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PRIMARY RESEARCH PAPER

Patterns and correlates of non-native inland fishes in the circum-Mediterranean region

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Abstract The circum-Mediterranean region is a global biodiversity hotspot, home to a highly distinctive freshwater fauna with a large proportion of endemic species, many of which are threatened. These ecosystems are increasingly impacted by biological invasions, particularly by non-native fishes. Here, we provide a comprehensive, updated inventory and analysis of non-native fishes recorded in inland waters across all countries bordering the Mediterranean Sea, based on an extensive review of scientific literature, databases and technical reports. A total of 151 non-native fish species were recorded in circum-Mediterranean inland waters, with Italy, Spain, Bosnia and Herzegovina, France and Croatia exhibiting the highest numbers of established species. Certain orders, such as Salmoniformes and Esociformes, were significantly overrepresented among established non-native species, whereas others, including Siluriformes and Characiformes, were underrepresented. Most introductions came from other European countries, Asia and North America, primarily through escapes or intentional releases. Non-native fish species richness showed a strong positive correlation with gross domestic product, precipitation and the number of dams, underscoring the influence of economic development and habitat availability as key drivers of species establishment. We also discuss the implications for regional biodiversity

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conservation and highlight the need for coordinated transnational strategies.

Keywords Europe · Freshwater ecosystems · Invasive species · Middle East · Northern Africa · Socioeconomic drivers

Introduction

The introduction of organisms beyond their native range represents a major threat to global biodiversity, contributing to species extinctions and to the alteration of ecosystem functions (Clavero & García-Berthou, 2005; Vilà et al., 2010; Gallardo et al., 2016; Soto et al., 2024). Non-native species introductions also have important societal and economic impacts, including an estimated annual economic cost of at least $26.8 billion (Diagne et al., 2021) and an increased risk of human disease transmission (Zhu et al., 2019). To date, more than 37,000 established non-native species have been registered worldwide (IPBES, 2023). However, the number of new introductions is still growing, with approximately 300 new introductions occurring annually (Seebens et al., 2017; IPBES, 2023), and no sign of the number of established non-native species declining in the near future (Seebens et al., 2021). The main drivers of species introductions are global economic activities and human-mediated environmental changes, which facilitate the transport, establishment and spread of non-native species (Arranz et al., 2025). Key factors such as trade volume, infrastructure development and habitat alterations create favorable conditions for biological invasions, shaping non-native species richness patterns worldwide (Hulme, 2009; Cano-Barbacil et al., 2022).

More specifically, inland fish introductions have increased substantially since the start of the twentieth century because of aquaculture, efforts to improve wild stocks and the growth of the pet trade (Gozlan et al., 2010; Novák et al., 2025; Oficialdegui et al., 2025). The introduction of non-native fishes, combined with habitat loss or degradation, pollution and hydrological alteration, often act synergistically toward the reduction of native inland fish populations (Bernery et al., 2022). Non-native fishes negatively impact native species through predation, hybridization, behavioral interference, disease and parasite spread, disruption of food webs and competition for resources (Cucherousset & Olden, 2011; Britton, 2023). In fact, invasive non-native fishes are often better competitors than the evolutionary-isolated native populations, and have a high reproductive potential, better predation strategies and a broader environmental tolerance (Mills et al., 2004; Cano-Barbacil et al., 2023b).

The circum-Mediterranean region is one of the world's biodiversity hotspots (Fensham et al., 2023). Its freshwater ecosystems harbor a very particular ichthyofauna, possessing a high proportion of range restricted endemic fishes (Kottelat & Freyhof, 2007; Doadrio, 2011), 56% of which are currently threatened (Smith & Darwall, 2006). However, they also host a high proportion of non-native species, with some catchments, such as the Segura River (Spain) and Pamvotis Lake (Greece), having an ichthyofauna comprised more than 70 and 80% of non-native fishes, respectively (Piria et al., 2018; Sánchez-Pérez et al., 2020). In fact, invasive non-native species have been highlighted as one of the greatest threats to the future decline of the endemic ichthyofauna of this region (Hermoso et al., 2011; Ribeiro & Leunda, 2012; Freyhof et al., 2020).

Lists of non-native species have been compiled for various countries and regions in Europe, northern Africa and the Middle East including Italy (Gherardi et al., 2008), Germany (Gollasch, 2006; Haubrock et al., 2025), the Iberian Peninsula (Elvira & Almodóvar, 2001; Muñoz-Mas & García-Berthou, 2020; Zamora-Marín et al., 2023), the Balkans (Piria et al., 2018), Morocco (Clavero et al., 2015; Taybi et al., 2023), Algeria (Kara, 2012), and Israel (Roll et al., 2007). In addition, an inventory of freshwater non-native species present in Europe was collected by the European Alien Species Information Network (EASIN) (Katsanevakis et al., 2012; Nunes et al., 2015). However, a detailed and updated analysis of the invasion records of inland fishes in the circum-Mediterranean area, is still lacking despite it is crucial for understanding the main patterns and drivers of biological invasions.

Here, we aimed to (1) compile a comprehensive and updated inventory of non-native fish species distributed across the inland waters of the circum-Mediterranean region by extensively reviewing published literature, online databases (e.g., GISD, EASIN and CABI), and technical reports; (2) identify the most commonly introduced species and taxonomic groups; (3) analyze the primary introduction pathways and native regions of the recorded species; and (4) determine the main socioeconomic and environmental variables that explain the occurrence patterns of non-native inland fishes. This study can guide the development of effective local and regional management strategies, including the identification of high-risk species that should be prioritized to prevent further introductions.

Methods

Geographic scope

This study focuses on the circum-Mediterranean area, defined as (1) river basins that drain into the Mediterranean Sea, or (2) river basins that experience—wholly or partially—a Mediterranean-type climate (Csa, Csb, Csc, BSh, BSk according to the Köppen-Geiger classification) with hot, dry summers and mild, wet winters (Perea et al., 2010; Vannière et al., 2011). Rainfall in the region is subject to high inter-annual and seasonal variability, and there exist a wide range of local climates with mean annual precipitation ranging from 100 to more than 3000 mm (Lionello, 2012). Thus, studied basins are located within the territories of Spain, Portugal, France, Italy, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Albania, North Macedonia, Greece, Turkey, Syria, Israel, Lebanon, Jordan, Egypt, Libya, Tunisia, Algeria, Morocco, Cyprus and Malta (Fig. 1). The overseas departments and regions of France, as well as the islands in Macaronesia belonging to Spain and Portugal (i.e., the Canary

