Environmental filtering governs the spatial distribution of alien fishes in a large, human-impacted Mediterranean river

Johannes Radinger¹,² | Juan Diego Alcaraz-Hernández¹ | Emili García-Berthou¹

¹GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Spain
²Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

Correspondence
Johannes Radinger, GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Spain.
Email: johannes.radinger@udg.edu

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Abstract

Aim: To analyse the occurrence and abundance of native versus alien fish species in relation to climate, land use, hydrologic alteration and habitat fragmentation in a heavily invaded and human-impacted riverine ecosystem. To test whether co-occurrence patterns of native versus alien species are structured by environmental filtering or biotic associations.

Location: Mediterranean, Iberian Peninsula, Ebro River catchment.

Methods: We modelled freshwater fish distributions and their association with environmental conditions using a hurdle model-like approach involving boosted regression trees. Additionally, we applied a joint species distribution model to quantify the co-occurrence of native versus alien fish species that can be attributed to shared environmental responses or potentially to biotic interactions.

Results: Our results point to environmental factors, rather than biotic associations, as major correlates of the increase of alien and the decline of native fishes in the Ebro River. We observed contrasting patterns of native versus alien species along the upstream-downstream gradient. Alien species dominated in the lower reaches associated with warmer temperatures, higher shares of intensive land use and appeared facilitated by dams and river regulation. Native species richness was highest in the larger tributaries followed by a strong decline in the main stem which was related to the river network position and land use type. Fragmentation played a subordinate role in explaining fish richness and abundance patterns.

Main conclusions: Given the strong association with temperature, a further range expansion of alien fishes in the Ebro with future climate change may be expected. More local-scale factors related to habitat degradation and hydrologic alteration will further exacerbate the invasion success of many alien fishes. Further multiple, independent species introductions might mask isolation and fragmentation effects of dams on the future spread and distribution of alien fish.

KEYWORDS
boosted regression trees, Ebro River, environmental filtering, freshwater fish, habitat degradation, invasive alien species, joint species distribution model, native species decline, species co-occurrence
1 | INTRODUCTION

Understanding species distribution patterns and causes of species co-occurrence is a major focus in ecology. A variety of factors, most prominently including abiotic environmental conditions and biotic interactions, are considered to determine where species occur at larger spatial scales, and why (Hutchinson, 1957; Kissling et al., 2012; Pollock et al., 2014). This topic is also a fundamental question in invasion ecology, in order to understand the proliferation of alien species and the often simultaneous decline of many native species and to implement suitable management measures. Whether introduced species colonize a certain habitat depends on the number of individuals introduced (i.e., propagule pressure, Lockwood, Cassey, & Blackburn, 2005, 2009), is driven by environmental filters, such as climate, that determine if propagules can survive (Theoharides & Dukes, 2007), and might be further limited by the dispersal abilities of species (e.g., Radinger & Wolter, 2015; Radinger et al., 2017; Stoll, Sundermann, Lorenz, Kail, & Haase, 2013). The subsequent establishment of a species might also be mediated by biotic interactions, such as competition or predation that affect population growth (Theoharides & Dukes, 2007). Particularly in a changing world, it is of great interest whether alien species are the direct drivers of the loss of native species through biotic interactions, or the passengers of decline caused by environmental change (e.g., habitat degradation) (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; Didham, Tylianakis, Hutchison, Ewers, & Gemmell, 2005; Hermoso, Clavero, Blanco-Garrido, & Prenda, 2011; MacDougall & Turkington, 2005). For example, Hermoso et al. (2011) and Light and Marchetti (2007) identified alien species as the primary driver of the decline of natives. However, many other examples revealed environmental change as a leading cause of native species loss irrespective of the presence of alien species (e.g., Kominoski et al., 2018; MacDougall & Turkington, 2005). Both aspects are not mutually exclusive and there is increasing evidence that environmental degradation and invasive species interact and jointly govern biodiversity loss and the decline of many native species (Didham et al., 2007). For example, environmental change causing a loss of refugia habitats might enhance the predation risk of invasive on native species (Didham et al., 2007; Hermoso et al., 2011). Identifying the leading causes of native species decline and the underlying processes related to the driver versus passenger hypotheses has major implications for environmental management. For example, invasive species eradication might be inefficient and unrewarded if native species loss is merely a result of environmental degradation and alien species have no effect on the decline of native species (Zavala, Hobb, & Mooney, 2001). The complex interactions of abiotic and biotic determinants of species co-occurrence have also been reflected in the recent development and increasing application of so-called joint species distribution models (JSDM), which aim to discern whether larger-scale patterns of species co-occurrences can be attributed to similar environmental responses or biotic associations (D’Amen, Mod, Gotelli, & Guisan, 2018; Kissling et al., 2012; Pollock et al., 2014).

