PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

The role of connectivity in the interplay between climate change and the spread of alien fish in a large Mediterranean river

Johannes Radinger[1,2] ⬤ | Emili García-Berthou[2] ⬤

[1]Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

[2]GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Spain

Correspondence
Johannes Radinger, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany.
Email: jradinger@igb-berlin.de

Abstract

Understanding how global change and connectivity will jointly modify the distribution of riverine species is crucial for conservation biology and environmental management. However, little is known about the interaction between climate change and fragmentation and how movement barriers might impede native species from adjusting their distributions versus limit the further spread of alien species. In this study, we modelled the current and future distributions of 11 native and five alien fishes in the large and heavily fragmented Ebro River, located within the Mediterranean region, which has many freshwater endemics severely threatened by global change. We considered 10 climate change models and five modelling algorithms and assessed the effects of connectivity on the accessibility of future suitable habitats. Thereby, we identify most conflict-prone river reaches, that is, where barriers pose a particular trade-off between isolating and negatively impacting native species versus potentially reducing the risk of alien species spread. Our results projected upstream habitat shifts for the vast majority of the species. Climate change affected species differently, with alien species generally showing larger habitat gains compared to natives. Most pronounced distributional changes (i.e. losses of native species and gains of alien species) and compositional turnover might be expected in the lower and mid reaches of large tributaries of the Ebro River. The role of anthropogenic barriers in this context is often ambiguous but rather unfavourable, as they not only restrict native fishes but also alter stream habitats and flow conditions. However, with our spatial modelling framework, we could identify specific river reaches where the connectivity trade-off in the context of climate change is particularly relevant. Overall, our findings emphasize the importance of the complex effects that climate change, riverine connectivity and alien species are expected to impose on river communities and the urgent need to adapt management strategies accordingly.

KEYWORDS
barriers, Ebro River, fragmentation, freshwater fish, non-native species, species distribution models

1 | INTRODUCTION

Climate change has become a major driver of unprecedented rates of global biodiversity change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Climate change causes expansions and contractions of suitable habitats and species range shifts (e.g. Loarie et al., 2009; Radinger et al., 2017) and might alter the structure and functioning of entire species communities (e.g. Davey, Devictor, Jonzén, Lindström, & Smith, 2013; Lurgi, Lopez, & Montoya, 2012). In addition, it has become clear that invasive alien species pose a further dominant threat to biodiversity worldwide that also interacts with climate change (Bellard, Jeschke, Leroy, & Mace, 2018; Ziska & Dukes, 2014). In fact, climate change has enabled alien species to expand into regions in which they previously could not survive and reproduce and has created new opportunities for them to become invasive (Bellard et al., 2018; Stachowicz, Terwin, Whitlatch, & Osman, 2002; Walther et al., 2009).

Fresh waters, which are among the most diverse ecosystems worldwide (Dudgeon et al., 2006; Lévêque, Oberdorff, Paugy, Stiassny, & Tedesco, 2008), are especially vulnerable and threatened by climate change and species invasions (Reid et al., 2019). For example, climate change affects populations and assemblages of riverine species via changes to temperature, flow conditions, sediment regimes and water quality (Palmer et al., 2008; Pletterbauer, Melcher, Ferreira, & Schmutz, 2015; Reid et al., 2019). Ultimately and in consequence of their physiological link to local climatic and flow conditions, freshwater fish species are particularly affected by climate change. For example, 33% of the European freshwater fishes, especially those in the Mediterranean, are already recognized as susceptible to climate change (Jarić, Lennox, Kalinkat, Cvijanović, & Radinger, 2019). Fish thermal habitats, in particular those of cold water river species, are commonly projected to shift to higher altitudes (Comte & Grenouillet, 2013; Isaak & Rieman, 2013; Pörtner & Farrell, 2008); however, specific spatial realizations of habitat shifts are further complicated by interactions with other anthropogenic drivers of global change such as land use change or habitat degradation and fragmentation by barriers (Grenouillet & Comte, 2014; Herrera-R et al., 2020; Radinger et al., 2016, 2017).

Regarding alien species in riverine ecosystems, to date more than 8,000 successful introductions of fish species into river basins outside their native range have been recorded worldwide (Leprieur et al., 2017; Tedesco et al., 2017). These introductions contribute to changes in fish species and functional diversity (Matsuzaki, Sasaki, & Akasaka, 2013; Toussaint et al., 2018; Villéger, Grenouillet, & Brosse, 2014). While aquatic invasions might have been understudied in the broader context of climate change (Bellard et al., 2018) in the past, assessing the effects of future climate change on the distribution of alien species constitutes an active area of research (Walther et al., 2009) with a growing number of case studies also for the aquatic realm (Bellard et al., 2018).

The pace of global change may actually exceed the capacity of many fishes to track suitable habitats (Comte & Grenouillet, 2013; Radinger et al., 2017). Whether species are able to track global change depends on their species-specific responses to climatic conditions, the spatial extent of projected habitat shifts and the capabilities of species to track these shifts by means of dispersal (Radinger et al., 2017). Species dispersal is particularly limited in heavily fragmented landscapes such as river ecosystems, where anthropogenic barriers to movement (e.g. weirs, dams) might disconnect the only route between two locations and the related loss of connectivity may prevent fish from keeping pace with future environmental changes (Radinger et al., 2017; Radinger, Hölker, Hölker, Horký, Slavík, & Wolter, 2018). Barriers to movement substantially impact riverine fishes (Gido, Whitney, Perkin, & Turner, 2016), for example, by disconnecting them from spawning sites (e.g. Carvajal-Quintero et al., 2017; Fagan, 2002; Jager, Chandler, Lepla, & Winkle, 2001), or by preventing recolonization from other river reaches (e.g. Lasne, Sabatié, Jeannot, & Cucherousset, 2015; Radinger & Wolter, 2015).

