Management of Biological Invasions (2025) Volume 16, Issue 1: 277–294

Special Issue: Advances in the study of the management of biological invasions in inland waters and the legacy of Gordon Howard Copp (1956−2023)
Guest editors: Lorenzo Vilizzi and Calum MacNeil

Research Article

Species traits and invasion history as predictors of freshwater fish invasion success in Europe

Fabio Marcolin[1,3,4], Paulo Branco[1], José Maria Santos[1], Luís Reino[2,3,4], Joana Santana[2,3,4], Joana Ribeiro[2,3,4], Daniel Chamberlain[5] and Pedro Segurado[1]

[1]*Forest Research Centre, Associate Laboratory TERRA, School of Agriculture, University of Lisbon, Tapada da Ajuda, P-1349-017 Lisboa, Portugal*
[2]*CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*
[3]*CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal*
[4]*BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal*
[5]*Dipartimento di Scienze Della Vita e Biologia dei Sistemi, Università di Torino, Turin, Italy*

Corresponding author: Fabio Marcolin (fabiomarcolin@isa.ulisboa.pt)

Co-Editors' Note: This paper was contributed as part of the Special Issue "Advances in the study of the management of biological invasions in inland waters and the legacy of Gordon Howard Copp (1956–2023)". This collaborative effort has attracted some of the most prominent invasion biologists who have contributed a diverse collection of high-profile papers addressing current knowledge gaps, research advances, and future opportunities in the management of biological invasions.

Citation: Marcolin F, Branco P, Santos JM, Reino L, Santana J, Ribeiro J, Chamberlain D, Segurado P (2025) Species traits and invasion history as predictors of freshwater fish invasion success in Europe. *Management of Biological Invasions* 16(1): 277–294, https://doi.org/10.3391/mbi.2025.16.1.16

Received: 29 February 2024
Accepted: 23 July 2024
Published: 15 January 2025

Handling editor: Lorenzo Vilizzi

Abstract

Despite the growing literature on the topic of freshwater fish invasions, few studies have employed a comprehensive analysis of the stages characterizing the invasion process with reference to the invasion pathway. There is therefore a need to understand more fully invasion pathways to avoid incomplete and biased conclusions and to support adequate management strategies. This study aims to provide a complete analysis of the species traits and invasion history that are associated with the successful passage of an alien freshwater fish species through the invasion pathway stages in European river basins. To predict how likely a freshwater fish species moves from each stage of the invasion pathway (release, establishment, spread and impact) to the next, generalized linear mixed models were run, using 23 species traits and seven variables describing introduction history as predictors for 127 established alien freshwater fish species in Europe. The results showed that the release and spread stages were driven primarily by variables related to invasion history (i.e. the type and number of causes of introduction). The establishment stage was driven mainly by functional and ecological traits, while the impact stage was driven both by functional and ecological traits and invasion history. Identifying the main drivers of alien species success at each invasion stage is key to designing stage-specific target management actions and thus contributing to an effective control of alien populations.

Key words: alien species; non-native species; ecological traits; functional traits; invasion pathway; invasion stage

Introduction

Invasive Alien Species (IAS; *sensu* Regulation 1143/2014: European Commission 2014) threaten native biota worldwide, from local to continental scales. They negatively affect ecosystem health and services (Simberloff et al. 2013; Early et al. 2016; Oficialdegui et al. 2023), causing annual economic losses of billions of euros (Cuthbert et al. 2021). Freshwater ecosystems are among the most threatened and impacted by biological invasions (Reid et al. 2019; Corrales et al. 2020). Freshwater IAS are associated with ecosystem degradation (Vandekerkhove et al. 2013), which is caused by competitive exclusion and predation on native species (Griffen and Delaney 2007; Rowles and O'Dowd 2007), ultimately leading to profound changes in native communities (Ehrenfeld 2010). This is particularly true for European native freshwater fish for which introduced fish species represent the second most common threat (Costa et al. 2021) as they contribute to taxonomic homogenization and negatively affect ecosystem functioning (Gallardo et al. 2016; Sommerwerk et al. 2017).

Introduced species become invasive when they successfully overcome environmental filters (acting as barriers) related to the different stages of the invasion process: transport, release, establishment, spread (Kraft et al. 2015; Bagnara et al. 2022; Chapple et al. 2022) and impact (García-Berthou 2007). The impact represents the last stage assuming that, despite being more adequately defined as an outcome of invasion (Blackburn et al. 2011), it is also likely to be driven by species traits. Identifying the traits acting at each stage of the invasion process is critical for predicting the invasive potential of alien species (Ribeiro et al. 2008), which is facilitated by the identification of management actions to control their establishment and spread. Moreover, these stages should be examined independently because each is mediated by a certain combination of species traits, and the same trait promoting the success of one stage may, in contrast, compromise the success of another (García-Berthou 2007).

Although the identification of freshwater fish traits responsible for invasion success has been extensively addressed, most studies have primarily focused on the establishment, spread and impact stages (e.g. Kolar and Lodge 2002; Marchetti et al. 2004a; Howeth et al. 2016). The establishment stage is the most studied for fish and seems to be related to reproductive strategy, size of native range, distance from native range', diet breadth, environmental tolerances (García-Berthou 2007; Peoples and Midway 2018) and invasion history (e.g. previous invasion success: Marchetti et al. 2004a; Ribeiro et al. 2008; Chan et al. 2021; Bernery et al. 2024). Similarly, the spread stage seems to be affected by previous invasion success, low parental care (Ribeiro et al. 2008) and larger adult size or longer lifespan (Moyle and Marchetti 2006). Conversely, the size of the native range has led to opposite conclusions, i.e. higher probability of spread related to small size of the native range (Moyle and Marchetti 2006; Ribeiro et al. 2008; but see Peoples and Midway 2018). Lastly, the impact stage has been reported to be driven by physiological tolerance, non-omnivorous diet (Moyle and Marchetti 2006), small native range size (Ribeiro et al. 2008), high fecundity, long lifespan and large body size (Su et al. 2023).

In contrast to the other stages, transport and release are poorly documented and therefore difficult to assess (Marchetti et al. 2004a; García-Berthou 2007; Alves and Tidbury 2022). Records of both successful and unsuccessful introductions are very scarce and tend to be strongly biased towards the successful ones (García-Berthou 2007). This data shortage could be tackled by obtaining more detailed information on propagule pressure, which, along with abiotic factors and a comprehensive knowledge of species traits, would help to understand how traits are filtered throughout the invasion process (Gulzar et al. 2024).

This study investigates the combination of functional traits, ecological traits and invasion history attributes that best correlate with the progressive success of alien species along their invasion pathway in European rivers. Functional traits are defined as any morphological, physiological, behavioural or phenological feature measurable at the individual level (Violle et al. 2007; De Bello et al. 2021), and ecological traits are defined as any feature based on the niche of a species (Violle et al. 2007; De Bello et al. 2021). In addition, how functional and ecological traits and invasion history explain the progressive success of alien fish species along the invasion pathway in European rivers is addressed. Four invasion stages were analysed independently – release, establishment, spread and impact – for both IAS and alien freshwater species. The objectives of this study are twofold: (i) to support the development of more effective management guidelines to prevent the invasion success of alien fish species in freshwater habitats; and (ii) to help to predict the future success of new alien fish species throughout the invasion pathway. This study provides a comprehensive approach that links species traits to the invasion success of alien freshwater fish species in Europe.

