



The importance of seawater tolerance and native status in mediating the distribution of inland fishes

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Abstract

Aim: Unravelling the ecological and historical factors that underlie species distributions has challenged ecologists for a long time. Thus, our objective is to understand the role of environmental variables explaining the distribution of three major eco-evolutionary groups of inland fishes (Darlington's divisions: primary, i.e. strict freshwater; secondary, i.e. salt-tolerant; and peripheral, i.e. diadromous and marine origin), and how these variables are related to fish traits.

Location: Iberian Peninsula.

Taxon: 51 native and 17 alien inland fish species from the Iberian Peninsula.

Methods: We modelled distributions of the most common inland fish species across the Iberian Peninsula to compare the importance of different predictors among the three Darlington's divisions and between native and alien species. To explore the importance of specific environmental variables in determining the distribution of different traits of inland fish, variable importances obtained from species distribution models were subjected to a redundancy analysis.

Results: Darlington's divisions differ significantly in salinity tolerance, in distribution overlap, in the importance of distribution predictors and associated life-history traits. Topographic and climatic variables were generally more important than land use and anthropogenic factors in explaining fish distributions. We found significant differences in the importance of variables explaining the distribution of native vs. alien species and especially among Darlington's divisions. River basin was most important for primary native and many alien species. Increasing mean temperature and damming were positively associated with the presence of tolerant, large-bodied and warm-water alien species from more hydrologically stable habitats.

Main conclusions: Despite marked differences in the distribution patterns of native and alien species, evolutionary and introduction histories as well as seawater tolerance are central factors explaining the current distribution of inland fishes. Darlington's divisions proved useful for addressing ecological and biogeographical questions at broader spatial scales.

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KEYWORDS

alien species, biological invasions, Darlington's divisions, endemic species, freshwater fish, hydrologic alteration, Iberian Peninsula, Mediterranean rivers, Myers' divisions, species distribution models

1 | INTRODUCTION

Unravelling the ecological and historical factors that underlie species distributions and biodiversity patterns has challenged ecologists and biogeographers for a long time. In an increasingly human-dominated world, where global biodiversity is changing at an unprecedented rate (Sala et al., 2000), unveiling the variables that explain the distribution of species is of key importance to understand environmental impacts, species invasions and the often simultaneous decline of many native species as well as to implement appropriate management measures (Markovic et al., 2014). This is particularly relevant in freshwater ecosystems, which are among the most diverse but, at the same time, most threatened ecosystems globally (Albert et al., 2021). Fresh waters are threatened by manifold interacting factors such as habitat degradation and alteration through land use changes and damming, pollution, invasive alien species and climate change (Grill et al., 2019). As a consequence, more than a quarter of all freshwater fauna is threatened or has recently become extinct (IUCN, 2019).

In contrast to terrestrial organisms, for which current climatic conditions and topography seem dominant in determining species' distributions, freshwater fish ranges are also markedly maintained by basin boundaries (Filipe et al., 2009). Thus, the historical connection among river basins and the fish tolerance to seawater are important factors to understand contemporary geographical patterns of freshwater fishes (Darlington, 1948; Filipe et al., 2009). Myers (1938, 1949) recognized that the distribution of fish is mediated by their different ability to survive and disperse through seawater, and proposed a classification of inland fish based on their eco-evolutionary history and euryhalinity. Darlington (1948) reviewed and simplified this classification of inland fish into three major eco-evolutionary groups (hereafter, Darlington's divisions): (1) primary fish, whose ancestors entered inland waters much earlier, cannot survive in seawater and are thus strictly confined to fresh water; (2) secondary fish, which mostly live in fresh waters but show some salt tolerance and can thus may survive in seawater; and (3) peripheral fish, which occur in fresh waters but have high salt tolerance, such as diadromous or species of marine origin. This classification is based on taxonomic families and in general primary species such as cyprinids, characids and most siluriforms have lower salinity tolerance in contrast to secondary species such as cichlids and cyprinodontiforms (McDowall, 2010), with the latter comprising certain species with the highest salinity tolerance known among fishes (Schultz & McCormick, 2013). Since its introduction, Darlington's classification has been frequently used to address questions in freshwater zoogeography and may be used as proxy of seawater tolerance (Berra, 2001). Primary fishes are naturally absent from oceanic islands such as New Zealand, Madagascar, the West Indies

and most of Australia in contrast to secondary and peripheral families, which were able to reach these areas because of their higher salinity tolerance (Darlington, 1948). For this reason, fish also reflect the faunal boundary between Australia and Southeast Asia (known as Wallace's line) better than other vertebrate groups (Berra, 2001). Similarly, secondary fishes are more prevalent and diversified in Central America because they colonized it before the final uplift of the Isthmus of Panama, and 10 million years before primary fishes (Smith & Bermingham, 2005). Myers' or Darlington's classifications are generally supported and used by many of the most comprehensive, recent fish monographs (Bănărescu, 1990; Berra, 2001; Doadrio, 2001; Kottelat & Freyhof, 2007; McDowall, 2010). Although numerous studies have analysed the relationships of environmental variables and the distribution of freshwater fish species (Carvajal-Quintero et al., 2019), the effect of seawater tolerance on contemporary inland fish distribution, and therefore, the differences among the three Darlington's divisions, has been barely investigated (Filipe et al., 2009; Smith & Bermingham, 2005).

An analysis of contemporary fish distributions must also consider the native status of a species (i.e. whether a species is native or not to a given region). This is relevant to draw meaningful conclusions about the importance of historical and ecological variables (Sax et al., 2005), as alien species have often different distribution patterns and drivers than native species. For instance, previous studies showed that temperature and other climate-related variables markedly influence freshwater fish invasion success (e.g. warm temperatures favour the establishment and spread of many alien species) (Bae et al., 2018).

In addition, anthropogenic factors such as land use change have altered the range size distribution of fish species (Radinger et al., 2016). Specifically, dams causing fragmentation of river networks and modifications of the natural flow and sediment regimes have been associated with changes in diversity and taxonomic homogenization of fish communities, favouring the presence of alien species and hindering native ones (Johnson et al., 2008). For instance, damming often facilitates the establishment and proliferation alien species with a suite of traits (Cano-Barbacil et al., 2020) that corresponds well to a periodic strategy (i.e. limnophilic and phytophilic species that maximizes age-specific fecundity at the expense of optimizing turnover time and juvenile survivorship; see Vila-Gispert et al., 2005; Winemiller & Rose, 1992). In addition, the distribution and abundance of migratory, estuarine, rheophilic and lithophilic species is heavily impacted by dams due to the loss of connectivity and accessibility to essential habitats and the alteration of the flow regime (Lassalle et al., 2009).