An important dilemma is that while barriers may negatively impact native species of conservation concern and may hinder from adjusting their distributions in response to global change, restoring river connectivity may also enable the spread of alien species (Fausch, Rieman, Dunham, Young, & Peterson, 2009; Kirk, Rosswog, Ressel, & Wissinger, 2018; Rahel & McLaughlin, 2018). Impoundments formed by dams are also more susceptible to higher propagule pressure and dams are likely to alter the flow regime in a way that may benefit alien species (Gido, Propst, Olden, & Bestgen, 2013; Johnson, Olden, & Vander Zanden, 2008; Liew, Tan, & Yeo, 2016). This potential conflict also affects river management where the objective of restoring connectivity to achieve ecological targets might be in apparent conflict with the objective to limit the spread of alien species.

While previous studies investigated distributions of freshwater fish in response to climate change, including alien species (e.g. Britton, Cucherousset, Davies, Godard, & Copp, 2010; Buisson, Thuiller, Lek, Lim, & Grenouillet, 2008; Fletcher, Gillingham, Britton, Blanchet, & Gozlan, 2016), as well as the combined effects of fragmentation and climate change (e.g. Kano et al., 2016; Radinger et al., 2017), no study has so far explicitly compared the combined effects of dams and climate change on the distribution of native and alien species. Consequently, there is an urgent need to better understand the interactive effects of climate change and the spread of alien species, especially in the context of riverine connectivity and the antithetical role of movement barriers. To address this question, we focus on the Ebro River, Spain, which is highly fragmented by anthropogenic barriers (Radinger, Alcaraz-Hernández, Alcaraz-Hernández, & García-Berthou, 2018), and located within the Mediterranean region, where many endemic species are particularly threatened by future climate change (Jarić et al., 2019; Maceda-Veiga, 2013). The Ebro River is characterized by many Iberian endemic fish species but also a large number of successful alien fish introductions (Almeida, Alcaraz-Hernández, Merciai, Benejam, & García-Berthou, 2017; Radinger, Alcaraz-Hernández, Alcaraz-Hernández, & García-Berthou, 2019). The main objectives of this study are: (a) to model the distributions of native and alien fishes in a large Mediterranean river for current and future climate scenarios, (b) to assess the effects of connectivity on the accessibility of future suitable habitats and compare native and

alien species, and thereby (c) to identify most conflict-prone river reaches (spread risk of alien species vs. isolation of native species). We expect species to modify their ranges in response to climate change in particular in upstream direction, but more importantly that alien species would benefit from climate change in contrast to many native species in the study area. Moreover, we expect that barriers impede species from tracking suitable habitats in particular those species that show largest climate change induced habitat shifts.

2 | MATERIALS AND METHODS

2.1 | Study area and environmental variables

The study area comprises the whole Ebro River basin, NE Spain, with a total catchment area of about 86,000 km². The Ebro River flows from the Cantabrian and Pyrenean Mountains to the Mediterranean Sea and discharges on average 452 m³/s at its mouth (Solans & Poff, 2013). The Ebro River and its tributaries are heavily regulated by about 300 large dams and over 2,100 smaller sized weirs, with the largest densities of dams, especially in the central and upper parts (Radinger, Alcaraz-Hernández, et al., 2018). For our analysis, we used a river network obtained from the official hydrographic network (CHE, Confederación Hidrográfica del Ebro, http://iber.chebro.es/geoportal/) at a spatial scale of 1:50,000 that has been complemented for some smaller tributaries from a river network at the 1:25,000 scale. The river network was segmented into 250 m long river reaches (n = 50,948) that represent the spatial units for all subsequent models and analyses.

Environmental data used in the models comprised of 15 moderately to weakly correlated variables ($|r| < .7$; Dormann et al., 2013) related to climate, land use, hydrological alteration, network connectivity/fragmentation and general basin topography/topology (Table 1).

Collinearity among variables was reduced using hierarchical clustering based on the correlation matrix (Dormann et al., 2013; Harrell, 2015) and selecting the best univariate predictor (i.e. ecologically more meaningful) of each cluster of two or more collinear variables.

As baseline climatic characterization of the Ebro River catchment, we generated three bioclimatic variables related to air temperature and precipitation patterns for the period 1992–2015 calculated from minimum and maximum temperature and precipitation data of the E-OBS data set (version 20.0e, spatial resolution: 0.1 degrees) of the European Climate Assessment & Dataset project (ECAD; Cornes, van der Schrier, van den Besselaar, & Jones, 2018; see Supplementary Material S1 for details). Bioclimatic variables were calculated using the 'biovars' function of the R-package '*dismo*' (version 1.1-4, Hijmans, Phillips, Leathwick, & Elith, 2017) and were spatially resampled using bilinear interpolation to correspond to the modelling grid with a spatial resolution of 50 × 50 m. For precipitation-related bioclimatic variables, we calculated average values for the catchment upstream of each river reach. Land use information was extracted from a raster map based on CORINE Land Cover 2000 level-3 classes (spatial resolution of 250 × 250 m; Büttner, Feranec, & Jaffrain, 2002). We calculated average shares of each of five aggregated thematic land use classes (built-up, arable, permanent crops, grassland and forest) for the catchment upstream of each river reach. To characterize hydrological flow alteration, we calculated the distance to the next upstream dam and the share of reservoir surface area in the catchment upstream of each reach. These two variables were identified in a previous study as relevant correlates of hydrologic alteration in the Ebro basin, with 'distance to the next dam' being particularly related to alterations of summer flow conditions (Radinger, Alcaraz-Hernández, et al., 2018). To describe network connectivity and fragmentation by dams, we calculated each reach's network closeness centrality using the Python *igraph* library

