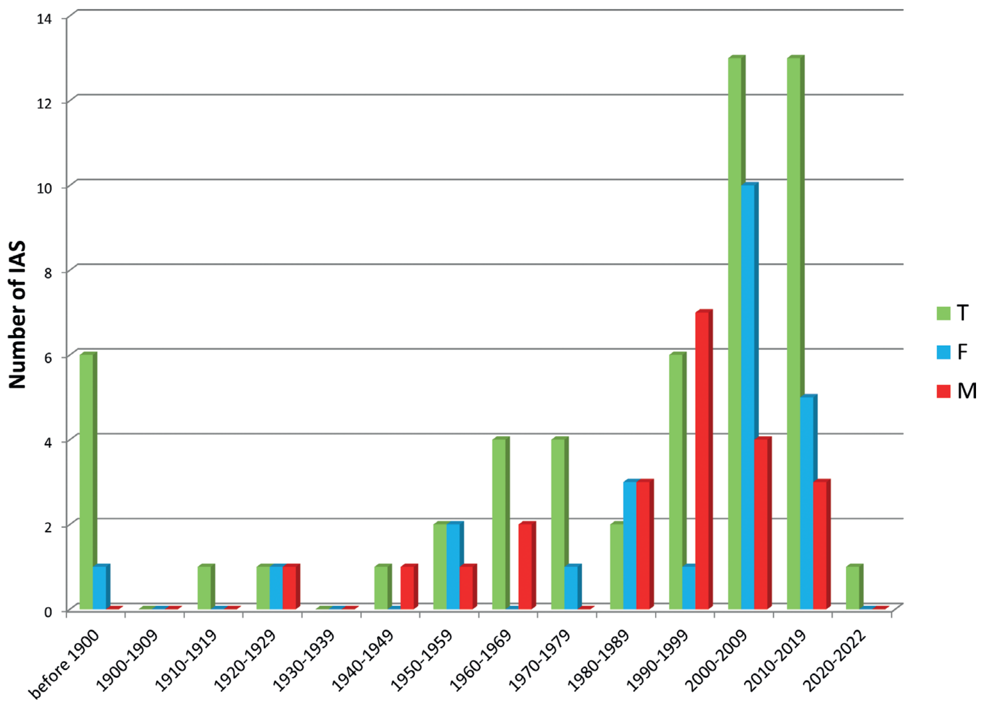

Figure 3. Number of new invasive alien species reported per decade and environment. T: terrestrial; F: freshwater; M: marine taxa.

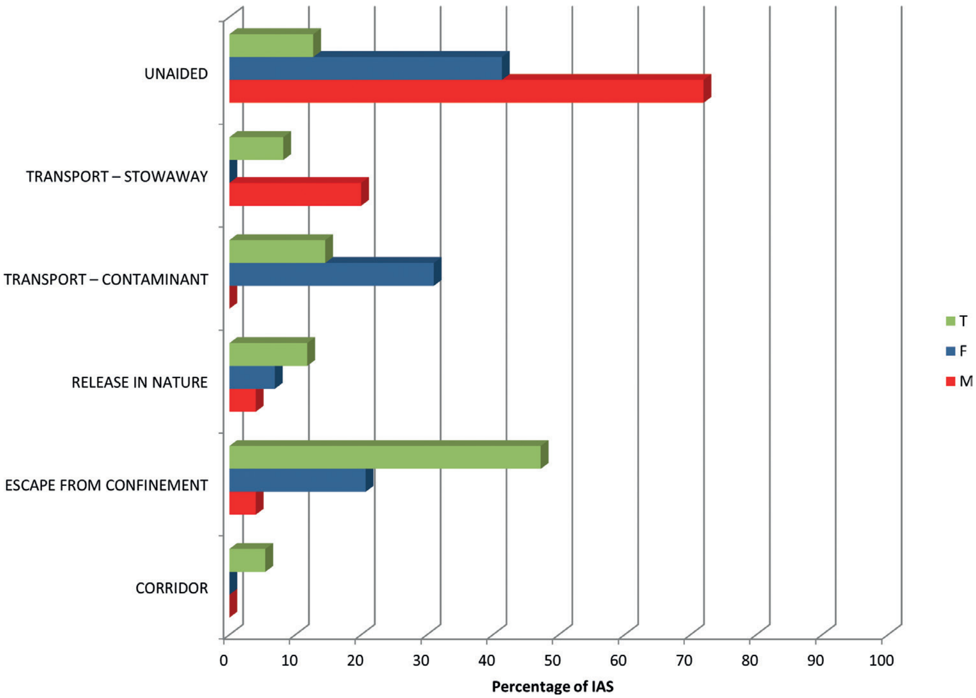

Figure 4. CBD principal introduction pathways for invasive species of Greece per environment. T: terrestrial; F: freshwater; and M: marine taxa.