Mediterranean climate regions are well suited to study the mechanisms that explain differences in the distribution patterns of inland



fish. They harbour a very particular fauna, rich in endemic but also alien species, and they often show strong anthropogenic perturbation (Leprieur et al., 2008). Specifically, the Iberian inland fish fauna comprises 68 native species, of which 41 are endemic and 32 alien species. Furthermore, numerous barriers cause rivers of the Iberian Peninsula to be more fragmented and impacted by dams than many other European rivers (Grill et al., 2019). Over the last decades, and concurrent with the proliferation of alien species and the increase in the number of dams, native fish populations of the Iberian Peninsula have considerably declined (Doadrio et al., 2011).

Against this background, the main objectives of this study are: (1) to assess the importance of climatic, topographic and anthropogenic variables in shaping the current distribution of primary, secondary and peripheral native and alien fish of the Iberian Peninsula; (2) to evaluate the role of hydrological alteration in the distribution of the three eco-evolutionary species' groups (Darlington's divisions); and (3) to understand the relationship between the importance of distributional drivers and fish traits. We hypothesized that primary, secondary and peripheral species would show contrasting importance of predictors because of their fundamental differences in evolutionary history and salinity tolerance. We expected that geographical restrictions by the river basin would be of particular importance for primary native species due to their limited dispersal ability. We also hypothesized that temperature and hydrological alteration would be important and positively correlated with alien species presence, because many of them are rather thermophilic and well adapted to stagnant waters. Finally, we hypothesized that limnophilic and tolerant species would be more prevalent at sites with warmer temperatures and higher hydrological alteration, while rheophilic fish presence would be negatively associated with these variables.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area comprised the Iberian Peninsula (see Figure 1a), which is characterized by its complex orography and high spatial and temporal climate variability. Following the Köppen-Geiger climate classification, the southern half of the Iberian Peninsula is dominated by a Mediterranean climate with dry and hot summers, SE Spain by a semiarid climate, the northern half by a Mediterranean oceanic climate with warm summers and mountainous areas by an oceanic climate (Kottek et al., 2006). Additionally, there are over 1500 large dams (MAPAMA, 2020), mostly for agricultural irrigation and other human uses.

2.2 | Fish data

We compiled occurrence data for all established Iberian inland fishes between 2000 and 2020. These comprise 68 native (including diadromous and estuarine) and 32 alien fish species. Presences

were mainly obtained from Global Biodiversity Information Facility (GBIF; GBIF.org, 2019) and the Portuguese 'Carta Piscícola Nacional' (Ribeiro et al., 2007), and complemented with 19 additional published studies (see Table S1). GBIF data were mainly based on Doadrio's atlas 2001, which is the most comprehensive fish study of Spain (Figure 1). The spatial resolution for subsequent modelling was set to 10 × 10 km which reflects the most widely used resolution in the species' occurrence records (see Doadrio, 2001). Darlington's divisions of the fish species were assigned using taxonomic families following Berra (Berra, 2001). We used this classification because (1) Darlington's divisions are well associated with salinity tolerance for the (few) species that have quantitative data (see Appendix S1); (2) other classifications (e.g. euryhalinity or use of brackish-water) are similar but generally more based on expert criteria than Darlington's classification; and (3) statistical analyses using data on salinity tolerance resulted in similar outcomes (see Appendix S1 for more details). Finally, we also compiled species-specific data of 16 morphological, reproductive and habitat use traits ('traits' hereafter; see Table S2) mainly from Cano-Barbacil et al. (2020) and complemented with other sources (Table S1).

2.3 | Environmental data

We compiled climatic, topographic, land use and anthropogenic variables (Table S3). We obtained environmental data layers from online databases and did subsequent calculations in QGIS 3.4.14 (QGIS Development Team, 2019). Predictor variables were rescaled to a modelling grid with a resolution of 10 × 10 km UTM (Universal Transverse Mercator, i.e. 100 km², $n = 6142$ total cells) to agree with the grain of our species occurrence data. Following Dormann et al. (2013), we removed strongly correlated variables with Pearson correlation coefficients $|r| \geq 0.7$. Using hierarchical cluster analysis based on the correlation matrix (Figure S1), we selected only one variable from each group of predictors based on its ecological relevance and literature. We then calculated variance inflation factors (VIF), using the R-package 'HH' (Heiberger, 2019), and checked that $VIF < 5$ (Kock & Lynn, 2012). A total of 13 predictor variables were finally used for species distribution model (SDM) development (Table S3; maps of all predictors are provided in Appendix S2).

As climatic predictors, we used mean air temperature as indicative of water temperature, which is a crucial driver of inland fish distributions (Bae et al., 2018; Murphy et al., 2015); average precipitation within each sub-catchment as representative of water discharge (Garvey et al., 2000); average precipitation seasonality (i.e. a measure of variation in monthly precipitation over the course of the year) as surrogate of the flow regime, a key environmental factor determining riverine dynamics (Lane et al., 2017); and solar radiation, reported as influential for spawning and growth of fishes (Williamson et al., 1997). As topographic variables, we selected: terrain slope; the topographic index, that is, a function of the catchment area and the slope gradient commonly used to quantify topographic control on hydrological processes (Sørensen et al., 2006); distance to the sea;