Mediterranean fresh waters are among the most heavily invaded ecosystems (Leprieur, Beauchard, Blanchet, & Oberdorff, 2008; Marr et al., 2013). Many freshwater species have been introduced in the Iberian Peninsula over the last century. While about 51 freshwater fish species are considered native in the Iberian Peninsula (excluding 10 diadromous species), over 26 alien fish species have successfully established, whereof 12 can be considered invasive, that is have spread (Doadrio, Perea, Garzón-Heydt, & González, 2011; Fauch & García-Berthou, 2013). Concurrent with the invasion by many alien fishes, the native fish fauna of the Iberian Peninsula, rich in endemics, has been substantially declining, with recent data suggesting that 49 (96%) of the native species being considered imperilled (Doadrio et al., 2011). Many riverine species native to the Iberian Peninsula are considered well adapted to the natural, Mediterranean climatic and hydrologic regimes, characterized by marked floods and droughts (Gasith & Resh, 1999). Consequently, anthropogenic impacts including habitat degradation, river regulation, water pollution and land use are considered major threats to the native fish fauna (Almeida, Alcaraz-Hernández, Merciai, Benejam, & García-Berthou, 2017; Benejam et al., 2015; Maceda-veiga, 2013; Santiago et al., 2016), are associated with community shifts and dominance in abundance of alien species (Aparicio, Vargas, Olmo, & Sostoa, 2000; Sommerwerk, Wolter, Freyhof, & Tockner, 2017) and might lead to marked changes in functional diversity (Colin, Villégér, Wilkes, Sostoa, & Maceda-veiga, 2018; Toussaint et al., 2018). In addition, climate change is considered a major threat to many, particularly endemic, fishes in the Mediterranean region (Jarić, Lennox, Kalinkat, Cvijanić, & Radinger, 2018; Maceda-veiga, 2013) and might facilitate the spread of alien species (e.g., Murphy, Grenouillet, & García-Berthou, 2015). The specific role of anthropogenic barriers such as dams and weirs in this context is less known but generally considered equivocal. In general, barriers negatively impact many native fishes, especially those that routinely migrate to the sea or within the river network or those that are intolerant to habitat degradation and alterations of the natural flow regime (Aparicio et al., 2000; Benejam et al., 2016). Barriers might prevent alien species from spreading within the river network, particularly upstream (Fauch, Rieman, Dunham, Young, & Peterson, 2009; Frings et al., 2013), but also facilitate the introduction, establishment and spread of alien species through the lentic impoundments that they create (Johnson, Olden, & Vander Zanden, 2008; Liew, Tan, & Yeo, 2016).

The specific environmental and biotic factors that shape the decline of native species and invasions by alien fishes of Mediterranean streams and rivers are unclear. Therefore, the main objectives of this study are (a) to analyse how the occurrence and abundance of alien fish species in the Ebro River are related to environmental variables describing climate, land use, hydrologic alteration, habitat fragmentation and river topography; and (b) to test whether co-occurrence patterns of native versus alien species are structured by environmental filtering or biotic associations using JSDM, which have been barely used for fish before. We hypothesized that: (a) as most introduced fishes in the Ebro River are warm-water species (Alcaraz, Vila-Gispert, & García-Berthou, 2005), the colonization of river habitats by alien species would be limited by temperature-related climate variables; (b) larger-scale variables
(e.g., climate, topology) would determine the general occurrence patterns and range limits of alien species, whereas more local-scale, habitat-related variables (e.g., hydrologic alteration) might determine their species richness and abundance; and (c) a combination of abiotic and biotic factors might structure both native and alien species occurrences.

2 | METHODS

2.1 | Study area and environmental variables

The study was conducted in the Ebro River basin, NE Spain, a large European river basin with a total catchment area of about 86,000 km² (Supporting Information Figure S1.1). The Ebro River flows from the Cantabrian and Pyrenean ranges to the Mediterranean Sea and discharges on average 452 m³/s at its mouth (Radinger, Alcaraz-Hernández, & García-Berthou, 2018). Climatic conditions and associated patterns of temperature and precipitation within the basin are very diverse with mean annual temperatures ranging from 0.8 to 16.2 °C and mean annual precipitation from >1,500 mm in the Pyrenees (with elevations >3,000 m a.s.l.) to <400 mm in the semi-arid interior (see e.g., Radinger, Alcaraz-Hernández, et al., 2018).

Land use is dominated by agriculture and the catchment is heavily regulated by about 300 large reservoirs and over 2100 smaller-sized weirs, with the largest densities of dams especially in the central and upper reaches (Supporting Information Figure S1.1). The native fish communities are dominated by Iberian endemic cyprinid species including Bermejuela (Achondrostoma arcsai), Iberian redfin barbel (Barbus haasi), Pyrenean gudgeon (Gobio lozanoi), Ebro barbel (Luciobarbus graellsi), Ebro nase (Parachondrostoma miegii), Pyrenean minnow (Phoxinus bigerri) and Ebro chub (Squalius laietanus). Many introduced species such as bleak (Alburnus alburnus), common carp (Cyprinus carpio) and Wels catfish (Silurus glanis) are increasingly dominant in the lower main stem reaches of Ebro River (Almeida et al., 2017).

The river network used in subsequent analyses was obtained from the official hydrographic network (CHE, Confederación Hidrográfica del Ebro, http://iber.chebro.es/geportal/) at a spatial scale of 1:50,000 and was partly complemented for some smaller tributaries from a river network at the 1:25,000 scale. In the following, we refer to the main stem and lower main stem as reaches with catchment size >10³ and >10⁴ km², respectively. Calculations of catchment characteristics were based on a European digital elevation model (EU-DEM version 1.1, https://land.copernicus.eu/pan-european/satellite-derived-products/ eu-dem/ue-dem-v1.1/) at a spatial resolution of 50 × 50 m. As environmental predictors for all further analyses, we used 24 uncorrelated variables (|r| < 0.7; Dormann et al., 2013) related to topography, climate, land use, hydrologic alteration and network connectivity/fragmentation (Supporting Information Table S1.1). Details on the calculation and selection of specific explanatory environmental variables are provided in the Supporting Information Appendix S1.