intentionally introduced as transport-contaminants during commercial fish stockings, two species (14.3%) have escaped from confinement from aquaculture units and two species (14.3%) have been released in nature for sport fishing (*Oncorhynchus mykiss*) and biological control of mosquitoes (*Gambusia holbrooki*) respectively (Suppl. material 3: fig. S2).

Regarding the IAS of the marine environment, all fish species (100%) have arrived unaided (Suppl. material 4: fig. S3). The introduction of marine invertebrate species was facilitated by a more diverse set of sub-pathways to enter or disperse in Greece: 67% have arrived unaided and 17% through transport-stowaway (Suppl. material 4: fig. S3). The majority of the marine plant species (60%) has arrived through transport-stowaway, while 40% have arrived unaided (Suppl. material 4: fig. S3).

Risk assessments and pathways

Out of the 126 taxa, 63% (79 taxa) were evaluated as of High-risk, 34% (43 taxa) as of Medium-risk and only 3% (4 taxa) as of Low-risk. High-risk taxa form the majority in all three environments (terrestrial, freshwater, and marine), with 65%, 60%, and

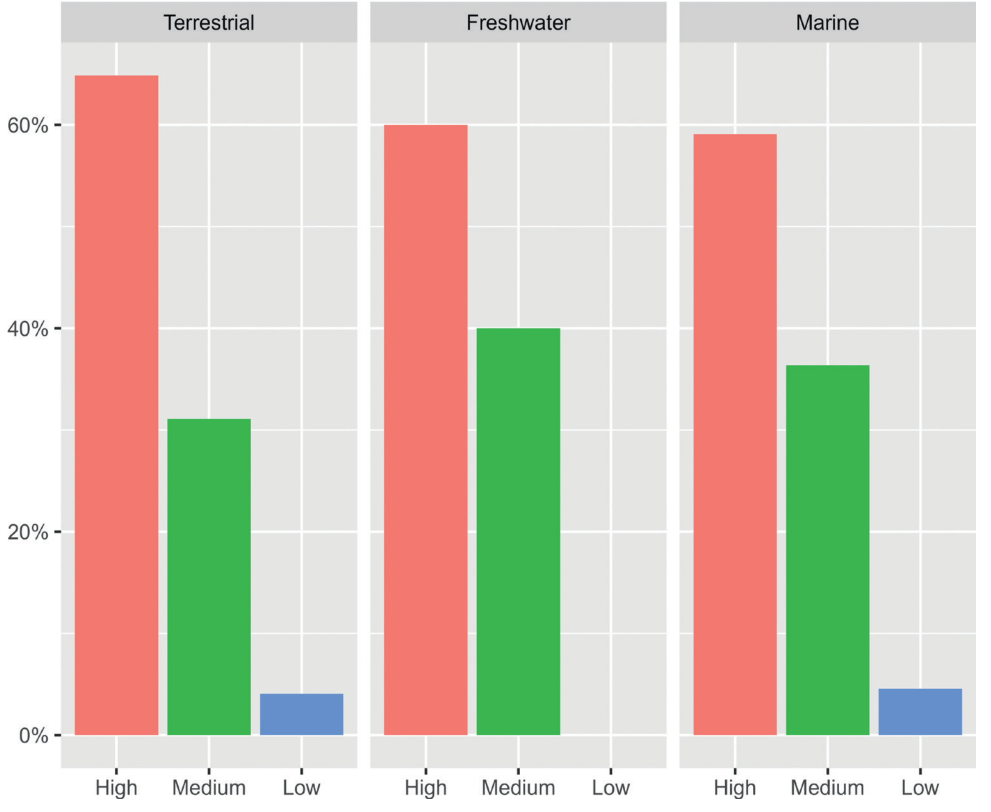

Figure 5. Grouped bar chart representing percentage of taxa per Risk Assessment category across different environments.

