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A multi-taxa assessment of aquatic non-indigenous species introduced into Iberian freshwater and transitional waters

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Abstract

Aquatic ecosystems are particularly vulnerable to the introduction of non-indigenous species (NIS), leading to multi-faceted ecological, economic and health impacts worldwide. The Iberian Peninsula comprises an exceptionally biodiverse Mediterranean region with a high number of threatened and endemic aquatic species, most of them strongly impacted by biological invasions. Following a structured approach that combines a systematic review of available information and expert opinion, we provide a comprehensive and updated multi-taxa inventory of aquatic NIS (fungi, macroalgae, vascular plants, invertebrates and vertebrates) in Iberian inland waters. Moreover, we assess overall patterns in the establishment status, introduction pathways, native range and temporal introduction trends of listed NIS. In addition, we discuss the legal coverage provided by both national (Spanish and Portuguese) and European NIS regulations. We inventoried 326 aquatic NIS in Iberian inland waters, including 215 established, 96 with uncertain establishment status and 15 cryptogenic taxa. Invertebrates (54.6%) and vertebrates (24.5%) were the groups with the highest number of NIS, with Arthropoda, Mollusca, and Chordata being the most represented phyla. Recorded NIS originated from diverse geographic regions, with North and South America being the most frequent. Vertebrates and vascular plants were mostly introduced through intentional pathways (i.e. release and escape), whereas invertebrates and macroalgae arrived mostly through unintentional ways (i.e. contaminant or stowaway). Most of the recorded NIS were introduced in Iberian inland waters over the second half of the 20th century, with a high number of NIS introductions being reported in the 2000s. While only 8% of the recorded NIS appear in the European Union list of Invasive Alien Species of Union concern, around 25% are listed in the Spanish and Portuguese NIS regulations. This study provides the most updated checklist of Iberian aquatic NIS, meeting the requirements set by the EU regulation and providing a baseline for the evaluation of its application. We point out the need for coordinated transnational strategies to properly tackle aquatic invasions across borders of the EU members.

Keywords

Alien species, checklist, environmental management, estuaries, inland waters, Portugal, regulation, Spain, Western Mediterranean

Introduction

Compared to terrestrial and marine ecosystems, freshwater and transitional waters (hereafter collectively referred to as inland waters) are especially vulnerable to biological invasions due to their intrinsic environmental features (Moorhouse and Macdonald 2015; McFadden et al. 2023), and the high introduction pressure promoted by the wide range of human activities developed in these aquatic habitats (Reid et al. 2019; Cabral et al. 2020). For instance, inland waters support commercial fisheries, aquaculture, shipping, and diverse recreational activities (e.g. sport fishing or navigation). In addition, inland waters are subject to different human infrastructures such as dams, ditches or water transfer systems (Ojaveer et al. 2018; Anastácio et al. 2019; Bailey et al. 2020). Such human activities are well-known drivers of the introduction and spread of non-indigenous species (hereafter, NIS) (Nunes et al. 2015). As a consequence, there is a growing evidence of major impacts caused by NIS at multiple ecological levels in inland waters, with well-demonstrated detrimental effects on native aquatic biota, ecosystem functions and services (Vilà et al. 2011; Gallardo et al. 2016; Guareschi et al. 2021). Under this scenario, management actions are urgently required to slow down the introduction rate of NIS in inland waters, to control populations of already established NIS and to prevent secondary spread towards still non-invaded aquatic ecosystems (Britton et al. 2023). In this context, updated inventories of NIS and comprehensive assessments on introduction pathways, native regions and temporal trends of introductions are fundamental for elucidating the causes and consequences of the invasion process (Seebens et al. 2017; Fuentes et al. 2020). Moreover, NIS management policies should be based on a transnational approach involving coordinated surveillance efforts (Bailey et al. 2020; Capinha et al. 2023). This is especially relevant when neighbouring countries share river basins and, consequently, aquatic ecosystems are largely interconnected. However, legislation and direct management are nowadays mostly implemented at national scale (Anastácio et al. 2019).

The Mediterranean basin is one of the major global hotspots of biodiversity, with the Iberian Peninsula comprising a particularly species-rich area and harbouring high numbers of endemic species (Araújo et al. 2007; Buira et al. 2017; Rosso et al. 2018). This is even more evident in the case of the Iberian aquatic biodiversity, which shows outstanding ratios of species singularity and endemicity (Doadrio et al. 2011; Hermoso et al. 2016). For instance, about 80% of freshwater fish, 40% of amphibian and 25% of water beetle species occurring in the Iberian Peninsula are endemic (Doadrio et al. 2011; Hermoso et al. 2016). However, most of these species are highly threatened and particularly vulnerable to NIS introductions (e.g. Cruz et al. 2008; Ruiz-Navarro et al. 2013; Romero 2015). In fact, the introduction of both animal and plant species in Iberian inland waters is a long-lasting and ongoing process, whose adverse effects have been largely documented from an ecological (Aguiar and Ferreira 2013; Anastácio et al. 2019), socioeconomic (Durán et al. 2012; Angulo et al. 2021) and public health (Collantes et al. 2015; Sánchez et al. 2021) perspective. In recent years, a few studies have provided reference NIS inventories and first assessments targeting different inland ecosystems (freshwater or transitional environments) and biotic groups, at Iberian, national (Spanish or Portuguese) and regional scales. For instance, García-Berthou et al. (2007) provided the first checklist of animal species naturalised in Iberian inland waters, and Cobo et al. (2010) provided a similar inventory for Galicia (Spain), adding plant species and comparing with other areas from the Iberian Peninsula. Aguiar and Ferreira (2013) conducted an overview of the available knowledge on invasive plants in Iberian rivers, whereas Rodríguez-Merino et al. (2017) focused on the potential distribution of non-native aquatic macrophytes in Iberian inland waters. Later, Anastácio et al. (2019) compiled records of animal NIS introduced across Portuguese freshwater ecosystems and provided a thorough assessment of the temporal introduction rate, native regions, reported impacts and legal coverage from both Portuguese and European lists of NIS. Muñoz-Mas and García-Berthou (2020) conducted a comprehensive review of aquatic non-indigenous fauna introduced in Iberian inland waters and compared temporal introduction rates between the Iberian Peninsula and two Iberian subregions (Portugal and Galicia). More recently, through a horizon scan exercise, Oficialdegui et al. (2023) have identified the most relevant NIS recorded or potential introductions to Iberian inland waters, but a relevant number of NIS that did not score high enough are missing from this list.

