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Ecological Processes

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A global analysis of the introduction pathways and characteristics associated with non-native fish species introduction, establishment, and impacts

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Abstract

Background The invasion success of introduced freshwater fishes is influenced by many factors, including ecological, species, and socioeconomic characteristics. Most studies that document the importance of these characteristics are conducted at local scales and/or focus on a single step of the invasion process. In this study, we aim to determine the species characteristics, ecological characteristics, and socioeconomic characteristics of non-native freshwater fish invasions. Our assessment was done at the global scale and considers all three steps of the invasion (i.e., introduction, establishment, and impact). For this purpose, we applied generalized linear models to 20 variables collected for 307 non-native species and modeled them as a function of ecological characteristics (i.e., environmental features), species traits (i.e., functional and morphological), and socioeconomic characteristics (i.e., human use and introduction pathways). We considered the number of countries in which each species was introduced, established, or had ecological impacts as a proxy of invasion step success. We also explored the specifics of species introduced through the aquaculture and the ornamental fish trade pathways.

Results We found that non-native freshwater fishes with broad diets, high parental care, and multiple introduction pathways are the most widely introduced and established worldwide. The number of countries with impacts reported was best explained by the type of introduction pathway (i.e., aquaculture or fisheries). Moreover, among non-native species introduced through aquaculture, those belonging to Cypriniformes and having broad diets were the most widely introduced and established species. In contrast, the species introduced through the ornamental fish trade pathway belonged to various taxonomic orders but were mainly native to tropical regions.

Conclusions Considering several types of factors is important when analyzing the invasion success of freshwater fish and disentangling the different invasion steps. These findings have strong implications for anticipating the profile of species with a high potential to invade many countries.

Keywords Aquaculture, Ecology, Exotic, Freshwater fish, Introduction pathway, Invasion step, Morphology, Ornamental fish trade, Socioeconomic, Trait

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Introduction

The rise of global trade has led to an increase in the introductions of invasive non-native species (Seebens et al. 2017). Presently, biological invasions of non-native species are recognized as a major threat to biodiversity at global scales (Bellard et al. 2016). In this study, a successful biological invasion was defined following IUCN (2000) as species transported and introduced beyond their natural geographical ranges by human pathways. Following introduction, species can potentially establish in the recipient environment by developing self-sustaining populations. At some point later, some of the established species can attain the invasion stage by expanding in the new environment and impacting native fauna and/or on the recipient environment (Lockwood et al. 2013).

Freshwater fishes are among the most introduced taxa, with non-native freshwater fishes now established in all biogeographical realms (Gozlan 2008; Leprieur et al. 2008; Bernery et al. 2022). The magnitude of introduced fishes is so significant that these biogeographical realms were irremediably altered, constituting evidence of the Anthropocene epoch (Leroy et al. 2023). Invasive non-native freshwater fish species have diverse impacts, ranging from local hybridization with native fish species, with the invasive rainbow trout (*Oncorhynchus mykiss*) and native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in Canadian rivers (Muhlfeld et al. 2009) being a well-known example. Invasions by freshwater fishes also lead to profound changes in native species assemblages, leading to taxonomic homogenization across large regions such as the Laurentian Great Lakes (Campbell and Mandrak 2020). Nonetheless, not all introduced non-native fish species become established and not all established species have impacts. Previous studies have shown that the success of each step of the invasion is influenced by different factors, namely, species characteristics, ecological characteristics of the native or recipient ecosystems, and socioeconomic characteristics that encompass introduction pathways of the introduced species. Regarding species characteristics, non-native fish species with a broad diet spectrum establish more easily than more specialized species (Ruesink 2005; Su et al. 2023). Concerning ecological characteristics, the size of the native range influences the establishment and spread of non-native species into new environments. Although the exact mechanism remains unclear, it is possible that species with expansive native ranges are adapted to broader ranges of climate and habitat (Marchetti et al. 2004a). Concerning socioeconomic characteristics, these are usually related to the intended uses of fishes by humans. Thus, the increasing use of fish in ornamental fish trade has caused a rise in fish introductions worldwide (Magalhães and Jacobi 2013; Bernery et al. 2022). Likewise, the aquaculture trade introduction pathways is also known to be an important source of freshwater fish introductions and establishments (Bernery et al. 2022). Furthermore, it is common to observe strong interactions between species characteristics and introduction pathways. For instance, species introduced through the aquaculture trade are more likely to be large-bodied omnivorous species (Su et al. 2020), while those introduced through ballast waters are more likely to be small-bodied species with lower spread rate (Wonham et al. 2000).

Understanding the different characteristics that promote invasion success is important in order to improve predictions about future invasions (Pyšek et al. 2020). Thus, several recent studies have used quantitative modeling to identify the characteristics of freshwater fish species that have successfully invaded (García-Berthou 2007; Snyder et al. 2014; Su et al. 2020, 2023). However, species, ecological, and socioeconomic characteristics of non-native freshwater fishes have never been studied jointly at the global scale while considering steps of the invasions separately. In fact, most studies are conducted at local scales and with a limited number of species (Marchetti et al. 2004b; Ribeiro et al. 2008), often without considering the different types of factors (Ribeiro et al. 2008) or the different steps of the invasion process (Ruesink 2005; García-Berthou 2007; Lawson and Hill 2022). Despite that Ruesink (2005) represents one of the most complete studies conducted to date that analyzed species, ecological, and socioeconomic characteristics of non-native freshwater fishes at the global scale, it focused on only the establishment step. As a result, there is currently no consensus about the factors characterising the species at each step of the invasion success of freshwater fishes globally.

To address this information gap, we conducted a multidimensional study to identify the species, ecological, and socioeconomic characteristics of non-native freshwater fish invasions. Our study used a statistical modeling approach and was conducted at the global scale and considered all three steps of the invasion process (i.e., introduction, establishment, and impact). For 307 introduced freshwater fish species, we considered their traits (i.e., functional and morphological), ecological characteristics (i.e., features of the species' native ecosystems), and socioeconomic aspects (e.g., introduction pathways including the aquaculture and ornamental fish trade). We investigated the link between these characteristics and the invasion patterns measured as the number of countries, where each species has been introduced, established, and reported to have impacted the native fauna and/or the all recipient ecosystem. We constructed our models based on initial assumptions for each invasion step. First, we hypothesized that the species characteristics influencing introduction success would be dependent on the introduction pathway (e.g., large-bodied fishes that are used as food fish have a greater likelihood of being introduced through the "aquaculture" pathway; Su et al. 2020). The introduction pathway also is, in turn, influenced by the native region of non-native species (e.g., species commonly associated with the ornamental fish trade tend to be native to tropical countries, Gertzen et al. 2008). Second, as the establishment step depends on the interplay between the recipient ecosystem fulfilling the introduced species' needs and the likelihood that individuals survive the transport and introduction steps, we hypothesized that generalist species (i.e., broader, more generalized diets) and species introduced in large numbers (i.e., high propagule pressure) would have greater establishment success. High parental care also has been highlighted in several studies as an important characteristic that favors successful establishment (Marchetti et al. 2004b; Lawson and Hill 2022). Finally, concerning the impact step, it has been demonstrated that invasive species at higher trophic levels tend to have greater impacts in recipient ecosystems, oftentimes because prey species in the recipient environment are naive to the new predator (Moyle and Light 1996; Howeth et al. 2016). Thus, we hypothesized that fish species with nektonic diets would have greater impacts than species at lower trophic levels that fed on more planktonic, plants, or detrital diets. However, only a few previous studies have focused on the impact step, mainly because impact data are scarce and difficult to compile (Bernery et al. 2022). Herein, we propose to analyze of the factors that drove the impact of non-native fishes in several countries.