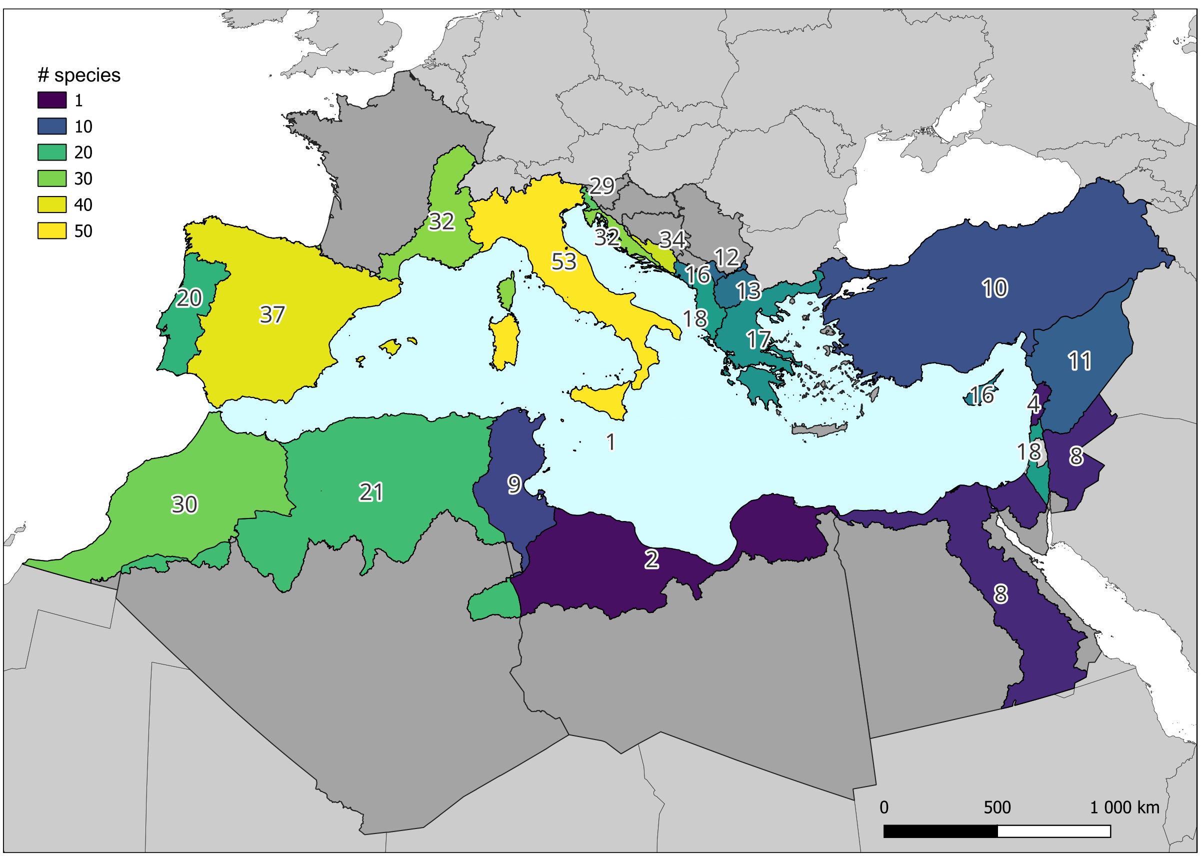

Fig. 1 Richness of established non-native inland fish species across the circum-Mediterranean region. Areas within the Mediterranean influence were defined as basins that either drain into the Mediterranean Sea or experience a Mediterranean-type climate (Csa, Csb, Csc, BSh, BSk according to the Köppen-Geiger classification)

Islands, Azores, Madeira and the Savage Islands), were excluded from this study and analysis. We considered species occurring in both lentic (i.e., ponds, lakes, wetlands, canals, and reservoirs) and lotic (i.e., rivers and streams) ecosystems. In addition, our analysis encompasses freshwater systems as well as transitional waters (e.g., saltmarshes, brackish zones, estuaries and coastal lagoons).

Data compilation

We employed a structured, integrative methodology to compile a comprehensive and up-to-date inventory of non-native inland fishes reported within the study basins defined above. This process began with an extensive review of available literature, encompassing peer-reviewed articles indexed in international databases, gray literature (e.g., regional journals, bulletins, technical reports) and online databases (see Cano-Barbacil et al., 2025a for a complete list of references). A systematic search was conducted in the Web of Science and Google Scholar using the following keywords: "freshwater fish" & "non-native" / "non-indigenous" / "allochthonous" / "exotic" / "alien" / "introduced" / "invasive" & "Mediterranean region" / "Portugal" / "Spain" / "France", etc. All retrieved publications were screened to extract records with explicit geographic attribution.

The preliminary inventory was subsequently cross-checked against national and regional sources, as well as major biodiversity and invasive species databases, including EASIN (European Alien Species Information Network; European Commission-Joint Research Centre, 2024), CABI-ISC (CABI´s Invasive Species Compendium; CABI, 2024), GISD (Global Invasive Species Database; ISSG, 2015), GRIIS (Global Register of Introduced and Invasive Species; Pagad et al., 2018), GBIF (Global Biodiversity Information Facility; GBIF.org, 2025) and FishBase (Froese & Pauly, 2025). For countries with mixed hydrographic drainage (i.e., France, Egypt and several Balkan states), only records explicitly referring to Mediterranean-draining basins were retained. When spatial resolution was insufficient to confidently assign a record to the defined study basins, the record was excluded. When inconsistencies arose regarding the presence and establishment status of non-native species, priority was given to regional and local studies over global databases, as the latter may contain errors or outdated information resulting from the aggregation of heterogeneous sources (see Online Resource 1). The final inventory includes all non-native fish documented in circum-Mediterranean inland waters up to January 2025. Fish taxonomy was based on FishBase (Froese & Pauly, 2025).

Non-native inland fishes were classified into established and not-established species following the definition provided by Soto et al. (2024). Established non-native are defined as those species that have established self-sustaining populations in their new location(s) in the wild. Thus, we classified as established only those species with studies providing explicit evidence of self-sustaining populations. Reports based solely on isolated records, stocking events without evidence of reproduction, or uncertain records were classified as not established. For certain species with uncertain establishment status, such as the rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792), we followed studies and reviews that explicitly evaluated their establishment status in Europe (Stanković et al., 2015). We also gathered information on the native range and the most likely introduction pathways for each non-native species from FishBase (Froese & Pauly, 2025) and CABI (2024). Then, we grouped the native range of each non-native species into the following regions: Europe, Africa, Asia, Australasia, Pacific, North America and South America. For species with more than one native region, equal weight was assigned to each region (i.e., the species was distributed in both regions). To categorize the introduction pathways of invasive species, we followed the classification established by the Convention on Biological Diversity (CBD 2014, see Online Resource 2).