2.2 | Fish data compilation

We collated a dataset of 614 samplings of the fish community in the Ebro River and its tributaries carried out between 1992 and 2015 (with >80% of the samples taken between 2002 and 2006, see Supporting Information Figure S2.3) provided by the CHE and the former Spanish Ministry of Agriculture and Fisheries, Food and Environment (MAPAMA). Sites were sampled only once and the fish sampling dataset constitutes an aggregation over multiple years, that is we did not consider temporal changes in fish communities. Fish sampling was conducted by electrofishing, either from boat or wading, with an average sampling length of 109 m (median = 99 m, IQR = 75–101 m) and an average sampled area of 760 m² (median = 581 m², IQR = 364–901 m²). Electrofishing, a standard method for sampling freshwater fish communities, is considered to capture highest numbers of species and represent well typical assemblages of streams and larger rivers (Zajicek & Wolter, 2018). Due to the high efficiency of electrofishing and spatial coverage and intensity of the fish sampling, we assume that species detection probability is high. From the 614 sampling sites, some sites were dry or not accessible due to high flows (n = 29) or had no fish captures (n = 63) and thus were excluded, leaving 522 samplings for further analyses (Supporting Information Table S2.2). For 394 samples, species abundance and the survey extent was recorded, while for the other samples only information on species presence was available. For further analyses, fish abundance data were standardized by the survey extent to catch per unit effort (CPUE, i.e., fish per 100 m fished length). For models based on occurrence-only information, the fish abundance data were transformed to presence/absence.

2.3 | Modelling framework

We modelled the richness of native and alien species and its association with environmental variables and the co-occurrence of native versus alien species using a combination of species distribution models: (a) a hurdle model-like approach involving boosted regression tree (BRT) models (Elith, Leathwick, & Hastie, 2008) to analyse which environmental variables are predominantly associated with the occurrence of alien species in the fish community; and (b) a joint species distribution model (JSDM; Pollock et al., 2014) to quantify the co-occurrence of (native and alien) fish species that can be attributed to shared environmental responses or to other ecological mechanisms such as biotic interactions.

2.3.1 | Modelling occurrence and relative abundance of alien fishes

We calculated BRT models using the package “dismo” (version 1.1-4, Hijmans, Phillips, Leathwick, & Elith, 2017) within the software R (version 3.4.3, R Core Team, 2017). BRT is a machine learning method that aggregates many simple single regression trees to a collective model of improved predictive performance (Elith et al., 2008). BRT models are considered to effectively select relevant
variables, identify variable interactions and avoid overfitting (Elith et al., 2008; Hastie, Tibshirani, & Friedman, 2009) and thus they are increasingly applied in ecology (Radinger et al., 2016; Radinger, Wolter, & Kail, 2015). Here, we applied a hurdle model-like (Zeileis, Kleiber, & Jackman, 2008) approach, that is a two-part model framework that specifies one model for the general occurrence of alien species and another for species richness. Specifically, we first used the full set of sampling sites (n = 522) to analyse which environmental variables best discriminate between sites inhabited by at least one alien species versus sites without alien species (i.e., occurrence of any alien species, O). Secondly, we focused on sites with at least one alien species (n = 187) and modelled the relationship between the environmental variables and the richness of native (S) and alien species (S) and the relative share of alien species (%S) and alien individuals within a sample (%I).

For modelling O, we applied a BRT model with a Bernoulli loss function (binomial model predicting presence vs. absence of any alien species); for S and S, we used a Poisson loss function; and for %S and %I, we considered a Laplace loss function that minimizes absolute errors. For each response variable, we fitted a BRT model including an automated stepwise variable selection (Radinger, Alcaraz-Hernández, et al., 2018; Radinger et al., 2016) and a 10-fold cross-validation. Cross-validation works by randomly splitting rows of the full dataset into K = 10 equally sized folds, repeatedly training the model on K – 1 folds and testing on the remaining fold. Tree complexity was set to 5 and learning rate to 0.0025 for all models to achieve the recommended number of more than 1,000 trees (Elith et al., 2008). To assess the model quality of the binomial O model, we calculated the mean and standard error (SE) of the AUC (area under the receiver operating characteristic curve) over all 10 folds. For the models of S, S, %S, and %I, we calculated the mean and SE of the correlation coefficient r between fitted and raw values. The relative importance (%VI) of each predictor variable in the final BRT model was quantified based on the number of times each variable was used for splitting, weighted by the squared improvement at each split and averaged over all trees (Elith et al., 2008; Radinger, Alcaraz-Hernández, et al., 2018).