Materials and methods

This study considers 127 alien fish species (both European non-native and translocated between European countries) belonging to 81 genera and 29 families that have been recorded as established in freshwater systems of one or more European country (Figure 1). As a first step, we included all species reported as 'established' (i.e. species with a self-reproducing population in the wild) in at least one European country. This information was obtained from several sources [e.g. Global Invasive Species Database (GISD); Pagad et al. 2018; Froese and Pauly 2020 and several scientific papers; all species traits and references are available in the Open Science Framework (OSF) online repository https://osf.io/p3qkj/; Marcolin et al. (2024)]. Whenever two or more sources provided contrary information about the establishment status of a species (i.e. one source reporting that the species was established in a country, whereas the other source considered it as not established), the most recent source was included. However, if these references were published in the same year, then we chose the species status as established, following the precautionary principle (Wood et al. 2020). Scientific names throughout follow the classification proposed by Fricke et al. (2024).

For each alien freshwater fish species, 23 species traits (11 functional and 12 ecological) and seven variables describing the species' introduction history were identified (Supplementary material Table S1). Data were retrieved from

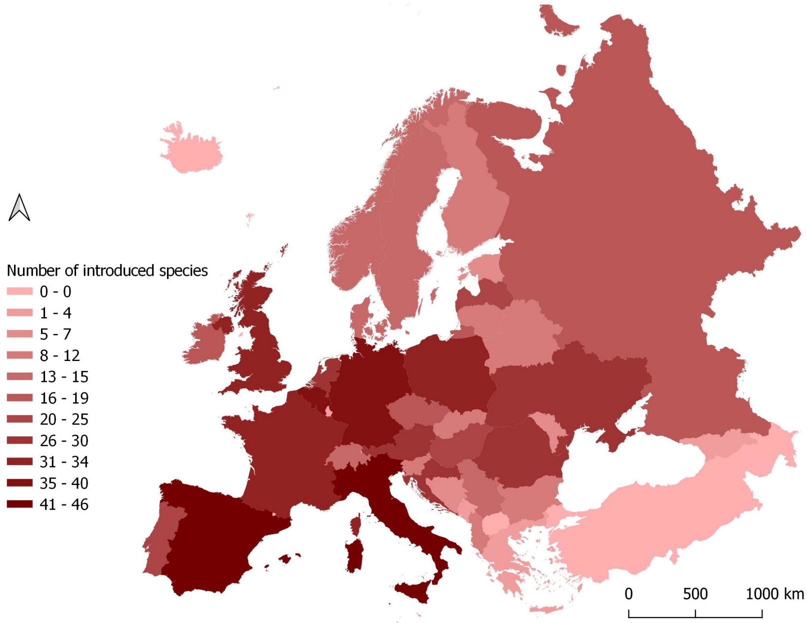

Figure 1. Study area and number of established alien freshwater fish per European country. The European borders follow Freyhof and Kottelat (2007). Countries with '0' alien fish species are due to missing information for the country. Turkey and Cyprus are represented for geographic reference purposes.

multiple sources including research studies, databases and fish index manuals (see Marcolin et al. 2024). If two or more sources provided contrary information regarding species traits, we only considered the most recent source of information, and if these references were published in the same year, then we followed the precautionary principle as above (i.e. selecting the trait class or value with potentially higher impacts on native ecosystems following the species introduction: Wood et al. 2020). For example, the vimba bream *Vimba vimba* (Linnaeus, 1758) was classified as an omnivore since it can be more impactful on the native fauna than an invertivore (Oberdorff et al. 2002). This approach allowed us to estimate the worst-case scenario for this species.

Information was successfully retrieved for 90% (3422 out of 3810) of the trait records among all species (Table S2). However, only 30% of the species (38 out of 127) had information for all traits. For the remaining 70% with missing traits, we used phylogenetic similarity (Troia and McManamay 2019) to assign the trait value, level or category of the closest species, which is that belonging to a common Genus or Family with known traits (77 out of 3810). If more than one closest species was available, we chose the value with potentially higher impact on the native ecosystem (see Marcolin et al. 2024).

Five traits had a high level of missing data (Acid tolerance, Habitat degradation tolerance, Water quality tolerance general, Water quality tolerance oxygen, Water quality tolerance toxic), thus these were aggregated into a single combined General tolerance trait, increasing the completeness of the records to 94% (3101 out of 3302). Following the precautionary principle approach, the level of the combined trait (tolerant, intermediate or intolerant) was based on the highest tolerance score found among the five tolerance traits. Whenever the available information was in the form of interval values [e.g. Female maturity of crucian carp *Carassius carassius* (Linnaeus, 1758) was reported to occur between 2 and 4 years of age], the precautionary principle approach was again followed by selecting the value leading to a higher impact on native ecosystems (e.g. the earliest age of Female maturity reported in the interval, i.e. 2 years for *Carassius carassius*).

Species trait filtering was investigated for the release, establishment, spread and impact stages of the invasion pathway. To model the influence of the different species traits on the invasive potential of alien species, proxies of the four invasion stages were used as response variables (Marchetti et al. 2004a; Ribeiro et al. 2008). Specifically: (1) the surrogate propagule pressure, as a proxy for the release stage; (2) the fraction of European countries with established populations where the species was released and has been reported as established, as a proxy for the establishment stage; (3) the number of European countries with established populations, as a proxy for the spread stage; and (4) the invasibility status, as a proxy of the impact stage (Table S1).

The intrinsic difficulty to assess the release stage lies mainly in the lack of documentation for most freshwater fish species introduction events (e.g. anglers discarding live baits: Peoples and Midway 2018), leading to the unavailability of estimates for propagule pressure. Recently, Peoples and Midway (2018) used the total number of references of human use of a species in discipline-specific literature databases (e.g. "species name AND aquaculture") as a surrogate for propagule pressure (following McGregor et al. 2012 and Procheş et al. 2012). Similarly, in this study the surrogate of propagule pressure was measured as the number of reported introduction events of a species in European countries, obtained from Froese and Pauly (2020) and the AquaNIS database (http://www.corpi.ku.lt/databases/index.php/aquanis). On one hand, this approach leads arguably to an underestimation of the number of introduction events (i.e. introduction events that occurred in several years are reported as one introduction event). On the other hand, it considers those introduction events for which human use is not reported. The Fraction of European countries with established populations was calculated as the proportion of the number of European countries where a species was introduced and established and the number of European countries in which the species was introduced (total of successful and unsuccessful introduction events). Hence, this variable provides a measure of establishment success that varies from 0 to 1, regardless of the total number of countries considered in the analysis. This variable was based on the same sources used to assess whether a species was established or not (see Section 2.1, above). The invasibility status was a binary variable with 0 representing alien species for which there is no evidence of being invasive and 1 representing IAS (i.e. established alien species having negative impacts in the introduced range; Regulation 1127/2014:

European Union 2014). A species was considered to be invasive (see Marcolin et al. 2024 for the full reference list) if it was known to be invasive in at least one country. However, 89 out of 127 species were evaluated using a classification provided by Vilizzi et al. (2019; see Table A5).