We gathered various country-level socioeconomic and environmental variables (see Cano-Barbacil et al., 2025a), including gross domestic product, an indicator of the intensity of commercial trade and industrialization (Leprieur et al., 2008), which was obtained primarily from the International Monetary Fund (International Monetary Fund, 2024). If data for a specific country was not available, we sourced it from the World Bank or the United Nations (United Nations Statistics Division, 2024; World Bank, 2024). We also retrieved the country area under the Mediterranean influence (i.e., surface of the basins that either flow into the Mediterranean Sea or exhibit a Mediterranean-type climate), total population from the Department of Economic and Social Affairs of the United Nations (United Nations, 2024), and the number of dams from the Commission Internationale des Grands Barrages (CIGB) database (ICOLD, 2024). Finally, we collected the mean temperature and mean total precipitation by country (Booth et al., 2014; Fick & Hijmans, 2017), and the percentage of the surface covered by desertic areas (i.e., BWh and BWk climates according to the Köppen-Geiger classification; see Online Resource 3) as an indicator of habitat availability for aquatic organisms (Beck et al., 2018).

Data analyses

We analyzed the taxonomic patterns of the 106 established non-native inland fishes in the circum-Mediterranean region by comparing the observed number of established species within each order to the number expected under a random selection scenario. In this approach, the expected number of established species for each order is estimated proportionally to the number of extant species in that order, assuming that species establishment occurs at random with respect to taxonomy (Alcaraz et al., 2005; Marr et al., 2010). Thus, we calculated *R* values, which represent the probability of observing a given number of established non-native fishes based on the proportion of extant species within each order (Lockwood, 1999) using the "stats" R-package (R Core Team, 2019). To determine *P* values, we controlled for the false discovery rate (i.e., the proportion of erroneously rejected null hypotheses) by applying the Benjamini & Hochberg (1995) correction to the *R* values. The total number of species within each order was obtained from FishBase (Froese & Pauly, 2025).

We calculated the establishment ratio for each species as the number of countries in which the species has established populations divided by the total number of countries where it was introduced. To examine whether establishment success was associated with taxonomic order and country, we performed chi-square tests of independence using the "stats" R-package (R Core Team, 2019).

We used principal component analysis (PCA) with a Hellinger transformation to summarize the variation in the number of introductions of the non-native fish species recorded by country. Additionally, we used a cluster analysis to group countries based on the species they harbor using the Jaccard method and the "hclust" function of the "cluster" R-package (Maechler et al., 2025).

We calculated the Pearson's correlation coefficient (*r*) to evaluate the relationships among non-native fish richness and the different environmental and socioeconomic variables compiled (i.e., gross domestic product, total population, population density, percentage of urban population, number of dams, area, precipitation, temperature and percentage of the surface covered by desertic areas). To visualize these correlations, we used a network representation as implemented in the "qgraph" package in R (Epskamp et al., 2023). We also used generalized linear models (GLMs) with the Poisson distribution to identify the most influential variables on non-native species richness. Model selection was performed using the "dredge" function of the "MuMIn" R-package (Barton, 2023). This procedure generates all possible sub-models nested within the global model (i.e., model including all the explanatory variables), selects the most plausible subset and ranks them according to the corrected Akaike Information Criterion (AICc). Model averaging was then conducted, including all models with $\Delta AICc < 4$ relative to the best-performing model. Gross domestic product, total population, population density, number of dams, area and temperature were $\log_{10}$-transformed prior to the analyses. All statistical analyses were conducted considering only the established species, and were performed in R version 4.4.0 (R Core Team, 2025).

Results

Taxonomic approach and distribution

A total of 151 non-native fish species in circum-Mediterranean inland waters, which included 106 clearly established and 45 present (i.e., not established). Italy, Spain, France, Bosnia and Herzegovina and Croatia, in that order, had the highest number of non-native fish species established in their inland water ecosystems. By contrast, Libya and Malta reported the fewest non-native fish species (Figs. 1 and 2). Cypriniformes ($n = 46$) had the highest number of established non-native species in the circum-Mediterranean region, followed by Salmoniformes ($n = 14$), Cichliformes ($n = 10$) and Cyprinodontiformes ($n = 10$). However, when considering the total number

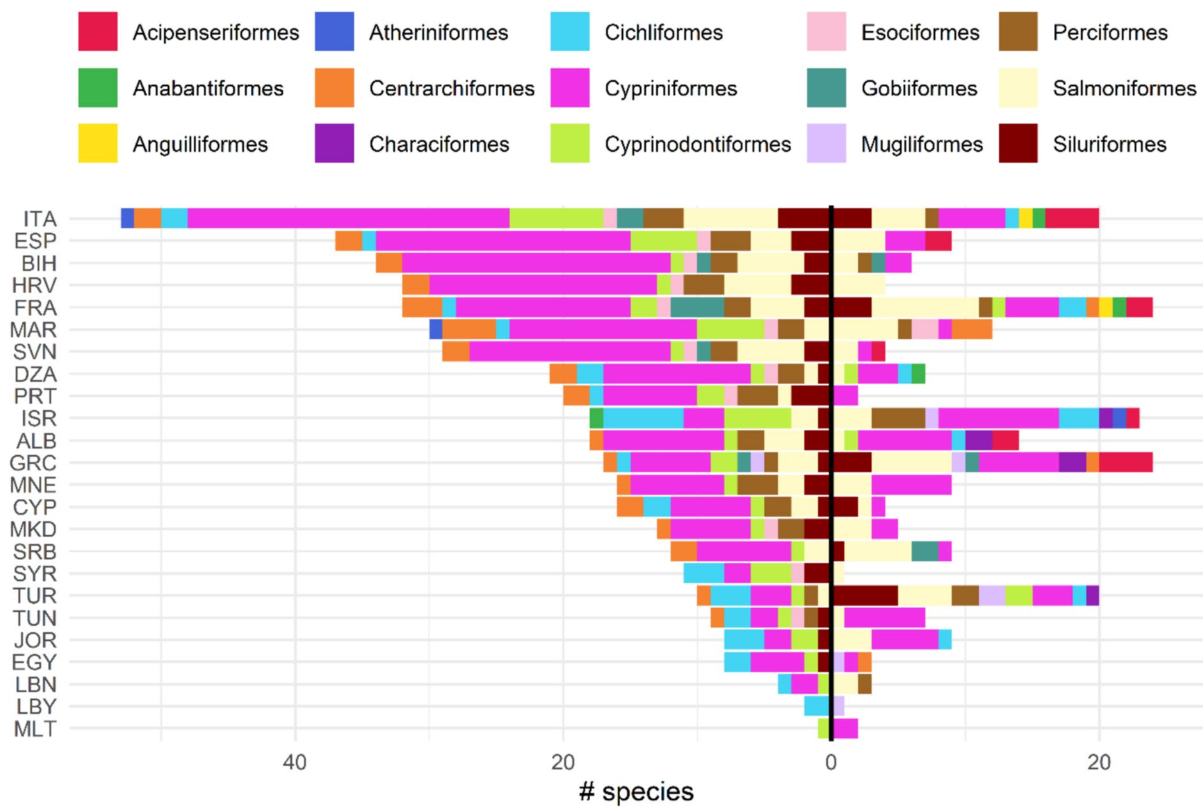

Fig. 2 Total number of established (left) and not-established (right) non-native inland fish species in circum-Mediterranean countries, colored by taxonomic order. The sum of both values represents the total number of introduced species in each country

of species within each order, Centrarchiformes, Esociformes and Salmoniformes were significantly overrepresented among established non-native species in the region (Table 1). By contrast, Characiformes and Siluriformes—two highly diverse fish orders—were significantly underrepresented among established non-native species in circum-Mediterranean countries.