Most of the above-mentioned studies retrieved NIS records exclusively from published scientific literature, thus overlooking grey literature and unpublished but validated NIS records from private inventories, institutional repositories and official databases. Because of time lags between detecting a NIS in the field and its corresponding publication (Zenetos et al. 2017), official online databases are currently essential resources for regularly updating NIS checklists and informing management policies more rapidly. Overall, NIS records concerning Iberian inland waters are scattered across several publications and data sources, thus posing a serious constraint for an integrated NIS management at different spatial scales. Moreover, they are often biased towards animal taxa and purely freshwater ecosystems, so studies concerning aquatic plants (e.g. Aguiar and Ferreira 2013) and transitional waters (Zorita et al. 2013; Cabral et al. 2020; Zamora-Marín et al. 2023) are scarce and conducted at local or regional scales. Hence, multi-taxa inventories of NIS introduced in Iberian inland waters (both fresh and transitional waters) are needed, since they comprise key tools in decision-making with potential implications on NIS regulation policies at national (Spanish and Portuguese) and European levels (e.g. the European Union list of Invasive Alien Species of Union concern, hereafter "the Union list"). In fact, the EU regulation No 1143/2014 on the prevention and management of the introduction and spread of invasive alien species (IAS) recommends the EU Member States to provide updated checklists on NIS introduced in their territory and conduct a comprehensive analysis of the unintentional introduction and spread pathways of the IAS of Union concern (Piria et al. 2018).

This study updates the information on aquatic NIS occurring in Iberian inland waters by combining knowledge from a diverse panel of experts with an extensive screening of published literature (both international and grey literature), online databases (e.g. GBIF, EASIN and CABI), and technical reports or off-line databases provided by environmental agencies. Through a broad multi-taxa approach including fungi, flora and fauna, this study aims (1) to provide an extensive and updated inventory of NIS introduced in Iberian inland waters, (2) to assess overall patterns in introduction pathways, native regions, and temporal introduction rates, and (3) to discuss the legal coverage of national (Spanish and Portuguese) and European IAS regulation. To make this study as robust as possible, this comprehensive assessment was conducted by an expert-consensus-based approach, which ensured a reliable checklist validation from a taxonomic and state-of-the-art viewpoint, since misidentification or distributional errors are common when no group-specific experts are involved in NIS multi-taxa studies (Zenetos et al. 2017).

Methods

Study area and target habitats

The Iberian Peninsula is mostly comprised of the mainland territory of Spain and Portugal. This area is characterised by a wide climatic gradient which extends from the northwestern (temperate oceanic conditions expressed as high rainfall and humidity values, and low continentality) to the southeastern edge (Mediterranean semiarid conditions), including also large parts of the territory exposed to Mediterranean climate with higher continentality. The coastline of the Iberian Peninsula extends over 3,904 km across the Mediterranean Sea (1,670 km), the Atlantic Ocean (1,367 km) and the Cantabrian Sea (867 km). Most of the Iberian territory is framed within major river basins, some of them shared between Spain and Portugal (e.g. Guadiana, Tagus and Douro catchments). Following the European Water Framework Directive (hereafter, WFD) (EC 2000), we considered inland waters as those standing or flowing surface aquatic ecosystems (both fresh and transitional waters) placed across land boundaries. Hence, this term included typically lotic (i.e. rivers and streams) and lentic freshwater ecosystems (i.e. lakes, wetlands and reservoirs), small water bodies (i.e. ponds and pools) and transitional or estuarine aquatic systems influenced by freshwater inputs (i.e. marshlands, brackish waters, estuaries and coastal lagoons). Here, all these aquatic ecosystems were collectively considered and referred to as inland waters. Inland waters from the Balearic and Macaronesia (i.e. Canary Islands, Madeira and the Azores archipelagos) islands were excluded.

Compiling records and attributes of NIS

An integrative and structured approach based on multiple data sources was applied to generate a comprehensive up-to-date inventory of all aquatic NIS occurring in Iberian inland waters. Firstly, we compiled all available literature on NIS occurrence in Iberian inland waters, including articles published in indexed international journals, grey literature (e.g. articles in regional journals or bulletins), online databases and technical reports. For peer-reviewed literature, we made a query in the Web of Science to retrieve all potential publications focused on NIS in Iberian inland waters. Boolean search terms included all words related to NIS or potential synonyms (i.e. alien, allochthonous, exotic, introduced, invasive, non-native and non-indigenous), target environments (i.e. freshwater, transitional, reservoir/s, lake/s, pool/s, pond/s, river/s, stream/s, estuary/ies and coastal lagoon/s) and the study area (i.e. Iberia, Iberian Peninsula, Spain and Portugal). Resulting publications were screened to generate a list of NIS introduced in Iberian inland waters. This preliminary list of NIS was further complemented with records from grey literature, national technical reports and regional checklists, as well as from the following databases: the European Alien Species Information Network (EASIN; http://easin.jrc.ec.europa.eu), CABI´s Invasive Species Compendium (CABI-ISC; http://www.cabi.org/isc/), the Global Invasive Species Database (GISD; www.iucngisd.org), the EXOCAT database (http://exocatdb.creaf.cat/base_dades/#), the AquaNIS database (http://www.corpi.ku.lt/databases/aquanis/) and the Global Biodiversity Information Facility database (GBIF; http://www.gbif.org/). We recorded all aquatic NIS introduced in Iberian inland waters up to August 2022.

We considered target taxa to be all those NIS able to live in freshwater and/or transitional waters at least during part of their life cycle. Aquatic taxa native from a given Iberian river basin but introduced in other Iberian catchments (i.e. translocated species) were excluded from our inventory. This preliminary list was agreed and validated by a panel of 65 experts in conservation biology and invasion science from Spain and Portugal, covering both types of target aquatic ecosystems (freshwater and transitional environments) and all biotic groups potentially containing aquatic NIS.

Following previous studies (see Muñoz-Mas and García-Berthou 2020), taxa clearly introduced into Iberian inland waters with self-sustaining populations were classified as "established" (most commonly referred as "naturalized" in plants), whereas those non-indigenous taxa reported to occur in the study area but without known self-sustaining populations were classified as "uncertain" (most commonly referred as "casual" in plants). Taxa with unclear biogeographic history in the Iberian Peninsula (i.e. native/introduced status) were considered as "cryptogenic". The recorded aquatic NIS were classified into five major biotic groups: vertebrates, invertebrates (both free-living and symbionts), vascular plants, macroalgae and fungi. From the screened data sources, we searched and retrieved the following four relevant species-specific attributes for all recorded NIS: native regions, introduction pathways, year of introduction and functional group. Native regions for the recorded NIS were divided into nine geographic regions: Africa, Antarctica, temperate Asia, tropical Asia, Australasia, Europe, Pacific Ocean, North America, and South America. According to the Convention of Biological Diversity (CBD 2014) and as stated by the EU regulation (European Commission 2017), which complemented the classification of introduction pathways previously proposed by Hulme et al. (2008), we used the following seven major categories to characterise the introduction pathways: Release, Escape, Contaminant, Stowaway, Corridor, Unaided and Unknown. Whenever possible, the most probable introduction pathways were based on published literature for the Iberian Peninsula.