TABLE 1 Descriptive statistics of the 15 environmental variables used in the analyses

Variable	Min	Q25	Median	Mean	Q75	Max
Annual mean temperature (°C)	3.3	10.7	12.0	11.9	13.8	17.6
Annual precipitation upstream (mm)	310	463	606	639	788	1,157
Temperature seasonality ($SD \times 100$)	487.2	594.2	634.9	627.1	665.9	717.7
Arable land use upstream (%)	0.0	1.0	15.5	20.8	35.0	100.0
Built-up land use upstream (%)	0.0	0.0	0.0	0.3	0.4	70.0
Forest land use upstream (%)	0.0	15.6	28.2	31.3	43.9	100.0
Grassland land use upstream (%)	0.0	5.9	12.7	16.3	21.0	100.0
Permanent crops land use upstream (%)	0.0	0.0	0.0	1.2	0.4	100.0
Share of reservoir area upstream (per mille)	0.0	0.0	0.0	3.5	2.7	473.3
Distance to next dam upstream (km)	0.0	6.1	15.9	21.3	31.1	126.4
Fragment size (length of connected river, km)	0.1	74.9	197.0	244.1	340.1	697.3
Sinuosity (−)	1.00	1.08	1.14	1.22	1.27	3.70
Network closeness centrality ($\times 10^{10}$)	63.37	88.67	96.27	99.61	108.81	146.10
Upstream basin size (km²)	0.00	35.27	153.43	3,245.17	721.52	85,710.79
Stream slope (per mille)	0.42	4.05	7.81	9.64	13.82	102.53

Abbreviation: *SD*, standard deviation.

(version 0.7.1, Csardi & Nepusz, 2006) and the fragment size (i.e. length of unfragmented river habitats) respectively. Closeness centrality of a reach is a measure of its centrality in the entire network (Freeman, 1978) and is an indicator of how well a reach is connected to all other reaches given the river network geometry. Network centrality has been identified as a significant predictor of α-diversity and community similarity in aquatic insect communities of river networks, and reflects dispersal pathways along the dendritic landscape structure and environmental characteristics that are linked to the network position (Altermatt, Seymour, & Martinez, 2013). Further stream network and basin topographical/topological variables included sinuosity and slope of single river reaches as well as the size of the catchment upstream of each reach. Variables related to the network position, sinuosity and distance to dams were based on the CHE vector hydrographic network. Other catchment characteristics (e.g. upstream catchment, climate, land use etc.) were calculated and resampled at a spatial resolution of 50 × 50 m and based on a European digital elevation model (EU-DEM version 1.1, https://land.copernicus.eu/pan-european/satellite-derived-products/eu-dem/eu-dem-v1.1/) and extracted for each river reach. For the extraction of environmental data and other spatial analysis, we used the free, open-source GRASS GIS (version 7.9, Neteler, Bowman, Landa, & Metz, 2012) and its tool *r.watershed*. Descriptive statistics of the explanatory environmental variables used in the models are provided in Table 1.

As future climatic conditions, we considered a range of regionalized climate change projections of global circulation models (GCM-RCM) from the EURO CORDEX project (see Supplementary Material S1 for details) based on the IPCC RCP 8.5 scenario (Moss et al., 2010). The RCP 8.5 climate scenario projects average global temperature increases of 1.4–2.6°C by 2050 (IPCC, 2013). Specifically, we computed four bioclimatic variables for the period 2051–2060 based on 10 selected GCM-RCM. The selected climate projections included, among others, global models such as MPI-ESM (Max Planck Institute Earth system model) and HadGEM2 (Hadley Global Environment Model 2) and regionalizations such as KNMI-RACMO (Regional Atmospheric Climate Model of the Royal Netherlands Meteorological Institute) and CLMcom (Climate Limited-area Modelling Community; see Table S1.1). For the study catchment and across the selected GCM-RCM, annual mean temperatures are projected to generally increase a median of 1.9°C; precipitation projections are spatially variable with median changes of 0.9 mm in the future scenario (Figure S1.1).

2.2 | Fish data

The native fish community of the Ebro River basin is characterized by many Iberian endemic cyprinid species (e.g. *Achondrostoma arcasii*, *Barbus haasi*, *Gobio lozanoi*, *Luciobarbus graellsii*, *Parachondrostoma miegii*). Many alien fish species have been introduced over the last century and have become increasingly dominant, especially in the lower reaches of the Ebro River (Almeida et al., 2017; Radinger, Alcaraz-Hernández, et al., 2019). Alien fishes have been introduced

for a variety of reasons including ornament (e.g. *Carassius auratus*), recreational fisheries (e.g. *Silurus glanis*, *Alburnus alburnus*), releases from aquaculture and aquaria (e.g. *Ictalurus punctatus*) or biological control (e.g. *Gambusia holbrooki*; Elvira & Almodóvar, 2001).