Materials and methods

Data sources of the species-level variables

To understand the factors facilitating the non-native freshwater fish introduction, establishment, and impact, we compiled species-level variables pertaining to their species, ecological, and socioeconomic characteristics. We chose these variables, because they were assumed to influence species invasions (see Table 1 for justifications and hypotheses; Pyšek et al. 2020). Overall, we obtained 20 species-level variables from five data sources:

(i) FishBase (Froese and Pauly 2019, version 19.04, accessed with the "rfishbase" R package; Boettiger et al. 2012), which included data on invasion status, characteristics, and human use of 34,300 fish species at the global scale. To date, FishBase is the most comprehensive global database on fish species. Despite some gaps and incompleteness, it gathers most of the current knowledge on fish species characteristics and human uses. FishBase has been widely used, notably in global studies determining characteristics of invasive fishes (e.g., Ruesink 2005; Bernery et al. 2023). Herein, we used FishBase to gather the diet, reproductive guild, human use, and introduction pathways that are fairly well informed for most fish species (Blanchet et al. 2010; Hirsch et al. 2021; Su et al. 2023). We also used the taxonomic classification of FishBase, where each species is associated to a unique code ensuring a consistent follow-up of species throughout taxonomic changes.

(ii) FISHMORPH morphological database (Brosse et al. 2021), which included information on the morphological traits of 9150 fish species.

(iii) database on freshwater fish occurrences complied by Tedesco et al. (2017), which has distribution data for 14,953 freshwater fish species in 3119 basins worldwide.

(iv) global biogeographical regions of freshwater fishes (Leroy et al. 2019).

(v) WorldClim world climate database (Fick and Hijmans 2017).

Species characteristics

We defined freshwater fish as all species with a freshwater habitat listed as one of their preferred habitats in the table *species()* of the "rfishbase" R package.

Main diet and diversity of diets

To retrieve data on species diets, we used the five types of diet filled in the "FoodI" column of the *fooditems()* table of the "rfishbase" R package: detritus, nekton, plants, zoobenthos, and zooplankton. Each species can be filled with several diets. Indeed, one species can have several iterations in the *fooditems()* table, following the locality, the experiment and/or the study, where the diet information was retrieved. For example, the Goldfish (*Carassius auratus*) had 10 iterations in the *fooditems()* table. In these 10 iterations, four diets were filled (detritus, plants, zoobenthos and zooplankton) with the zoobenthos being the most represented diet, representing 60% of the iterations). Thus, we compiled two variables: (i) the most represented diet for each species (hereafter referred as the main diet) and (ii) the diversity of diets, determined by the total number of diet categories (Table 1, e.g., 4 in the case of the Goldfish). In the cases (37 out of 307 species considered here), where several diets were equally represented, we chose the most represented diet within the taxonomic order. We made an exception for *Megalops*

Table 1 Descriptions of the type, the modalities and the hypothesis and justifications of all the variables used

Variable type	Variable	Variable modalities	Hypothesis/justification
Response variable	Number of countries, where the species: (i) is introduced (ii) is established (iii) has ecological impacts (for all species and the ornamental fish trade and aquaculture pathways)	Quantitative variables	–
Species characteristics	Main diet	• Detritus • Nekton • Plants • Zoobenthos • Zooplankton	Broad food spectrum, piscivorous diet, as well as some specialized diets facilitate establishment (Ruesink 2005; Tonella et al. 2018). A nekton diet can be associated with species having an impact (Moyle and Light 1996; Howeth et al. 2016)
	Number of diet categories	Quantitative variable	
	Hydrodynamics	Quantitative variable	Good swimming ability enables fish to colonize new regions, spread, establish, and have wide impacts (Carvajal-Quintero et al. 2019)
	Pectoral fin vertical position	Quantitative variable	
	Parental care	Ordered categorical variable • Non-guarder • Guarder • Bearer	A high level of parental care facilitates establishment (Marchetti et al. 2004b; Lawson and Hill 2022)
	Total length (TL)	Quantitative variable	At the introduction step, the body length of successful species is linked to the introduction pathway (Wonham et al. 2000; Su et al. 2020). At the establishment step, body length depends on the environmental conditions (Vila-Gispert et al. 2005). At the impact step, small species can have greater impacts (Marchetti et al. 2004a, b)
	Taxonomy	• Cypriniformes • Cyprinodontiformes • Siluriformes • Perciformes • Characiformes • Other	Taxonomic order is a surrogate for missing characteristics that could influence species success at different stages of the invasion
Ecological characteristics	Temperature range in the native basins	Quantitative variable	Temperature range in native basins can be a proxy of temperature tolerance. Temperature tolerance influences the establishment and spread of invasive species (Kolar and Lodge 2002; Marchetti et al. 2004b; Snyder et al. 2014)
	Maximum temperature in the native basins	Quantitative variable	
	Main native bioregion	• Nearctic • Palearctic • Sino-Oriental • Neotropical • Ethiopian • Madagascan	Native bioregions roughly reflect environmental conditions
Socioeconomic characteristics	Use by humans	Yes/no	Species used by humans have greater chances of being introduced than those not used by humans
	Aquaculture	1/0	Introduction pathways constrain the characteristics of introduced species (Wonham et al. 2000; Su et al. 2020) The number of introduction pathways is linked to high propagule pressure
	Sport/Angling	Quantitative variable	
	Accidental		
	Ornamental		
	Fisheries		
	Diffusion		
	Species control		
	Number of introduction pathways		

atlanticus which had two equally most represented diets even at the taxonomic order level. Therefore, we chose to associate the "nekton" main diet to this species, because *Megalops atlanticus* is a known predator of crabs and small fish (Planquette et al. 1996).

Swimming ability

To analyze the influence of swimming ability on invasion success, we used two variables from Su et al. (2019). First, we used the pectoral fin vertical position (i.e., ratio of pectoral fin position relative to body depth), which reflected the swimming style (Table 1). For example, lateral pectoral fins are used more for propulsion and fine movements, whereas ventral pectoral fins often typify fishes with less precise movements (Blake 2004; Su et al. 2019). Second, we quantified the hydrodynamics for each fish species as the ratio of body length to body depth (Villéger et al. 2017; Su et al. 2019) (Table 1).

Parental care

We used the parental care variable from the "RepGuild1" column of the *species()* table of the "rfishbase" R package (Table 1). The parental care variable considered three categories: "nonguarders" which do not guard eggs or nests, "guarders" which guard eggs and nests, and "bearers" which incubate eggs on or in parental body and give birth to live young.

Total length (TL)

To gather this information, we used the "TL" column of the *morphometrics()* table of the "rfishbase" R package. As a species can be filled with several different total lengths depending on the origin of the data (e.g., study, location) we took the median of all the given total length for each species. Indeed, we chose to use the species median rather than the maximum size to better capture intra-species size variation, which may impact the introduction pathway taken (e.g., ballast water).