For each recorded NIS, the year of introduction (i.e. first detection in the wild) in Europe and both Iberian countries was obtained. This date at European scale was mostly retrieved from EASIN, whereas at the national scale (for Spain and Portugal) was mainly retrieved from scientific literature providing first records for the Iberian Peninsula. When unreported in the literature, we applied a conservative approach and considered the year of the corresponding publication as the year of introduction, following Cobo et al. (2010) and Muñoz-Mas and García-Berthou (2020). In the case of host-specific alien invertebrate symbionts (e.g. *Onchocleidus dispar*), we considered the year of introduction to be that of the host. By contrast, in the case of generalist non-indigenous parasites (e.g. *Lernaea cyprinacea*), which can be introduced with many host species (native or non-indigenous species), we considered the first detection year of the parasite. Additionally, we retrieved from EASIN the name of the country/ies where a given NIS was detected for the first time within Europe. Recorded NIS were also classified into the following nine functional groups: primary producers, herbivores, predators or parasites, detritivores, filter feeders, omnivores, xylophages, pollinators and polyphagous. Lastly, we screened the current regulation to assess the legal coverage of the recorded NIS. In particular, we checked the inclusion of NIS in the Union list, the Spanish IAS Catalogue (Royal Decree 630/2013, latest update 1 December 2020), the Spanish Allochthonous List (Royal Decree 570/2020), and the Portuguese List of IAS (Decree-Law 92/2019).

Data analyses

We analysed which native regions, introduction pathways and functional groups were most prevalent for the recorded NIS. To avoid overrepresentation of those NIS associated with two or more categories, data on these attributes were down-weighted in frequency-related analyses following the strategy of Muñoz-Mas and García-Berthou (2020). We used data on the first year of introduction of the recorded NIS in Europe, Spain and Portugal to compare temporal trends. We also applied linear models to assess pairwise differences in introduction dates among both Iberian countries and Europe (e.g. Spain vs Europe) and to determine potential NIS introduction delays. Lastly, legal coverage of the listed NIS in the official European, Spanish and Portuguese regulation lists of NIS was visually assessed through Venn diagrams, obtained with the package VennDiagram (Chen 2022), implemented in the free software R v.4.0.3 (R Core Team 2022).

Results

Taxonomic approach

We recorded 326 non-indigenous taxa in Iberian inland waters, which included 215 clearly established, 96 uncertain and 15 cryptogenic taxa (Suppl. material 1). The listed aquatic NIS represented five major biotic groups, with invertebrates (54.6% of total taxa) being the dominant one, followed by vertebrates (24.5%), vascular plants (12.6%), macroalgae (7.4%) and fungi (0.9%). These aquatic NIS covered virtually all phyla (15) inhabiting Iberian inland waters, and belonged to 36 classes. The most represented phyla (or division in the case of plants) were Chordata (27.0%), Arthropoda (20.6%) and Mollusca (16.0%), whereas Magnoliophyta (10.7%), Rhodophyta (6.1%), Platyhelminthes (5.5%) and Annelida (5.2%) gathered a lower number of NIS, and the remaining phyla showed marginal values (≤ 2%) (Fig. 1). Overall, the ratio established/total NIS was congruent across all biotic groups, with the species-richest phyla having a greatest number of established NIS (range 47–94% of established taxa from the total NIS richness). At lower taxonomic resolution, Actinopterygii (14.1%) was the class with most species among all the taxa recorded, followed by Magnoliopsida (10.7%), Malacostraca (9.2%), Gastropoda (8.3%), Bivalvia (7.4%) and Florideophyceae (6.1%) (Suppl. material 2: fig. S1).

Most of the aquatic non-indigenous vertebrates (57.5%) were fish (Class Actinopterygii) and they mainly corresponded to NIS well established in Iberian inland waters (34 established; 12 uncertain taxa), with Cyprinidae being the dominant among the 16 recorded families (16 cyprinids out of 46 listed non-indigenous fish species). Reptiles were the second species-richest class among vertebrates (13 NIS, 16.2% of vertebrates) and they were exclusively represented by freshwater turtle species, with only one taxon being clearly established (*Trachemys scripta*). A similar pattern was found in birds and amphibians, with eight listed NIS for both classes but only two species of birds (*Alopochen aegyptiaca* and *Cairina moschata*) and three species of amphibians

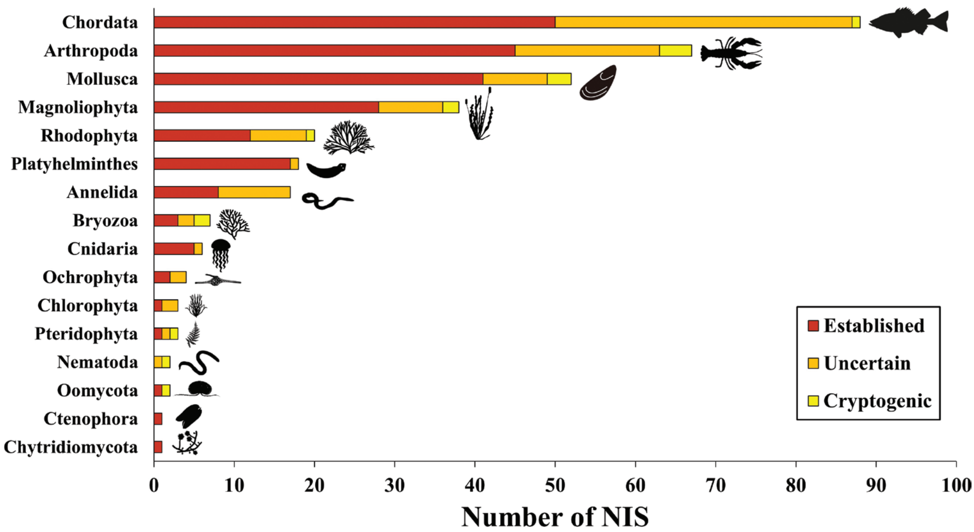

Figure 1. Cross-group richness of aquatic non-indigenous species (NIS) recorded in inland waters (including freshwater and transitional waters) from the Iberian Peninsula. Groups correspond to phyla (animals) or divisions (plants). Colours refer to the proportion of NIS belonging to each establishment stage (established, uncertain or cryptogenic). From top to bottom, groups are ranked from the species-richest to the species-poorest.

(*Discoglossus pictus*, *Pelophylax* kl. *grafi* and *Xenopus laevis*), respectively, were considered as established. On the other hand, the recorded non-indigenous invertebrates were represented by a widely diversified set of species that corresponded to 24 classes including 62 orders. Podocopida (19 NIS) and Decapoda (16 NIS) were the invertebrate orders with most species. Regarding vascular plants, our inventory included submerged, floating and emergent aquatic plants occurring in Iberian inland waters, which generally corresponded to hydrophytes and helophytes. Magnoliopsida (35 NIS) was the dominant group of vascular plants, 12 of these species belonging to the order Alismatales, whereas the class Polypodiopsida hosted three non-indigenous pteridophytes. Among macroalgae, Rhodophyta was the dominant group (20 NIS), whereas Ochrophyta (4 NIS) was much less represented. Lastly, non-indigenous fungi species (3 NIS) were exclusively represented by pathogens belonging to the genera *Batrachochytrium* and *Aphanomyces*, which mostly affect amphibians and crayfish, respectively.