We collated a data set of 614 fish samplings in the study area for our analysis. Fish sampling was carried out by electrofishing between 1992 and 2015, either from boat or wading (median sampling length = 99 m, IQR = 75–101 m) and provided by the CHE and the former Spanish Ministry of Agriculture and Fisheries, Food and Environment (MAPAMA). The original sampling sites were established as part of multiple independent monitoring programmes (e.g. for the EU Water Framework Directive) and selected by expert criteria to assure good spatial coverage of water bodies of the Ebro River catchment. From the 614 sampling sites we excluded dry or inaccessible sites due to high flows, those that had no fish captures or with incomplete environmental information, leaving 521 samplings for further analyses. Fish sampling data were transformed to presence/absence to be used in subsequent models. Only fish species with a minimum prevalence of 0.05 (>27 presence records in 521 sampling sites) were considered. The final fish data set comprised of 11 native and five alien species (Table 2). All considered alien species have naturally reproducing populations in the study catchment and, thus, can be considered 'naturalized' (sensu Richardson et al., 2000).

2.3 | Species distribution models

We calibrated species distribution models (SDMs) of 16 fishes in the Ebro using the '*biomod2*' framework (version 3.4.6; Thuiller, 2003; Thuiller, Georges, Engler, & Breiner, 2020) and five modelling algorithms that are commonly used in fish distribution models (e.g. Grenouillet & Comte, 2014; Markovic et al., 2014), including regression methods (generalized linear models, generalized additive models) and machine learning methods (boosted regression trees models, random forest, maximum entropy modelling). For all modelling algorithms, we used pseudo-absences selected from an ecologically informed background data set as observed absences might be affected by more than the lack of suitability related to our set of environmental variables. For example, observed absences might be affected by imperfect sampling, unconsidered environmental variables, dispersal and colonization processes or biotic interactions that prevent the presence at a given location (Lobo, Jiménez-Valverde, & Hortal, 2010). Thus, we used an approach of generating pseudo-absence data from outside the environmental domain where the species is present (Jiménez-Valverde, Lobo, & Hortal, 2008). More specifically, we followed an idea proposed by Chapman, Pescott, Roy, and Tanner (2019): as background data we combined both unsuitable and accessible river reaches for each species to account for species' environmental tolerances and potential dispersal constrains respectively. For alien species, we defined the accessible background area as all river reaches within a distance of 50 river km from known presence points but not further than the next upstream dam; for native species, we considered all river reaches as potentially accessible assuming no effects of

TABLE 2 Sixteen modelled fish species in the Ebro River basin and corresponding model performances. Species are characterized as native (N) or alien (A) to the Ebro River basin. Model performance is provided as mean and standard deviation (SD) of the area under the curve (cross-validation AUC) and mean sensitivity and specificity across all model runs and algorithms for a species

Code	Scientific name	Common name	N/A	Pres/Abs	Mean AUC	SD AUC	Mean sensitivity	Mean specificity
Ach_arc	*Achondrostoma arcasii*	Bermejuela	N	79/442	0.86	0.05	84.11	77.69
Alb_alb	*Alburnus alburnus*	Bleak	A	113/408	0.90	0.03	85.37	83.78
Bar_qui	*Barbatula quignardi*	Pyrenean stone loach	N	117/404	0.81	0.04	83.30	70.55
Bar_haa	*Barbus haasi*	Iberian redfin barbel	N	132/389	0.78	0.04	82.40	64.97
Car_aur	*Carassius auratus*	Goldfish	A	39/482	0.86	0.06	81.50	85.22
Cob_cal	*Cobitis calderoni*	Northern Iberian spined-loach	N	31/490	0.89	0.08	85.19	89.98
Cyp_car	*Cyprinus carpio*	Common carp	A	109/412	0.85	0.05	85.54	74.81
Gam_hol	*Gambusia holbrooki*	Eastern mosquitofish	A	28/493	0.92	0.08	87.76	94.72
Gob_loz	*Gobio lozanoi*	Pyrenean gudgeon	N	226/295	0.87	0.02	85.43	76.62
Luc_gra	*Luciobarbus graellsii*	Ebro barbel	N	299/222	0.84	0.02	83.50	71.55
Par_mie	*Parachondrostoma miegii*	Ebro nase	N	246/275	0.82	0.03	81.02	70.86
Pho_sp	*Phoxinus* sp.	Minnow	N	175/346	0.86	0.02	87.82	72.60
Sal_flu	*Salaria fluviatilis*	Freshwater blenny	N	32/489	0.79	0.09	78.80	78.07
Sal_tru	*Salmo trutta*	Brown trout	N	203/318	0.79	0.03	81.32	66.84
Sil_gla	*Silurus glanis*	Wels catfish	A	42/479	0.91	0.07	88.07	92.83
Squ_lai	*Squalius laietanus*	Ebro chub	N	50/471	0.87	0.05	83.51	84.23

anthropogenic barriers and dispersal constrains in an evolutionary timeframe. For each species, we defined the environmentally unsuitable background domain using a simple range envelope model (using the 'sre' function from the R-package '*biomod2*', Thuiller et al., 2020) based on known presence records and the 15 environmental variables. The range envelope is defined by minimum and maximum percentile values of the environmental conditions of the locations where a species is found. River reaches with an environmental variable falling outside this envelope were considered to be included in the data set of the environmentally unsuitable background domain.