Data analysis

To assess multicollinearity among variables, correlation tests were run using the Pearson correlation coefficient. All variable pairs showing $r > |0.7|$ were considered to be correlated. The Variance Inflation Factor (VIF; Zuur et al. 2007) was also computed in a stepwise fashion by excluding at each step the variable with the highest VIF, until all variables had a VIF lower than 2.5 (Johnston et al. 2018). A correlation coefficient of 0.70 was found between *maximum adult size* and *maximum lifespan* and, based on the stepwise VIF, *maximum adult size* was discarded from all models.

An empirical modelling approach based on Generalized Linear Mixed Models (GLLMs) was followed, both to estimate the importance of each variable at different invasion stages and to build predictive models for each invasion stage. GLLMs were used to account for the non-independence among traits induced by phylogenetic similarity (De Bello et al. 2021), specifying taxonomic classification at the family level as a random factor. Different distributions and link functions were specified according to the type of response at each stage (Table S1): Gaussian errors and link = 1 (multiple linear regression) for the release stage (*propagule pressure*; continuous), Poisson errors and log link (Poisson regression) for the spread stage (*Number of European countries with established populations*; discrete), and binomial errors and logit link (logistic regression) for the establishment (*Fraction of European countries with established populations*; proportion) and impact stages (*Invasive status*; binary). All predictor variables coded at the ordinal scale were treated as numeric in the models.

Along the sequence of analyses, the outcome of each stage was assumed to be dependent on the outcome of the previous stage(s). Hence, at each stage the effect of variables was tested while controlling for the effect of the previous stage by adding the response variables of all previous stages to the models of the subsequent stages as candidate independent variables. First, the probability of introduction of a species (release stage) was modelled specifying propagule pressure proxy as the dependent variable, and functional and ecological traits as potential predictors, as well as three variables related to the introduction history (cause of introduction, number of causes of introduction and prior invasion success outside Europe). Then, in a second model, the probability of a species to establishment in Europe (establishment stage) was modelled using the *fraction of European countries with established populations*, as the response variable. In this step, the same predictors were used as above, but the response variable of the *release* stage (*propagule pressure*) was added. In the next modelling step, prior invasion success in European countries (spread stage) was modelled as the dependent variable, adding the response variables of the previous stage (*fraction of European countries with established populations*) as a predictor variable. Finally, the *invasive status* (impact stage) was used as the response variable, adding the response variable of the spread stage (*number of European countries with established populations*) as a predictor variable. The analysis of the *impact* stage was an exception: the response variable of the release stage (*propagule pressure*) was not included as a candidate variable in the model since its correlation with the *spread* stage response variable ($r = 0.9$) was higher than the established threshold ($r = 0.7$).

For model selection, a multimodel inference approach (Burnham and Anderson 2002) was followed. To select a reduced subset of candidate variables, we first ran a backwards variable selection based on Akaike's Information Criterion (AIC) for each invasion stage model (four stages; as per Anderle et al. 2022). Based on this reduced subset of variables, a set of candidate models (Tables S3 to S6) was defined following two main a priori assumptions: (1) the success of alien species at each invasion stage always depends on the introduction history and the outcome of the preceding stages; (2) any other variable (functional and ecological traits) was allowed to enter the model if it did not exceed a total of five variables in each candidate model to avoid model overfitting and to keep the number of candidate models lower than the number of cases ($n = 127$; Burnham and Anderson 2002). We then used model averaging on the best model subset (whenever $\Delta AIC < 2$) and calculated the importance of each independent variable in the model. To estimate the goodness-of-fit of models, the marginal and conditional R^2 were computed: the first representing the variance explained by the fixed effects and the second representing the variance explained by the entire model (Nakagawa and Schielzeth 2013). When the final model resulted from averaging the best approximating models, a weighted average of the models' R^2 was computed, in which the weights corresponded to the respective Akaike weights (wi). The effect of the variables in the model were considered significant whenever the 95% confidence intervals of regression coefficients did not overlap 0 (gaussian regression models for the release stage) or the Odds Ratios (logistic regression models for the establishment and impact stages) and the Incident Rate Ratios (Poisson regression models for the spread stages) did not overlap one.

All analyses were performed with R version 4.0.0 (R Core Team 2020). The *vifstep* function of the usdm R package (Naimi 2015) was used to compute the VIF stepwise procedure. GLMM were performed using lme4 R package (Bates et al. 2007). Multimodel inference was performed with the MuMIn R package (Bartoń 2016).

Table 1. Importance of each candidate predictor variable considered at each stage, based on the sum of the Akaike's weights (see text for further details).

Trait	Release	Establishment	Spread	Impact
Functional trait				
Female maturity	0.07			0.63
Length of breeding season	0.18			
Maximum fecundity		0.83	0.21	
Maximum lifespan		0.66	0.07	0.62
Migratory behaviour	0.48			0.62
Parental care	0.72	0.07	0.35	0.18
Reproductive guild		0.01	0.07	
Spawning frequency		0.09	0.57	
Ecological trait				
Feeding habitat		0.06		
Flow preferences		0.04		
General tolerance	0.05			
Salinity tolerance			0.07	0.00
Spawning habitat preferences	0.10	1.00		
Temperature tolerance		0.25		0.24
Trophic level/index				0.30
Climate zone		0.00		0.86
European native	0.28	1.00		
Invasion history				
Cause of introduction	1.00	1.00	0.79	
Fraction of European countries with established populations (establishment stage)			1.00	
Number of causes of introduction	1.00		0.85	
Number of European countries with established populations (spread stage)				1.00
Prior invasion success outside Europe	1.00	0.00		
Propagule pressure (release stage)		0.00	1.00	

Results

The release stage model showed moderate support (wi = 0.35, marginal R^2 = 71%). *Migratory behaviour*, *parental care*, *prior invasion success outside Europe*, *number of causes of introduction*, and *cause of introduction* were the most important predictors for alien species to be released (Table 1). In particular, *prior invasion success outside Europe* and *number of causes of introduction* showed strong positive effects on *propagule pressure*. According to *cause of introduction*, alien species with release records that were identified as accidental or both accidental and intentional tended to show a lower propagule pressure than species with exclusively intentional releases. Both *migratory behaviour* and *parental care* showed a significant negative effect on *propagule pressure* at this stage (Figure 2A, Figure S1).

The establishment stage model showed good support (wi = 0.49, marginal R^2 = 53%). Among the selected quantitative variables, three - *maximum lifespan*, *spawning habitat preferences* and *maximum fecundity* – had a negative effect on the establishment likelihood, while two - *temperature tolerance* and European origin (*European native*) - had a positive effect (Figure 2B, Figure S2). Moreover, alien species with release records that were identified as accidental, intentional and through dispersion tended to show a higher establishment probability than species with exclusively intentional releases.