Species taxonomy

We used FishBase as the taxonomic reference (Froese and Pauly 2019). We classified each species to taxonomic order using the *load_taxa()* table from the "rfishbase" R package. The number of species classified per taxonomic order was heterogeneous, which sometimes creates statistical issues due to class imbalances, especially for orders with few representative species. Therefore, we kept the five main taxonomic orders (i.e., Characiformes, Cypriniformes, Cyprinodontiformes, Perciformes, and Siluriformes) separated during modeling and grouped all the remaining 16 taxonomic orders under an "Other" category.

Ecological characteristics

Main native bioregion

Freshwater fishes have evolved in isolated biogeographical regions for the past 10–20 million years (Leroy et al. 2019). Consequently, each bioregion has distinct characteristics pertaining to its environmental conditions, faunistic composition, and associated interactions. In addition, biogeographical regions broadly cover the main geopolitical regions of the world, with distinct intra-region and inter-region properties in terms of species displacement and propagule pressure. Hence, the region of origin of a species is a proxy of several characteristics: environmental conditions, diversity of interactions throughout their evolutionary history, and the likelihoods of introduction to non-native ecosystems (Table 1). We defined two variables based on the biogeographical regions following Leroy et al. (2019), namely, the number of native bioregions (defined as bioregions, where the species has native occurrences) and the main bioregion, defined as the bioregion with the greatest number of native basins, where the species is found. It is important to note that 85% of the species considered here have only one bioregion. Two species equally occurred in two native bioregions. For these species, we selected one region at random and verified whether this choice had an impact on the model results using sensitivity analyses.

Temperature range, minimum and maximum temperature in the native basins

We used the minimum temperature of the coldest month and the maximum temperature of the warmest month from WorldClim (Fick and Hijmans 2017) to derive two variables: annual maximum temperature and temperature range (Table 1). We excluded the annual minimum temperature, as this variable was correlated to temperature range. We only considered the 0.95 quantile of the maximum temperature of the warmest month and the 0.05 quantile of the minimum temperature of the coldest month across the native basins for each species to avoid extreme outlier values.

Socioeconomic characteristic

Use by humans

Four columns of the *species*() table in the "rfishbase" R package indicate the human use of species through fisheries ("Importance" column), bait ("Usedasbait" column), sport ("GameFish" column), or aquariums ("Aquarium" column). If a species is used in at least one of these four sectors (i.e., belonging to a category other than "never/rarely", "of no interest", "of potential interest" or "potential"), we considered this species to be used by humans. The species considered as used by human are filled with "yes", while the others are filled with "no".

Introduction pathways

Using the *introduction()* table from the "rfishbase" R package, we considered each pathway as an independent variable (Table 1). Therefore, a given species could have several introduction pathways. We filtered out pathways containing only a few species. Thus, we reclassified pathways documented in FishBase into the seven following categories: aquaculture, sport/angling, species control (e.g., weeds, mosquitos, plankton, and snails), diffusion (e.g., Lessepsian migration, spread from other countries, removal of natural barriers), accidental (e.g., ship ballasts), fisheries, and ornamental fish trade.

Response variables

In this study, we considered three steps of the invasion: introduction, establishment, and impact. We gathered FishBase data on variables that reflected the three invasion steps: (1) the number of countries, where species has been introduced, (2) the number of countries, where introduced species are established, and (3) the number of countries, where established species have had impacts. To obtain information about these three variables for each species, we used the table given by *introductions()* function of the "rfishbase" R package. This table describes the introduction events of each fish species, provides the location of each introduction, and the establishment and impact status of each species. We used the data from FishBase, whereby the impact was defined as a significant ecological interaction of the non-native species with the non-native ecosystem (Froese and Pauly 2019). Note that the impact data from FishBase are probably not exhaustive but surely provide a preliminary overview of the link among pathways, traits, and impacts in a standardized way.

Number of countries where species have been introduced, established, and have had impacts

We used the locations found in the "TO" column of the *introduction()* table of the "rfishbase" R package. It should be noted that some species might have simply been transported to a new location without being introduced to the wild, though this is unlikely because most alive imported species are introduced either intentionally or accidentally to the natural environment (Su et al. 2020). Thus, we assumed that all the species transported to a country were introduced in the wild. The locations listed in FishBase were not standardized at a specific spatial scale (i.e., names ranged from the names of cities to entire continents), so we manually harmonized names to the country scale as follows. First, we excluded all records above the country scale. Second, we grouped islands located far from their country by archipelago or considered them separately when they did not comprise an archipelago. As some of the introductions were old, some of the listed countries no longer existed and/or could not be grouped or assimilated with any new country (e.g., USSR and Korea). We therefore considered these countries independently. When the spatial scale was the river or lake, we considered all the riparian countries independently. We listed as "Unknown" any locations given at a larger scale than a country (e.g., "Europe") or locations that could not be identified. 208 countries were considered in this study.

For each species, we counted the number of countries, where the species was introduced, established, and had impacts. Concerning the establishment step, all species recorded as "Yes," "Probably Yes," "Established," or "Probably established" in the "Estabwild" column of the *introduction()* table were accepted as species established in the wild in the considered locations. We removed from the analysis species that were listed as established but not introduced beforehand, as we could not access the establishment location of these presumably "non-introduced" species. We also took as established any species that had impacted an ecosystem but were not established (i.e., "No" or "Probably no" in the "Estabwild" column) or had an unknown establishment status. This allowed to consider in the analysis established the species artificially maintained in the recipient environment by constant releases (e.g., rainbow trout in many European countries) (Stanković et al. 2015). Concerning the impact step, we considered that all the species noted as "Yes," "Probably some," or "Some" in the "EcolEff" column of the *introduction()* table had likely ecological impacts in the considered locations.

Following data compilation, we obtained 840 species with all the considered predictive variables available and with an introduction status: 307 species were classified as introduced, while 533 were considered as non-introduced. Of the 307 introduced species, the total number of countries where the species had been introduced was provided. Among these 307 introduced species, 217 species were established in at least one country and 117 had ecological impacts in at least one country.

Statistical analysis

To determine the characteristics of the species at each step of the invasion process, we used generalized linear models (GLM) to analyze the influence of species, ecological, and socioeconomic characteristics on the number of countries, where the species was introduced, established, and/or have had impacts. First, we assessed the Spearman correlations between all the 20 explanatory variables using the *ggcorr()* R function of the GGally package (Schloerke et al. 2022). We also used the *model.matrix()* from the stats package (R Core Team 2022) to separate each modality of the numerical variables into binary variables. We then used the *cor()* function (stats package; R Core Team 2022) to explore the Pearson correlations between the new binary variables and between the binary and quantitative variables. To reduce structural multicollinearity, we centered (i.e., subtracted the variable mean from all observations so the mean equaled zero) the variables "total length", "temperature range in the native region", and "number of diet categories", which were then used in interaction terms.