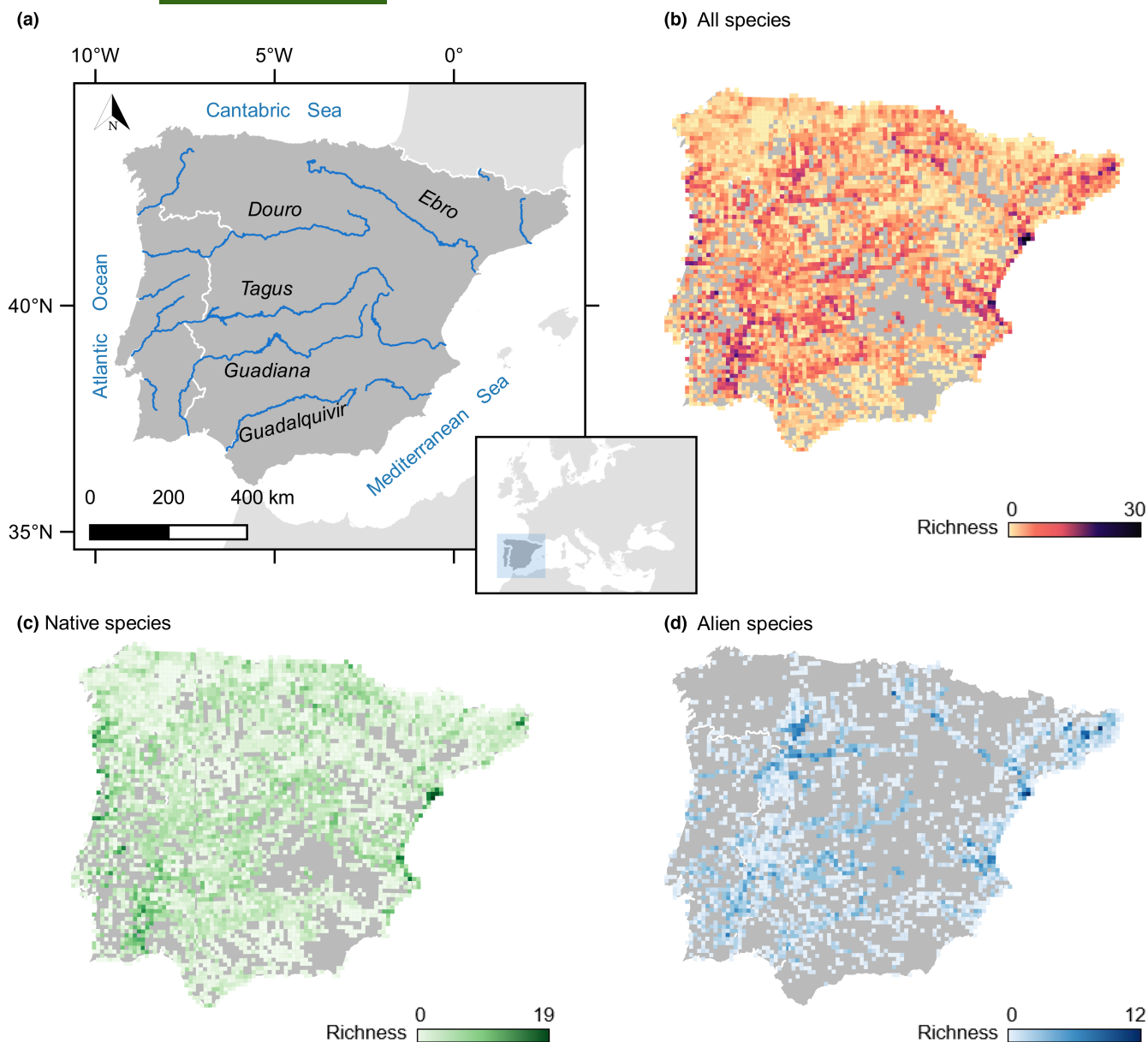


FIGURE 1 (a) Map of the Iberian Peninsula with its major rivers. (b) Observed total fish species richness, (c) richness of native fish species and (d) richness of alien fish species in the Iberian Peninsula. Projection: WGS 84/Pseudo-Mercator–EPSG:3857.

and Strahler's stream order as a proxy of stream size and longitudinal position within a river system (Strahler, 1957). As indicators of anthropogenic perturbation, we used: percentage of agricultural and urban land use in the catchment upstream (i.e. percent surface of altered land use in the river basin upstream of a certain grid cell), which are, for example, correlated to impairment of water, habitat quality and siltation (Bae et al., 2018); upstream accumulated reservoir capacity (i.e. the accumulated volume of water stored in reservoirs upstream of each modelling grid in the river network), as an indicator of the changes in flood magnitude and mean flow produced by damming (Bae et al., 2018; Batalla et al., 2004); and local reservoir capacity (i.e. the volume of water stored in each 10×10 km modelling grid cell), as a measure of the direct influence of reservoirs on fish species occurrence (Rahel, 2002). Finally, we also included the

water district (hereafter, 'basin ID') to account for biogeographical units and evolutionary history since our main focus is to understand factors explaining the current distribution of fish species rather than to know their potential distribution. 'Basin ID' consisted of single river basins in the case of large rivers, or sets of small coastal rivers that share similar faunas and environmental characteristics (see Appendix S2).

2.4 | Statistical analysis

We first used a multivariate permutational analysis of variance (PERMANOVA) to test for differences in the current distribution of primary, secondary and peripheral native and alien species. We used



the 'adonis2' function of the R-package 'vegan' (Oksanen et al., 2017). We used 999 permutations and Jaccard distances. Compared to other methods, PERMANOVA has the advantage of not making distributional assumptions and permitting various distance measures and designs. We also calculated the distribution similarity of the three Darlington's divisions using the Jaccard index (J). For that purpose, we used the functions 'vegdist' and 'meandist' of the R-package 'vegan'.

To develop SDMs, we used the BIOMOD computational framework, as implemented in the R-package 'biomod2' (Thuiller et al., 2019). To avoid potential biases, we did not model recently established introduced species and only analysed distributions of species with occurrence records in at least 20 modelling grid cells. In total, 51 native and 17 alien species were considered in our distribution models. We used four different algorithms that have been frequently applied to a variety of taxa and that showed good accuracy and complementary advantages: generalized linear models (GLM), boosted regression trees (BRT), random forests (RF) and Maxent. GLM are an extension of linear models to allow for heteroscedasticity and non-normal errors (McCullagh & Nelder, 1989). We used GLMs with binomial distribution and a logit link function. BRT combine the strengths of regression trees (i.e. models that relate a response variable to their predictors by recursive binary splits) and boosting (Elith et al., 2008) by proceeding through sequential improvements using a numerical optimization algorithm that adds a new tree at each step. RF are model-averaging approaches where each tree depends on the values of a randomized subset of predictors and with the same distribution for all trees in the forest (Breiman, 2001). RF showed better prediction accuracy than other SDM techniques with minimal overfitting (Marmion et al., 2009). Maxent-based species distribution models use species' presence records and a 'background' sample of environments in the study area, and apply the maximum-entropy principle for model fitting (Guillera-Arroita & Lahoz-Monfort, 2014). For additional details of the selected modelling options, see Table S4.

Our datasets did not include reliable absence locations because of inconsistent sampling effort. Therefore, we generated three pseudo-absence datasets (each $n = 1000$) among background grid cells for each species (Barbet-Massin et al., 2012). We used a random selection of pseudo-absences, a procedure generally yielding reliable SDMs (Barbet-Massin et al., 2012). Random selection of pseudo-absences is the best strategy when using regression techniques (e.g. GLM) and yields good models when using classification and machine-learning techniques (e.g. RF, BRT) (Barbet-Massin et al., 2012). We calibrated the models 10 times using randomly selected 70% of the data and validated against the remaining 30% based on cross-validation. We evaluated the predictive accuracy of the different SDM algorithms using four statistics (Table S5): the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), sensitivity and specificity. We computed an ensemble forecast, built for each species using models with a AUC score greater than 0.7, weighted by their AUC to increase prediction accuracy and to overcome prediction uncertainty from individual modelling techniques (Marmion et al., 2009).