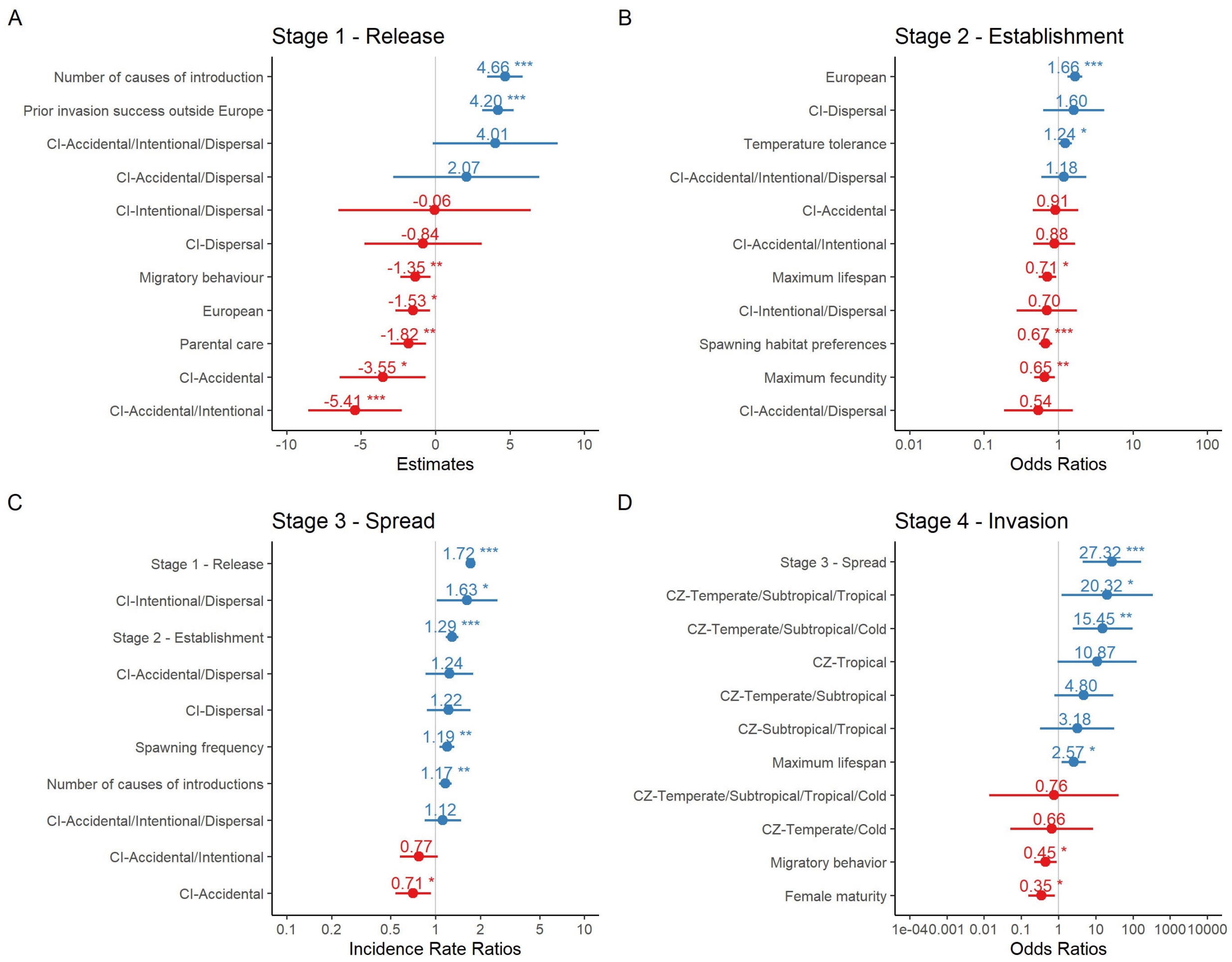

Figure 2. Selected predictor Estimates and 95% confidence intervals of regression coefficients (invasion stage 1), Odds Ratios (i.e. the change in the likelihood [log] of the establishment given a unit change in the predictor; invasion stages 2 and 4) and Incident Rate Ratios (i.e. the rate of the expected counts after one unit change in the predictor; invasion stage 3) of the Generalized Linear Mixed Models relating the proxy of each one of the four invasion stages with predictor variables (see text for further details; CI – Cause of Introduction, with "exclusively intentional releases" as the reference category; CZ – Climatic Zone, with "temperate zone" as the reference category).

The spread stage model showed good support (wi = 0.49, marginal R^2 = 71%). No model averaging was required because the second best model showed a ΔAIC higher than 2. All quantitative variables included in the model showed a positive effect on the *number of European countries with established populations* (Figure 2C, Figure S3 of Suppl. information). These included four variables: *spawning frequency*, *number of causes of introduction*, *propagule pressure* (*release* stage response variable) and *fraction of European countries with established populations* (establishment stage response variable). According to the *cause of introduction* variable (Figure 2C), alien species with release records that were identified as both intentional and through dispersal tended to be established in more European countries than species with exclusively intentional releases.

The resulting impact stage model showed moderate support (wi = 0.24, marginal R^2 = 84%). No model averaging was required because the second best model showed a ΔAIC higher than 2. All quantitative explanatory variables had coefficients with confidence intervals that did not contain zero. These included two variables showing a positive effect – *maximum lifespan* and *number of European countries with established populations* (*spread* stage response variable) – and two variables showing a negative effect – *migratory behaviour* and *female maturity* (Figure 2D, Figure S4). For *climate zone*, the categories whose odds ratio confidence intervals did not include zero were tropical, temperate/subtropical/tropical and temperate/subtropical/cold (Figure 2), which means that species belonging to these trait categories tended to have higher invasiveness than species restricted to the temperate zone (reference category).

Discussion

This study supports the idea that in successfully established alien freshwater fish species (that eventually become invasive), the most relevant combination of traits differs throughout the invasion pathway. This was true despite the effect of variables related to the history of alien species introductions. Moreover, by incorporating the probability of success at the previous stages, we could disentangle which traits drive a species' success at each individual stage of the invasion pathway. Both release and spread stages tended to be primarily related to the introduction history of the species, such as the causes of introduction or the invasion success outside Europe, whereas the establishment and impact stages tended to be primarily related to functional traits.