2.3.2 Modelling the co-occurrence of native versus alien species

We applied a joint species distribution model (JSDM) to investigate our dataset for patterns of species co-occurrence with a specific focus on native versus alien species. JSDM quantify the leftover residual correlation (Rho) among multiple species after accounting for the correlation that can be attributed to shared environmental responses (EnvRho; Pollock et al., 2014; Warton et al., 2015). The basic idea of JDSM is that species that co-occur more frequently than expected given the environment (positive Rho) might either indicate some sort of dependence (e.g., facilitation) or may simply point to missing relevant environmental variables, while negative values of Rho may indicate some sort of negative species association (e.g., competitive exclusion; Pollock et al., 2014). Specifically, we fitted a JSDM using the code provided by Pollock et al. (2014), which is a hierarchical multivariate probit regression model that relates the environmental variables (Supporting Information Table S1.1) to a binary response variable (presence/absence) involving latent variables (Pollock et al., 2014). Further details on the JSDM are described in Pollock et al. (2014). The JSDM was fitted for the subset of the species with a minimum prevalence of 0.05 (>27 presence records in the 522 sampling sites; Supporting Information Table S2.2) using the Markov chain Monte Carlo (MCMC) algorithm from the software JAGS (version 4.3.0) via the R package “R2jags” (version 0.5-7, Su & Yajima, 2015). In total, we calculated five chains of 200,000 iterations with a burn-in of the first 50,000 iterations and a thinning rate of 20 to reach model convergence, retaining 7,500 samples for further analyses. Model convergence was informally assessed for all relevant parameters using diagnostic trace plots and the Gelman-Rubin convergence diagnostic (Gelman & Rubin, 1992). To avoid potential overfitting, we calculated a preliminary JSDM and excluded all environmental variables that were insignificant with a 95%-highest posterior density interval (HPDI) of the Beta coefficients including zero for all species in the final JSDM run. The JSDM yields two matrices, with the first providing pairwise environmental correlations, EnvRho, and the second providing pairwise residual correlation among species occurrences, Rho, after accounting for their shared environmental response (Bar-Massada & Belmaker, 2017). We calculated the median and the 95% HPDI of EnvRho and Rho from the posterior distributions of the environmental and residual correlation matrix. Correlations were considered significant when the HPDI did not include zero (Zurell, Pollock, & Thullier, 2018). We applied permutation tests (asymptotic general independence test; R package “coin,” version 1.2-2, Hothorn, Hornik, Wiel, & Zeileis, 2008) and pairwise permutation post hoc tests with a p-value adjustment that controls the false discovery rate (FDR, Hochberg & Benjamini, 1995; R package “companion,” version 1.11.1, Mangiafico, 2017) to test for differences in the distribution of the environmental and residual correlations among pairs of native and alien species.

3 RESULTS

3.1 Occurrence and relative abundance of alien species

Of the 522 fish community samples available, 187 had one or more alien species (Figure 1). The most frequent alien species in the Ebro basin were bleak (n = 113 presence records), common carp (n = 109) and Wels catfish (n = 42). By contrast, the three most frequent native species were Ebro barbel (n = 299), Ebro nase (n = 247) and Pyrenean gudgeon (n = 227), which are all endemic to the Iberian Peninsula. Along the upstream-downstream gradient native species richness was hump-shaped, with only a few native species inhabiting the headwaters, higher richness in the larger tributaries and upper main stem with catchment sizes up to about 10⁵ km² and followed by a strong decline in the lower main stem (Figure 2 and Supporting
Information Figure S3.4). In the most downstream reaches (downstream of the Flix dam, Supporting Information Figure S1.1), native species richness was increasing again. By contrast, alien species were only present in the lower main stem parts of the Ebro River (catchment >10,000 km²) and increased in downstream direction (Figures 1 and 2). The number and share of alien species per site was on average 0.78 species (range = 0–9, IQR = 1–5) and 16% (range = 0%–100%, IQR = 25%–0%), respectively. The number of native species was weakly positively correlated with the number of alien species (Spearman correlation, $r_s = 0.12$, $p < 0.01$, Figure 2). The share of individuals of alien species ($\%S_A^i$) on the total number of individuals was on average 16% (range = 0%–100%, IQR = 14%–0%)

The occurrence of alien fishes, $Q_A$, in the Ebro River could be modelled with high accuracy, as indicated by a cross-validation AUC of 0.90 (SE = 0.01, see Supporting Information Table S4.3). Ten out of 24 variables were selected as important in the final $Q_A$ model, that is discriminating between sites inhabited by at least one alien species versus sites without alien species while other predictor variables were less important and not selected (Table 1). Specifically, the size of the upstream catchment (44% VI) was the by far most influential variable (Figure 3), followed by the minimum temperature of the coldest month (9% VI) and arable land use (7% VI). Sites inhabited by alien species were generally located more downstream in the Ebro River main stem, had upstream catchments $>10^3$ km² (Figure 2), had a minimum temperature of the coldest month $>-0.5^\circ C$ and had larger shares of arable land use in their catchments.

The richness of native ($S_N^i$) and alien species ($S_A^i$) as well as the share of alien species ($\%S_A^i$) and alien individuals ($\%I_A^i$) could be modelled with moderate to good accuracy as indicated by the correlation between model-fitted and observed values ($S_N^i$: $r = 0.71$, SE = 0.04; $S_A^i$: $r = 0.65$, SE = 0.06; $\%S_A^i$: $r = 0.71$, SE = 0.04; $\%I_A^i$: $r = 0.70$, SE = 0.05, Supporting Information Table S4.3). The final models of $S_N^i$ and $S_A^i$ were less complex and selected 11 and 7 environmental variables, respectively, compared to the models of $\%S_A^i$ and $\%I_A^i$, which selected $\geq 19$ variables (Table 1).