Native regions

Native regions of the recorded NIS corresponded to all geographic areas, with the exception of Antarctica (Fig. 2). North America (26.8%) and temperate Asia (18.8%) were the most common native regions of Iberian aquatic NIS. We found 197 NIS (60.8%) that were native to a single geographic region (Suppl. material 2: fig. S2a). Overall, NIS belonging to all biotic groups were native to a wide variety of geographic regions (Fig. 2). Particularly, vertebrates were mostly native to North America, Europe and temperate Asia, whereas invertebrates were native to all geographic regions and they comprised

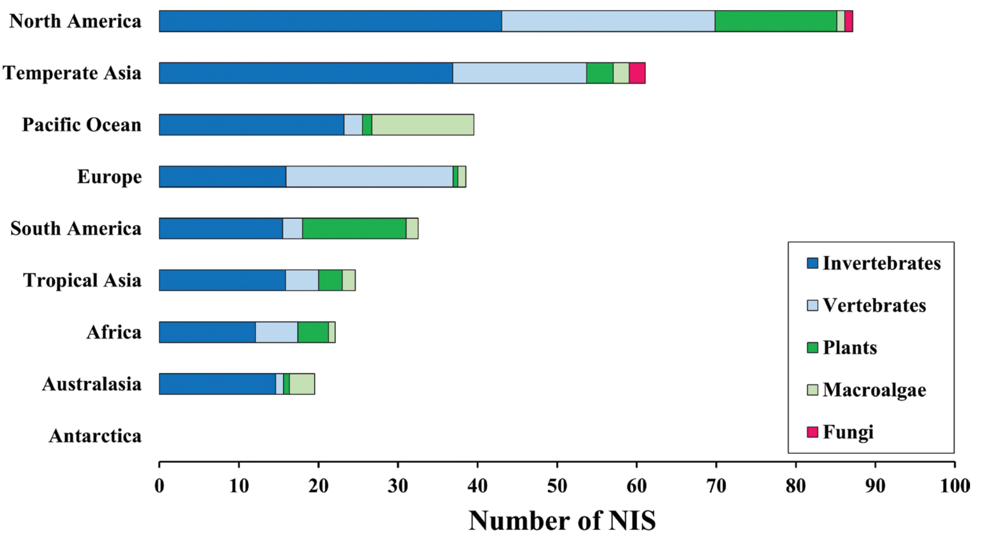

Figure 2. Native regions for the aquatic non-indigenous species (NIS) recorded in inland waters (both freshwater and transitional waters) from the Iberian Peninsula. Results are displayed according to the five main biotic groups considered. As several NIS presented two or more native regions, data were down-weighted to avoid overrepresentation.

about half of the NIS considered as native to each region. Vascular plants were mainly native to North and South America, whereas most non-indigenous macroalgae were native to the Pacific Ocean. Fungi were native from temperate Asia and North America.

Pathways of introduction

We identified four major pathways as responsible of NIS introductions in Iberian inland waters, which totalled about 90% of the recorded taxa: Stowaway (26.1%), Contaminant (25.6%), Escape (21.2%) and Release (17.1%) (Suppl. material 2: fig. S3). The vast majority of recorded NIS were introduced through a single pathway (170 NIS, 53.8%) or two pathways (127 NIS, 40.2%) (Suppl. material 2: fig. S2b). This pattern in the number of introduction pathways was homogenous across biotic groups. Taxonomic-related patterns of NIS arrival were observed across major biotic groups (Fig. 3). For instance, non-indigenous invertebrates and macroalgae arrived mostly through stowaway and contamination (i.e. unintentional pathways), whereas vertebrates and vascular plants were mainly intentionally introduced through escape and release.

Timeline of NIS introduction

Year of introduction was available for most of the recorded NIS (283/326 for Europe, 280/305 for Spain, and 151/178 for Portugal), thus ensuring representative data on NIS introduction to ascertain temporal arrival rates. From the 1860s to 1960s, the

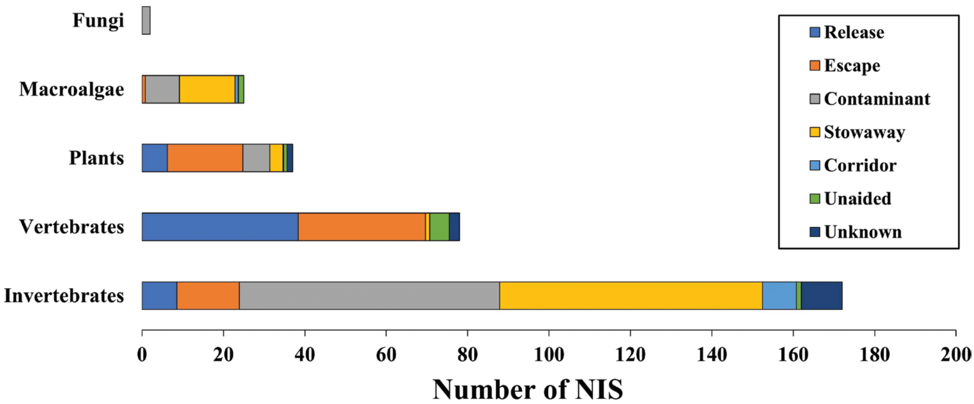

Figure 3. Contribution of the categories of introduction pathways to the arrival of aquatic non-indigenous species (NIS) to inland waters (including freshwater and transitional waters) from the Iberian Peninsula. NIS are grouped into the five major biotic groups considered. As several NIS were introduced through two or more pathways, data were down-weighted to avoid overrepresentation of these categories.