Traits filtering at each invasion stage

This study confirmed the importance of three traits as drivers of alien fish species release, establishment and impact along the invasion pathway stages in Europe: *maximum lifespan*, *migratory behaviour* and *European native* (native from Europe or not). *Maximum lifespan* was also found in other studies to have a significant effect on alien fish invasion stages (Marchetti et al. 2004a; Jeschke and Strayer 2006; Liu et al. 2017; Peoples and Midway 2018). In these studies, this trait was found to be important for the establishment, spread and impact stages, most often showing a positive correlation with the probability of success at each stage. *Maximum lifespan* has likely an indirect effect on species' success at different invasion stages, because fish with a longer lifespan typically attain larger maximum body sizes (not considered here as a candidate predictor due to collinearity problems), which confers enhanced dispersal abilities and possibly increased competitive advantages. However, studies differ in their conclusions on the effect of lifespan on alien fish invasion success, which possibly reflects the scale and the environmental gradients that are covered. For example, a negative effect of lifespan was found in California, USA (Marchetti et al. 2004a; Moyle and Marchetti 2006), and in Iberian Mediterranean streams (Vila-Gispert et al. 2005), which share some common environmental features, whereas no significant effect was found in the Appalachian (USA) river basin (Buckwalter et al. 2020). Positive effects of lifespan were more often found in larger scale studies (Jeschke and Strayer 2006; Liu et al. 2017; Su et al. 2023). Lifespan may influence the success of alien fish species in two distinct directions. On one hand, species with a shorter lifespan often share a set of life-history characteristics related to high reproductive capacity, including a short generation time and higher population growth rates (Bernery et al. 2024), which may favour establishment success. This is the typical *r*-selection model that confers advantages in unstable habitats with limited resources and harsh environments (MacArthur and Wilson 1967). On the other hand, species with a longer lifespan, i.e. *k*-selection species adapted to more stable conditions (MacArthur and Wilson 1967), tend to show higher dispersal ability (Su et al. 2024), higher fecundity (Marchetti et al. 2004a), and are usually preferred for recreational angling (a major trait of introduction in non-native areas; Davis and Darling 2017), commercial fisheries and aquaculture, all of which may favour their success as invasive species. This is supported by the results of this study, which suggest that short-lived species tend to be more successful during the establishment stage, whereas long-lived species tend to be more successful during the impact stage. Nevertheless, methodological issues cannot be discarded as data on population dynamics tend to be scarcer for short-lived species, as more sampling effort is required to capture accurate data on population trends.

According to the models for the release and impact stages, *Migratory behaviour* tends to be related to a lower success during these two stages. A similar trend was found in alien fish from Californian basins (Moyle and Marchetti 2006), where frequent unsuccessful introductions of migratory fish seem to be related to their typical homing behaviour and to the difficulties associated with their varying physiological and habitat requirements at different life history stages, coupled with their high mortality during migration (Moyle and Marchetti 2006).

The *European native* variable was the third showing a significant effect in more than one stage. European native species were found to have lower chances of being released, although they had a higher probability of successfully establishing populations in non-native European countries. Therefore, results suggest that the number of release records is lower for European species than for non-European species, although European species show higher establishment success because they are probably better adapted to similar European climatic conditions. This variable could be interpreted as a proxy for distance to the nearest native source or region, which was found to be important in the establishment stage in other studies (Marchetti et al. 2004b; Ribeiro et al. 2008). Nonetheless, this result should be interpreted with caution, since the database sources used in this study are more likely to report species introduced from outside Europe than translocated species.

Moreover, the set of European species that were considered in the present analysis have in common an overall low commercial value in comparison to non-native species occurring in Europe, which may also explain the lower number of release records.

Other traits significantly affected the success of alien freshwater fish species along the invasion pathway, despite their effect being limited to a single invasion stage. This was the case of *female age at maturity*, *parental care*, *spawning frequency*, *spawning habitat preferences*, *temperature tolerance* and *climatic zone* of the native range. A negative association of *female maturity* at the impact stage was found, despite a positive association with *maximum lifespan*, suggesting that fish with long lifespans, but early female maturity, are favoured at this stage. Moreover, *parental care*, another trait related to reproduction, was negatively associated with propagule pressure at the release stage. This result is consistent with the trend found in the Iberian Peninsula, where alien species would arguably benefit from having similar life-history strategies to native Iberian species, which typically show low parental care (Ribeiro et al. 2008). Nonetheless, an opposite trend was found in other studies, where high parental care was found to favour fish invasions (Marchetti et al. 2004a; Jeschke and Strayer 2006; Buckwalter et al. 2020; Lawson and Hill 2022; Bernery et al. 2023; Bernery et al. 2024).

Spawning frequency was also found to be a relevant factor during the spread stage. Accordingly, in other parts of the world, such as North America, fish species that spawn more frequently per season were found to colonize a wider range of non-native watersheds (Peoples and Midway 2018). In the Iberian Peninsula, a lower spawning frequency along the year was more frequently found among successful fish invaders that originated outside the Iberian Peninsula, while higher *spawning frequency* was associated with translocated Iberian fish species (Vila-Gispert et al. 2005). *Spawning habitat preference* was found to be one of the most important traits for the establishment of alien fish in Europe. The models showed that limnophilic spawners (spawners in low current waters) tend to establish populations more successfully than rheophilic spawners (spawners in high current waters). Traits related to habitat characteristics are often disregarded in studies that investigate relationships between fish invasiveness and functional traits. In one of the few exceptions, it was shown that most alien fish from Catalonian watersheds tend to prefer lower and more lentic stream reaches, although this refers to general habitat preferences (Vila-Gispert et al. 2005). Among the traits related to tolerance, *temperature tolerance* was the only one to show a significant effect at the establishment stage. As expected, eurythermal species tended to establish populations more successfully. This is consistent with most studies, which often found that successful fish invaders showed higher thermal tolerance (Kolar and Lodge 2002; Peoples and Midway 2018) or higher physiological tolerance (Marchetti et al. 2004a;

Moyle and Marchetti 2006; García-Berthou 2007). Finally, the *climate zone* of provenance, which reflects the latitudinal extent of the native species range, was found to be positively related to invasion success during the impact stage. This variable is related to the size of the native range and has been commonly found to be an important characteristic across different invasion stages (Marchetti et al. 2004a; Jeschke and Strayer 2006; Moyle and Marchetti 2006; Ribeiro et al. 2008; Peoples and Midway 2018; Buckwalter et al. 2020).

Invasion history as a driver of alien fish invasion

This work supports previous studies that suggested a strong positive association of human-related and invasion history characteristics on the success of alien fish species throughout the invasion pathway (Kolar and Lodge 2002; Marchetti et al. 2004a; Jeschke and Strayer 2006; Ribeiro et al. 2008; Peoples and Midway 2018; Su et al. 2023; Bernery et al. 2024). The *cause of introduction* was found to significantly affect the release and spread stages, with species unintentionally introduced or both unintentionally and intentionally having lower probability to be introduced or spread compared to only intentionally introduced species. This characteristic was also found to be important for the worldwide success of alien fish (Ruesink 2005). As expected, the *number of causes of introduction* also positively influenced introduction success, again during the release (due to higher *propagule pressure*) and spread stages (possibly due to translocation, e.g. live baits, of an established species within the basins of the same country; Lenhardt et al. 2011; Hirsch et al. 2021). *Prior invasion success outside Europe*, was found to significantly promote success during the release stage. Other studies reported the importance of this characteristic for the success of both establishment and spread of alien fish species (Marchetti et al. 2004a; Ribeiro et al. 2008).

As expected, the proxies of one stage were good predictors of the stages that followed. For example, *propagule pressure*, here used as a proxy of release probability, was found to be positively associated with the spread of alien fish, and was among the most important predictor variables during this stage. This is often identified as one of the predictors that most strongly influences invasion success (Lockwood et al. 2005), namely during the establishment stage (Marchetti et al. 2004a; Ruesink 2005; Ribeiro et al. 2008; Bernery et al. 2024). The establishment probability, as measured by the fraction of countries with reported releases where confirmed established populations were recorded, was positively associated with the spread stage and found to be an important predictor during this stage. Finally, the spread stage, as measured by the *number of European countries with established populations*, was the most important variable affecting the invasion probability during the impact stage.