At species level, *Gambusia holbrooki* Girard, 1859 (established in 21 countries), *Cyprinus carpio* Linnaeus, 1758 (20) and *Lepomis gibbosus* (Linnaeus, 1758) (16) were the most widespread fish among the inventoried taxa making them the three most introduced species in the circum-Mediterranean region (Fig. 3a). Another 14 species were established in at least 10 countries, whereas 38 of the recorded species were established in only one country. The establishment rates varied notably among species (Fig. 3b). For 58 species, all introductions were successful, resulting in self-sustaining populations in every circum-Mediterranean country where they were introduced. By contrast, all introductions of 45 species failed to result in viable populations. Establishment rates varied markedly among orders ($\chi^2 = 118.2$, df = 14, $P < 0.001$), and were higher for Cyprinodontiformes, Esociformes and Centrarchiformes and lower for Anguilliformes, Acipenseriformes and Characiformes (Online Resource 4a). Similarly, establishment patterns vary across countries ($\chi^2 = 85.3$, df = 23, $P < 0.001$), being lower in certain countries of the eastern Mediterranean basin (e.g., Turkey, Malta, Greece or Israel, Online Resource 4b).

Cichliformes and Cyprinodontiformes species have established self-sustaining populations primarily in Eastern Mediterranean and North African countries (Fig. 4). For example, Syria, Lebanon, Israel, Jordan and all northern African countries have recorded the presence of at least one *Oreochromis* species. By contrast, countries such as Italy, France, Spain and Portugal are characterized by the presence of non-native

Table 1 Number of non-native fishes established in the circum-Mediterranean region by taxonomic order compared to their total known number of species (Froese & Pauly, 2025)

Order	Total spp.	Established spp.	Expected established spp.	Bias	*R*	*P*
Acipenseriformes	27	0	0.170	=	0.843	1.000
Anabantiformes	258	1	1.622	=	0.517	1.000
Anguilliformes	90	0	0.566	=	0.567	1.000
Atheriniformes	312	1	1.962	=	0.416	1.000
Centrarchiformes	162	5	1.019	↑	**< 0.001**	**0.046**
Characiformes	2208	0	13.882	↓	**< 0.001**	**< 0.001**
Cichliformes	1759	10	11.059	=	0.452	1.000
Cypriniformes	4564	46	28.695	=	**0.001**	0.075
Cyprinodontiformes	1372	10	8.626	=	0.250	1.000
Esociformes	14	2	0.088	↑	**< 0.001**	**< 0.001**
Gobiiformes	1060	6	6.665	=	0.500	1.000
Mugiliformes	61	1	0.384	=	0.057	1.000
Perciformes	479	5	3.012	=	0.084	1.000
Salmoniformes	226	14	1.421	↑	**< 0.001**	**< 0.001**
Siluriformes	3832	5	24.093	↓	**< 0.001**	**< 0.001**

R values are the binomial probabilities of selectivity of established non-native species. *P* values are the *R* values adjusted for multiple comparisons (Benjamini & Hochberg, 1995). Only taxonomic orders that have established species in the region are shown

Arrows up (↑) indicate positive bias, arrows down (↓) negative bias and equal symbols (=) indicate no clear bias

Significant results ($P < 0.05$) are highlighted in bold

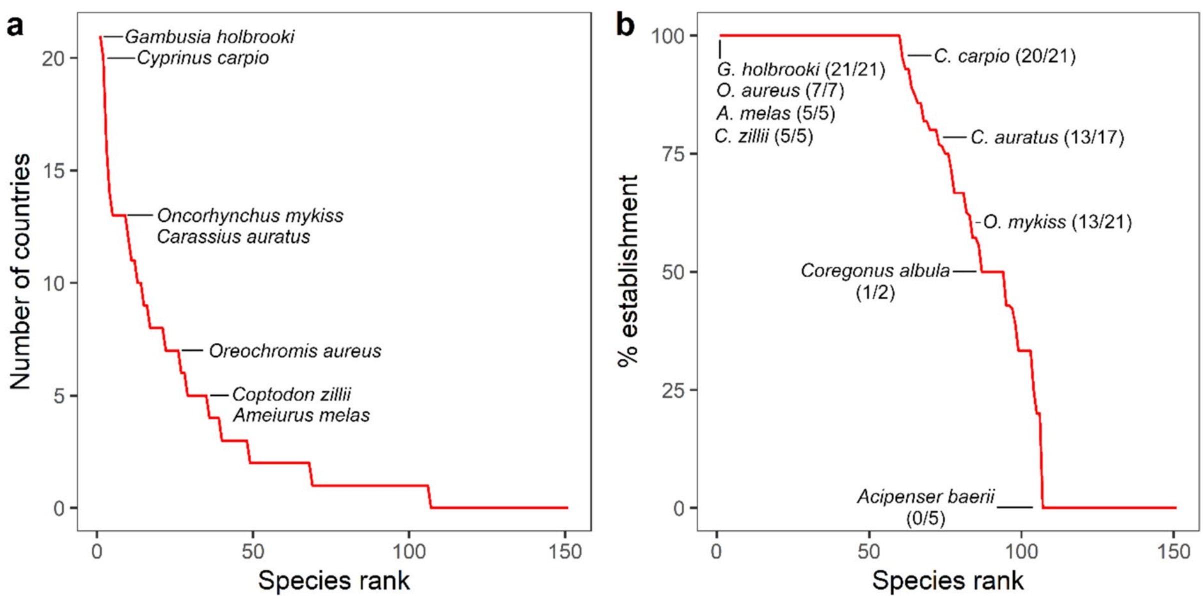

Fig. 3 Rank frequency curves showing **a** the extent of occurrence and **b** the establishment success of non-native fish species recorded across circum-Mediterranean countries (the number of countries in which the species has established populations and the total number of countries where it was introduced are shown in brackets). Species are ranked from most to least widespread, and from highest to lowest percentage of establishment, respectively. Representative taxa are labeled along the curves to highlight their relative positions