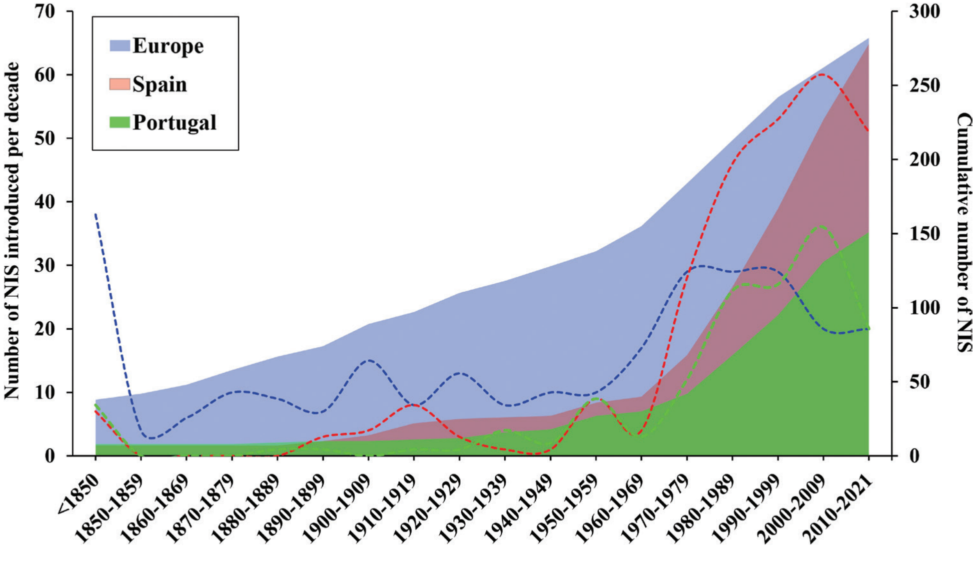

Figure 4. Temporal introduction rates of aquatic non-indigenous species (NIS) recorded in inland waters (including freshwater and transitional waters) from the Iberian Peninsula. Filled areas represent the cumulative number of introduced NIS in European, Spanish and Portuguese inland waters, whereas lines represent the decadal pace of NIS introduction. Note that the last decade includes two additional years (2020–2021) to allow for reliable data representation.

recorded NIS were introduced in European inland waters at a pace of 5–15 species per decade, reaching introduction rates of 30 species per decade over the end of the 20th century (1970s–2000s), though this pace has slightly decreased in the past two decades (Fig. 4). In both Spain and Portugal, some widespread NIS were introduced before the

1850s, such as the common carp (*Cyprinus carpio*), the goldfish (*Carassius auratus*) and the tadpole snail (*Physella acuta*). On the other hand, a clear temporal variation was observed in the contribution of each introduction pathway to the arrival of the recorded NIS to Iberian inland waters (Suppl. material 2: fig. S4). For instance, intentional pathways (i.e. Release and Escape) made a higher contribution to the arrival of aquatic NIS to Iberian inland waters before 1950, whereas unintentional pathways (i.e. Contaminant and Stowaway) gained relevance during the second half of the 20th century.

The delay in aquatic NIS introductions among the three regions (Europe, Spain and Portugal) was only evident for pairwise comparisons between national and continental scales (Fig. 5), with no significant differences being observed between both Iberian countries (Fig. 5c). Results from linear models conducted separately across taxonomic groups supported the similar pace of NIS introduction among both countries, particularly in the case of invertebrates (R^2 = 0.5168) and vertebrates (R^2 = 0.8497). When compared to the year of introduction in Europe (Fig. 5a, b), both Spain and Portugal showed a

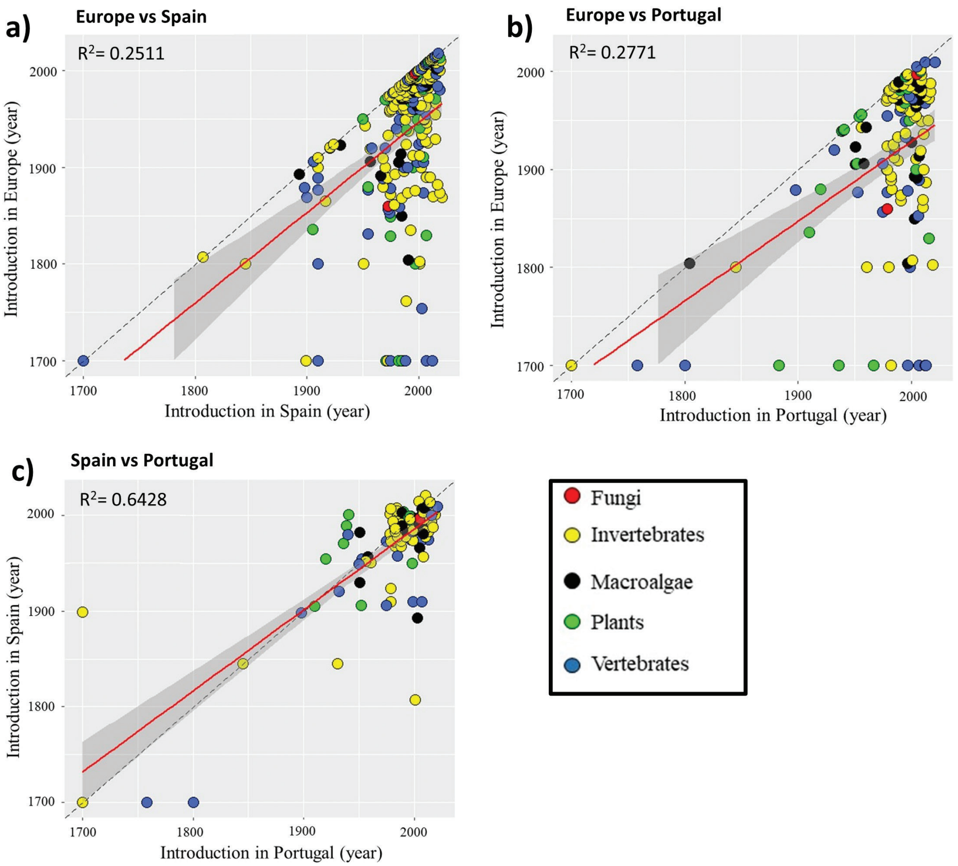

Figure 5. Scatterplots and linear regression functions (red line) of the year of introduction of aquatic non-indigenous species (NIS) in three regions: Europe vs Spain (a), Europe vs Portugal (b) and Spain vs Portugal (c). Each dot represents a given NIS, with colour indicating the five considered biotic groups. Dashed lines represent the equality line and grey shadow correspond to confidence intervals.

similar pattern in the delay of NIS introductions. This situation was particularly evident after the 1900s, when both countries received new NIS with an average delay of about 50 years after their introduction in European inland waters. Interestingly, both Spain and Portugal comprised major countries of first detection in Europe (i.e. European countries acting as gateways for aquatic NIS introduction at continental scale) to a large number of the recorded NIS. For instance, at a continental scale, 51 NIS were firstly detected in Spain and 22 in Portugal, whereas UK (38 NIS), France (35) and Italy (31) were also relevant countries of first introduction in Europe (Suppl. material 2: fig. S5).

Functional groups

The recorded NIS spanned a wide variety of functional groups (Suppl. material 2: fig. S6), but they were mostly represented by predators (26.4%), filter-feeders (24.7%), primary producers (20.1%) and omnivores (18.5%). No alien pollinator species were detected, whereas the cryptogenic ship worm (*Teredo navalis*) was reported as the single xylophagous (i.e. wood-eating) species inhabiting Iberian inland waters.