We computed variable importances for each species-specific ensemble model to determine the most influential environmental factors, using the internal procedure of 'biomod2'. This methodology applies Pearson correlation between the standard predictions (i.e. fitted values) and predictions where the variable under investigation has been randomly permuted. If the correlation is high (i.e. small difference between both predictions), a variable is considered less important for the model (Thuiller et al., 2009). Variable importance ranges from 0 to 1, with higher values indicating greater importance of a predictor. As the variable 'basin ID' could potentially mask effects of other environmental predictors, we additionally computed all the SDMs without considering 'basin ID' to compare results. Models including 'basin ID' resulted in similar importance of the other variables but generally higher predictive accuracy (see Appendix S3). Therefore, we decided to base all subsequent analyses on the set of SDMs including 'basin ID' as predictor variable.

To test for differences in variable importance of predictors and AUC of models among primary, secondary and peripheral native and alien fish species we used PERMANOVA. We used univariate PERMANOVAs to analyse differences of variable importance of predictors and AUC in native status and Darlington's divisions and its interaction, and a multivariate PERMANOVA including all predictor variable importances. We used 999 permutations and Euclidean distances for the PERMANOVA. We also tested for homogeneity of dispersions for the different predictors among groups using the function 'betadisper' of the R-package 'vegan'.

To explore the importance of specific environmental variables in determining the distribution of different traits of inland fish (see e.g. Magadzire et al., 2019), variable importances obtained from our SDMs were subjected to a redundancy analysis (RDA) (Legendre & Legendre, 2012), using the 'rda' function of the R-package 'vegan'. This technique extracts and summarizes the variation in a set of response variables (i.e. variable importances) that can be explained by a group of explanatory variables (i.e. fish traits). We used 'arcsin' transformation for response variables to ameliorate linearity and normality. We assessed the significance for each term using permutation tests (999 permutations). As the trait dataset contained missing data, we imputed the 2.6% of missing values to avoid potential drawbacks of analyses that omit these cases (Nakagawa & Freckleton, 2008), and because it allowed us to increase the overall number of species with complete data by 29.4%. We used the 'imputeFAMD' function of the R-package 'missMDA', which allows the imputation of missing values of mixed datasets comprising of continuous and categorical variables. We used five components to predict the missing entries as estimated using the 'estim_ncpFAMD' function. We then computed two analyses of variance (ANOVA) to analyse how the scores of the two first axis varied among native status and Darlington's divisions and its interaction. As a complementary approach (de Bello et al., 2015), to account for the non-independence of trait data among species due to phylogenetic relatedness (Felsenstein, 1985), we also performed a principal components analysis (PCA) on the variable importance dataset to extract synthetic axes, and then we related

the first two axes to the set of species traits using phylogenetic generalized least squares (PGLS), using the 'pgls' function of the 'caper' package (Orme et al., 2018). The maximum likelihood estimate of λ was incorporated as a parameter in the PGLS model, thus controlling for phylogenetic dependence in the data in a manner that is optimal for the dataset (Freckleton et al., 2002). The phylogenetic tree of the studied species was obtained from a recent ray-finned fishes phylogeny (Rabosky et al., 2018), using the function 'fishtree_phylogeny' of the R-package 'Fish Tree' (Chang et al., 2019). All statistical and modelling tasks were performed with the software R, version 3.5.1 (R Core Team, 2020).

3 | RESULTS

We found that actual distributions of fish (as mapped in current fish atlases) varied between native and alien species (PERMANOVA, $R^2 = 0.023$; $P = 0.007$), but especially among the three Darlington's divisions ($R^2 = 0.065$; $P = 0.001$). Although the similarity of species distributions was generally very low (different species are often found in different basins; see Appendix S4), secondary and peripheral species are more similar in their distributions (mean $J = 0.056$) compared to primary species ($J = 0.030$ with secondary and 0.026 with peripheral).

For all species ensemble models, average cross-validated AUC scores were high (ranging from 0.856 to 0.990 with a mean value of 0.945, Table S5) but varied among Darlington's divisions (PERMANOVA, $R^2 = 0.115$; $P = 0.014$), between native and alien species ($R^2 = 0.049$; $P = 0.045$), and with significant interaction between Darlington's divisions and native status ($R^2 = 0.108$; $P = 0.022$). AUC were lower for alien than for native species and particularly higher for native primary fish (Figure S2). High values of TSS ranging from 0.604 to 0.977 with a mean value of 0.829 also indicated good performance of the models (Table S5). High specificity (ranging from 81.4 to 98.9 with a mean value of 91.8) and sensitivity (ranging from 78.9 to 99.1 with a mean value of 91.3) of the models pointed to a great proportion of correctly predicted background points and presences, respectively (Table S5). Projected SDM maps for the 68 inland fish in the Iberian Peninsula are provided in Appendix S4.

In general, climatic and topographic predictors were more important than land use and anthropogenic predictors (Figure S3). However, multivariate PERMANOVA revealed significant differences in the importance of predictors explaining the distributions of native vs. alien species and even larger differences among Darlington's divisions (25 and 6.5% of explained variation, respectively), with no clear interactions or differences in dispersions (Figure 2 and Table 1). Specifically, 'basin ID' was the most important predictor across species (Figure S3) but showed marked differences in variable importance among Darlington's divisions. It was particularly important for primary species (mean = 0.429; SD = 0.244), but less important for secondary (mean = 0.292; SD = 0.253) and peripheral species (mean = 0.210; SD = 0.151; Figure 2b). 'Basin ID' was the most important variable for many