Management recommendations

The results of our study not only further support well-established recommendations, but also may provide new directions to prevent or manage biological invasions. Although the transport stage was not considered in our analysis, given the lack of data available at the European scale, this study remains one of the few to evaluate the release stage for invasive alien fishes. The release stage was found to be mostly governed by human-related variables, namely the *introduction history*. Thus, actions to manage alien species should primarily focus on controlling intentional releases of alien fish, especially of species with a known introduction success outside European borders. It is nevertheless possible that our work underestimated the introduction of European translocated species, as these may be less likely to be reported to the database used. During the establishment stage, management actions are more limited since the human component is not the most important in determining the success of alien species. Nonetheless, the results suggest that control actions should be primarily focused on European-origin fish species with a shorter lifespan, low maximum fecundity, limnophilic spawning habits and high thermal tolerance. For example, culling, using different removal techniques, is a good alternative to eradicate alien fish species at this stage, as this method is particularly effective in the very initial stages of invasion, especially for species with low dispersal abilities (Almela et al. 2021). The spread stage was again mostly governed by introduction history and human interest, although also positively associated with fish that showed higher yearly spawning frequency. At this stage, actions to manage alien species should mainly focus on controlling the number of causes of introductions, namely intentional releases and dispersion among basins. Nonetheless, avoiding their success in the previous two stages, in particular for species with higher spawning frequency, would be more effective since alien fish species are still spatially constrained and in low abundances in the initial period of the invasion process (Rytwinski et al. 2019). Finally, the results found for the impact stage support management actions that are more focused on controlling species that succeeded in the spread stage, in particular non-migratory fish showing longer lifespans, lower female age at maturity and occupying wider latitudes in their native ranges. At this stage, to increase eradication probability or to constrain invasion (for invasive species with high dispersal ability), long-term management control actions (i.e. culling) should be implemented (Almela et al. 2021).

Author contribution

All authors contributed to the research conceptualization and design. FM, PB, JMS and PS collected the data. FM and PS analysed the data with input from all authors. LR and PS provided logistical and funding provision. FM and PS wrote the manuscript with contributions from all authors. DC contributed to the writing and the final revision of the manuscript. All authors read and approved the final version of the manuscript.

Acknowledgements

We thank Lorenzo Vilizzi and an anonymous reviewer for the valuable comments on the manuscript. This work was supported by FCT – Fundação para a Ciência e Tecnologia, I.P. through project references UIDB/00239/2020 (DOI 10.54499/UIDB/00239/2020) and UIDP/00239/2020 (DOI 10.54499/UIDP/00239/2020).

Funding declaration

This research was supported by FCT – Fundação para a Ciência e a Tecnologia project "ALIENTRADE project: something in the way they move: How global pattern of wildlife trade influence global invasion success" (PTDC/BIA-ECO/30931/2017-POCI-01-0145-FEDER-030931). This work was also supported by the FCT funded project UnRAVEL with the reference 10.54499/PTDC/BIA-ECO/0207/2020 and DOI identifier https://doi.org/10.54499/PTDC/BIA-ECO/0207/2020. FM, JR and JS were funded by Fundo Europeu de Desenvolvimento Regional through the Operational Competitiveness Factors Program "COMPETE" and by National Funds through the FCT) within the framework of ALIENTRADE project (PTDC/BIA-ECO/30931/2017-POCI-01-0145-FEDER-030931). LR was supported by Portuguese National Funds through FCT, I.P. (DL57/2016/CP1440/CT0011 and CEECIND/00445/2017, respectively). Forest Research Centre (CEF) is supported by FCT – Fundação para a Ciência e Tecnologia, I.P., Portugal (UIDB/00239/2020; DOI:10.54499/UIDB/00239/2020). The Associate Laboratory TERRA (LA/P/0092/20202020 - DOI 10.54499/LA/P/0092/2020) is also funded by FCT. The Open Access was funded by CEF Project UIDB/00239/2020.
Publication of this study was supported by the European Union's Horizon Europe HORIZON-CL6-2024-BIODIV-01 project "GuardIAS - Guarding European Waters from IAS", under grant agreement no. 101181413 (Katsanevakis et al. 2024).
The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

Almela VD, Palmer SC, Andreou D, Gillingham PK, Travis JM, Britton JR (2021) Predicting the outcomes of management strategies for controlling invasive river fishes using individual-based models. *Journal of Applied Ecology* 58: 2427–2440, https://doi.org/10.1111/1365-2664.13981

Alves MT, Tidbury HJ (2022) Invasive non-native species management under climatic and anthropogenic pressure: application of a modelling framework. *Management of Biological Invasions* 13: 259–273, https://doi.org/10.3391/mbi.2022.13.2.01

Anderle M, Paniccia C, Brambilla M, Hilpold A, Volani S, Tasser E, Seeber J, Tappeiner U (2022) The contribution of landscape features, climate and topography in shaping taxonomical and functional diversity of avian communities in a heterogeneous Alpine region. *Oecologia* 199: 499–512, https://doi.org/10.1007/s00442-022-05134-7

Bagnara M, Nowak L, Boehmer HJ, Schöll F, Schurr FM, Seebens H (2022) Simulating the spread and establishment of alien species along aquatic and terrestrial transport networks: A multi-pathway and high-resolution approach. *Journal of Applied Ecology* 59(7): 1769–1780, https://doi.org/10.1111/1365-2664.14184

Bernery C, Marino C, Bellard C (2023) Relative importance of exotic species traits in determining invasiveness across levels of establishment: Example of freshwater fish. *Functional Ecology* 37: 2358–2370, https://doi.org/10.1111/1365-2435.14393

Bernery C. Bellard C, Courchamp F, Brosse S, Leroy B (2024) A global analysis of the introduction pathways and characteristics associated with non-native fish species introduction, establishment, and impacts. *Ecological Processes* 13: 22, https://doi.org/10.1186/s13717-024-00495-8

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339, https://doi.org/10.1016/j.tree.2011.03.023

Buckwalter JD, Frimpong EA, Angermeier PL, Barney JN (2020) Species traits predict stream-fish invaders in an Appalachian (USA) river basin. *Freshwater Biology* 65: 552–564, https://doi.org/10.1111/fwb.13453

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, second ed. Berlin, Germany: Springer 63(2020), 10

Chan J, Zeng Y, Yeo DCJ (2021) Invasive species trait-based risk assessment for non-native freshwater fishes in a tropical city basin in Southeast Asia. *PLOS ONE* 16: e0248480, https://doi.org/10.1371/journal.pone.0248480

Chapple DG, Naimo AC, Brand JA, Michelangeli M, Martin JM, Goulet CT, Brunton DH, Sih A, Wong BBM (2022) Biological invasions as a selective filter driving behavioral divergence. *Nature Communications* 13: 5996, https://doi.org/10.1038/s41467-022-33755-2

Corrales X, Katsanevakis S, Coll M, Heymans JJ, Piroddi C, Ofir E, Gal G (2020) Advances and challenges in modelling the impacts of invasive alien species on aquatic ecosystems. *Biological Invasions* 22: 907–934, https://doi.org/10.1007/s10530-019-02160-0