59% of taxa respectively (Fig. 5). The highest percentages of High-risk assessed taxa were found specifically for marine plants (100%), birds (92%), terrestrial invertebrates (86%), mammals (75%), freshwater fishes (71%), and reptiles (60%). Most of the High-risk taxa (84%) are already present in the country either in the wild or in cultivation/captivity.

In the High-risk RA category, 37 taxa have entered or are expected to enter Greece through escape from confinement, while 29 taxa have arrived or are expected to arrive in Greece unaided. In the Medium-risk RA category, 18 taxa entered, or are expected to enter, Greece through escape from confinement, 14 taxa have reached or are expected to reach Greece unaided, and 13 taxa have contaminated, or are expected to contaminate unintentionally, transferred commodities. All taxa using corridors as a pathway category (exclusively terrestrial plants) are of High-risk (Fig. 6). Details on the numbers of taxa per pathway of introduction and environment can be found in the Suppl. material (Suppl. material 5: fig. S4).

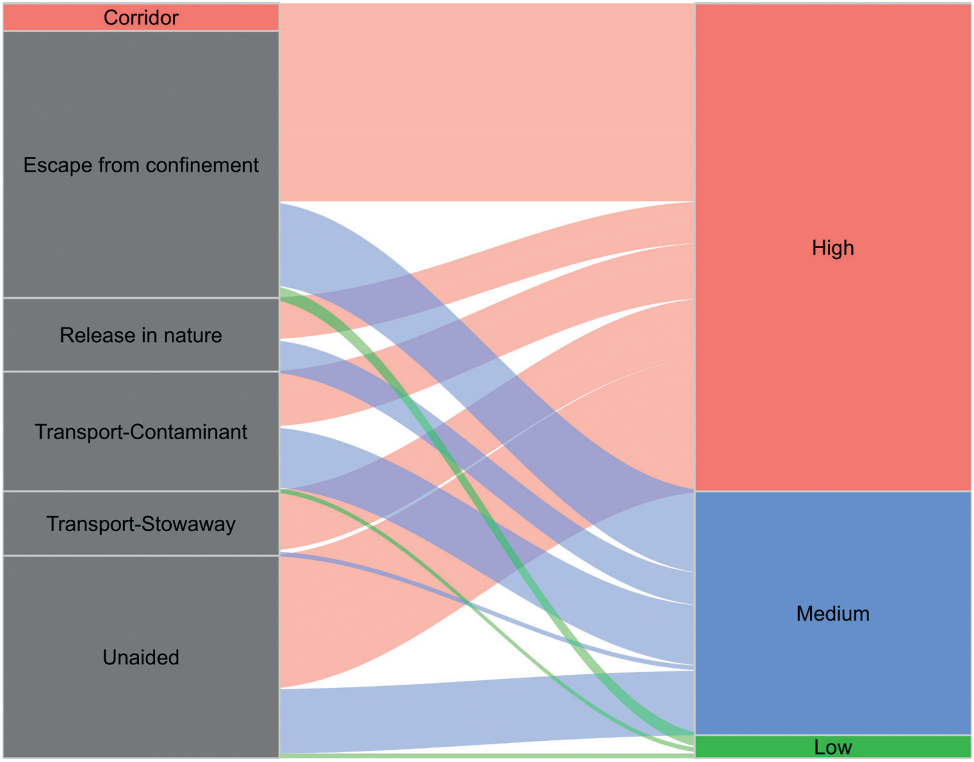

Figure 6. Alluvial diagram showing the distribution of introduction pathways across impact categories for all taxa. Nodes on the left represent different CBD principal pathways and nodes on the right the classification of taxa by Risk Assessment categories. Same colour between pathway and risk assessment nodes indicates that all taxa using the specific pathway are exclusively classified in the particular impact category.

Discussion

The scope of the EU 1143/2014 Regulation is to prevent new arrivals and the establishment of IAS in the member states. Consequently, the compilation of national lists and prioritization of their pathways of introduction are of high importance for managing biological invasions. The current study provides a solid scientific base to meet these requirements.

The rate of introductions varied over time, with the number of new IAS arrivals increasing after 1970. Similarly, the introduction rate of species follows a sharp increase after the same period. Records for terrestrial taxa seem to predominate. This could reflect the emphasis placed on monitoring the terrestrial environment, the fact of more frequent introductions in this environment, or the fact that the effects of invasions are more easily detected. Unfortunately, studies on biological invasions in both aquatic and terrestrial environments are rather sparse, so there is not much comparison possible within this field. Seebens et al. (2017), showed that the annual rate of first records worldwide has increased during the last 200 years, with 37% of all first records reported recently (1970–2014).