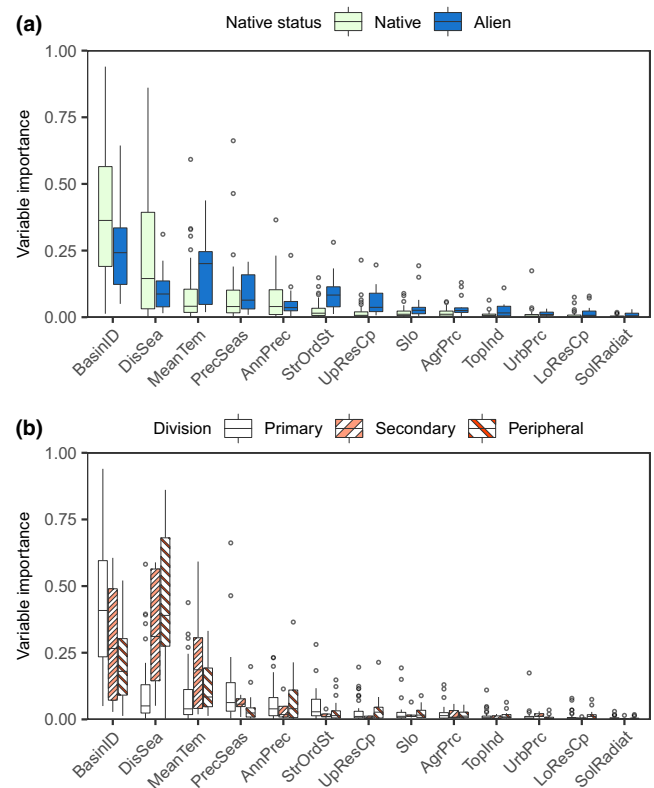


FIGURE 2 Importance of the different predictor variables used in the species distribution models (a) across native status (i.e. alien vs. native) and (b) Darlington's divisions of inland fish (i.e. primary, secondary and peripheral). Boxes correspond to the 25th and 75th percentiles; lines inside a box show the median; whiskers extend to the last observation within 1.5 times the interquartile range from the quartiles and outliers are indicated by empty circles. Predictor variable abbreviations are defined in Table 1.

endemic species (Figure 3a) and those alien species that are present yet in a few specific basins (Figure S4). Overall, 'distance to the sea' was the second most important variable in our models (Figure S3). It was the most important variable for several peripheral (mean = 0.452; SD = 0.268) and secondary (mean = 0.401; SD = 0.304) native species present in estuaries or coastal lagoons (Figures 2, 3b and S5) where it was negatively related to their occurrence probability. 'Annual mean temperature' was overall the second most important variable for alien species (mean = 0.174; SD = 0.122; Figure 2a). Its importance was significantly greater than for native fish (mean = 0.086; SD = 0.113). With increasing temperatures, the occurrence probability was increasing for 15 out of the 17 alien species studied (Figure S6). Conversely, increasing temperatures were associated with decreasing occurrence probability of some native fish, such as *Salmo trutta* (Figure 3c) or *Achondrostoma arcasii*. The importance of 'annual mean temperature' was also higher for secondary species than for peripheral and primary fish (Figure 2b).

'Upstream reservoir capacity' was overall the sixth most important variable (Figure S3). Its variable importance differed among the three Darlington's divisions studied but mainly between native and

TABLE 1 Results of the PERMANOVA and homogeneity of dispersions analysis across native status (NS) and Darlington's fish divisions (D)

Response Variable	PERMANOVA										Homogeneity Of dispersions P
	NS	D	NS×D	Residuals	Mean effect						
					PrN	SeN	PeN	PrA	SeA	PeA	
All	0.064 **	0.242 ***	0.031	0.661	NA	NA	NA	NA	NA	NA	0.324
Basin ID	0.038	0.228 ***	0.028	0.705	NA	NA	NA	NA	NA	NA	0.150
DisSea	0.082 **	0.368 ***	0.027	0.523	+	-	-	+	-	+	0.032
MeanTem	0.101 **	0.116 *	0.062 .	0.721	-	+	+	+	+	-	0.017
PrecSeas	0.006	0.075	0.037	0.881	-	+	+	-	+	-	0.183
AnnPrec	0.007	0.014	0.010	0.969	-	-	+	-	-	+	0.383
StrOrdSt	0.280 ***	0.041	0.018	0.660	+	+	+	+	+	+	0.144
UpResCp	0.196 ***	0.081 *	0.054	0.669	+	+	+	+	+	-	0.037
Slo	0.114 *	0.020	0.003	0.863	-	-	-	-	-	+	0.211
AgrPrc	0.159 **	0.001	0.031	0.809	+	+	-	+	+	-	0.139
TopInd	0.151 **	0.040	0.013	0.796	+	+	+	+	+	+	0.101
UrbPrc	0.003	0.008	0.015	0.975	-	+	+	+	+	-	0.950
LoResCp	0.084 *	0.087 *	0.048	0.781	+	-	-	+	+	-	0.050
SolRadiat	0.173 **	0.015	0.010	0.802	+	+	-	+	+	-	0.183

Note: Coefficients of determination (R^2) and positive/negative mean effects for the six groups are shown for PERMANOVA. P values for PERMANOVA are expressed with asterisks (***) ≤ 0.001 ; ** ≤ 0.01 ; * ≤ 0.05 ; . ≤ 0.1). P values are also shown for homogeneity of dispersions analysis.

Abbreviations: AgrPrc, average agricultural land use with a given sub-catchment; AnnPrec, average annual precipitation within sub-catchment; DisSea, distance to the sea; LoResCp, local reservoir capacity; MeanTem, annual mean temperature; NA, not applicable; PeA, peripheral alien species; PeN, peripheral native species; PrN, primary native species; PrA, primary alien species; PrecSeas, average precipitation seasonality within sub-catchment; SeA, secondary alien species; SeN, secondary native species; Slo, slope; SolRadiat, solar radiation; StrOrdSt, Strahler stream order; TopInd, topographic index; UpResCp, upstream reservoir capacity; UrbPrc, average urban land use within a given sub-catchment.

alien fish. 'Upstream reservoir capacity' variable importance was significantly greater for alien and peripheral fish (Figure 2). Analysis of homogeneity of dispersions showed also that the dispersion across groups was not homogeneous (Table 1). Specifically, alien species showed greater variability in the importance of the 'upstream reservoir capacity' (mean = 0.064; SD = 0.053) than native ones (mean = 0.020; SD = 0.033). This variable was especially important and positively related with the occurrence of several alien species like *Silurus glanis*, *Esox lucius* or *Cyprinus carpio* (Figures 3d and S7). 'Upstream reservoir capacity' was negatively but less markedly related with the occurrence of 12 out of the 29 primary native species studied. Moreover, SDMs revealed a positive relationship between 'upstream reservoir capacity' and the occurrence of peripheral native species. By contrast, the mean effect of 'local reservoir capacity' on this group of species was negative. Finally, the variables 'slope', 'topographic index' and 'solar radiation', or those related to anthropogenic disturbance, such as percentage of 'agricultural' or 'urban' land use were, in general, much less important predictors of fish species distribution at the scale of the Iberian Peninsula.