Legal coverage of NIS regulation

Only 26 (8.0%) out of the 326 recorded NIS are included in the Union List of the EU Regulation (Fig. 6). Both national lists of IAS provided a higher legal coverage, since 86 (26.4%) and 80 (24.5%) out of the total recorded NIS were included in the Portuguese and Spanish lists of IAS, respectively. Although both national lists shared two thirds of the listed NIS, we found a clear regulation mismatch between them. For instance, the Portuguese list of IAS did not include 15 Spanish-listed taxa despite being

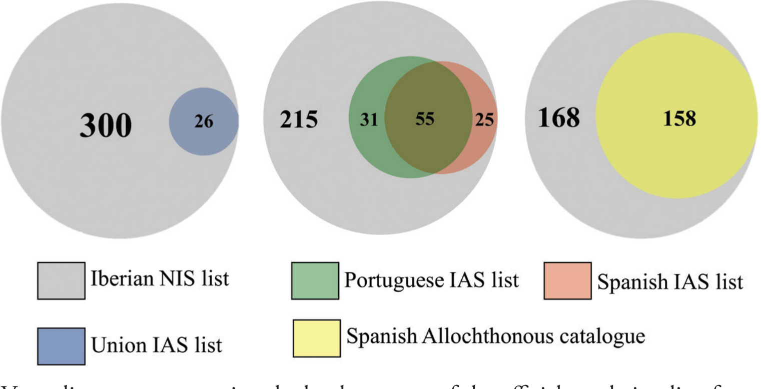

Figure 6. Venn diagrams representing the legal coverage of the official regulation lists for aquatic non-indigenous species (NIS) in Europe, Spain and Portugal. Large circles represent the pool of 326 NIS introduced in Iberian inland waters (Iberian NIS list), whereas smaller circles represent the number of aquatic Iberian NIS which are listed in the Union IAS list, in the Portuguese IAS list, in the Spanish Catalogue of Invasive Alien Species (Spanish IAS list) and in the list of allochthonous species able to impact on Spanish native biodiversity (Spanish Allochthonous catalogue). The number of NIS exclusive to and shared by each list is indicated within circles.

also introduced in Portugal, and 29 out of the 31 Portuguese-listed were not considered in the Spanish regulation. The highest legal coverage was provided by the Spanish allochthonous catalogue, since it included 158 out of the 326 recorded NIS (48.5%). Some taxonomic groups were clearly underrepresented in the European and national regulation lists (Suppl. material 2: fig. S7). For instance, none of the 52 recorded non-indigenous mollusc species were included in the Union list, and no alien platyhelminthes were included in any of the official lists of IAS (EU, Spanish and Portuguese). Chordata and Magnoliophyta were always the best represented ones in NIS regulations, whereas Arthropoda and Mollusca were comparatively the least considered.

Discussion

Checklist of NIS in Iberian inland waters

Our multi-taxa assessment provides the most updated and comprehensive inventory of NIS occurring in freshwater and transitional waters from the Iberian Peninsula (mainland Spain and Portugal). By gathering expert knowledge, published literature and other available data sources, we recorded 326 taxa of fungi, macroalgae, vascular plants, invertebrates and vertebrates already introduced and detected in Iberian inland waters, including established, uncertain and cryptogenic taxa. As compared to other reference checklists (Table 1), our multi-taxa inventory supports the occurrence of 258 aquatic animals and 41 plants introduced in Iberian inland waters, which is twice the number of NIS provided by previous reference studies (Rodríguez-Merino et al. 2017; Muñoz-Mas and García-Berthou 2020). These differences in NIS richness are likely due to the fact that former assessments were exclusively based on partial accounts of the available evidence (i.e. only NIS records published in international literature). Here, by combining information from multiple data sources (i.e. published international and grey literature, official online databases and technical reports) and looking for consensus among a widely diversified panel of Iberian experts, we achieved the most reliable and updated NIS checklist. In this context, official data repositories have emerged in recent years as essential tools to periodically update NIS checklists and assist management actions (Katsanevakis et al. 2014). Hence, online open-access databases provide a source of NIS records complementary to published literature, which suffers from long lag times that occur from field NIS detection to publication (Zenetos et al. 2017). Our integrative approach ensures a comprehensive assessment that will optimally support prioritising actions on NIS management (Katsanevakis et al. 2014).

In addition, most of the reference checklists (Table 1) focused only on non-indigenous fauna and/or freshwater environments as target systems, with NIS inventories on aquatic flora or transitional waters being much more limited. As stated here, information on NIS occurrence in Iberian inland waters is notably scattered across different data sources, which may place constraints on prospective data analysis and implementation of management actions by national or regional governments and river basin authorities. Moreover, the lack of integrated studies at national or regional scales precludes the assessment of global patterns and correlates in NIS introduction (Lonsdale 1999; Vilà et al. 2001). Therefore, our multi-taxa assessment is particularly valuable from a management viewpoint, because it unifies scattered NIS records and provides an updated inventory of aquatic NIS established (or potentially established) in Iberian inland waters, as well as includes a freely available database containing relevant species-specific information (Suppl. material 1). However, this inventory is likely to be subject to potential taxonomic biases derived from knowledge gaps of some poorly-known taxa, because of various biotic groups that are especially diverse and able to thrive in inland waters (e.g. annelids, nematodes, flatworms or chlorophytes) were underrepresented in our checklist. To date, research efforts focused on such biotic groups in Iberian inland waters have been sparse and scattered, which could have limited the number of recorded NIS. Through an expert-consensus-based approach, our study likely reduces the risk of taxonomic uncertainties typically occurring during the process of listing invasive species (McGeoch et al. 2012), thus providing a reliable and valuable list for environmental agencies, policy-makers and conservationists.

Table 1. Number of non-indigenous species (NIS) reported by the main previous studies providing reference checklists in the study area or related geographical regions. NA means no data available.

Reference checklist	Target environments	Target taxa	Study area	*N* established	*N* uncertain	*N* cryptogenic	*N* total
This study	Freshwater and transitional	Fungi, macroalga, plants, and animals	Iberian Peninsula	215	96	15	326
Zamora-Marín et al. 2023	Transitional	Animals	Spanish Mediterranean coast	93	30	6	129
Oficialdegui et al. 2023	Freshwater and transitional	Plants and animals	Iberian Peninsula	103	21	2	126
Muñoz-Mas and García-Berthou 2020	Freshwater and transitional	Animals	Iberian Peninsula	125	18	6	149
Anastácio et al. 2019	Freshwater	Animals	Mainland and insular Portugal	67	NA	NA	67
Rodríguez-Merino et al. 2018	Freshwater	Vascular plants	Europe	NA	NA	NA	60
Gofas et al. 2017	Marine	Molluscs	Mainland and insular Spain	36	NA	2	38
Rodríguez-Merino et al. 2017	Freshwater	Macrophytes	Iberian Peninsula	20	NA	NA	20
Chainho et al. 2015	Marine and transitional	Algae, plants and animal	Mainland and insular Portugal	78	46	NA	133
Aguiar and Ferreira 2013	Freshwater (rivers) and riparian	Plants	Iberian Peninsula	NA	NA	NA	NA
Cobo et al. 2010	Freshwater	Animals	Iberian Peninsula	NA	NA	NA	78
Sanz-Elorza et al. 2001	Terrestrial and freshwater	Plants	Spain	NA	NA	NA	176