We performed GLMs considering all the species, regardless of their introduction pathway, to explain the number of countries, where the species (i) were introduced, (ii) were established, and (iii) had impacts (Appendix 1). We used the 20 explanatory variables and six interactions between the variables: the interactions between total length and temperature range, between total length and taxonomic order, between total length and ornamental fish trade pathway, between total length and sport/angling pathway, between total length and aquaculture pathway, and between number of diet categories and taxonomic order (Appendix 1). Indeed, we hypothesized that species belonging to the same taxonomic order could have the same characteristics, and that the length of species can influence the introduction pathway (Wonham et al. 2000; Su et al. 2020).

We also specifically explored the characteristics of species introduced through the aquaculture and ornamental fish trade pathways, which were the two most common pathways of fish species' introduction. We conducted the same GLM analyses as above while considering only the species introduced through the aquaculture or ornamental fish trade pathways. With these models, we considered 11 variables and three interactions with the variable "introduction pathways" removed from these models (see Appendix 1). Given the paucity of impact data, we conducted these GLMs only on the introduction and establishment steps. In FishBase, it is stated that the species introduced through the ornamental fish trade pathway should be all considered as established (Froese and Pauly 2019). However, as a precautionary principle, we chose to distinguish introduced and established species from the ornamental fish trade pathway. Indeed, the rise of introductions from the ornamental fish trade pathway is relatively recent (Bernery et al. 2022) and evidence of establishment is insufficiently available to consider all ornamental fish trade introduced species as truly established species. As our data were count data, we computed these GLMs with Poisson distributions or negative binomial distributions when our response variables were overdispersed. To check for overdispersion, we used the *dispersiontest()* function from the "AER" R package (Kleiber and Zeileis 2008). We then used the *stepAIC()* function from the "MASS" R package (Venables and Ripley 2002) and a stepwise selection procedure to choose the best model based on the Akaike information criterion. For each model, a pseudo-r^2 was estimated using the following formula: 1—Model Deviance/Model Null Deviance. We identified the significant variables of each model using the *Anova()* function from the "car" R package (Fox and Weisberg 2019). The variable importance of each variable in the models (i.e., absolute value of the *t*-statistic of each model variable) was calculated using the *varImp()* function from the "caret" R package (Kuhn 2008).

To address potential fluctuations due to the randomly chosen main diet and main regions for some species, we performed a sensitivity analysis. For the species with several main diets or several main native regions, we randomly selected the main diet and the main native region, and then performed the above GLMs on the new dataset. We repeated the process 100 times to observe the variation in the results due to the random choices. We observed that the random choice of the main diet did not significantly affect model results (Appendix 2).

Results

All species

With regard to the introduction model, species introduced in a high number of countries were associated with a high number of different introduction pathways (variable importance [VI] = 10), a high level of parental care (VI = 5.3 for the linear relation), had aquaculture (VI = 4.5) or fisheries (VI = 2.7) as one of their introduction pathways, and had a high number of diet categories (VI = 2.4). Siluriformes with a high number of diet categories also tended to be introduced into many countries (VI = 2.3) (Figs. 1a, 2). The establishment step model exhibited similar results to the introduction model for selected variables (Figs. 1b, 2), except for species established in a greater number of countries for which the aquaculture pathway had no effect. Finally, species with impacts in a high number of countries were associated with most of the pathways (except for species control, accidental, and aquaculture), a high level of parental care, and a high number of diet categories when species were from the Siluriformes order (Figs. 1c, 2). Nonetheless, parental care was only significant in 22% of models in sensitivity analysis, thus, reducing the variable importance (Appendix 2).

Species introduced through the aquaculture pathway

Our analysis on the 154 species introduced through the aquaculture pathway revealed that these species

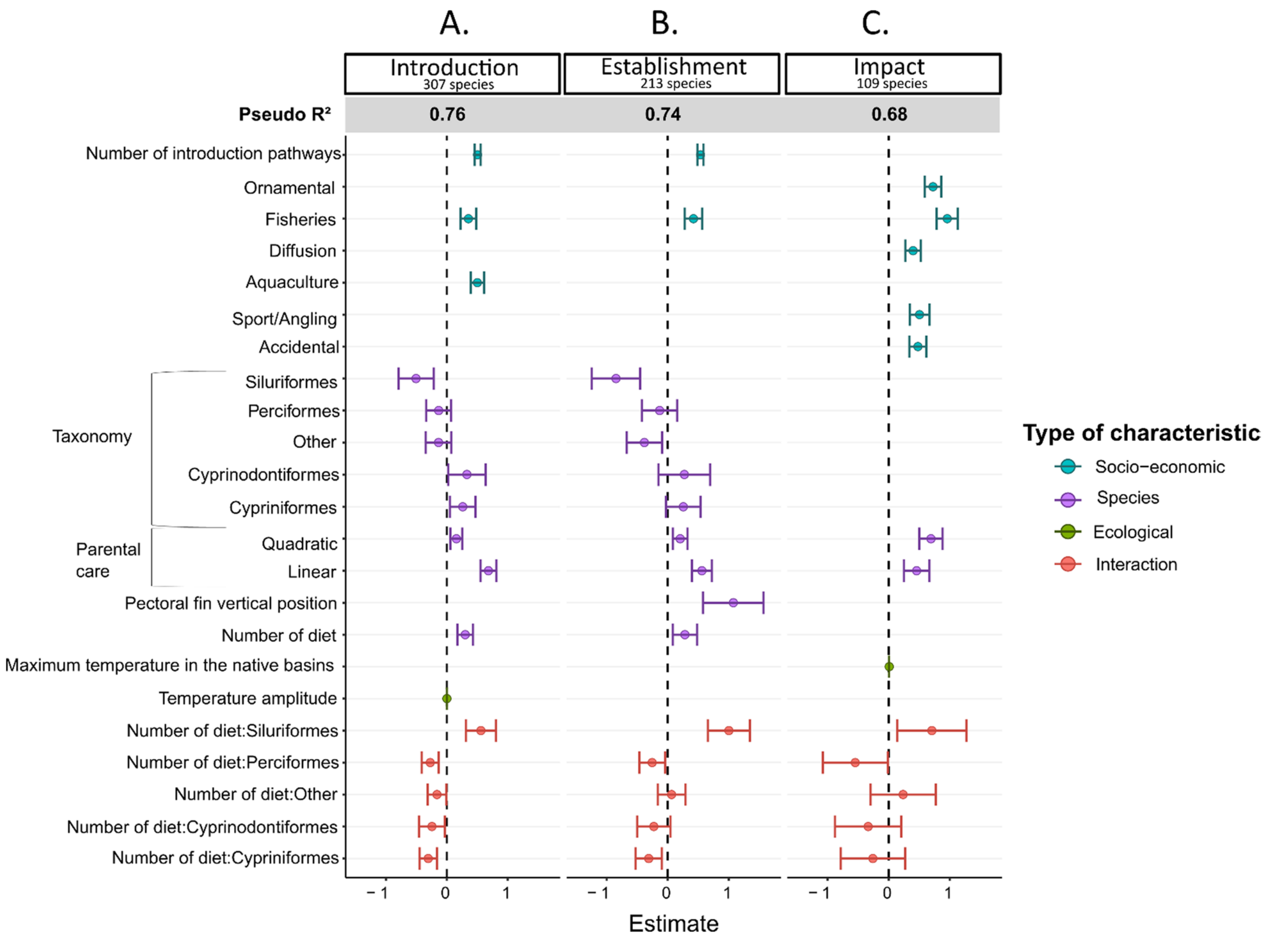


Fig. 1 Estimates (with standard errors) of significant variables resulting from the generalized linear model for all the introduced species and for each step of the invasion. The sign of the coefficients depends on the category of reference for the Taxonomy and Major native bioregion variables. For taxonomy, the reference is the Characiformes order. Introduction step intercept: 0.676 (SE = 0.209). Establishment step intercept: 0.249 (SE = 0.305). Impact step intercept: −3.813 (SE = 1.036)

introduced in a high number of countries were associated with a high number of diet categories (VI = 2.9) and with the Cypriniformes order (VI = 1.6) (Fig. 3a). These species also were associated with high parental care (significant variable in 57% of models in sensitivity analysis, Appendix 2). This finding suggests that introduced non-Cypriniforms were species that preferentially exhibited high parental care.