RDA revealed that 35.3% of the variation in variable importance can be explained by differences between fish traits ($F_{16,51} = 1.737$, $P = 0.001$). Species whose distributions were highly sensitive to 'annual mean temperature', 'stream order', 'upstream reservoir capacity' and 'slope' were mainly characterized by being tolerant and

larger-bodied species (Figure 4). Moreover, many of these species were alien fish (Figure S8). Primary native species, whose distributions were particularly conditioned by 'basin ID', were mainly rheophilic, invertivory and potamodromous (Figure 4). RDA indicated that most peripheral species are diadromous and larger-bodied species (Table S2). The ANOVA results showed that the scores of the first axis (i.e. RDA1) varied among Darlington's divisions ($F_{2,62} = 15.1$; $P < 0.001$), between native and alien species ($F_{1,62} = 43.3$; $P < 0.001$), and with significant interaction between Darlington's divisions and native status ($F_{2,62} = 3.3$; $P = 0.042$; Figure S9). The ANOVA of the second axis did not show clear differences among Darlington's divisions nor between native and alien fish.

The PCA explained 40.3% of the variable importance variation with two axes (Figure S10). The first PCA axis identified a dominant gradient of variable importances that contrasts species whose distribution is mainly constrained by river basin boundaries with species whose distribution is more influenced by climatic and anthropogenic factors (e.g. precipitation, temperature and human impacts). The second axis contrasts species whose distribution is affected by the continentality (i.e. species that occur in coastal areas vs. species that occur in the interior of the Iberian Peninsula). In contrast to the results of the RDA, PGLS only showed a positive relationship between omnivory and the first axis of the PCA (estimate = 2.534, $t = 3.240$, $P = 0.002$; Table S6).

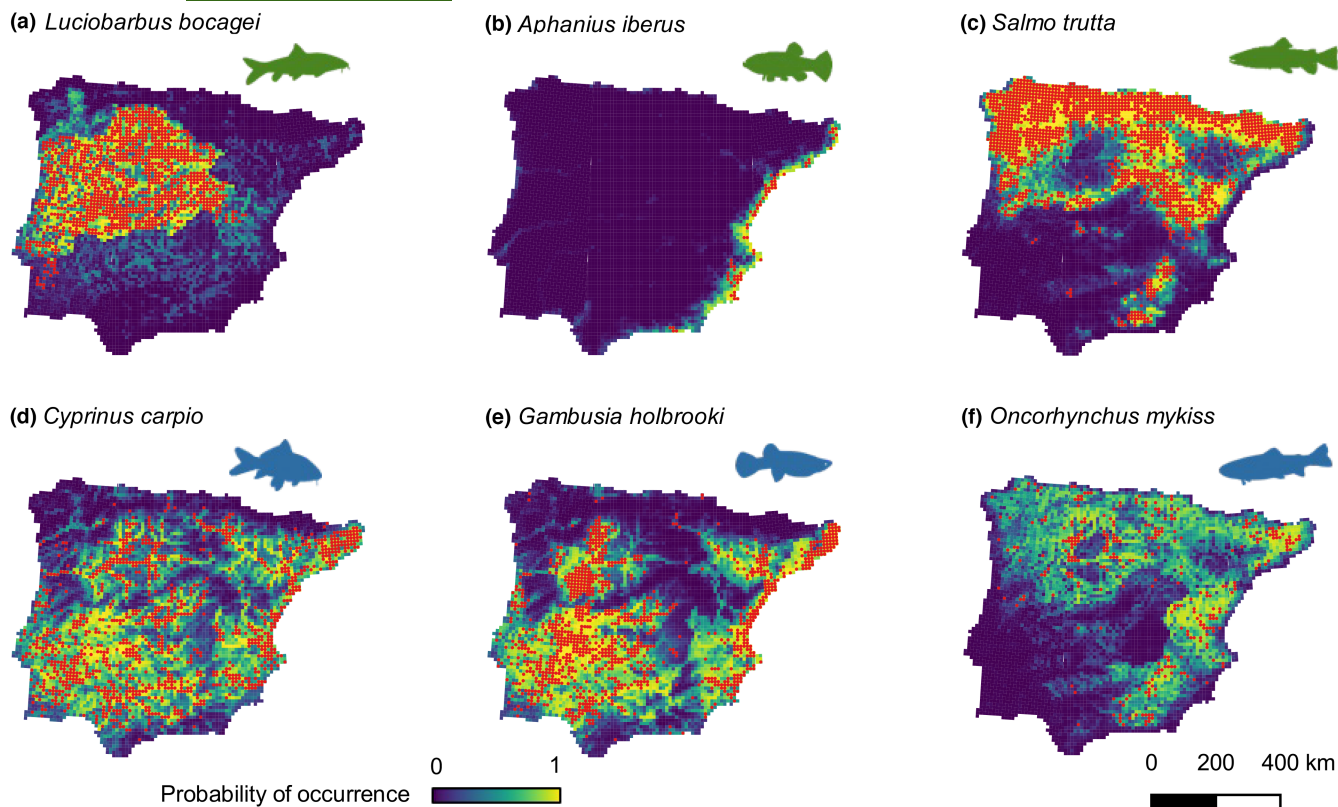


FIGURE 3 Projected species distribution models maps for six paradigmatic inland fish species in the Iberian Peninsula. Upper panels with green silhouettes show native species; lower panels with blue silhouettes show alien species. Red points correspond to species occurrences. Pri = primary; Sec = secondary; Per = peripheral. Projection: WGS 84/Pseudo-Mercator—EPSG:3857. Silhouettes were obtained from <http://phylopic.org/>.