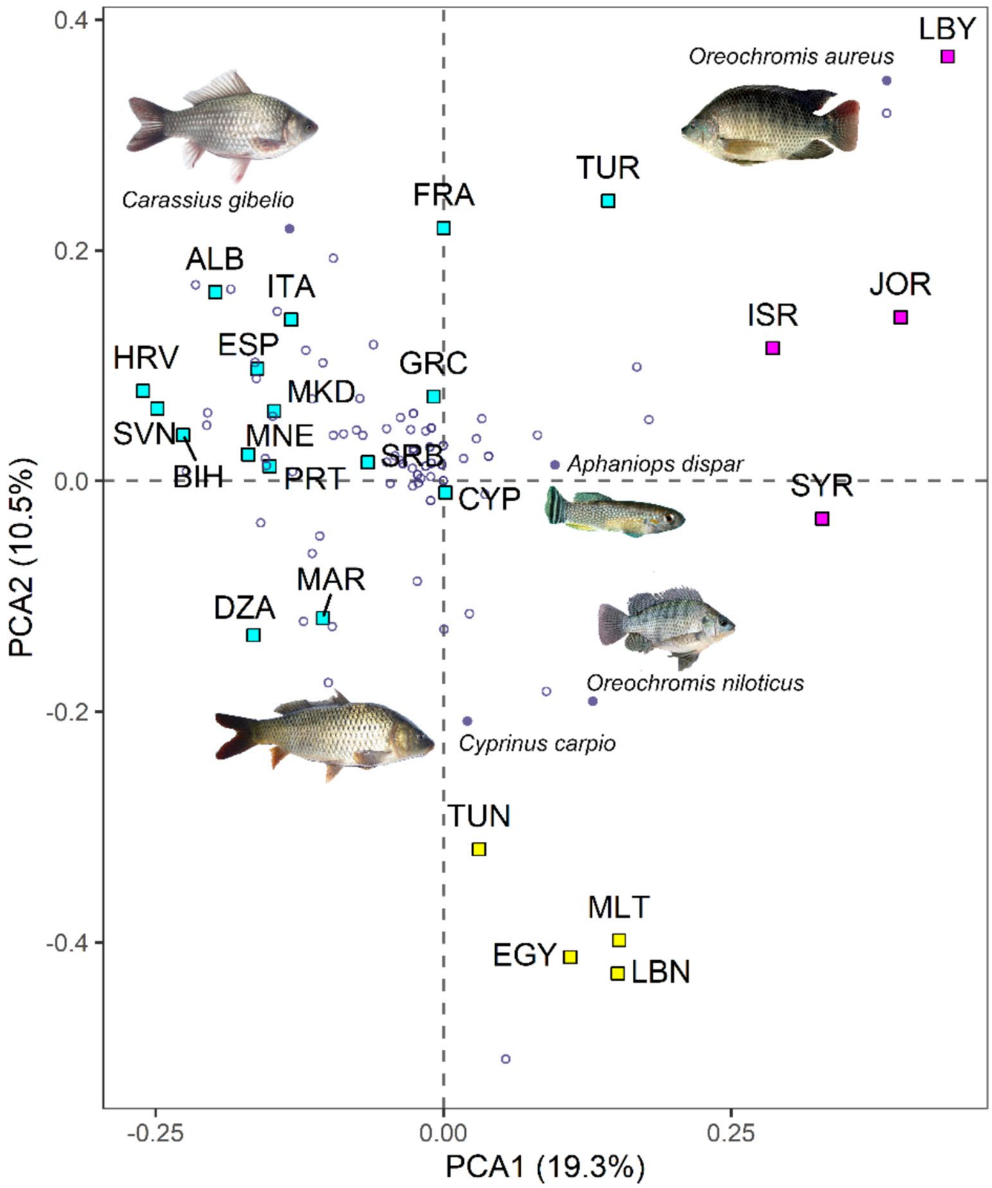

Fig. 4 Principal component analysis (PCA) of established non-native species by country in the circum-Mediterranean region. Purple circles represent species scores, while squares represent country scores. Square colors represent the three country groups derived from cluster analysis. The first two dimensions account for 29.8% of the total variance. Image sources: Wikimedia Commons

Cypriniformes from neighboring European countries. For instance, *Luciobarbus graellsii* (Steindachner, 1866), native to Spain, is well established in Italy, while *Alburnus alburnus* (Linnaeus, 1758), a species native to Central and Eastern Europe, has been introduced to Spain and Portugal, as well as to Morocco and Algeria. The Balkan countries exhibit a high proportion of non-native Salmoniformes compared to other regions, including *Salmo trutta* Linnaeus, 1758, *Thymallus thymallus* (Linnaeus, 1758), *Salvelinus* spp. and *Coregonus* spp. Based on these introduction patterns, circum-Mediterranean countries can be grouped into three main clusters (Online Resource 5): (1) European countries, Morocco, Algeria and

Turkey; (2) Israel, Syria, Jordan and Libya; and (3) Tunisia, Egypt, Lebanon and Malta.

Biogeographic origin and pathways of introduction

Most non-native fish species established in inland water ecosystems across the circum-Mediterranean region are native to Europe ($n=58$), Asia ($n=39$) and North America ($n=24$) (Fig. 5). Species from Africa ($n=11$), South America ($n=3$), and the Pacific region ($n=2$) were less commonly introduced. In European countries such as Italy, Spain, France, and Portugal, most non-native fish species originate from within Europe itself. Similarly, the non-native fish fauna of Balkan countries and Turkey includes a significant proportion of species introduced from Europe, but also from Asian countries. By contrast, non-native fishes in Israel, Syria, Jordan, and Libya predominantly originate from Africa, whereas in Tunisia, Egypt, Lebanon, and Malta they mainly originate from Asia.

We identified two major pathways responsible for fish introductions in the circum-Mediterranean: escape from confinement ($n=105$) and intentional release into the wild ($n=57$). By contrast, introductions via interconnected waterways ($n=6$) and unintentional transport ($n=9$, including stowaways and contaminants) were less common. Most recorded non-native fish were introduced through a single pathway ($n=110$, 72.8%) or two pathways ($n=41$, 27.2%).