In addition, the 90 species established through aquaculture had a high number of diet categories (VI = 3.8) and belonged to all taxonomic orders except Characiformes and Cyprinodontiformes (i.e., they belonged to the Perciformes, Cypriniformes and "other" taxonomic orders). They were also often associated with high parental care (significant variable in 76% of models; Fig. 3b, Appendix 2).

Species introduced through the ornamental fish trade pathway

We analyzed the characteristics of 126 species introduced through the ornamental fish trade (Fig. 4a). Species introduced to many countries tended to be less hydrodynamic (i.e., lower ratio of body length to body depth (VI = 5.5), were native to the Neotropical (VI = 2.5) or Sino-Oriental regions (VI = 2.3) and had a greater number of diet categories (VI = 1.6).

Concerning the establishment step (Fig. 4b), we considered a subset of 70 established species among those introduced through the ornamental fish trade pathway. Species established in many countries were less hydrodynamic (VI = 4.9), were from the orders Cyprinodontiformes (VI = 4.3) or Cypriniformes (VI = 2.4), and primarily came from the Ethiopian (VI = 1.2) or Neotropical (VI = 1.1) regions.

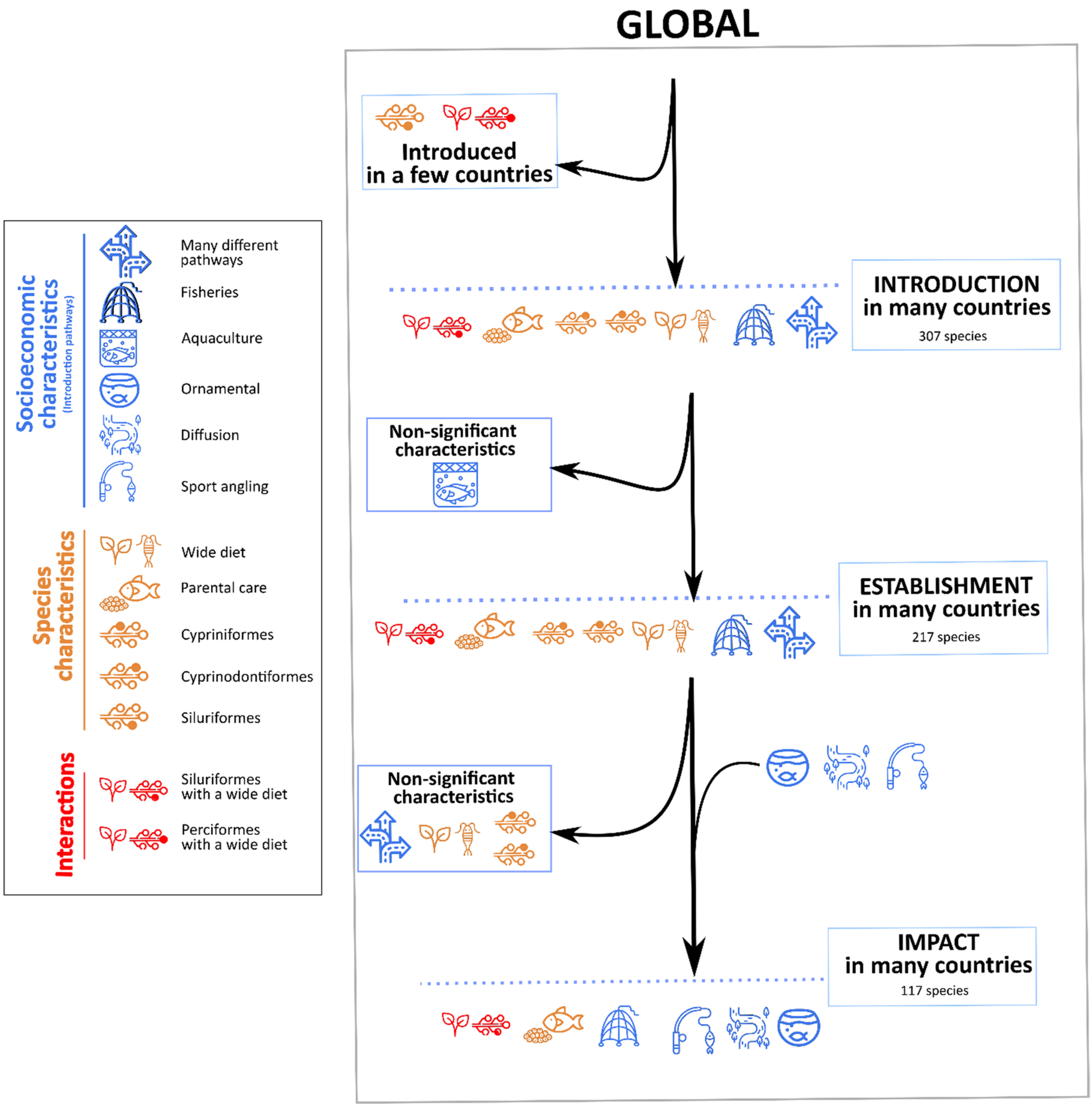


Fig. 2 Main characteristics explaining the success of each step of the invasion process for freshwater fishes

Discussion

Using the socioeconomic, ecological, and species characteristics of 307 non-native freshwater fish species, we were able to identify a profile of pathway-dependent characteristics related to successful invasions for each step of the invasion process. As we hypothesized, we detected that species characterized by broad diets and high parental care as well as multiple socioeconomic introduction pathways (e.g., fisheries and aquaculture) were particularly successful at being introduced and established in multiple countries. However, contrary to our hypothesis, diet did not significantly affect the success of the establishment step. Furthermore, socioeconomic characteristics seemed important to explain the impact of freshwater fishes in many countries. Overall, species socioeconomic history as related to the introduction pathways appeared to play a primary role in species introduction and establishment success, while ecological