As previously mentioned, terrestrial plants were the first invasive species to be recorded, with some records dating back to the first half of the 19th century. *Phytolacca americana* (A. Strid, pers. comm. 2022) and *Datura stramonium* (Bory de Saint-Vincent and Chaubard 1832-33) were the alien species first observed in the wild (ca. 1830). Similar to other studies (e.g., Nikolić et al. 2013; Sirbu et al. 2022) the accumulation rate of invasive plant species occurrences shows an increasing tendency after the 1950s. The highest number of new introductions per decade is recorded for the periods 1960–1969 and 1970–1979, a fact that could potentially be attributed to more intense field studies. Although the number of alien plant species deliberately introduced for ornamental reasons has generally increased, alien plants' records in the wild have been decreasing during the last two decades, probably due to the raised awareness about the risk of using non-native species, at least for landscape restoration practice.

All terrestrial vertebrates of the HELLAS-ALIENS were introduced into the wild after 1960, except for the Ring-necked Pheasant, which has been intensively reproduced and released as game during the 20th century all over Greece; yet there is no information on the date and place of its first introduction in the wild (Handrinos and Akriotis 1997). There seems to be a constant rate of one terrestrial vertebrate introduction in the wild per decade, which concerns solely animals farmed for food and fur (e.g., the American Bullfrog and the Coypu, respectively) or released intentionally to the wild as game (e.g., Red-legged Partridge). Our data suggest that until the 1990s introductions were attributed predominantly to farmed animals imported into Greece for economic production, while onwards, and especially after 2000, the high increase in introduction rate is mainly attributed to introductions of animals used for human companionship. These pet species were mostly mammals or amphibians and reptiles imported directly into Greece. The European Wild Bird Trade Ban may have reduced bird invasion risks in the recent 15 years (Carrete and Tella 2008; Cardador et al. 2019), a period when there is only one record of invasive pet-bird introduction to the wild in HELLAS-ALIENS, the Common Myna observed in Rhodos Island in 2017, a case that may have to be treated as an unaided spread to Greece from Turkey.

Regarding the twelve terrestrial invertebrates already present in Greece, all first records are after 2003 with the exceptions of the harlequin ladybird *Harmonia axyridis* which was introduced intentionally in the early 1990s (Angelidou et al. 2022) and *Solenopsis geminata* that the only record dates back in 1993 (Salata et al. 2019). The giant resin bee *Megachile sculpturalis* and the pine wood nematode *Bursaphelenchus xylophilus* have not been recorded yet in the country. In Greece, recording terrestrial invertebrates, and insects in particular, has sparked more interest in the early 2020s through citizen science platforms such as the iNaturalist and social media. It is anticipated that this interest will produce more reports and first records in the coming years.

As for the new records of alien freshwater organisms, they seem to have peaked in the period 2000–2010 and, to a lesser degree, in 2010–2020, probably reflecting the increasing negative impacts of globalization on native freshwater biodiversity (Reid et al. 2019). At the same time, they are also correlated to the application of more efficient sampling techniques (e.g., electrofishing for freshwater fishes), wider scale field surveys of lotic and lentic freshwater ecosystems, as well as dedicated efforts to compile annotated lists of the Greek freshwater fauna (Economou et al. 2007; Zenetos et al. 2009; Koutsikos et al. 2012; Barbieri et al. 2015; Vardakas et al. 2022).

The highest number of new introductions for the marine environment of Greece dates back to the 1990s. While only five IAS had entered the Greek marine waters by 1970, and none in the 1970–1980 period, the trend of new introductions appears to be increasing and culminates in the 1990–2000 period with seven new marine IAS. In the last two studied periods, the number of IAS ranges from four to five per decade. This trend in marine waters follows the pattern observed in the Mediterranean Sea for all new alien species introductions (not only invasive ones). Zenetos et al. (2022) documented that the rate of new introductions (excluding parasites, pathogens, and microalgae) on an annual basis, has increased in the Mediterranean since the late 1990's reaching 14 species per year in the period 2012–2017. The increased trend of marine aliens observed in the 1990s (seven IAS) can be attributed either to the increased sampling effort following the interest of the scientific community (Shirley and Kark 2006) or to climate change as documented in Raitsos et al. (2010). The relevant lower number of IAS in the following decades could be an artifact as some of the alien species already introduced in Greek waters might turn out to be invasive. Nevertheless, it is expected that in addition to the time-lapse in reporting IAS (Zenetos et al. 2019), future studies of old data sets, including museum collections, will reveal IAS is already present but neglected to date (Oliver 2015).