Fitting SDMs for each of the 16 species comprised 10 replicate model runs of each of the five modelling algorithms. For each replicate model run, we used three pseudo-absence data sets of 5,000 randomly sampled points from the background domain of each species to reduce sampling variation. These settings were based on a preliminary analyses of the data set which revealed that further increasing the size and number the pseudo-absence data sets and replicate model runs did not improve overall model quality while being computationally cumbersome. We complemented the pseudo-absence data set during model configuration (function 'BIOMOD_FormatingData' of the R-package '*biomod2*') with true absences (Table 2), that is, reaches that have been sampled but where the target fish species was not detected.

The modelling resulted in 150 SDMs (5 × 10 × 3) for each of the 16 species. For each replicate model run, the species occurrence data were randomly split into a training (70%) and testing set (30%). The models were fitted by balancing the weight of presences and pseudo-absences such that prevalence was 0.5, meaning that the presences

will have the same importance as the absences in the calibration process of the models (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Thuiller et al., 2020). SDMs were fitted using the default settings in '*biomod2*' (Thuiller et al., 2020). Withhold testing data were then used to assess the models' predictive performance for each run and pseudo-absence data set. We then calculated the mean and standard deviation (SD) of the area under the curve (AUC), and the mean sensitivity (proportion of correctly predicted presences) and specificity (proportion of correctly predicted absences) for each species over all model runs to evaluate model quality and performance.

We used the fitted species-specific SDMs to map habitat suitabilities of single river reaches across the entire Ebro River network for the baseline and the 10 future GCM-RCM projections. Therefore, the 150 species-specific models were merged to a single ensemble model for each species and modelling algorithm (i.e. averaged over 10 replicate model runs and three pseudo-absence data sets; five models per species) using the models' AUC as a proportional weighing factor (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). Single models of poor performance (AUC < 0.70) were excluded from ensemble model building.

Finally, each species- and algorithm-specific ensemble probability map for each climate scenario (baseline + 10 GCM-RCM; 55 maps per species) was transformed into a presence/absence map using a threshold provided by '*biomod2*' that minimizes the absolute difference between specificity (true negative rate) and sensitivity (true positive rate), which is similar to the sensitivity–specificity sum maximization approach (described e.g. in Liu, Berry, Dawson, & Pearson, 2005).

2.4 | Analysis of species range shifts and connectivity

To evaluate species range shifts, we first calculated spatial descriptors of each species' habitat range for the modelled baseline and future GCM-RCM scenarios and each modelling algorithm describing: (a) the centre of their distribution, (b) the lower and upper range limits, and (c) the overall extent of their suitable habitats (adapted from Comte & Grenouillet, 2013). The centre of a species distribution along the upstream–downstream gradient was defined as the mean Strahler stream order (H_{Str}) across all river reaches (total $n = \sim51k$) that were projected suitable under a given climate scenario. The lower (H_{lwr}) and upper (H_{upr}) range limits were defined as the 2.5% and 97.5% percentiles of the distance from the source (km) of all suitably projected river reaches (Comte & Grenouillet, 2013; Quinn, Gaston, & Arnold, 1996). The overall extent of suitable habitats (H_{suit}) was defined as the total river length (river km) of all reaches projected suitable. We calculated species-specific median values and their 95% confidence intervals (CI, based on 5,000 nonparametric bootstrap simulations, percentile method) of H_{Str}, H_{lwr}, H_{upr} and H_{suit} across GCM-RCM and modelling algorithms.

Furthermore, for each spatial descriptor and species, we calculated pairwise differences (Δ) between a future scenario (GCM-RCM and modelling algorithm) and the corresponding baseline scenario modelled with the same algorithm ($n = 50$ per species). From these pairwise differences, we calculated species-specific median values and their 95% CI across GCM-RCM and modelling algorithms to describe future species range shifts. Here, ΔH_{lwr} and ΔH_{upr} describe shifts of the lower and upper distributional limits of a species respectively. ΔH_{Str} constitutes a robust metric of a species' range centre shift with negative and positive values indicating upstream and downstream shifts, respectively, and the absolute value corresponding to the magnitude of a shift (e.g. -0.1 ΔH_{Str} corresponds to an upstream shift of 10% of a species distributional area by one stream order). Additionally, we calculated Wilcoxon signed rank tests with continuity correction to test whether median ΔH_{Str}, ΔH_{lwr}, ΔH_{upr} and ΔH_{suit} across species were statistically different from 0.

To visualize directional consistency in fishes' responses to climate change, we plotted species range shifts based on a layout introduced by Comte and Grenouillet (2013). We used permutation tests (approximative general independence test [AGIT], R-package '*coin*', Hothorn, Hornik, Wiel, & Zeileis, 2008) to compare ΔH_{Str}, ΔH_{lwr}, ΔH_{upr} and ΔH_{suit} between alien and native fish species.

To assess projected changes in fish species composition, we calculated the richness-based species-exchange ratio, SER_r (Hillebrand et al., 2018), as a measure of temporal species turnover (temporal β-diversity) between the baseline scenario and each future scenario (GCM-RCM and modelling algorithm). The SER_r is the complement of the Jaccard similarity coefficient (Legendre & Legendre, 2012), a commonly applied measure in studies of biodiversity change (e.g. Olden & Poff, 2003) and quantified as:

$$SER_r = \frac{S_{imm} + S_{ext}}{S_{tot}},$$

where S_{imm} is the number of newly recorded species in a reach, S_{ext} is the number of species lost from a reach and S_{tot} is the number of species across both samples (baseline and future scenario). The SER_r quantifies the gross change in species composition and ranges between 0 (all species persist, identical species composition) and 1 (all species are exchanged, no species in common; Hillebrand et al., 2018). The SER_r was calculated for each future scenario (GCM-RCM and modelling algorithm) and then averaged across models. To assess the relationship between temporal β-diversity and change in α-diversity (i.e. species richness), we calculated Pearson correlations between SER_r and the absolute values of projected (native and alien) species net gain across all river reaches.