Patterns in aquatic NIS introduction

Aquatic non-indigenous vertebrates and invertebrates were generally native to North America and temperate Asia, though a relevant proportion of taxa were also originated from Europe, being all these patterns congruent with previous studies (Anastácio et al. 2019; Muñoz-Mas and García-Berthou 2020). For vertebrates, this pattern was mainly due to the high number of non-indigenous fish species native to North America, Asia and Europe, which have been intentionally introduced (i.e. released) in Iberian inland waters to promote recreational fishing (García-Berthou et al. 2007). Most of these introduced fish corresponded to large piscivorous species (e.g. *Micropterus salmoides* and *Esox lucius*) and small-sized fish (e.g. *Alburnus alburnus* and *Abramis bjoerkna*) used as forage species for non-indigenous piscivores (Elvira and Almodóvar 2001). A non-negligible number of non-indigenous fish have also been intentionally released for ornamental purposes (e.g. *Carassius auratus*) or as a consequence of the aquarium trade (e.g. *Aphanius fasciatus*, *Poecilia reticulata* and *Misgurnus bipartitus*) (Maceda-Veiga et al. 2013; Clavero et al. 2023), whereas few of them became naturalised through escapes from fish farm facilities (e.g. *Ictalurus punctatus*) (Elvira and Almodóvar 2001; Maceda-Veiga et al. 2013). Non-indigenous fish introduced in Iberian inland waters but native to Europe are of particular interest because they have arrived through diverse introduction pathways, either intentionally as described above, or following a clear introduction route from French to north-eastern Iberian basins (Clavero and García-Berthou 2006). The remaining non-indigenous vertebrates were evenly native to all the considered regions (Suppl. material 2: fig. S8a), though non-indigenous reptiles were mostly native to North America, as previously documented for Spain (Vilà et al. 2001; Poch et al. 2020). However, this pattern in reptile introductions contrasts with that reported for non-indigenous herpetofauna naturalised in Europe, which was mostly native to Asia and Africa (Kark et al. 2009). Overall, non-indigenous vertebrates were almost exclusively introduced through intentional pathways (i.e. release and escape) (Suppl. material 2: fig. S8b), which is in accordance with continental patterns reported for Europe (Nunes et al. 2015; Saul et al. 2017). Native biogeographic regions for non-indigenous vertebrates correspond to temperate regions with climate regimes similar to the Iberian Peninsula. In this context, NIS introductions from regions with similar climate regimes are more likely to be successful and lead to established NIS (i.e. self-sustaining populations), as these species could be physiologically already adapted to the environmental conditions of the recipient aquatic ecosystems (Ribeiro et al. 2008).

Unlike vertebrates, invertebrate NIS were mostly introduced in Iberian inland waters through two unintentional pathways: contaminant and stowaway. They were native to almost all geographic regions, with North America and temperate Asia being the predominant. Previous studies have shown that most estuarine NIS of non-mollusc and non-arthropod invertebrates (e.g. annelids or platyhelminthes) reached the Iberian coast as hitchhikers through ballast water or hull fouling vessels from global maritime trade (Zorita et al. 2013; Chainho et al. 2015; López and Richter 2017; Cabral et al. 2020). This vector of introduction has been also highlighted as responsible for the arrival of some arthropods (e.g. estuarine crabs) to Iberian transitional waters. Several non-indigenous invertebrates (e.g. ostracods) have been also passively imported with rice culturing from Asia (Forès 1998; Valls et al. 2014). Non-indigenous decapods were composed by two separate groups, with freshwater crayfish being mostly native to North America and introduced intentionally (i.e. escape or release) for commercial purposes (Vedia and Miranda 2013), whereas estuarine crabs arrived unintentionally through stowaway and were mostly native to America (Muñoz-Mas and García-Berthou 2020). Non-indigenous molluscs arrived to Iberian inland waters mostly through stowaway, contaminants and escape, most of them associated with aquaculture facilities (López-Soriano and Quiñonero-Salgado 2016). The opening and subsequent enlargement of the Suez Canal in 1869 also allowed several estuarine gastropods of Indo-Pacific origin (the so-called Lessepsian migrants) to colonise the Mediterranean Sea (Nunes et al. 2014), and spread over transitional waters of the Iberian coast. For instance, such is the case of the molluscs *Fulvia fragilis*, *Bursatella leachii*, *Pinctada radiata* and *Cerithium scabridum* (López-Soriano et al. 2020). Moreover, anthropogenic modifications of Iberian estuaries may facilitate the establishment of those NIS that are more environmentally tolerant (González-Ortegón and Moreno-Andrés 2021).

The recorded non-indigenous aquatic vascular plants are mainly native to South and North America, and most of them were introduced through escape and release, although a non-negligible number of them also arrived as contaminants. Moreover, up to five different introduction pathways were exclusively associated with the arrival of some non-indigenous aquatic plants (e.g. *Heteranthera limosa*) (Suppl. material 2: fig. S2b). This pattern in non-indigenous plant introduction is congruent with that reported at continental scale in Europe, with escape being the major introduction pathway and vascular plants being also the biotic group introduced through more diverse vectors (Pergl et al. 2017).

Almost half of the recorded non-indigenous macroalgae was native to the Pacific Ocean and considered Lessepsian migrants, whereas the other half was native to the remaining geographic regions and introduced presumably passively through maritime traffic (Chainho et al. 2015; Orlando-Bonaca et al. 2021). Fungi corresponded to pathogens and were exclusively introduced as contaminants, but results provided here for this group are likely biased due to important challenges for taxonomic identification and poor knowledge of their biogeography (Bailey et al. 2020; Turbelin et al. 2022).

Legal coverage and policy implications

Legislative instruments (e.g. regulation lists or catalogues) are developed at European, national and even regional level to prevent the introduction and spread of enlisted NIS through direct management actions. The Regulation (EU) No 1143/2014 established a list of IAS of Union concern which entails that all EU Member States must implement specific management actions to prevent new introductions and further spread across European countries (Genovesi et al. 2015). Spain and Portugal have developed and adapted their IAS legislations to the EU Regulation, with the Spanish IAS catalogue and the Portuguese national IAS list being pivotal for providing legally binding lists that imply a generic prohibition on possession, transport and trade of listed taxa. We found that about 8% of the NIS recorded in Iberian inland waters were included in the Union list, which is the core of the EU Regulation. On the other hand, 26% and 25% of the recorded NIS were included in the Portuguese and Spanish IAS catalogues respectively, although it is understandable that the national IAS regulations do not necessarily include all the non-indigenous species recorded in their territories. Additionally, almost half (48.5%) of the listed NIS were also listed in the Spanish Allochthonous List, but this regularly upgraded list is focused on taxa potentially introduced in the near future and aims to regulate the importation of new NIS (other than those listed in the Union List and the Spanish IAS List) from other countries that are not part of the European Union and to promote adequate risk assessment. This moderately high percentage is explained by the fact that the Spanish Allochthonous List includes several entire genera (e.g. *Alternanthera* ssp. and *Lepomis* ssp.) and a very large number of species with the aim of regulating the potential importation of allochthonous taxa which are actually sibling species of already introduced NIS (e.g. *Alternanthera sessilis* and *Lepomis gibbosus*) and could lead to similar impacts in Iberian inland waters.