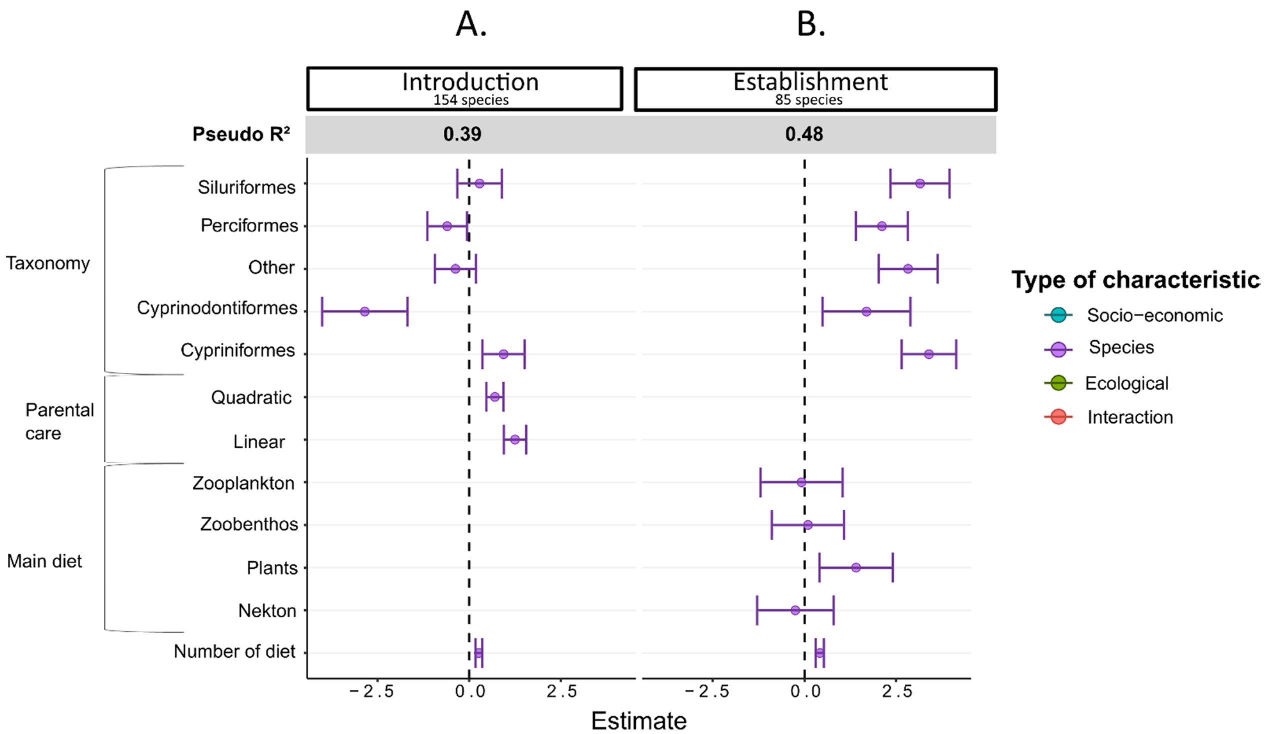


Fig. 3 Estimates (with their standard errors) of significant variables resulting from the generalized linear model for the established species introduced through the aquaculture pathway and for the introduction and establishment steps. The sign of the coefficients depends on the category of reference for the Taxonomy, Main diet, and Major native bioregion variables. For taxonomy, the reference is the Characiformes order. For diet, it is the detritus diet. Introduction step intercept: 2.367 (SE = 0.538). Establishment step intercept: − 0.95 (SE = 1.227)

characteristics seemed to only influence the invasion success in a secondary manner.

Introduction step

We highlighted specific characteristics and socioeconomic histories for species introduced to many countries. As hypothesized, multiple introduction pathways favored widespread introductions, with different introduction pathways increasing the likelihood of being transported and introduced in many locations. For example, the common carp (*Cyprinus carpio*) was introduced through six of the seven possible pathways considered here, though some pathways are specific to certain countries. Indeed, the common carp was introduced to several countries through aquaculture (e.g., Australia, Shearer and Mulley 1978), to New Zealand and South Africa for ornamental fish trade purposes (De Moor and Bruton 1988; Froese and Pauly 2019), and to Finland for angling (Froese and Pauly 2019). Species introduced to high numbers of countries also tended to have specific species characteristics such as higher levels of parental care and a higher number of diet categories. For example, *Oreochromis mossambicus* and *Oreochromis niloticus* were introduced to 97 and 94 countries, respectively, and are bearers with at least four different diets (Froese and Pauly 2019). This result supports our initial hypothesis, as these two characteristics have already been highlighted in previous studies, though only at the state or country scales and/or for the establishment step (Marchetti et al. 2004a in California; Tonella et al. 2018 in Brazil; Chan et al. 2021 in Singapore; Lawson and Hill 2022 in Peninsular Florida, Bernery et al. 2023). Nonetheless, the role played by parental care in the introduction step of the invasion process has not yet been reported, with the underlying mechanisms remaining to be elucidated (e.g., Marchetti et al. 2004a). One possible explanation could be that species with high parental care tend to be introduced more, because their reproduction may be easier in captivity. For instance, several species of poecilids (e.g., guppies [*Poecilia reticulata*]) and Cichlids (e.g., *Haplochromis* sp. or *Cichlasoma* sp.) are popular aquarium fishes known to be highly prolific and easy to rear (Bianchi 1993).