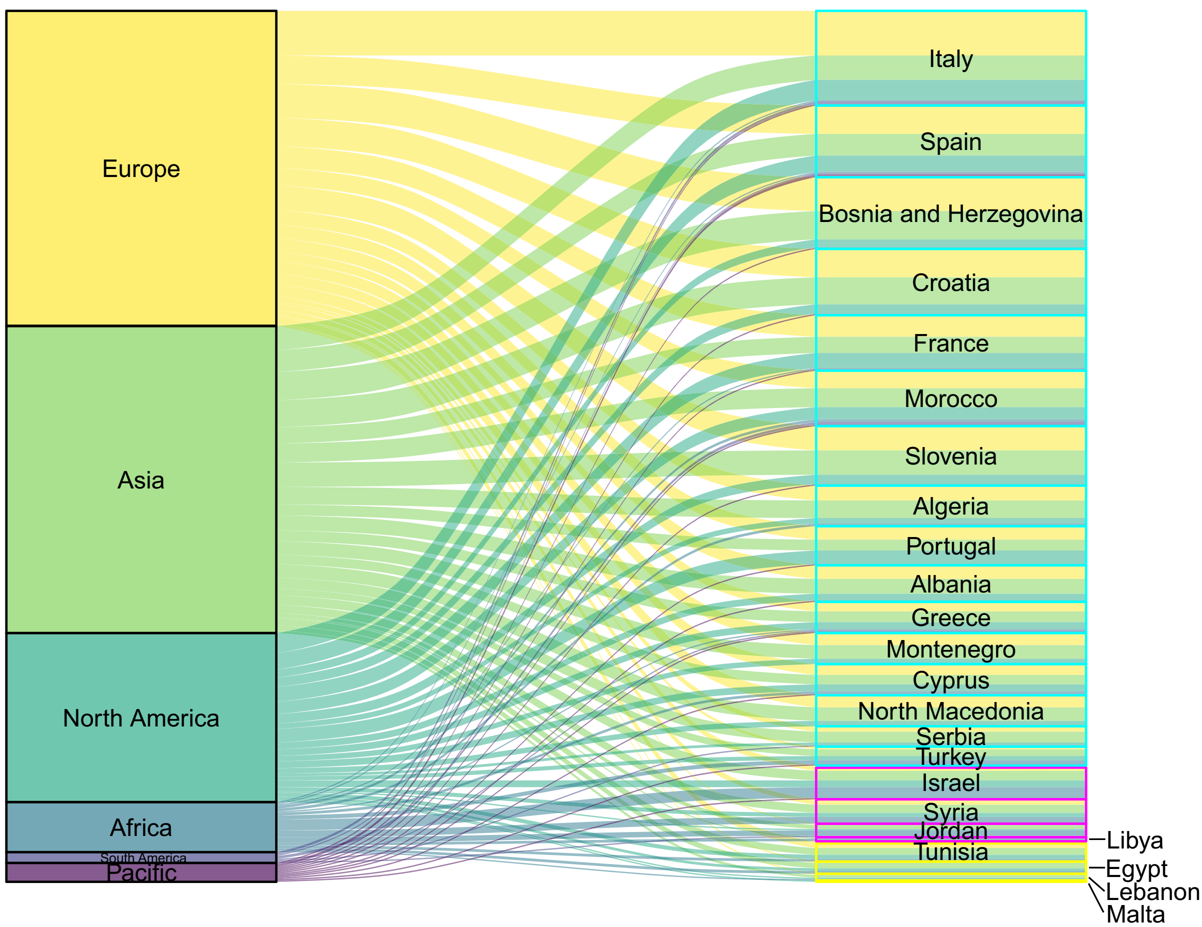

Fig. 5 Biogeographical origin of established non-native fishes from each country, with the width of the flows proportional to the number of species. Colors in the right column represent the three country groups derived from cluster analysis

Effect of environmental and socioeconomic variables

Non-native fish richness per country was positively correlated to gross domestic product ($r = 0.61$, $P = 0.001$), the number of dams per country ($r = 0.61$, $P = 0.002$), and total precipitation ($r = 0.42$, $P = 0.042$); while it was negatively correlated to mean temperature ($r = -0.43$, $P = 0.037$; Fig. 6). Similarly, GLM results showed that the most influential predictors of non-native fish species richness were gross domestic product (Estimate = 0.354, $P = 0.001$), country area under the Mediterranean influence (Estimate = 0.274, $P = 0.036$), and annual precipitation (Estimate = 0.001, $P < 0.001$; Table 2). Gross domestic product and precipitation were included as explanatory variables in the six selected models (i.e., models with ΔAICc < 4), while area was included in five. The three variables showed a positive effect to non-native fishes' richness, reflecting the role of economic development and habitat availability in facilitating the introduction and establishment of non-native fish species.

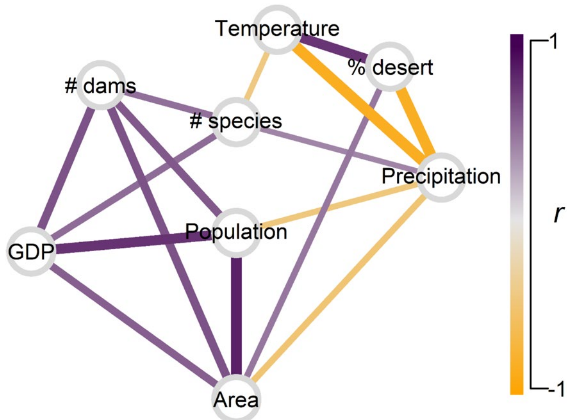

Fig. 6 Network representation of correlations among environmental and socioeconomic variables, with edges indicating correlation strength and direction. The color gradient reflects correlation coefficients (r). Note that only significant relationships are represented. The percentage of urban population was removed because it was not significantly correlated to any other variable. GDP gross domestic product

Discussion

Our study provides the most up-to-date and comprehensive inventory of non-native inland fish occurring in freshwater and transitional waters across the circum-Mediterranean region. By compiling published literature and other available data sources, we recorded 151 non-native fish species introduced in inland waters, including both established and not-established taxa. In recent years, official data repositories and monitoring programs have emerged as essential resources for regularly updating non-native species checklists. These open-access online databases serve as a valuable complement to the published literature, which often suffers from significant delays between field detection and formal publication (Zenetos et al., 2017). Our integrative approach to data collection ensures a broader and more robust

Table 2 Results of model averaging from the nine selected generalized linear models (GLMs) (i.e., models with ΔAICc < 4)

Variable	Estimate	Std. error	z	P	n models	Sum of weights
(Intercept)	− 0.587	0.749	0.747	0.455		
GDP	0.354	0.104	3.243	**0.001**	6	1.00
Precipitation	0.001	< 0.001	4.657	**< 0.001**	6	1.00
Area	0.274	0.123	2.096	**0.036**	5	0.92
# dams	− 0.128	0.135	0.887	0.375	1	0.14
Population	− 0.215	0.242	0.833	0.405	1	0.13
% desert	0.211	0.275	0.721	0.471	1	0.12
Temperature	− 0.413	0.692	0.559	0.576	1	0.10

Conditional average model estimates, standard errors, z-values and P values are shown. Additionally, the number of selected models in which each predictor was included and the sum of weights are reported

GDP gross domestic product

Significant predictors ($P < 0.05$) are highlighted in bold assessment, which can effectively support the prioritization of management actions targeting non-native inland fish in circum-Mediterranean countries (Katsanevakis et al., 2014).