Temporal trends within taxonomic groups, which constitute the sum for each environment, are observed and can be explained by the different pathways of introductions of species that differ in their ecology. We must note here that the species included in our analysis are in their majority established species that have been evaluated as invasive.

Terrestrial and freshwater plants constitute a large portion of the species comprising the national list of Greece. This is probably because plant species are easier to be studied but also to the fact that plant species are widely used for ornamental purposes, combined with the fact of easily escaping from confinement. The use of exotic plants in landscape improvement and reforestation used also to be a very common practice; hence, these plants could easily escape and expand their distribution and finally become invasive. The current list comprises 32 terrestrial and freshwater plant taxa of which 84% have escaped from confinement. This is in agreement with relevant studies (Essl et al. 2015; Pergl et al. 2017, 2020; Saul et al. 2017; McGrannachan et al. 2021; Sandvik et al. 2022), which report that plants are the most prominent taxonomic group among those invading an area. Several studies (Essl et al. 2015; Pergl et al. 2017, 2020; Saul et al. 2017; McGrannachan et al. 2021; Sandvik et al. 2022; Sirbu et al. 2022) also agree on the finding that alien plant species are predominantly introduced by means of escape from confinement, as they are mainly used for ornamental purposes. Ornamental horticulture is recognized as an important pathway for introducing and dispersing alien species (Drew et al. 2010). At the European level, Hulme et al. (2008) point to escape from confinement as the most frequent pathway for the introduction of alien species.

Fifteen plant taxa were classified as of High-risk and 16 as of Medium-risk, while only one species (*Matricaria discoidea*) was classified as of Low-risk. *M. discoidea* has been present in Greece since 1994 and, although it is considered an invasive species, its populations are spatially limited to specific mountains where they are found mainly at high altitudes, in stony/gravelly places (Greuter and Raus 2008; Greuter and von Raab-Straube 2008; Dimopoulos et al. 2013). Therefore, the risk of its future expansion is low if the secondary introduction pathways are properly controlled. Similarly to our findings, most of the plant taxa included in relevant works are classified as of High-risk (Sandvik et al. 2022). Twelve of the 15 High-risk plant species (80%) are already present in the country (in the wild or in cultivation), seven out of the 15 are present in the wild (47%), seven are hydrophytes (47%), while 70% of the hydrophytes are of High-risk.

Most alien invasive plants in Greece originate from the Americas followed by Asian and African species. This pattern is similar to that observed for all alien plants recorded in Greece (Arianoutsou et al. 2010) and it is in accordance with findings for other Mediterranean countries (see for example Celesti-Grapow et al. 2009). This is most probably linked to their pathways of introduction, as the majority of plants have been introduced through escape from confinement. The alien established plant species represent 4.5% of the Greek flora (including archaeophytes and established aliens) while the ratio of established alien to native plant species is 1:12.7 or 0.079. Invasive alien plant taxa account for 12.1% of the established alien plant species.

A published consolidated list of alien terrestrial vertebrates in Greece is missing. According to the HELLAS-ALIENS list, invasive terrestrial vertebrates already present in the wild add approximately 8%, 3%, 2% and 6% to the native amphibians, reptiles, birds and mammals, respectively.

HELLAS-ALIENS contains three terrestrial vertebrate IAS that are native to other parts of Europe and thus cannot be considered for the EU list: *Alectoris rufa*, *Podarcis siculus*, and *Triturus carnifex*. The latter is highly likely to invade the country within the next 10 years as the Horizon exercise performed has shown. *Alectoris rufa*, has been introduced in the wild as game since at least 1979 (Handrinos and Akriotis 1997) and until 2009, when the intentional release of exotic species as game was prohibited; yet, the genetic pollution of *Alectoris graeca*, through hybridization was already evident (Barilani et al. 2007). *Podarcis siculus*, has conquered several new areas inside and outside the EU arriving as a stowaway on cargo and nursery trade (Silva-Rocha et al. 2014; Scalera 2019) which seems to be the case for the Greek colony as well (Adamopoulou 2015). It has exhibited negative impacts on native species mostly through competitive exclusion (e.g., displacement of the critically endangered *P. raffonei*, see Capula et al. 2002) and hybridization with native *Podarcis* (Capula 1993, 2002). An unfortunate but probable consequence of its accidental entry in the Aegean islands is that it may threaten island endemic lizards that for the most part have evolved without the presence of competitors, and some are already endangered (Lymberakis et al. 2018).