Costa MJ, Duarte G, Segurado P, Branco P (2021) Major threats to European freshwater fish species. *Science of Total Environment* 797: 149105, https://doi.org/10.1016/j.scitotenv.2021.149105

Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Essl F, Gozlan RE, Haubrock PJ, Kourantidou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021) Global economic costs of aquatic invasive alien species. *Science of the Total Environment* 775: 145238, https://doi.org/10.1016/j.scitotenv.2021.145238

Davis AJS, Darling JA (2017) Recreational freshwater fishing drives non-native aquatic species richness patterns at a continental scale. *Diversity and Distributions* 23: 692–702, https://doi.org/10.1111/ddi.12557

De Bello F, Carmona CP, Dias AT, Götzenberger L, Moretti M, Berg MP (2021) Handbook of trait-based ecology: from theory to R tools. Cambridge, UK, 312 pp, https://doi.org/10.1017/9781108628426

Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Gonzalez P, Grosholz ED, Ibañez I, Miller LP, Sorte CJB, Tatem AJ (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nature Communications, Nature Publishing Group 7, https://doi.org/10.1038/ncomms12485

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 41: 59–80, https://doi.org/10.1146/annurev-ecolsys-102209-144650

European Commission (2014) Commission Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. Bruxelles, Belgium, 21 pp

Freyhof J, Kottelat M (2007) Handbook of European freshwater fishes. Cornol, Switzerland, 646 pp

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22: 151–163, https://doi.org/10.1111/gcb.13004

García-Berthou E (2007) The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology* 71: 3–55, https://doi.org/10.1111/j.1095-8649.2007.01668.x

Griffen BD, Delaney DG (2007) Species invasion shifts the importance of predator dependence. *Ecology* 88: 3012–3021, https://doi.org/10.1890/07-0172.1

Gulzar R, Hamid M, Hassan T, Rashid I, Khuroo AA (2024) Different sets of traits determine transition of alien species along the invasion continuum. *Science of The Total Environment* 912: 169137, https://doi.org/10.1016/j.scitotenv.2023.169137

Hirsch PE, N'Guyen A, Burkhardt-Holm P (2021) Hobbyists acting simultaneously as anglers and aquarists: Novel pathways for non-native fish and impacts on native fish. *Aquatic Conservation* 31: 1285–1296, https://doi.org/10.1002/aqc.3557

Howeth JG, Gantz CA, Angermeier PL, Frimpong EA, Hoff MH, Keller RP, Mandrak NE, Marchetti MP, Olden JD, Romagosa CM, Lodge DM (2016) Predicting invasiveness of species in trade: climate match, trophic guild and fecundity influence establishment and impact of non-native freshwater fishes. *Diversity and Distributions* 22: 148–160, https://doi.org/10.1111/ddi.12391

Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology* 12: 1608–1619, https://doi.org/10.1111/j.1365-2486.2006.01213.x

Johnston RJ, Jones K, Manley D (2018) Confounding and collinearity in regression analysis: a cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. *Quality & Quantity* 52: 1957–1976, https://doi.org/10.1007/s11135-017-0584-6

Katsanevakis S, Zaiko A, Olenin S, Costello MJ, Gallardo B, Tricarico E, Adriaens T, Jeschke JM, Sini M, Burke N, Ellinas K, Rutten S, Poursanidis D, Marchini A, Brys R, Raeymaekers JAM, Noé N, Hermoso V, Blaalid R, Lucy FE, Verbrugge LNH, Staehr PAU, Vandepitte L, de Groot D, Elliott M, Reuver M, Maclaren J, Li M, Oldoni D, Mazaris A, Trygonis V, Hablützel PI, Everts T, Pistevos JCA, Dekeyzer S, Kimmig SE, Rickowski FS, Panov VE (2024) GuardIAS – Guarding European Waters from Invasive Alien Species. *Management of Biological Invasions* 15: 701–730, https://doi.org/10.3391/mbi.2024.15.4.14

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessments for non-native species. *Science* 298: 1233–1236, https://doi.org/10.1126/science.1075753

Kraft NJ, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29: 592–599, https://doi.org/10.1111/1365-2435.12345

Lawson KM, Hill JE (2022) Life history strategies differentiate established from failed non-native freshwater fish in peninsular Florida. *Diversity and Distributions* 28: 160–172, https://doi.org/10.1111/ddi.13448

Lenhardt M, Markovic G, Hegedis A, Maletin S, Cirkovic M, Markovic Z (2011) Non-native and translocated fish species in Serbia and their impact on the native ichthyofauna. *Reviews in Fish Biology and Fisheries* 21: 407–421, https://doi.org/10.1007/s11160-010-9180-8

Liu C, Comte L, Olden JD (2017) Heads you win, tails you lose: Life-history traits predict invasion and extinction risk of the world's freshwater fishes. *Aquatic Conservation* 27: 773–779, https://doi.org/10.1002/aqc.2740

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20: 223–228, https://doi.org/10.1016/j.tree.2005.02.004

MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, N.J., 203 pp

Marchetti MP, Moyle PB, Levine R (2004a) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49: 646–661, https://doi.org/10.1111/j.1365-2427.2004.01202.x

Marchetti MP, Moyle PB, Levine R (2004b) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* 14: 587–596, https://doi.org/10.1890/02-5301

McGregor KF, Watt MS, Hulme PE, Duncan RP (2012) What determines pine naturalization: species traits, climate suitability or forestry use? *Diversity and Distributions* 18: 1013–1023, https://doi.org/10.1111/j.1472-4642.2012.00942.x

Moyle PB, Marchetti MP (2006) Predicting invasion success: freshwater fishes in California as a model. *BioScience* 56: 515–524, https://doi.org/10.1641/0006-3568(2006)56[515:PISFFI]2.0.CO;2

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from Generalized Linear Mixed-effects Models. *Methods in Ecology and Evolution* 4: 133–142, https://doi.org/10.1111/j.2041-210x.2012.00261.x

Oberdorff T, Pont D, Hugueny B, Porcher JP (2002) Development and validation of a fish-based index for the assessment of 'river health'in France. *Freshwater Biology* 47: 1720–1734, https://doi.org/10.1046/j.1365-2427.2002.00884.x

Oficialdegui FJ, Zamora-Marín JM, Guareschi S, Anastácio PM, García-Murillo P, Ribeiro F, Miranda R, Cobo F, Gallardo B, García-Berthou E, Boix D, Arias A, Cuesta JA, Medina L, Almeida D, Banha F, Barca S, Biurrun I, Cabezas MP, Calero S, Campos JA, Capdevila-Argüelles L, Capinha C, Casals F, Clavero M, Encarnação J, Fernández-Delgado C, Franco J, Guillén A, Hermoso V, Machordom A, Martelo J, Mellado-Díaz A, Morcillo F, Oscoz J, Perdices A, Pou-Rovira Q, Rodríguez-Merino A, Ros M, Ruiz-Navarro A, Sánchez MI, Sánchez-Fernández D, Sánchez-González JR, Sánchez-Gullón E, Teodósio MA, Torralva M, Vieira-Lanero R, Oliva-Paterna FJ (2023) A horizon scan exercise for aquatic invasive alien species in Iberian inland waters. *Science of the Total Environment* 869: 161798, https://doi.org/10.1016/j.scitotenv.2023.161798