The three most important variables related to the number of native species, $S_N^i$, were network closeness centrality (22.3% VI), forest land use (19.1% VI) and upstream basin size (9.8% VI). Specifically, sites with more native species were generally less centrally located within the network, more upstream and had higher shares of forest (>30%) in their catchment. By contrast, the richness of alien species, $S_A^i$, was predominantly related to annual mean temperature (41.3% VI) followed by upstream basin size (15.5% VI) and minimum temperature of the coldest month (12.5% VI). Temperature constituted a limiting factor for alien species, that is sites with higher $S_A^i$ were located in regions with a mean annual temperature $>15.5^\circ C$ and a minimum temperature of the coldest month $>-0.5^\circ C$ (Supporting Information Figure S4.5). Moreover, $S_A^i$ steadily increased with catchment size and was relatively lower in 15–25 km but higher in 25–60 km distance downstream a dam.

The three most important variables for $\%S_A^i$ were upstream basin size (10.7% VI), distance from the next upstream dam (8.6% VI),
and minimum temperature of the coldest month (7.9% VI). The $S_A$ steadily increased with catchment size and was elevated in 25–60 km downstream of dams (Supporting Information Figure S4.5). The three most important variables for $\%I_A$ were distance from the next upstream dam (10.2% VI), sinuosity (7.9% VI), and mean annual temperature (7.6% VI). The $\%I_A$ increased with distance from dams and higher $\%I_A$ was found in river reaches of low sinuosity and with mean annual temperatures >14.5°C (Supporting Information Figure S4.5).

3.2 | Co-occurrence of native and alien species

The JSRM revealed that co-occurrence patterns of the 17 most frequent species could be mainly attributed to shared environmental responses (EnvRho). Shared environmental responses were divergent among the modelled pairs of species with a median EnvRho of 0.34 (IQR = −0.14 to 0.62). We detected instances of positive ($n = 71$), negative ($n = 27$) and nonsignificant ($n = 38$, i.e., the 95% HPDI included zero) pairwise environmental correlation (Figure 4). Common carp and bleak showed the strongest positive (EnvRho = 0.90, HPDI = 0.82–0.96), while Wels catfish and brown trout showed the strongest negative environmental correlation (EnvRho = −0.84, −0.93 to −0.71). In contrast, pairwise residual correlation among species Rho was generally weaker than EnvRho. Median Rho was 0.08 (IQR = −0.09 to 0.27) and mainly positive ($n = 38$), or nonsignificant ($n = 91$) and less frequently negative ($n = 7$; Figure 4). The strongest positive residual correlation was detected between Ebro nase and Ebro barbel (Rho = 0.72, 0.61–0.81), whereas the strongest negative, but not significant residual correlation was between Pyrenean stone loach and European eel (Rho = −0.35, −0.59 to −0.08).

Environmental correlations were significantly stronger among pairs of alien species (median EnvRho = 0.83) than between native and alien species (median EnvRho = 0.10) or among native species (median EnvRho = 0.36), as indicated by pairwise permutation tests (maxT = 4.1, $p < 0.005$, Figure 5). Residual correlations were significantly higher among pairs of native species (median Rho = 0.15) than pairs of native versus alien species (median Rho = 0.01, maxT = 2.8, $p < 0.05$, Figure 5).

4 | DISCUSSION

Our initial hypothesis that the distributional range of alien, mainly warmer-water fish species in the study area is largely co-determined by temperature-related climate variables was fully supported by our results. We observed contrasting patterns of native versus alien
| Variable                          | $O_A$ | $S_N$ | $S_A$ | $\%S_A$ | $\%I_A$ |
|----------------------------------|-------|-------|-------|---------|---------|
| Upstream basin size              | 44.24 (1) | 9.82 (3) | 15.52 (2) | 10.66 (1) |
| Annual mean temperature          | 6.88 (4) | 6.39 (7) | 41.33 (1) | 5.34 (7) | 7.61 (3) |
| Distance to next dam upstream    | 5.45 (7) | 6.88 (6) | 9.49 (4) | 8.58 (2) | 10.18 (1) |
| Network closeness centrality     | 4.81 (10) | 22.29 (1) | 4.12 (11) | 5.06 (8) |
| Min temperature of coldest month | 9.26 (2) | 12.45 (3) | 7.92 (3) | 4.7 (11) |
| Built-up land use                | 4.9 (9) | 3.95 (10) | 8.09 (5) | 6.02 (4) | 5.19 (6) |
| Forest land use                  | 19.14 (2) | 3.18 (15) | 4.41 (14) |
| Sinuosity                        | 4.94 (9) | 5.73 (7) | 5.84 (5) | 7.87 (2) |
| Arable land use                  | 7.47 (3) | 6.13 (8) | 4.33 (10) | 5.04 (9) |
| Mean temperature of driest quarter | 3.81 (11) | 7.38 (6) | 5.28 (8) | 3.49 (17) |
| Temperature seasonality          | 8.97 (4) | 3.42 (14) | 5.07 (7) |
| Number of barriers upstream      | 7.67 (5) | 3.53 (13) | 4.86 (10) |
| Grassland land use               | 5.08 (8) | 5.6 (6) | 4.32 (15) |
| Annual precipitation             | 5.51 (6) | 2.63 (18) | 5.39 (5) |
| Permanent crops land use         | 6.41 (5) | 2.46 (20) | 4.64 (12) |
| Isothermality                    | 4.54 (9) | 6.91 (4) |
| Rel. area of reservoirs upstream | 4.03 (12) | 4.22 (16) |
| Density of dams upstream         | 3.07 (16) | 4.48 (13) |
| Palmer Drought Severity Index    | 2.65 (17) | 3.24 (19) |
| Stream slope                     | 2.47 (19) | 3.31 (18) |
| Number of barriers within 10 km  | 2.19 (21) |
| Fragment size                    | 1.72 (22) |
| Impounded river length within 10 km upstream | 0.46 (23) |
| Number of reservoirs within 10 km upstream | |