About 17.6% of the listed NIS in the present study have their native range within Europe, thus placing important challenges for transnational regulation and cooperation at Europe scale. This situation may lead to a complex conservation paradox when some aquatic species are native and even threatened in certain EU Member States but they have been introduced and become invasive in others (Marchetti and Engstrom 2016). Hence, national-level regulation instruments must be properly designed and implemented to deal with NIS that are particularly harmful to a given region and address these inherent constraints derived from managing NIS at European scale (Baquero et al. 2023). Consequently, effective management will require that national NIS catalogues are complemented to include all taxa that are considered a priority for management (Angulo et al. 2021). In this context, horizon scan exercises may become particularly useful to identify those high-risk NIS requiring priority management actions within a given region. In fact, Oficialdegui et al. (2023) highlighted a concern list of 126 taxa (all of them included in our inventory making up 38.6% of our listed NIS), as the most relevant invasive alien species already present in Iberian inland waters. Despite the effort made in these kinds of exercises, further research is needed to update the lists, and to address other aquatic invasive taxa that are continually being reported for the first time. The inventory presented here may be useful for this purpose.

On the other hand, our assessment on legal coverage provided by regulation lists highlighted important taxonomic-related biases. For instance, the Union list does not include any non-indigenous mollusc despite most of them being non-indigenous to Europe and some are already causing important ecological and economic impacts in Iberian inland waters (Sampaio and Rodil 2014; Gilioli et al. 2017). Therefore, further European-scale efforts should be done to include non-indigenous molluscs in NIS regulation. Although the Iberian Peninsula can be considered a single biogeographical entity, our results pointed to a considerable mismatch in the criteria followed for species listing between both Spanish and Portuguese catalogues. For instance, several NIS already introduced in both Iberian countries were included in the Spanish IAS catalogue but excluded from the Portuguese one, and vice versa. Hence, independent NIS management in neighbouring countries belonging to the same biogeographical region can jeopardise resource optimization and ultimately hinder effectiveness of management actions. Supra-national coordinated management actions are particularly needed, as they are generally more effective than national or regional ones (Faulkner et al. 2020). In fact, the Article 11 of the EU Regulation states that coordination and cooperation among MS is pivotal to address a strategic management. Owing to the several river basins shared by Spain and Portugal, the creation of an Iberian office for a coordinated NIS management would likely enhance the effectiveness of control measures and prevention protocols, as well as inter-sectorial communication for improving stakeholder engagement, as already suggested for other regions (Caffrey et al. 2014; Piria et al. 2017). Within the framework of this coordination office, national governments should channel management strategies on aquatic NIS through inter-regional regulation institutions (i.e. river basin authorities and coastal demarcations) to ensure coordinated efforts and avoid constraints from political borders among autonomous communities. The management of NIS is therefore a complex and transnational challenge that requires multi-faceted actions involving diverse institutions and stakeholders at different spatial scales (Baquero et al. 2021). For that purpose, the EU Regulation allows MS to list NIS of regional concern that require enhanced cooperation among involved countries. To inform these NIS management strategies, further research efforts in invasion science should be more applied and focused on cost-efficient actions (Muñoz-Mas et al. 2021).

Conclusions

The introduction of NIS in Iberian inland waters is a long-lasting process affecting many facets of biodiversity, but also local economies and public health. Managing aquatic NIS in the Iberian Peninsula requires a well-coordinated strategy among decision-makers and stakeholders. Nowadays, the increase of human pressure on natural habitats, the climate change and the expanding international trade are promoting the entry, spread, and establishment of new non-native taxa, particularly in inland waters. Hence, effective NIS management requires updated and detailed information on main introduction-related attributes. This study provides a comprehensive multi-taxa inventory of aquatic NIS introduced in Iberian freshwater and transitional waters. This baseline information is delivered through a freely available database intended to become a key tool for improving NIS prevention, monitoring and management at Iberian level. For instance, our assessment may serve as a useful resource for managing NIS introduction pathways into freshwater and estuarine ecosystems, as well as for communicating the magnitude of aquatic invasions to all related authorities and stakeholders. Moreover, this inventory also aims to meet the requirements on updated NIS data stated by the EU Regulation on IAS. Ultimately, our study provides valuable information on the implementation of other EU policies with implications on NIS management, such as the EU Biodiversity Strategy to 2030, the Birds and Habitats Directives, the Marine Strategy Framework Directive, and the Water Framework Directive.

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Supplementary material 1

All data of the recorded NIS

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Data type: xlsx

Explanation note: Excel file containing all data of the recorded NIS, as well as a corresponding legend for an easier interpretation and all the references supporting the NIS inventory.

Link: https://doi.org/10.3897/neobiota.89.105994.suppl1

Supplementary material 2

Supplementary images

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Data type: docx

Explanation note: **fig. S1**: Number of aquatic non-indigenous species (NIS) recorded in Iberian inland waters (including freshwater and transitional waters) across taxonomic classes; **fig. S2**: Number of native regions (a) and introduction pathways (b) associated to the five major biotic groups containing all aquatic non-indigenous species (NIS) introduced in Iberian inland waters (including freshwater and transitional waters); **fig. S3**: Contribution of the seven categories of introduction pathways to the arrival of aquatic non-indigenous species (NIS) to Iberian inland waters (both freshwater and transitional waters); **fig. S4**: Temporal variation in the overall contribution of the seven introduction pathways to the arrival of aquatic non-indigenous species (NIS) to Iberian inland waters (including freshwater and transitional waters); **fig. S5**: By-country distribution of first European records of aquatic non-indigenous species (NIS) introduced in Iberian inland waters (including freshwater and transitional waters); **fig. S6**: Distribution across functional groups (i.e. trophic groups) of aquatic non-indigenous species (NIS) recorded in Iberian inland waters (including freshwater and transitional waters); **fig. S7**: Legal coverage of official regulation lists for aquatic non-indigenous species (NIS) introduced in Iberian inland waters (including freshwater and transitional waters); **fig. S8**: Distribution of native regions (a) and introduction pathways (b) across taxonomic classes containing all aquatic non-indigenous species (NIS) introduced in Iberian inland waters (including freshwater and transitional waters)

Link: https://doi.org/10.3897/neobiota.89.105994.suppl2