4 | DISCUSSION

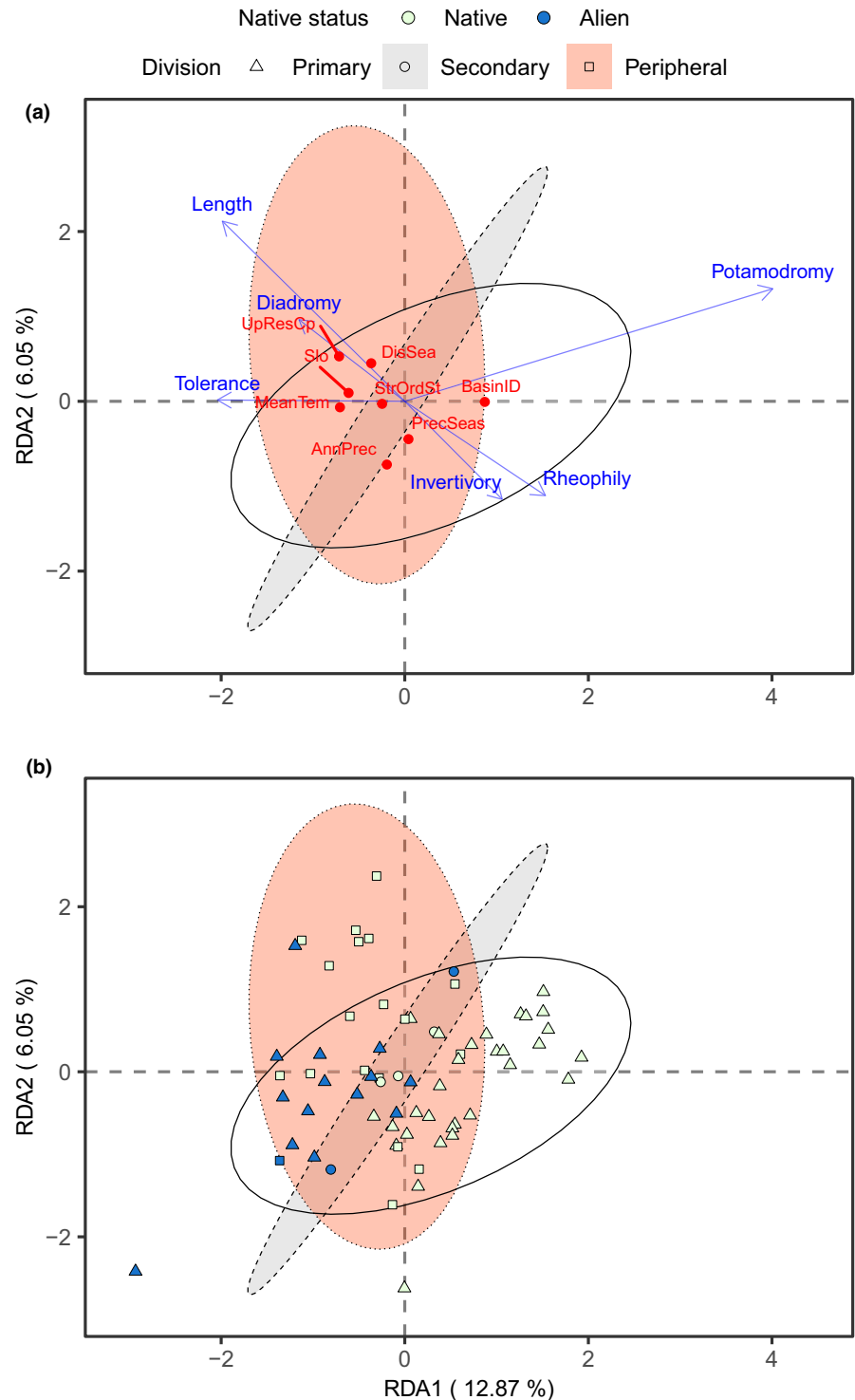
Our results showed that regardless of differences in the distribution patterns between native and alien species, evolutionary and introduction histories as well as seawater tolerance are central factors explaining the current distribution of Iberian inland fishes. For instance, we found that secondary species have a more similar distribution to peripheral than to primary species. The distribution of *Fundulus heteroclitus* in the Atlantic coast of North America or in southwestern Iberia (where it was introduced and dispersed to different river estuaries) and *Aphanius spp.* along Mediterranean salt marshes exemplifies that despite the likely absence of long-distance movements through salt waters in modern times (Moyle & Cech, 2004), the distribution patterns of such secondary species are very different from primary fishes, which are often confined to a few river basins.

Hence, our hypothesis that primary, secondary and peripheral fish species would generally show contrasting importance of different climatic, topographic and anthropogenic predictors in explaining their distribution was supported by our results. Results revealed marked and clear differences between the eco-evolutionary groups suggested by Darlington (1948), which were even more pronounced than differences between native and alien species. More specifically, our results showed that 'basin ID' was the most important variable for primary native species, suggesting that these species are

confined to their particular and potentially isolated drainage systems and that any migration to other basins might (naturally) only be enabled by slow geological processes (e.g. river captures or changes in sea level) (Myers, 1938). For example, native *Squalius* and *Luciobarbus* genera as well as other native cyprinids have experienced extensive speciation processes in the Iberian Peninsula after the formation of the different basins and geographical barriers (Doadrio et al., 2011). Correspondingly, a recent study investigating global fish distributions revealed that the historical connection among river basins during Quaternary low sea-level periods constitutes a good predictor explaining range sizes in freshwater fishes (Carvajal-Quintero et al., 2019). Although its effect is not as remarkable as for primary native species, 'basin ID' was also the most important variable for several alien species such as *Australoheros facetus*, mostly present in the Guadiana basin (Hermoso et al., 2008); and *Scardinius erythrophthalmus*, whose distribution is mainly restricted to the basins of the Ebro and Eastern Pyrenees (Doadrio, 2001). By contrast, 'basin ID' was much less important for peripheral fish, as their geographical ranges are not necessarily restricted by the sea given their ability to migrate, or disperse through seawater (McDowall, 2010) and thereby enter and colonize other river catchments.

In accordance with our hypothesis and previous studies (Murphy et al., 2015), temperature was found to be a key environmental variable for explaining the distribution of alien species. This further

FIGURE 4 (a) Correlation biplot based on redundancy analysis (RDA) of variable importance of the different environmental predictors used in the species distribution models. Species traits are shown as blue arrows. For clarity, only significant and marginally significant traits ($P < 0.10$, see Table S5 for further information) and 8 most important environmental variables in species distribution models are shown. Predictor variable abbreviations are defined in Table 1. Note that continuous traits (e.g. fish maximum length) were previously \log_{10} -transformed. (b) Individual plot where each dot represents one species. Light green shows native species, while dark blue shows alien species. 95% confidence ellipses are shown for primary (white), secondary (grey) and peripheral (light red) fish.



emphasizes the thermophilic character of many alien species (e.g. *Gambusia holbrooki*), with higher temperatures favouring their reproduction and competitive capacity (Carmona-Catot et al., 2013). Climate change models for the Iberian Peninsula predict temperature increases, most pronounced during the summer months, and changes in precipitation with increased variability over the year (Álvarez Cobelas et al., 2005). Warmer temperatures and reduced flows could create novel suitable habitats for introduced

species in future, thereby facilitating their establishment and invasion (Carmona-Catot et al., 2013). 'Annual mean temperature' also showed an important effect on several secondary species that are also thermophilic such as the native *Aphanius baeticus* and *Valencia hispanica*. Some native species showed considerable negative effects of temperature on their geographical distributions. This includes, for example, *S. trutta*, a well-known cold-water species that is mainly distributed through the north of the Peninsula and in mountain

ranges (Elliott & Elliott, 2010). Thus, climate change could produce severe impacts on both taxonomic and functional components of the native ichthyofauna (de Oliveira et al., 2019).