To evaluate potential effects of barriers, we determined all river reaches that are considered suitable for a given species but are concurrently inaccessible via dispersal routes from known species-specific source (i.e. presence) points. For this purpose, dams in the Ebro River were considered as impassable in upstream direction, hence restricting fish in moving upstream, but passable in downstream direction. Dispersal routes and connectivity along the network were assessed using the Python *igraph* library. Subsequently, we determined the share (%) of habitats that are projected suitable but inaccessible ($\%H_{inaccess}$) for each species and how this might change under the climate scenarios. We calculated permutation tests (AGIT, R-package '*coin*', Hothorn et al., 2008) to compare $\Delta\%H_{inaccess}$ between alien and native fish species.

To investigate for longitudinal patterns, we obtained for each stream order class the average (across river reaches) of the number of alien and native species per reach that would find suitable but concurrently inaccessible habitat. We plotted maps of suitable but inaccessible habitats for both groups (alien vs. native species) and calculated their relative shares to identify most conflict-prone river reaches (spread risk of alien species vs. isolation of native species) related to the management of river connectivity.

We used multiple factor analysis (MFA, R-package '*FactoMineR*', version 1.42, Lê, Josse, & Husson, 2008), a generalization of principal component analysis (Abdi, Williams, & Valentin, 2013), to reduce the multidimensional attribute space of the variables ΔH_{Str}, ΔH_{lwr}, ΔH_{upr}, ΔH_{suit} and $\Delta\%H_{inaccess}$ of the future GCM-RCM scenarios to a smaller set of principal components (PC) that describes the species' responses to climate change under consideration of restricted connectivity. Analysis of the variables' contributions to the PCs and calculating 95% confidence ellipses of group means (R-package '*ellipse*', version 0.4.1, Murdoch & Chow, 2018) were then used to describe differences between the groups of alien and native species.

Spatial analyses were carried out in GRASS (version 7.9, Neteler et al., 2012); spatial maps were plotted using QGIS (version 3.10, QGIS Development Team, 2018); statistical analysis was carried out in the software R (version 3.6.1, R Core Team, 2019).

3 | RESULTS

The distributions of 16 fish species in the Ebro River network were successfully modelled with a mean (across replicate model runs and

algorithms) cross-validated AUC across species of 0.85 (Table 2). Of all considered species, *G. holbrooki*, *S. glanis* and *A. alburnus* yielded the best performing models. The SDMs projected future changes in habitat range descriptors across the modelled species (Figure 1; Supporting Information S2).

The centre of species distributions described by mean Strahler stream order H_{Str} ranged between 1.7 (*B. haasi*) and 5.2 (*S. glanis*) with an overall median across all species of 2.9 (CI = 2.7–3.2) for the baseline scenario (Table S2.1). For the future scenario, H_{Str} was projected to shift upstream for the vast majority of species with largest shifts found for *G. holbrooki* (ΔH_{Str} = −0.7), *S. glanis* (−0.5) and *Cyprinus carpio* (−0.4; Table S2.3). Median upstream shift ΔH_{Str} across all models and species was −0.16 (CI = −0.18 to −0.13) and statistically clear
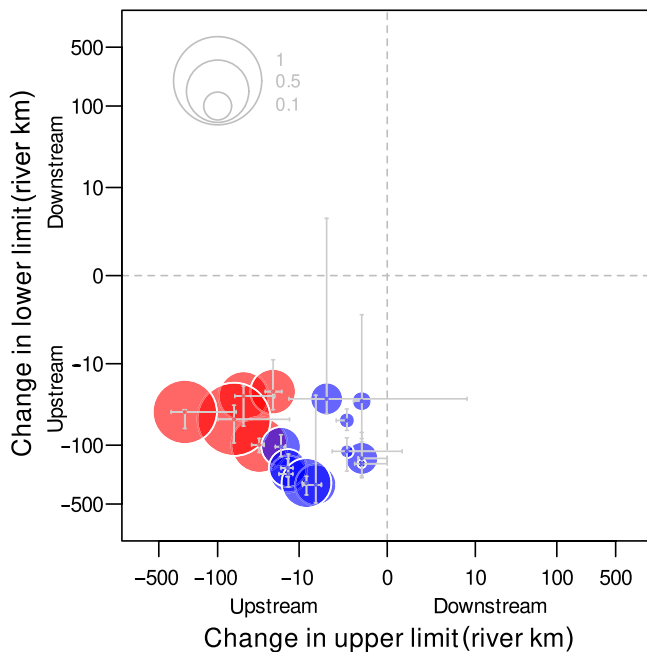
FIGURE 1 Changes in the upper and lower range limits between the baseline and future climate change scenario for native (blue) and alien (red) fish species. Representation of range shift metrics is based on Comte and Grenouillet (2013). Each circle represents the median range shift of a single species calculated over all modelling algorithms and GCM-RCM. Sizes of the circles refer to changes in the mean Strahler stream order of a species' distribution (ΔH_{Str}). Error bars indicate the corresponding 95% confidence interval of the median range shift. Species-specific data on range shifts are provided in Tables S2.1–S2.3

as indicated by a Wilcoxon signed rank test (V = 62,402, p < .001). This shift in mean stream order corresponds to an upstream shift of 16% of a species distributional area by one stream order. Over all modelling algorithms and GCM-RCM, alien species exhibited larger upstream shifts of their distribution centres compared to native species (Table 3). Differences in ΔH_{Str} between alien and native species were statistically clear (AGIT; Z = −12.51, p < .001).