Note. Variables are displayed in descending order based on the sum of VI across the models. The importance rank of each variable is provided in parenthesis. Variables without information were not selected in the final model.

Species along the upstream-downstream gradient. This longitudinal pattern might be caused by several factors that change along the stream course such as slope, discharge, depths, flow velocities, substrates and temperature (Allan & Castillo, 2007). Besides catchment size also the minimum temperature during the cold winter period and the mean annual temperature themselves appeared as decisive environmental predictors of the occurrence and richness of alien fish species in our study. As most fish are ectothermic organisms, this suggests physiological mechanisms related to lower temperature limits (e.g., for spawning or survival) which might restrict these alien species (Portner & Farrell, 2008). For example, suitable temperatures during the spawning period for the alien cyprinid species carp and bleak are considered 16–22 and 17–28°C, respectively (Mann, 1996). For the nonnative Eastern mosquito fish (Gambusia holbrooki), Pen and Potter (1991) reported relatively warm spawning temperatures >15–16°C. This roughly corresponds with our findings of mean annual temperatures of approximately 15.5°C as a lower threshold for the occurrence of many alien fishes in the study area. Since the distributions of alien species in the Ebro River are strongly temperature related, it might be expected that with future climate change alien species will further expand their upper range limits into upstream tributaries, as observed for other fishes (Comte, Buisson, Daufresne, & Grenouillet, 2013; Isaak & Rieman, 2013). However, whether fish can track future climate change-related habitat shifts also depends on the species’ dispersal ability and might be limited by migration barriers as observed elsewhere (Radinger et al., 2017; Radinger, Hölker, Horký, Slavík, & Wolter, 2018).

While larger-scale variables related to catchment size and temperature were related to the general occurrence of alien species, local-scale, often habitat-related variables such as sinuosity or distance to the next dam (i.e., proxy for local hydrologic alteration, particularly increased summer flows, Radinger, Alcaraz-Hernández, et al., 2018) were found to be important correlates of the relative abundance of alien fish. By that, our results support several previous studies suggesting that alteration of the seasonal and inter-annual flow variability of rivers as caused by dams (e.g., Poff, Olden, Merritt, & Pepin, 2007; Radinger, Alcaraz-Hernández, et al., 2018) is favouring alien species at the expense of locally adapted native species (Aparicio et al., 2000; Bunn & Arthington, 2002; Hermoso et al., 2011; Poff et al., 2007). In addition, dams can also favour alien
species through the created impoundments (Johnson et al., 2008; Liew et al., 2016). Hydrologic impacts of dams on native versus alien fish largely depend on the complex interaction of species-specific habitat requirements with the magnitude and type of flow regulation (Gido, Propst, Olden, & Bestgen, 2013). Interestingly, while Batalla, Gómez, and Kondolf (2004) and Radinger, Alcaraz-Hernández, et al. (2018) revealed that hydrologic alteration in the Ebro basin is most pronounced in downstream proximity to dams, our results revealed highest numbers of alien species in 25–60 km distance downstream of dams. The ultimate reason for this downstream shifted effect remains unclear, but might be related to the so-called “rithralization” effect (Hohensinner, Hauer, & Muhar, 2018). By that, reaches immediately downstream of dams may show relatively elevated flow velocities and larger grain sizes of the substrate, which might benefit the native rheophilic, lithophilic species (e.g., Ebro barbel) rather than the limnophilic alien species (e.g., largemouth black bass [Micropterus salmoides]). With increasing distance from a dam, the likelihood of impounding effects (e.g., slower flow velocities and/or siltation, Schmutz & Moog, 2018) induced by the next downstream dam increases, which might additionally promote the abundance of limnophilic alien fishes. Similarly to previous findings (e.g., Murphy et al., 2015), variables related to the total of dams/barriers in the entire upstream catchment were also found relevant pointing to the cumulative effects of dams. Specifically, the sediment transport is severely altered by dams with approximately 25%–30% of the pre-disturbance sediment flux being trapped in reservoirs globally.

**FIGURE 3** Response of the occurrence of alien fish species, $O_{an}$, to the three most influential environmental predictors. Lines show the fitted functions of the marginal effect of a given predictor based on the results of the boosted regression tree model. Grey open circles indicate the sampling sites with (1) or without (0) alien species.