Another vertebrate worth mentioning in the HELLAS-ALLIENS is *Neovison vison*, (American mink) which is already established in Northwest Greece (Adamopoulou and Legakis 2016) and is expanding (Galanaki and Kominos 2022). It is an IAS with significant adverse impacts on European biodiversity (Bouros et al. 2016), affecting 47 native species (Genovesi et al. 2012). However, it is not listed in the EU list due to the consideration of costs and socioeconomic aspects; concerned Member States could address such species through national measures (European Commission 2021).

Importation of pets followed by either their deliberate release or escape from confinement seems to be an important pathway for several terrestrial vertebrates in accordance with the general pattern in Europe (Roy et al. 2019; Tedeschi et al. 2021). Apart from one, all reptile species in the HELLAS-ALIENS are pet trade species. Among mammal species, escape from confinement is the major pathway, as many of them are kept as pets in private or public collections or bred for their fur. Only *Nyctereutes procyonoides* (the racoon dog) and *Ondatra zibethicus*, (muskrat), seem to enter the country through natural dispersal across Greece's northern borders. Both species have confirmed occurrences in the Balkans (Ćirović 2006; Popova and Zlatanova 2017) and their few verified records are currently restricted to North Greece (Catsadorakis and Bousbouras 2010; Adamopoulou and Legakis 2016).

Twenty-one terrestrial vertebrate species have been assessed as of High-risk, five as of Medium-risk and two of Low-risk for the native biodiversity. High-risk species include, among others, the well-established in Crete *Lithobates catesbeianus*, (the American bullfrog), a carrier of the lethal chytrid fungus that threatens amphibian populations worldwide (Miaud et al. 2016). This species threatens local subpopulations of the endemic, declining Cretan frog, *Pelophylax cretensis*, which is recently assessed as Vulnerable since it occurs in ten or fewer threat-defined locations (IUCN SSC Amphibian Specialist Group 2020).

Most of the terrestrial invertebrates on HELLAS-ALIENS are likely to have detrimental impacts to economic sectors such as agriculture, forestry, the tourism industry and human health (IUCN 2000; Mazza and Tricarico 2018; Haubrock et al. 2021). Unlike plant taxa, most terrestrial invertebrates are unintentionally introduced (Saul et al. 2017; Riera et al. 2021). Most of the terrestrial invertebrates on HELLAS-ALIENS are of Asian origin. Knowing the origin of the non-native terrestrial invertebrates is important during the establishment of early warning systems at points of entry and border controls, however, for terrestrial insects, it was shown that it is generally unknown whether their introduction to Greece is the result of a primary introduction event from their area of origin or a secondary translocation from an already invaded country that either shares borders with Greece or is a major trading partner, e.g. Italy or Germany (Demetriou et al. 2021). Deciphering the biological invasion history, distribution, impacts and species interactions of non-native terrestrial invertebrates by utilising classical methods, citizen science and molecular tools will help us understand better their impacts on ecosystems and native biodiversity and it has been described as a desirable strategy in other Mediterranean countries such as Cyprus (Demetriou et al. 2021).

Updated, relatively recent compilations available for freshwater fishes indicate that alien freshwater fish species of the HELLAS-ALIENS list add approximately 17% to the native freshwater ichthyofauna of Greece (Barbieri et al. 2015). Freshwater invertebrates and fishes also constitute a large part of the national list of invasive species of Greece. This is in agreement with recent studies, focusing on the more well-studied freshwater fishes of Greece (as opposed to invertebrates) and of the Balkans that report a high percentage of alien species in freshwater ecosystems (15%–23%, for Greece, see Barbieri et al. 2015; for all Balkans, see Piria et al. 2018, also for Bulgaria, North