The composition and establishment patterns of non-native inland fish across the circum-Mediterranean region differed extensively among countries. While most non-native established species were Cypriniformes, followed by Salmoniformes, Cichliformes and Cyprinodontiformes, their frequency of introductions and establishment rates varied among nations. These differences can be partially explained by several factors, including geographical proximity and similarities in environmental conditions (Chapman et al., 2017). For example, Spain, France, Italy and Portugal have exchanged multiple freshwater fish species, with introductions often facilitated by common trade routes and similar cultural practices related to fisheries and aquaculture (García-Berthou et al., 2005; Clavero & García-Berthou, 2006; Cobo et al., 2010; Anastácio et al., 2019). Thus, their non-native ichthyofauna is characterized by a high diversity of non-native Cypriniformes and Perciformes in comparison to other countries. Similarly, North African and Eastern Mediterranean countries have introduced similar warm-water fish species (e.g., *Oreochromis* spp. and Cyprinodontiformes) well-adapted to their particularly arid conditions (Clavero et al., 2015; Pritchard Cairns et al., 2024). In fact, introductions of non-native inland fish originating from regions with similar climatic regimes are more likely to succeed and result in established populations, as these species may already be physiologically adapted to the environmental conditions of the recipient ecosystems (Ribeiro et al., 2008). In addition, shared historical connections is another key factor shaping the introduction patterns of non-native species. This is especially evident in the Balkan countries (i.e., former Yugoslavia), where past shared environmental policies and practices led to the introduction of similar non-native species (Piria et al., 2018); but was observed as well in other European countries (García-Berthou et al., 2005; Rabitsch et al., 2013).

Our results also showed that the taxonomic distribution of non-native established inland fishes in the circum-Mediterranean region is biased and some fish orders such as Centrarchiformes, Esociformes and Salmoniformes are significantly overrepresented in relation to their world diversity. In agreement with our results, Salmoniformes show clear evidence of positive selection among non-native species in the Iberian Peninsula and exhibit high non-native species diversity in the Balkan Peninsula (Alcaraz et al., 2005; Marić et al., 2022; Zamora-Marín et al., 2023). Similarly, other taxonomic groups such as birds (Lockwood, 1999; Blackburn & Duncan, 2001) and plants (Pyšek, 1998; Richardson & Rejmánek, 2004) also exhibited non-random introduction patterns. These biases are strongly linked to the deliberate introduction of organisms that have particular characteristics and interest for humans, and that have been successfully introduced elsewhere (Alcaraz et al., 2005; García-Berthou, 2007; Cano-Barbacil et al., 2022).

Influence of biogeographic origin and pathways on species introductions

Overall, introductions of European fishes were the most common in the circum-Mediterranean region, a pattern consistent with that observed across various biogeographic regions of the northern Mediterranean arc, namely the Iberian, Italian, and some Balkan countries (Bianco, 2014; Piria et al., 2018; Zamora-Marín et al., 2023). For instance, large-bodied piscivorous fish species and European cyprinids have been extensively introduced and established into Western and Southern Europe (Latorre et al., 2023), as well as into some Northern African countries (e.g., Morocco) (Taybi et al., 2023), from their native ranges in Central and Eastern Europe (Copp et al., 2005). However, introductions from temperate regions of Asia and North America were also very common compared to other biogeographic regions, suggesting that introduction pathways involving long distance transport played an important role in the entry and establishment of non-native fishes (Piria et al., 2018; Muñoz-Mas & García-Berthou, 2020).

The reasons for, and pathways through which, these intra- and inter-continental introductions occurred are diverse. Overall, the non-native inland fish recorded in this study were introduced almost exclusively through deliberate pathways, namely release and escape (see Online Resource 2), a pattern that aligns with continental trends reported for freshwater fishes in Europe (Nunes et al., 2015) and in specific biogeographic regions such as the Iberian Peninsula (Zamora-Marín et al., 2023). Escape from confinement was the most important introduction pathway mainly due to "facilitated" escapes of ornamental fishes and to the introduction of different species for aquaculture. Despite its long tradition, ornamental fishkeeping has become one of the most popular hobbies in recent decades, with species from around the globe now being available in pet stores and through the online pet trade (Novák et al., 2025). *Carassius auratus* (Linnaeus, 1758), *C. carpio*, Cyprinodontiformes such as *Fundulus heteroclitus* (Linnaeus, 1766), *Poecilia* spp. and *Xiphophorus* spp., as well as the Asian loaches *Misgurnus anguillicaudatus* (Cantor, 1842) and *Misgurnus dabryanus* (Guichenot, 1872) have been widely introduced as ornamental fishes in the studied countries (Cano-Barbacil et al., 2025b; Novák et al., 2025). Similarly, aquaculture has a long history in the circum-Mediterranean region, dating back to ancient times when civilizations such as the Romans and Egyptians cultivated fish for food, a practice that was later continued in monasteries during the Middle Ages (Nash, 2010). In modern times, aquaculture has expanded significantly and many countries have invested heavily in this activity (Gyalog et al., 2022). The most commonly cultured species include non-native species such as the Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758), rainbow trout *O. mykiss*, and different catfish species such as *Clarias gariepinus* (Burchell, 1822) or *Ictalurus punctatus* (Rafinesque, 1818), which have been introduced due to their adaptability and fast growth rates (Milstein, 2017; Pasch & Palm, 2021). However, it is important to note that some species that are now used in aquaculture were originally introduced for other purposes (Savini et al., 2010). *O. mykiss*, *Salvelinus fontinalis* (Mitchill, 1814), *Ameiurus* spp., *I. punctatus*, and *Sander lucioperca* (Linnaeus, 1758) were initially introduced in some countries for angling, but were later incorporated into hatchery programs for restocking purposes and food production (Molony et al., 2003). In fact, intentional releases due to angling and biocontrol were another major pathway of non-native species introduction and dispersal. In countries such as Italy, Spain or Morocco the introduction of game fishes has particularly been a common practice during the twentieth century (Carpio et al., 2019). Species such as *Esox lucius* Linnaeus, 1758, *S. lucioperca, Micropterus nigricans* (Cuvier, 1828) or *Silurus glanis* Linnaeus, 1758 have expanded their non-native ranges due to continuous introductions by anglers (Martelo et al., 2021; Banha et al., 2024). Similarly, *Gambusia* spp. and other invertivorous species have been introduced across all the circum-Mediterranean region for mosquito population control and to help reduce disease transmission (Pyke, 2008). In some regions, introduced inland fish populations are managed to provide socioeconomic benefits for people. For example, species such as common carp (*C. carpio*) and largemouth bass (*M. nigricans*) are actively managed in many countries to support recreational angling, which generates substantial income for local economies. Similarly, rainbow trout (*O. mykiss*) is widely stocked in rivers and reservoirs for sport fishing and aquaculture purposes. Hence, it is crucial to consider both the environmental and socioeconomic impacts of non-native fish when assessing their impacts in recipient countries.