**FIGURE 4** Heatmap (a and c) and network diagram (b and d) visualization of environmental correlation, EnvRho (a and b) and residual correlation, Rho (i.e., co-occurrence after accounting for shared environmental responses) (c and d) among the 17 most frequent fish species (see Supporting Information Table S2.2 for species codes) in the Ebro River catchment. Colours of the correlation heatmaps indicate negative (red) to positive (blue) correlations; asterisks indicate significant correlations (95% HPDI did not include zero). Only significant correlations are displayed in the network diagrams; bold lines indicate strong correlations $|r| > 0.7$. Alien species displayed in bold font in the network diagram.
Given the characteristic dendritic structure of river networks (Fagan, 2002; Grant, Lowe, & Fagan, 2007), the upstream-downstream gradient of species richness observed in this study is also closely linked to the connectivity of sites within the network. Specifically, the main stem is more centrally located and better connected than peripheral headwater streams, which is commonly associated with greater local species richness at downstream sites and lower richness at headwater sites (Altermatt, Seymour, & Martínez, 2013; Muneeppearakul et al., 2008; Seymour, Fronhofer, & Altermatt, 2015). However, partly contrasting with these previous studies, a connectivity-richness relationship was confirmed by our results only for alien fishes, while the richness of native fishes was negatively associated with connectivity. In fact, sites that were topologically less connected (i.e., central), showed relatively greater native species richness. Whether this connectivity effect on the native (endemic) fish fauna is related to any evolutionary adaptive capability to maintain populations in even unconnected sites or if the presence of alien species in the main stem causes native species to evade or decline in such areas, remains unclear. However, native species richness in the Ebro River main stem is also diminished by the lack of several native, diadromous species (e.g., European eel, thhlip grey mullet [Chelon ramada], Twait's shad [Alosa fallax], sturgeon [Acipenser sturio]) that have locally vanished as their migration has been impeded by large dams in the lowermost reaches (Aparicio, Pintor, Durán, & Carmona-Catot, 2012; Clavero & Hermoso, 2015; Elvira, Almodóvar, & Llobón-Cerviá, 1991; López, Gázquez, Olmo-Vidal, Aprahamian, & Gisbert, 2007). Therefore, dams located in critical sections of the river network (e.g., the topologically highly connected main stem) can cause severe upstream effects especially on migratory species (Brevé, Buijse, Kroe, Wanningen, & Vriese, 2014; Segurado, Branco, & Ferreira, 2013). Fragmentation by barriers (dams and weirs), as investigated in our analysis, played only a subordinate role to explain fish richness and abundance (see also Branco, Segurado, Santos, Pinheiro, & Ferreira, 2012). However, we used fragmentation indices (e.g., numbers of barriers in proximity to a site and fragment size), whereas explicitly modelling fish dispersal (Radinger et al., 2017; Radinger, Hölker, et al., 2018; Radinger, Kail, & Wolter, 2014; Radinger & Wolter, 2015) or analysing time-series of species distribution patterns might be more appropriate in explaining if and to what degree barriers impede dispersal. Although isolation by dams may prove beneficial for native biota by blocking the entry of invasive species (Fausch et al., 2009; Liermann, Nilsson, Robertson, & Ng, 2012; McLaughlin et al., 2013), the distribution of many alien fish in the Ebro River is the result of potentially multiple introductions related to accidental releases from aquaculture (e.g., channel catfish [Ictalurus punctatus]) or deliberate stockings, for example as game or bait fish for recreational fisheries (e.g., European eel, large-mouth black bass, bleak; Elvira & Almodóvar, 2001). These introductions might mask isolation and fragmentation effects of dams on the spread and distribution of alien fish.

The novel JSAM approach revealed that environmental filtering rather than biotic interactions govern the co-occurrence of native and alien fish in the Ebro River. This contrasts with a previous study.
in another Mediterranean river basin (Guadiana River, Spain) suggesting that biotic interactions with invasive species are the leading driver of the decline of native freshwater fish assemblages (Hermoso et al., 2011). Whether these differences are related to the different geographical, ecological context or to methodological differences remains unclear and requires further investigation, also with a particular focus on the fast-moving advances in JSMDs (D’Amen et al., 2018; Húi, 2016; Kissling et al., 2012; Ovaskainen, Abrego, Halme, & Dunson, 2016; Pollock et al., 2014; Tikhonov, Abrego, Dunson, & Ovaskainen, 2017; Warton et al., 2015). We found limited evidence for biotic-driven co-occurrence patterns in fish communities in the Ebro River as indicated by weak positive or negative pairwise species correlations after accounting for shared environmental responses (Figure 4). However, several facilitative interactions between fish as detected by our model seem unlikely, but positive residual correlations between fishes could have been due to a shared response to an abiotic variable that was not considered (Pollock et al., 2014; but see also Zurell et al., 2018). For example, the strongest positive residual correlation was detected between Ebro nase and Ebro barbel, that is two lithophilic species, indicating that our JSDM might lack information on bottom substrates.