Results indicated that topographical and climatic variables were more influential drivers of the distributions of Iberian inland fishes than anthropogenic factors. In agreement with previous studies (Bae et al., 2018), variables such as 'agricultural' and 'urban land uses' had little effect on fish distribution at the spatial scale of the Iberian Peninsula. This contrasts with other previous studies, which found land use an important driver of fish distributions in large river catchments (Radinger et al., 2016; Radinger et al., 2019). This disagreement may result from the different spatial scales considered and because climatic predictors are often more important especially at larger spatial scales (Guisan & Thuiller, 2005).

'Local reservoir capacity', which indicates the presence and size of local reservoirs, was also of less importance for explaining fish distributions in our study. This partly contrasts with previous studies describing local reservoirs as an important predictor of the distribution of some alien species (e.g. *Micropterus salmoides*) that dominate Iberian reservoirs, and whose presence can be explained by altered environmental conditions and increased propagule pressure (Johnson et al., 2008). Surprisingly, the observed importance of dams in explaining native fish distributions was relatively low compared to topographical and climatic variables. We found a negative effect of 'local reservoir capacity' on peripheral fish distribution. As migratory and estuarine species cannot pass river barriers, their presence is negatively associated with reservoirs. It is well documented that dams and other river barriers have greatly reduced the range sizes and spawning areas of many anadromous species. In the Iberian Peninsula, anadromous species lost up to 80% of habitats in many river basins (Mateus et al., 2012). Nevertheless, the variable 'upstream reservoir capacity', which describes the degree of modification of the natural flow regime and other ecological features resulting from upstream impoundment, was the most important anthropogenic factor, especially related to the distributions of alien and peripheral species. This might point to the importance of cumulative effects of dams on fish distributions which might differ from local impacts of single reservoirs.

Our results agree with previous studies, which have indicated that dams and their associated alteration are likely to favour alien fish (Radinger et al., 2019). The greater importance of 'upstream reservoir capacity' than 'local reservoir capacity' for alien species might indicate that the presence of these fish is not only associated to the reservoir itself—which is often considered a site of high propagule pressure of alien species—but rather to the regulated river reaches that are severely hydrologically altered. Moreover, the RDA showed that alien species are mainly tolerant fish with rather large flexibility in their requirements regarding water quality and habitats, and are larger-bodied than primary native species. These traits were mainly related to the variable importance of 'mean annual temperature' and 'upstream reservoir capacity'. Our results agree with previous studies of the Iberian Peninsula (Vila-Gispert et al., 2005) showing that alien species correspond well to the periodic life-history strategy defined

by Winemiller and Rose (1992): alien fish represent large-sized species with long longevity, late maturity, high fecundity, few spawning bouts per year and short reproductive span. However, traits of many alien fishes result from human selection of species with particular desirable features such as large body-size (e.g. game and commercial fishes) or wide ecological tolerance to ensure successful establishment (Alcaraz et al., 2005; Grabowska & Przybylski, 2015). In contrast, primary native fish show more opportunistic traits, that is, they show early maturation, frequent reproduction over an extended spawning season, rapid larval growth and rapid population growth rates. By altering environmental conditions and reducing flow variability with the construction of barriers and dams, the introduction of alien fish from seasonal habitats (central European and southeastern North American streams) that are more hydrologically stable has been favoured (Vila-Gispert et al., 2005). The disagreement observed between the results of the RDA and the results after accounting for phylogenetic relatedness among species (i.e. PGLS) could be due to the absence of an evolutionary relationship between the distributional drivers considered in this study and fish traits.

The weaker performance of the SDMs of alien species as indicated by lower AUC values might reflect that they have not yet fully realized their distributions in the Iberian Peninsula. For example, some alien species have only been found in single drainage basins, which does not mean that environmental conditions in other basins are unsuitable for future colonization. Therefore, their current distributions are also much influenced by their introduction histories and basin boundaries. Nevertheless, SDMs constitute a valuable tool to identify those regions which are particularly vulnerable to the establishment of invasive alien species (Perrin et al., 2021).

Although Darlington's classification has received some criticism (Rosen, 1974; Sparks & Smith, 2005), it is widely applied and well related to experimental seawater tolerance (see Appendix S1). Our results showed that it is a useful classification system to address ecological and biogeographical questions as the species of the same division are generally closer in their distribution patterns. The scarcity of quantitative data on seawater tolerance of many fish species makes this classification a helpful proxy. We also note that there are some limitations that might have affected our modelling results, related to both methodological issues and uncertainties associated with observational data. For instance, the variables upstream and local reservoir capacity explained much of the shifts below dams in flood magnitude and mean monthly flow, but not changes in annual runoff or median daily flows (Batalla et al., 2004), as the effect of a reservoir depends not only on its capacity, but also on its operation. Thus, these metrics only represent a portion of the potential hydrologic alterations that rivers suffer. Finally, the dendritic structure of river networks has been frequently argued against the use of species atlas grid-based data for modelling freshwater fish distributions. However, SDMs based on grid could also show high predictive performance and are a good alternative in those cases where stream network-related data are not available (Markovic et al., 2012).

In summary, our results shed light on a central topic in fish biogeography and reveal the main variables that shape the distribution

patterns of Iberian inland fishes. Specifically, we found that topographic and climatic predictors are more important than land use and anthropogenic variables in explaining fish distributions. Native and alien species showed marked differences in the importance of factors explaining their distribution. Thus, our results are an important contribution to the prioritization in alien species management and to identify the areas that might become invaded. Particularly, the marked differences among Darlington's divisions reflect that this eco-evolutionary classification is strongly related to environmental variables driving species distributions, with species of the same division generally showing analogous distribution patterns. This further leads to the conclusion that different tolerances to salinity of the three divisions studied and possibly associated factors largely influence the current distribution of inland fish at larger scale.

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CONFLICT OF INTEREST

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

Species occurrence, environmental data, variable importance results and scripts underlying our analyses are available via figshare (DOI: <https://doi.org/10.6084/m9.figshare.12696428.v1>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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