The lower range limit H_{lwr} was projected to shift upstream for all modelled species, with a median ΔH_{lwr} across all species of −90.1 km (CI = −100.7 to −78.8 km) for the future scenario. Upstream shifts in H_{lwr} across species were statistically clear (Wilcoxon signed rank test; V = 35,313, p < .001). However, differences in ΔH_{lwr} between the groups of alien and native species were statistically not clear (AGIT; Z = 0.34, p = .74; Table 3). Shifts in the upper range limit H_{upr} were consistently upstream for the modelled species (negative ΔH_{upr}; Table S2.3). Median ΔH_{lwr} across species was −8.0 km (CI = −11.0 to −6.0 km) for the future scenarios compared to current climate conditions and was statistically clear (Wilcoxon signed rank test; V = 81,073, p < .001). Differences in ΔH_{upr} between alien and native species were statistically not clear (AGIT; Z = −0.35, p = .73).

Projections of climate-related changes in the overall extent of suitable habitats, H_{suit} were variable among species (Figure 2; Table S2.3) with habitat losses (ΔH_{suit} < 0) for five and habitat gains (ΔH_{suit} > 0) for 11 species. Across all species and models, median ΔH_{suit} was generally positive for the future climate scenarios (+242 km [+20.3%], CI = 192.0–348.9 km) thus indicating overall range gains (Wilcoxon signed rank test; V = 234,940, p < .001). Specifically, *G. holbrooki* (+201%), *Squalius laietanus* (+262%) and *S. glanis* (+92%) showed largest relative habitat gains, while *A. arcasii* (−49%), *Salmo trutta* (−25%) and *C. calderoni* (−23%) showed largest relative habitat losses (Table S2.3). Over all modelling algorithms and GCM-RCM, differences in ΔH_{suit} between alien and native species were statistically not clear (AGIT; Z = 0.05, p = .96).

When restricted connectivity caused by dams was considered, the share of suitable but concurrently inaccessible habitat, $\%H_{inaccess}$, was projected to increase from 4.4% (median across all species and models; CI = 2.1–6.1%) for the baseline scenario to 8.6% (CI = 7.6–9.3%) for the future scenarios (Figure 2; Tables S2.1 and S2.2). Median $\Delta\%H_{inaccess}$ across species, modelling algorithms and GCM-RCM was 2.7% (CI = 2.2–3.1%). Differences in $\Delta\%H_{inaccess}$ between alien and native species were statistically clear (AGIT; Z = 6.40, p < .001; Table 3). Largest shares of suitable but

TABLE 3 Summary of spatial shifts of species distributions under scenarios of future climate change across modelled native and alien species: ΔH_{Str} = difference in mean Strahler stream order; ΔH_{lwr} and ΔH_{upr} = differences in the lower and upper range limits; ΔH_{suit} = difference in the overall extent of suitable habitats; and $\Delta\%H_{inaccess}$ = difference in the share (%) of habitats that are projected suitable but inaccessible. Negative ΔH_{Str}, ΔH_{upr} and ΔH_{lwr} refer to upstream shifts. Results represent medians and CI (in parentheses) for both groups and calculated from pairwise differences between a future scenario (GCM-RCM and modelling algorithm) and the corresponding baseline scenario

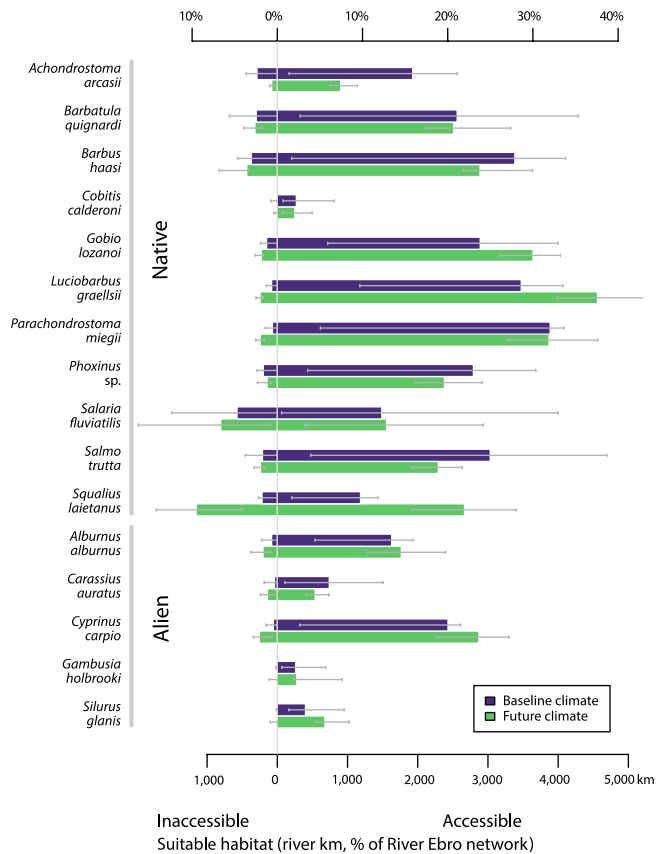|	ΔH_{Str} [–]	ΔH_{lwr} [km]	ΔH_{upr} [km]	ΔH_{suit} [km]	$\Delta\%H_{inaccess}$ [%]
Native spp.	−0.09 (−0.11 to −0.07)	−112.9 (−127.3 to −99.8)	−3.0 (−4.0 to −2.4)	107.8 (18.0–230.9)	2.4 (2.0–2.9)
Alien spp.	−0.42 (−0.48 to −0.32)	−47.6 (−60.0 to −39.0)	−38.5 (−49.5 to −27.7)	376.5 (301.5–457.7)	3.9 (2.3–5.6)