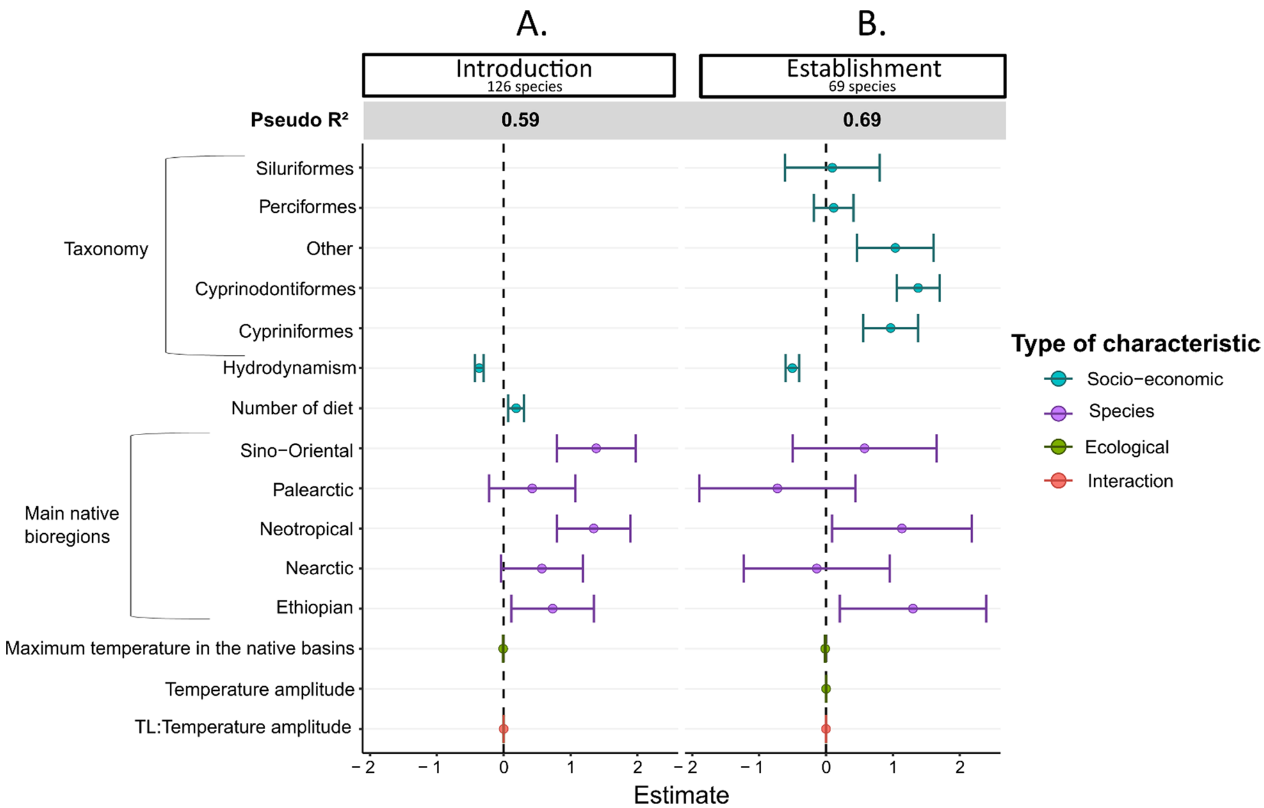


Fig. 4 Estimates (with their standard errors) of significant variables resulting from the generalized linear model for the species introduced through the ornamental pathway. The sign of the coefficients depends on the category of reference for the Taxonomy and Major native bioregion variables. For the taxonomic order, the reference is the Characiformes order. For the major native bioregion, the reference is the Australian region. Introduction step intercept: 1.752 (SE = 1.31). Establishment step intercept: 4.6 (SE = 1.9)

Establishment step

The variables influencing the total number of countries, where species established were similar to those for introductions. Species that established in higher numbers of countries were associated with greater numbers of pathways, higher parental care, and greater number of diet categories. The greater numbers of introduction pathways was linked to the higher propagule pressure, which has been demonstrated to be one of the main characteristics of invasion success (Jeschke and Strayer 2006). Higher parental care maximizes offspring survival in the presence of competitors, thus, providing an advantage that can favor successful establishment (Levine and D'Antonio 1999). Moreover, generalist diets allow introduced species to adapt to different environments, and thus, allow establishment in a wider range of environments (Tonella et al. 2018). In a recent study on 222 non-native fishes, Bernery et al. (2023) reported similar results at the global scale, finding that varied diets, higher temperature range within the native ranges, and greater levels of parental care were associated with widely established fishes.

Despite this common overall pattern of introduction and establishment characteristics, we found several noteworthy differences with previous studies. For example, although species introduced through the aquaculture pathway were introduced in many countries, their establishment success remained limited. This result was counterintuitive, as aquaculture is recognized as the most important introduction pathway of non-native freshwater fishes worldwide (Gozlan 2008; Bernery et al. 2022). Our results suggest that although aquaculture allows the establishment of many different species, it does not necessarily result in these species becoming established in many different countries. This trend can be explained by the concentration of aquaculture production in Asia (especially China), which cultures a greater diversity of species (Metian et al. 2020). In addition, there may be long delays between the establishment of species and their range expansion into new countries, which is one of the aspects of the 'invasion debt' (Rouget et al. 2016). Thus, at present, we may not yet have enough hindsight to detect the eventual effects of aquaculture. The way in which the species are cultured in each country also affects the probabilities of establishment. For example, species cultured in and escaping from natural ponds are more likely to establish, because the individuals often escape in high numbers (Gu et al. 2022). This trend also could reflect the efficiency of management methods set by governments to limit or avoid fish escapes (Kolar et al. 2010). We also can surmise that some species introduced through the aquaculture pathway were not able to survive and reproduce in recipient environments (e.g., East Asian carp in northern Europe; Lehtonen 2002).

Ecological impact

At the global scale, data on freshwater fish impacts in general are incomplete, which hinders the identification of important characteristics for the invasion step (Vitule et al. 2009; Bernery et al. 2022). However, herein we propose a first characterization of non-native species with impacts in several countries based on the available global-scale data. The variables influencing the number of countries where species have ecological impacts were distinct from those influencing the introduction and establishment steps. Contrary to our hypothesis, diet did not significantly influence the impact step. Conversely, human uses such as fisheries, ornamental fish trade, and angling along with the diffusion of already established species tended to be the major pathways favouring non-native species' impacts. Surprisingly, the aquaculture pathway did not stand out as an important variable despite the substantial impact of some cultured fishes. In fact, the impacts of fishes introduced through the aquaculture pathway may be understudied due to their economic benefits (Gozlan 2008; Haubrock et al. 2022), which may partly explain why aquaculture did not appear to be an important variable. For example, the channel catfish (*Ictalurus punctatus*) is known to be responsible for the decline of many native species outside its native range (Townsend and Winterbourn 1992). Although widely introduced in Brazil for aquaculture, no ecological impact has been recorded in FishBase for channel catfish in this country (Vitule et al. 2009; Froese and Pauly 2019). This absence of reported impacts can also be attributed to the ecosystem's existing richness in Siluriformes, that already fill similar niche to the one occupied by the channel catfish, and thus limits its impact. However, introduction pathways are not the only important variables leading to ecological impact. For instance, Siluriformes have been introduced, established, and have had impacts in many countries, though only when they have broad diets. This tendency seems to be driven by a few species with broad diets that are present in a higher number of countries (e.g., *Clarias anguillaris*, *Ictalurus punctatus*, *Ameiurus melas*, *Ameiurus nebulosus*, and *Silurus glanis*).

Importance of interactions between pathways and species characteristics

In this study, we highlighted the interaction between species characteristics and introduction pathways as they affected invasion success. Considering all the species, the overrepresentation of species native to the Palearctic and Sino-Oriental regions among the introduced species could be due to the influence of the two most important introduction pathways, namely, aquaculture and ornamental fish trade. Indeed, these regions are economically well developed, making them more prone to export fish species for aquaculture (FAO 2012). This may also be linked to the early development of aquaculture in these regions, the Palearctic region in particular (Balon 1995). With the development of aquaculture occurring in tropical countries (Garlock et al. 2020), this trend is likely to continue to spread throughout developing regions of the world. Considering the models per pathway, species introduced and established in many countries through aquaculture are similar to those of the global pool (i.e., higher number of diet categories, higher parental care). These species also tended to be from the order Cypriniformes, which include many carps that have been cultured for centuries (Balon 2004), but are also complemented by representants of other taxonomic orders caring for their offspring such as cichlids and catfishes. In fact, these species continue to be the main production species in global aquaculture (FAO 2020).

In contrast, species introduced and established in many countries through the ornamental fish trade are less hydrodynamic and more often native to the Neotropical and Sino-Oriental regions. These characteristics are associated with the most popular aquarium fishes, including poeciliids and tetras (Duggan et al. 2006; Gertzen et al. 2008), thus, highlighting the strong influence of propagule pressure.