Pagad S, Genovesi P, Carnevali L, Schigel D, McGeoch MA (2018) Introducing the global register of introduced and invasive species. *Scientific Data* 5: 1–12, https://doi.org/10.1038/sdata.2017.202

Peoples BK, Midway SR (2018) Fishing pressure and species traits affect stream fish invasions both directly and indirectly. *Diversity and Distributions* 24: 1158–1168, https://doi.org/10.1111/ddi.12747

Procheş Ş, Wilson JR, Richardson DM, Rejmánek M (2012) Native and naturalized range size in *Pinus*: relative importance of biogeography, introduction effort and species traits. *Global Ecology and Biogeography* 21: 513–523, https://doi.org/10.1111/j.1466-8238.2011.00703.x

Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews, Blackwell Publishing Ltd* 94: 849–873, https://doi.org/10.1111/brv.12480

Ribeiro F, Elvira B, Collares-Pereira MJ, Moyle PB (2008) Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biological Invasions* 10: 89–102, https://doi.org/10.1007/s10530-007-9112-2

Rowles AD, O'Dowd DJ (2007) Interference competition by Argentine ants displaces native ants: implications for biotic resistance to invasion. *Biological Invasions* 9: 73–85, https://doi.org/10.1007/s10530-006-9009-5

Ruesink JL (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology* 19: 1883–1893, https://doi.org/10.1111/j.1523-1739.2005.00267.x-i1

Rytwinski T, Taylor JJ, Donaldson LA, Britton JR, Browne DR, Gresswell RE, Lintermans M, Prior KA, Pellatt MG, Vis C, Cooke S (2019) The effectiveness of non-native fish removal techniques in freshwater ecosystems: a systematic review. *Environmental Review* 27: 71–94, https://doi.org/10.1139/er-2018-0049

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: What's what and the way forward. *Trends in Ecology and Evolution* 28: 58–66, https://doi.org/10.1016/j.tree.2012.07.013

Sommerwerk N, Wolter C, Freyhof J, Tockner K (2017) Components and drivers of change in European freshwater fish faunas. *Journal of Biogeography* 44: 1781–1790, https://doi.org/10.1111/jbi.13019

Su G, Mertel A, Brosse S, Calabrese JM (2023) Species invasiveness and community invasibility of North American freshwater fish fauna revealed via trait-based analysis. *Nature Communications* 14: 2332, https://doi.org/10.1038/s41467-023-38107-2

Troia MJ, McManamay RA (2020) Biogeographic classification of streams using fish community– and trait–environment relationships. *Diversity and Distributions* 26: 108–125, https://doi.org/10.1111/ddi.13001

Vandekerkhove J, Cardoso AC, Boon PJ (2013) Is there a need for a more explicit accounting of invasive alien species under the Water Framework Directive? *Management of Biological Invasions* 4: 25, https://doi.org/10.3391/mbi.2013.4.1.04

Vila-Gispert A, Alcaraz C, García-Berthou E (2005) Life-history traits of invasive fish in small Mediterranean streams. *Biological Invasions* 7: 107–116, https://doi.org/10.1007/s10530-004-9640-y

Vilizzi L, Copp GH, Adamovich B, Almeida D, Chan J, Davison PI, Dembski S, Ekmekçi FG, Ferincz Á, Forneck SC, Hill JE, Kim J-E, Koutsikos N, Leuven RSEW, Luna SA, Magalhães F, Marr SM, Mendoza R, Mourão CF, Neal JW, Onikura N, Perdikaris C, Piria M, Poulet N, Puntila R, Range I.L, Simonović P, Ribeiro F, Tarkan AS, Troca DFA, Vardakas L, Verreycken H, Vintsek L, Weyl OLF, Yeo DCJ, Zeng Y (2019) A global review and meta-analysis of applications of the freshwater Fish Invasiveness Screening Kit. *Reviews in Fish Biology and Fisheries* 29: 529–568, https://doi.org/10.1007/s11160-019-09562-2

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116: 882–892, https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wood CM, Gutiérrez RJ. Keane JJ, Peery MZ (2020) Early detection of rapid Barred Owl population growth within the range of the California Spotted Owl advises the Precautionary Principle. *The Condor* 122: duz058, https://doi.org/10.1093/condor/duz058

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3–14, https://doi.org/10.1111/j.2041-210X.2009.00001.x

Websites, online databases and software

Bartoń K (2016) MuMIn: Multi-model Inference. R Package Version 1.15.6.

Bates D, Sarkar D, Bates MD, Matrix L (2007) The lme4 package. R package version, 2(1), 74

Fricke R, Eschmeyer WN, Van der Laan R (2024) Eschmeyer's catalog of fishes: genera, species, references. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 15 May 2024)

Froese R. Pauly D (eds) (2020) FishBase. World Wide Web electronic publication. www.fishbase.org (accessed 15 April 2020)

Marcolin F, Branco P, Santos JM, Reino L, Santana J, Ribeiro J, Chamberlain D, Segurado P (2024) Dataset for "Species traits and invasion history as predictors of freshwater fish's invasion success in Europe". Retrieved from https://osf.io/p3qkj/

Naimi B (2015) Usdm: Uncertainty Analysis for Species Distribution Models. R Package Version 1.1–15. http://CRAN.R-project.org/package=usdm

R Core Team (2020) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Supplementary material

The following supplementary material is available for this article:

Table S1. Functional and ecological traits, and invasion history information compiled for the alien freshwater fish in Europe.
Table S2. Trait data retrieved for the 127 non-native fish species (number of values, number of missing values, and percentage of missing values per trait).
Table S3. Set of candidate and ranked models for the release stage.
Table S4. Set of candidate and ranked models for the establishment stage.
Table S5. Set of candidate and ranked models for the spread stage.
Table S6. Set of candidate and ranked models for the impact stage.
Figure S1. Partial dependence plots of the mean predicted values for the release stage model
Figure S2. Partial dependence plots of the predicted values for the establishment stage model
Figure S3. Partial dependence plots of the predicted values for the spread stage model
Figure S4. Partial dependence plots of the predicted values for the impact stage model

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2025/Supplements/MBI_2025_Marcolin_etal_SupplementaryTables_1_2.pdf
http://www.reabic.net/journals/mbi/2025/Supplements/MBI_2025_Marcolin_etal_SupplementaryTable_3.xlsx
http://www.reabic.net/journals/mbi/2025/Supplements/MBI_2025_Marcolin_etal_SupplementaryTable_4.xlsx
http://www.reabic.net/journals/mbi/2025/Supplements/MBI_2025_Marcolin_etal_SupplementaryTable_5.xlsx
http://www.reabic.net/journals/mbi/2025/Supplements/MBI_2025_Marcolin_etal_SupplementaryTable_6.xlsx
http://www.reabic.net/journals/mbi/2025/Supplements/MBI_2025_Marcolin_etal_SupplementaryFigures.pdf