Macedonia and Serbia, see e.g., Simonović et al. 2013; for Croatia and Slovenia, see Piria et al. 2016). Most of the freshwater species of the list are of North American origin, and in this, the list mirrors the dominant origin of introduction of alien fish species also in the Balkans (Piria et al. 2018). Natural dispersal occurs through the several transboundary rivers and lakes shared with neighboring Balkan countries, such as the Prespa lake, the Kerkini lake (Strymon river basin), and the Evros river (Barbieri et al. 2015; for recent invasions see Erőss et al. 2005; Zogaris and Apostolou 2011; Petriki et al. 2014; Karaouzas et al. 2020) is the main pathway of freshwater species invasion in Greece. Other pathways include, for invertebrates, transport contaminants on plants for Botanical gardens/greenhouses or commercial crops (Vinarski 2017; Cianfanelli et al. 2007; Beran and Glöer 2006), as well as the aquarium pet trade (Marrone et al. 2011). In contrast, most fish species introduced as transport contaminants, entered Greek freshwaters accidentally during fish stockings with carp, mostly in lake ecosystems (Perdikaris et al. 2012; Piria et al. 2018). Finally, there are also fish escapes in Greece from aquaculture, the dominant pathway of alien fish introductions in other Balkan countries (Barbieri et al. 2015; Economou et al. 2007; Piria et al. 2018) and, importantly, potential escapes of two highly invasive crayfish species (*Procambarus clarkii* and *Procambarus virginalis*) from the aquarium trade (Papavlasopoulou et al. 2014) the major pathway for new non-indigenous crayfish species introductions into Europe as well (Chucholl 2013).

Invasion by alien species constitutes a leading cause of the rapid global freshwater biodiversity loss (Reid et al. 2019); similarly invasive species are a major driver of the geographic range reduction and population decline of the endemic, threatened freshwater fauna of Greece (Perdikaris et al. 2010, 2016; Barbieri et al. 2015; Kalogianni et al. 2019, 2022). Thus, it is not surprising that High-risk species dominate the freshwater taxa of the current list (18 species, including all six species expected to invade Greek freshwaters in the next ten years), with six species in the EU list (such as the highly invasive fish *Lepomis gibbosus* and *Pseudorasbora parva*, widespread in Greece, and the crayfish *Pacifastacus leniusculus*) and conversely, no Low-risk species present.

The origin of the vast majority of marine IAS included in the HELLAS-ALIENS was the Indo-Pacific and in particular the west Indo-Pacific. Most marine IAS have entered Greek waters via the Suez Canal, but not directly. Indeed, the impact of the Suez Canal in the introduction of marine aliens has been previously documented (e.g., Zenetos et al. 2012; Galil et al. 2017; Tsiamis et al. 2018) and accounts for more than half of Mediterranean aliens, and the vast majority of fishes (e.g., Zenetos et al. 2012). However, corridor is not the main pathway of most IAS in the Greek Seas. Although marine species in the HELLAS-ALIENS have progressively entered the eastern Mediterranean via the Suez, they were first established in the Levantine sea from where they invaded the Greek Seas unaided or with vessels (Transport-Stowaway) (Zenetos et al. 2020). In a recent analysis of biological traits that could potentially favor the introduction and establishment of alien fishes in the Mediterranean, Karachle et al. (2022) show that temperature is the most important factor. This finding, combined with the abrupt rising temperature since the end of the 1990s that has modified the potential thermal habitat available for warm-water species and facilitating their settlement at an unexpectedly rapid rate (Raitsos et al. 2010), further explains the participation of Indo-Pacific taxa in the HELLAS-ALIENS. In particular, Transport – Stowaway – Machinery/equipment is the main vector of macrophytes introduction whether of Indo-Pacific origin e.g., *Womersleyella setacea* or of NE Pacific or Tropical Atlantic e.g., *Codium fragile*, *Asparagopsis taxiformis*. In the case of marine plants, although many are also of Indo-Pacific origin, their introduction is related to shipping and not corridors. The Indo-Pacific origin does not imply an unaided introduction for all invertebrates introduced to the Greek Sea. For example, Transport-Stowaway is suspected to be the mode of introduction of the bivalve mollusc *Fulvia fragilis* (Crocetta et al. 2017). On the other hand, the blue crab *Callinectes sapidus* native to the western Atlantic has invaded the Aegean Sea either via ballast waters (Transport-Stowaway) or Unaided from the neighboring Turkish waters. Finally, another species that is worth mentioning is the Atlantic northern shrimp *Penaeus aztecus*. The pathway of its introduction in the Mediterranean is not very clear, with the aquaculture release/escape prevailing as the most likely pathway (Galil et al. 2016; Karachle et al. 2017). This is also true for the Greek Seas, as the species is considered to enter Greece either unaided from neighboring countries (i.e. Turkey) and/or as an escape from confinement.