Limitations and recommendations for future studies

It is important to note that the similarity between the introduction and establishment steps can be partly explained by a detection bias, namely, that introductions that fail to establish have less chance of being reported and/or detected than successful introductions (Drake 2007). We used the number of countries, where species were introduced, established, and have had impacts as an indicator of non-native invasion success. However, the sizes of the countries are highly variable, which implied possible biases. Species established in many small countries are considered to be more established than species established in a limited number of large countries despite that they both may encompass the same area. This bias could be corrected by using the number of basins, though we only had this information for the establishment step

(Tedesco et al. 2017). Nonetheless, the number of countries, where species have become established was significantly positively correlated to the number of basins, thus, minimizing the severity of the bias ($R = 0.85$, $p < 2.2e-16$; 161 species considered). Moreover, some of our results can vary at local scales, because the characteristics of the recipient environment can significantly influence the outcome of an introduction (Vila-Gispert et al. 2005). Furthermore, concerning the impact step, the global paucity of some data made it more difficult to conduct studies and interpret analyses that were global in scope (Bernery et al. 2022). For example, ecological impacts of invasive species can be unnoticed for decades, leading to species being wrongly classified as having had no impacts (Courchamp et al. 2017). Thus, the results concerning the impact stage must be viewed as preliminary until more time has passed and more data becomes available. In this regard, data on invasive species' impacts tend to more frequently reported from developed countries supporting research dedicated to biological invasions and towards species with low economic benefits (Zengeya et al. 2017; Bernery et al. 2022). Therefore, there are new initiatives to address this data shortcoming, such as the development of a EICAT database for freshwater fish species, which could allow future works to resolve the question of the characteristics of high-impact species. Thus, to improve future studies, more data should be collected in relation to the impact step as well as certain characteristics (e.g., species fecundity), which has been shown to influence the establishment of species at local scales (Vila-Gispert et al. 2005).

Conclusion

Based on information that was available in the current literature, this study provided a global snapshot of the characteristics that supported the success of the whole invasion process for freshwater fishes. It highlighted the importance of separately considering different types of factors (e.g., species, ecological, and socioeconomic characteristics) across the different steps of the invasion process to disentangle the effects of different introduction pathways. These results can be useful to improve screening tools. For example, the invasiveness tool of FishBase only considers the introduction pathway and the climate adequacy between the native and recipient environment to determine the potential invasiveness of a species (Froese and Pauly 2019). By contrast, our results stress the importance of considering a wider variety of characteristics. Our findings also demonstrated the importance of determining not only the invasive status of a species but also the profile of species with the potential to invade large areas. Ultimately, this approach considering the different steps and pathways of invasion could be helpful to better identify the determinants of invasion success in other taxa (Capellini et al. 2015).

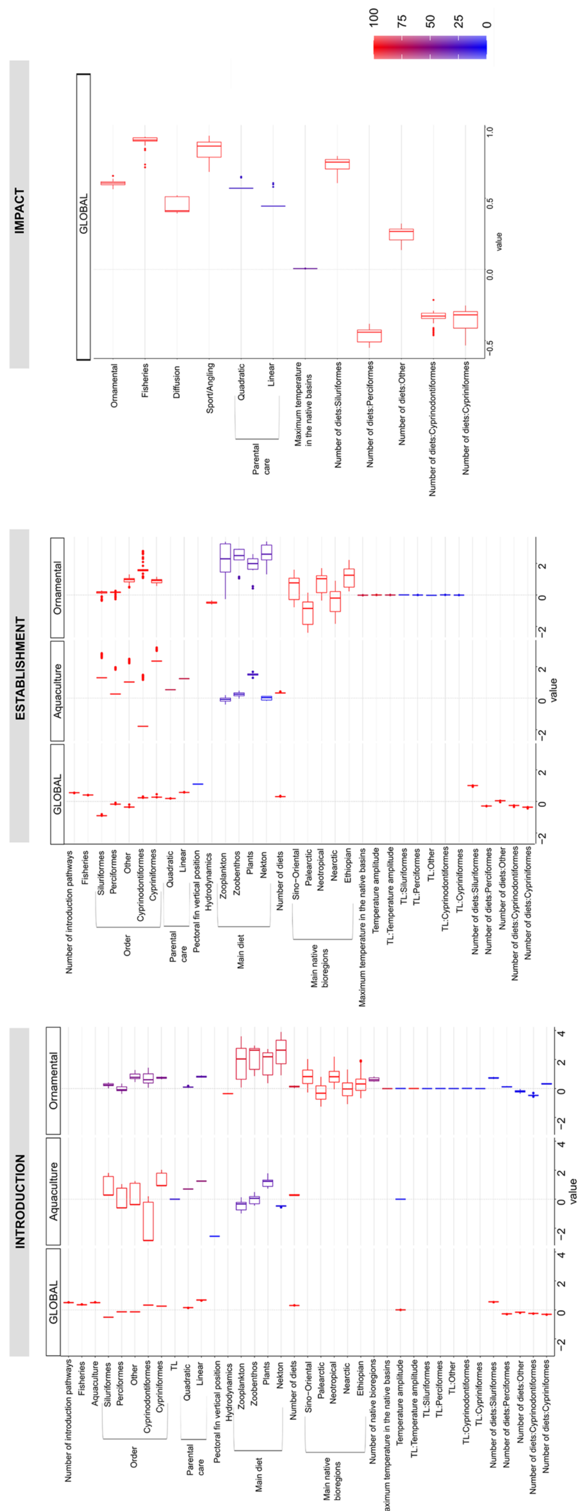
Appendices

Appendix 1: Variables used in each model

Introduction—Global Establishment—Global Impact—Global	*Life history traits* Main diet Number of diets Hydrodynamics Pectoral fin vertical position Parental care Total length Order	*Socioeconomic characteristics* Aquaculture Sport/Angling Accidental Ornamental Fisheries Diffusion Species control Number of introduction pathways Human use
	Ecological characteristics Temperature amplitude in the native basins Maximum temperature in the native basins Main native bioregion Number of native bioregions	*Interactions* Between Temperature amplitude and Total length Between Order and Number of diets Between Order and Total length Between Ornamental and Total length Between Sport/Angling and Total length Between Aquaculture and Total length
Introduction—Aquaculture Introduction—Ornamental Establishment—Aquaculture Establishment—Ornamental	*Life history traits* Main diet Number of diets Hydrodynamics Pectoral fin vertical position Parental care Total length Order	*Interactions* Between Temperature amplitude and Total length Between Order and Number of diet Between Order and Total length
	Ecological characteristics Temperature amplitude in the native basins Maximum temperature in the native basins Main native bioregion Number of native bioregions	

Appendix 2: Sensitivity analysis

Boxplots represent the estimates (without standard errors) of 100 models. We varied the main diet of species with several main diets and the main native bioregion of species with several main native bioregions. The color gradient represents the number of models in which the considered variable is significant (1: blue, 100: red). "TL" refers to total length.


INTRODUCTION
ESTABLISHMENT
IMPACT
GLOBAL
Aquaculture
Ornamental
value

Author contributions

CaB, CéB, FC and BL conceived the ideas and designed the methodology; CaB collected the data, analyzed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Availability of data and materials

All the R code necessary to generate the data and the results present in the paper will be available on GitHub after the acceptance of the paper. Used data also include open access data: (i) FishBase (Froese and Pauly 2019, version 19.04, accessed with the "rfishbase" R package; Boettiger et al. 2012); (ii) the FISHMORPH morphological database (Brosse et al. 2021); (iii) the database on freshwater fish occurrences complied by Tedesco et al. (2017); (iv) the global biogeographical regions of freshwater fish (Leroy et al. 2019); and (v) the world climate database WorldClim (Fick and Hijmans 2017).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

All authors declare that they have no competing interests.

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