Influence of economy and habitat availability on species introductions

Our findings showed that economic activities, habitat availability and habitat alteration play an important role in driving the overall richness of non-native fishes. Consistent with previous studies, our results underscore the predominant influence of macroeconomic factors, climate and reservoirs as hotspots for non-native fishes introductions (Cano-Barbacil et al., 2022; Arranz et al., 2025). Countries with higher economic resources (i.e., gross domestic product) tend to host more non-native fish species due to increased international trade, aquaculture production and angling activities, which lead to a higher number of both intentionally and unintentionally species introductions (Sharma et al., 2010; Gallardo & Aldridge, 2013). Similarly, regions with more reservoirs support greater non-native fish richness because they experience higher propagule pressure and provide stable habitat conditions that are usually well-suited for non-native species establishment (Cano-Barbacil et al., 2022). Finally, annual precipitation and area were also positively correlated with non-native species richness. This suggests that countries with larger habitat availability may provide more suitable environments for both the introduction and successful establishment of non-native species.

By contrast, we found a negative correlation between temperature and non-native species richness, whereas no clear relationship was observed with human population. Typically, warmer climates are known to facilitate biological invasions at both global and regional scales (Bellard et al., 2016; Radinger et al., 2019). Similarly, total population is usually strongly associated with non-native species richness, as densely populated areas provide more opportunities for species introductions (García-Berthou et al., 2005). However, in the circum-Mediterranean region, the presence of vast desert and arid areas in large, warm and highly populated countries such as Algeria, Libya, and Egypt, where conditions are unsuitable for the establishment of aquatic organisms, might explain the opposite pattern.

Under the current climate change scenario, habitat suitability for aquatic organisms in the circum-Mediterranean region is expected to be further altered, potentially influencing the dynamics of invasions in freshwater ecosystems (Woodward et al., 2010; Carosi et al., 2021). Predicted increases in aridity and the amplification of extreme events may lead to the drying of river stretches, changes in hydrological regimes, and modifications in the availability of stable freshwater habitats. Such changes could disadvantage some currently established species while simultaneously creating opportunities for more thermophilic species—already widespread in the region, such as *Oreochromis* spp.—to expand their range and establish in new areas better suited to their ecological preferences (Cano-Barbacil et al., 2023a; Oficialdegui et al., 2023). In addition, species that are currently present but not yet established may face increased opportunities to become established under these new conditions, particularly those pre-adapted to warmer, more variable environments.

Considerations and limitations of the study

This study presents several inherent limitations related to data availability and quality, which may affect the completeness and accuracy of the compiled inventory. First, although the final dataset was carefully verified using recent regional studies and expert knowledge to ensure that only non-native species occurring within the defined study basins were included, some uncertainty may remain because many national datasets report species presence at the country level without distinguishing among individual river basins. To reduce potential biases, we prioritized local and regional sources providing geographically explicit information whenever possible. Second, the establishment status of certain species is not always consistently reported. While some studies follow categorization frameworks such as that proposed by Blackburn et al. (2011), others use ambiguous or non-standard terminology, reducing comparability of establishment status among countries (Cano-Barbacil et al., 2020; Haubrock et al., 2024). These inconsistencies may lead to misclassification of certain species, potentially biasing cross-country comparisons and affecting estimates of establishment rates. To mitigate this issue, we applied a conservative classification approach and prioritized studies providing explicit evidence of self-sustaining populations. Finally, despite recent advances in genetic studies, taxonomic uncertainties persist for several taxa. For example, current evidence indicates that *Gambusia affinis* (Baird & Girard, 1853) is largely absent from most Mediterranean systems, whereas *G. holbrooki* is the dominant established species, although both taxa may co-occur in a few countries (Srean, 2015). Similar taxonomic complexities occur within the genus *Phoxinus* in Spain, where multiple lineage and hybrid populations have been reported (Corral-Lou et al., 2019). Despite these limitations, the dataset represents the most comprehensive synthesis currently available for the circum-Mediterranean region and provides a robust basis for large-scale comparative analyses.

Conclusions

The occurrence of non-native inland fishes in the circum-Mediterranean region results from a complex interplay of socioeconomic, ecological, geographic and historical drivers. Human activities that facilitate the movement of aquatic fauna into inland waters—such as aquaculture, recreational angling or ornamental trade—are expected to intensify in the coming decades, with projections indicating significant increases in the number of non-native species introductions across circum-Mediterranean countries (Seebens et al., 2020). Since the eradication and control of non-native inland fish populations is usually challenging and costly once they become established (Britton et al., 2011), with only a few documented exceptions (Weyl et al., 2014), a clear distinction between introduced (but not yet self-sustaining) species and established species remains fundamental for defining effective management strategies. Introduced species require rapid detection and immediate response measures, as early intervention offers the highest likelihood of successful eradication or containment. In contrast, established species typically demand long-term management strategies, focused on impact mitigation, habitat restoration, and preventing further spread. Accordingly, management priorities in the region should include: (1) implementing stringent biosecurity protocols and effective prevention measures to reduce the likelihood of new introductions; (2) developing robust predictive risk assessments to anticipate which species are likely to establish in specific regions (Roy et al., 2019; Cano-Barbacil et al., 2023a); and (3) reinforcing surveillance programs to ensure early detection and the prompt activation of response protocols (Reaser et al., 2020). Given the strong influence of economic activities on biological invasions, management efforts should prioritize enhanced monitoring programs as well as coordinated and stricter regional policies to control international trade and the introduction of high-risk species associated with aquaculture, angling and fishkeeping. Adaptive governance and targeted monitoring efforts should focus on well-known invasion hubs—such as reservoirs and highly transformed and populated catchments—where propagule pressure is consistently high. Ultimately, addressing the challenges posed by non-native inland fishes in the circum-Mediterranean region requires an integrated approach that combines scientific research, evidence-based policy, and public awareness. Such coordinated efforts are essential to minimize biodiversity loss and ecological disruptions, and ensure that management strategies remain socially and economically feasible in a region where human–environment interactions are exceptionally strong.

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Data availability Tables containing species and environmental data by country are available on figshare (DOI: https://doi.org/10.6084/m9.figshare.29656604).

Declarations

Competing interests We have no conflicts of interest to disclose.

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