For the marine environment, ten (45% of taxa) and seven (32% of taxa) of High and Medium-risk taxa respectively have arrived unaided. It is worth noting that *Penaeus aztecus*, the only taxon that has potentially escaped from confinement, is of High-risk, while the pearl oyster *Pinctada radiata* which has been intentionally released, is of Medium-risk. All marine plants are of High risk. Finally, alien marine taxa add approximately 7% to the native marine biota (Simboura et al. 2019, UNEP/MAP-SPA/RAC 2021).

Conclusions

The present study provides a thorough analysis of the IAS of Greece. Our results based on the systematic review of existing literature reveal that a considerably high number of terrestrial plants and freshwater organisms are threatening local biodiversity and may also pose serious problems in the economy and society, as is the case of marine species (Oliver 2015; Zenetos et al. 2019). One of the most important findings of the study focuses on the pathways of introduction of IAS indicating that escape from confinement is the most frequent pathway of terrestrial taxa. This has serious implications for decisions on the importation of horticultural and ornamental plants as well as on pets and their subsequent accidental (or not) release in the wild. As biological invasions are a dynamic field, surveillance and management of pathways can provide an efficient method to prevent the arrival of new IAS (McGeoch et al. 2016). However, monitoring the pet and aquarium trade (on line trading also included) is rather challenging since it requires detailed knowledge of the species imports (numbers, taxa) through legal or illegal trade or data such as the number of pets kept in captivity and/or sold, which are usually absent. Natural dispersal is the dominant pathway of aquatic taxa, both freshwater and marine, indicating that monitoring of freshwater transboundary waterways and marine corridors and vessels respectively should be a priority. Our work sets the basis for management plans. National and international experts in invasive species could address specific objectives such as assessing the feasibility of eradicating established invasive alien species either countrywide or from the islands which are high in endemic species. Ranking established invasive alien species based on the threat they pose to locations across the Greek mainland, islands and seas, where they are not currently established, should also be a priority. Raising awareness programs to competent authorities, schools and members of the public should take place highlighting the importance of biosecurity to better protect the native biodiversity in the Greek mainland and the islands from invasive alien species should also be a priority.

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Supplementary material 1

List of HELLAS-ALIENS species

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Data type: excel file with a list of species

Explanation note: The file contains the full list of alien invasive species of Greece.

Link: https://doi.org/10.3897/neobiota.86.101778.suppl1

Supplementary material 2

CBD principal introduction pathways for terrestrial invasive alien species of Greece per different categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos

Data type: figure

Explanation note: fig. S1: CBD principal introduction pathways for terrestrial invasive alien species of Greece per different categories. The category vertebrates includes amphibians, reptiles, birds and mammals.

Link: https://doi.org/10.3897/neobiota.86.101778.suppl2

Supplementary material 3

CBD principal introduction pathways for freshwater invasive alien species of Greece per different categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos

Data type: figure

Explanation note: fig. S2: CBD principal introduction pathways for freshwater invasive alien species of Greece per different categories. The category vertebrates corresponds to fishes.

Link: https://doi.org/10.3897/neobiota.86.101778.suppl3

Supplementary material 4

CBD principal introduction pathways for marine invasive alien species of Greece per different categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos

Data type: figure

Explanation note: fig. S3: CBD principal introduction pathways for marine invasive alien species of Greece per different categories. The category vertebrates corresponds to fishes.

Link: https://doi.org/10.3897/neobiota.86.101778.suppl4

Supplementary material 5

Alluvial diagram showing the distribution of introduction pathways across impact categories

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Data type: figure

Explanation note: fig. S4: Alluvial diagram showing the distribution of introduction pathways across impact categories. Nodes on the left represent different CBD main pathways and nodes on the right the classification of taxa by Risk Assessment categories. Same colour between pathway and risk assessment nodes indicates that all taxa using the specific pathway are exclusively classified in the particular impact category. A: terrestrial; B: freshwater; C: marine taxa.

Link: https://doi.org/10.3897/neobiota.86.101778.suppl5