The high degree of shared environmental responses among alien fish (compared to native vs. alien species, Figure 5) suggests strong environmental filtering and that alien fish occur in distinct downstream habitats largely affected by river regulation. This is also supported by the fact that the native Iberian fish fauna has very few limnophilic species, that is species that prefer stagnant waters and could thus colonize novel ecosystems such as reservoirs. Thus, our results might also be viewed in the context of Darwin’s naturalization conundrum, which postulates the importance of functional distinctiveness of alien species from native species to avoid competition and, at the same time, the importance of shared similarity to pass environmental filters and successfully establish (Diez, Sullivan, Hulme, Edwards, & Duncan, 2008; Marx, Giblin, Dunwiddie, & Tank, 2016; Thuiller et al., 2010). Although in our study, we did not measure functional or phylogenetic relatedness, differences in functional traits between alien and native species (e.g., related to limnophily, spawning substrate, temperature) have been shown elsewhere (Alcaraz et al., 2005; Vila-Gispert, Alcaraz, & García-Berthou, 2005). Moreover, the alien fish that have been introduced in the Ebro River are from genera without close native relatives (congeners, see Supporting Information Table S2.2).

Although our results suggest that alien species are rather passengers of ecological changes than the leading driver, we acknowledge that habitat degradation and alien species might complexly interact and jointly govern the decline of native species (Didham et al., 2007). Thus, effective conservation of native fishes in the Ebro River should focus on both the restoration of habitats and the natural hydrologic regime and the control of invasive species, particularly the prevention of further introductions.

There are some limitations that might affect our modelling results. Despite our efforts to minimize multicollinearity and to select methods that are relatively robust to it, we acknowledge the general intercorrelated nature of environmental variables. Specifically, rivers are hierarchically nested ecosystems, where larger-scale watershed attributes (e.g., climate, land use, catchment size) affect reach-scale or habitat-related variables (e.g., hydraulic conditions, sinuosity; Dollar, James, Rogers, & Thoms, 2007; Thorp, Thoms, & Delong, 2006). Furthermore, we note that our study is limited by not considering temporal dynamics, that is changes in species assemblages or environmental conditions over time which might have also influenced our model results. Our analysis represents a snapshot based on aggregated fish samplings over multiple years and assuming constant land use, climate, number of barriers etc. over that time. However, we acknowledge that the introduction, establishment and spread of alien species are complex time-dynamic processes in a changing environment and involve potential interactions with native species that might also be variable in time. Consequently, we strongly encourage further studies to use comprehensive time-series datasets documenting biological invasions (potentially also including numbers of propagules and failed introductions) and to investigate the dynamics of species invasions and potential biotic interactions with native species over time (Kuczynski & Grenouillet, 2018).

In summary, our results revealed the proliferation of alien fishes in the Ebro River and the simultaneous decline of many native fish species to be more strongly correlated with environmental rather than biotic associations. Particularly, the distributional limits of alien fishes were strongly related to larger-scale temperature-related climatic factors. Additionally, local-scale factors related to habitat degradation and hydrologic alteration were found to be important correlates of the spatial distribution of many alien fishes. However, detecting biotic effects (e.g., predation, competition) causing the proliferation of alien fishes in our study proves challenging because (a) habitat alteration is spatially co-correlated with the occurrence of alien species; and (b) we only investigated co-occurrence patterns based on presence/absence of species. Although we acknowledge that invasive species can cause extirpations of native species (Clavero & García-Berthou, 2005; García-Berthou & Moreno-Amich, 2000; Miller, Williams, & Williams, 1989; Pyšek, Blackburn, García-Berthou, Perglová, & Rabitsch, 2017) biotic interactions might more likely first express in abundance declines, which are often noisy and were beyond the scope of this study. In a changing world increasingly impacted by humans, research is urgently needed to develop a mechanistic understanding of whether and why alien fishes spread and native species decline.

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DATA ACCESSIBILITY

Species and environmental data, and BRT and JSMD models used in this study are available as csv files and R scripts from the figshare repository: https://doi.org/10.6084/m9.figshare.6530588.

ORCID

Johannes Radinger https://orcid.org/0000-0002-2637-9464
Juan Diego Alcaraz-Hernández https://orcid.org/0000-0002-6885-6695
Emil García-Berthou https://orcid.org/0000-0001-8412-741X

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**BIOSKETCHES**

**Johannes Radinger** is currently a postdoc researcher in river ecology working at the Institute of Aquatic Ecology, University of Girona, Spain. His research interests include modelling of spatial patterns and processes such as species-habitat relationships and dispersal of freshwater biota to aid conservation and management of rivers.

**Juan Diego Alcaraz-Hernandez** is currently a postdoc researcher at the Institute of Aquatic Ecology of the University of Girona, Spain. He has experience in population dynamics, species distribution models in river ecosystems and current research focuses on biogeography and human pressures on freshwater fish.

**Emili García-Berthou** is a professor of ecology at the Institute of Aquatic Ecology of the University of Girona, Spain. His research interests include invasion biology, ecology of freshwater fish and statistical ecology. Further information on his laboratory and publications is available at http://invasiber.org/egb.html.

Author contributions: J.R. and E.G-B. conceived the study; J.D.A-H. and J.R. compiled the data. J.R. analysed the data and led the writing; all authors contributed to the writing.

**SUPPORTING INFORMATION**

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

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