FIGURE 2 Extent of suitable habitat (H_{suit} in river km) that is accessible (right segments of the bars) versus inaccessible (left segments) for 11 native and 5 alien species and for the baseline and future climate scenarios. Error bars indicate the 95% confidence interval of the median value calculated over all modelling algorithms and GCM-RCM. Bottom and top axes refer to the absolute (river km) and relative length of the Ebro River network respectively

FIGURE 3 Multiple factor analysis (MFA) biplot of habitat shifts metrics for native (blue circles) and alien (red diamonds) fish species for the first two dimensions. Ellipses indicate 95% confidence areas of the group means of alien and native species respectively. Positively correlated variables are grouped together and arrow lengths reflect their contributions to the factor map. The 0 species (black triangle) shows the position of a generic species without any change in the considered metrics. Species codes are explained in Table 2

inaccessible habitats for the future scenario were identified for *Salaria fluviatilis* (median = 34.7%, CI = 22.5–36.4%), *S. laietanus* (median = 30.1%, CI = 27.6–32.4%) and *B. haasi* (median = 14.2%, CI = 12.5–16.3%).

The MFA revealed clear differences between the groups of native versus alien species in response to climate change and restricted connectivity apparent from the first two dimensions (Figure 3). These two dimensions jointly explained 44.7% of the variance among species in ΔH_{Str}, ΔH_{lwr}, ΔH_{upr}, ΔH_{suit} and $\Delta\%H_{inaccess}$ and across all modelling algorithms and future GCM-RCM. ΔH_{Str} and $\Delta\%H_{inaccess}$ were particularly contributing to the first dimension (Table S3.2), and thus associated with observed differences between alien and native species while ΔH_{lwr} contributed particularly to the second dimension. Further details on the MFA results are provided in Supplementary Material S3.

Patterns of habitat gains and losses were variable between species and in space. Overall, many reaches, particularly those in the down- and midstream reaches of larger tributaries to the Ebro River main stem (e.g. Rivers Guadalope, Matarraña, Segre), were identified as becoming potentially suitable for alien species in the
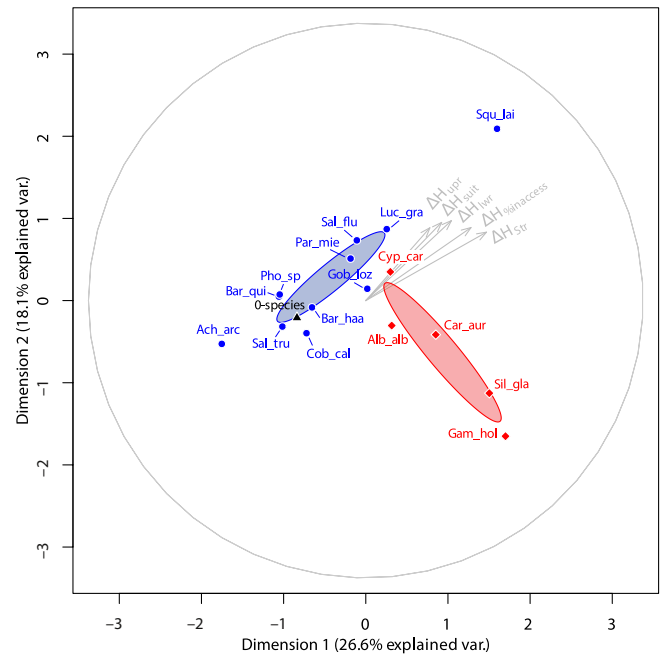
future and constitute reaches where already introduced species might spread (Figure 4; Figure S4.1). Concurrently, these down- and midstream reaches of tributaries and the upper Ebro main stem were projected as areas that will most likely exhibit losses of suitable habitats of native species. More upstream headwater reaches were identified as becoming potentially suitable for native species.

Across the entire Ebro basin, mean SER_r of fish communities between the baseline and the projected future scenario was 0.38 (Figure 4; Figure S4.1). High species turnover indicated by an $SER_r > 0.5$ was detected for 20% of the river reaches, particularly in the down- and midstream reaches of larger Ebro tributaries. Species turnover (SER_r) was clearly positively but weakly correlated with the mean absolute change in richness of all (Pearson's $r = .35$, $p < .001$), native ($r = .28$, $p < .001$) and alien ($r = .25$, $p < .001$) species (Figure S4.3).

Under consideration of restricted connectivity, mainly lower order headwater reaches of many Ebro tributaries (stream order 1–3) were identified as suitable but inaccessible due to dams, especially for native species (Figure 5). By contrast, for alien species, the mainly central reaches (stream order 3–5) of the Rivers Segre, Jalón, Guadalope and Matarraña as well as the upper Ebro main stem were identified as potentially suitable in future but where dams might restrict their spread from downstream reaches (Figure 5).
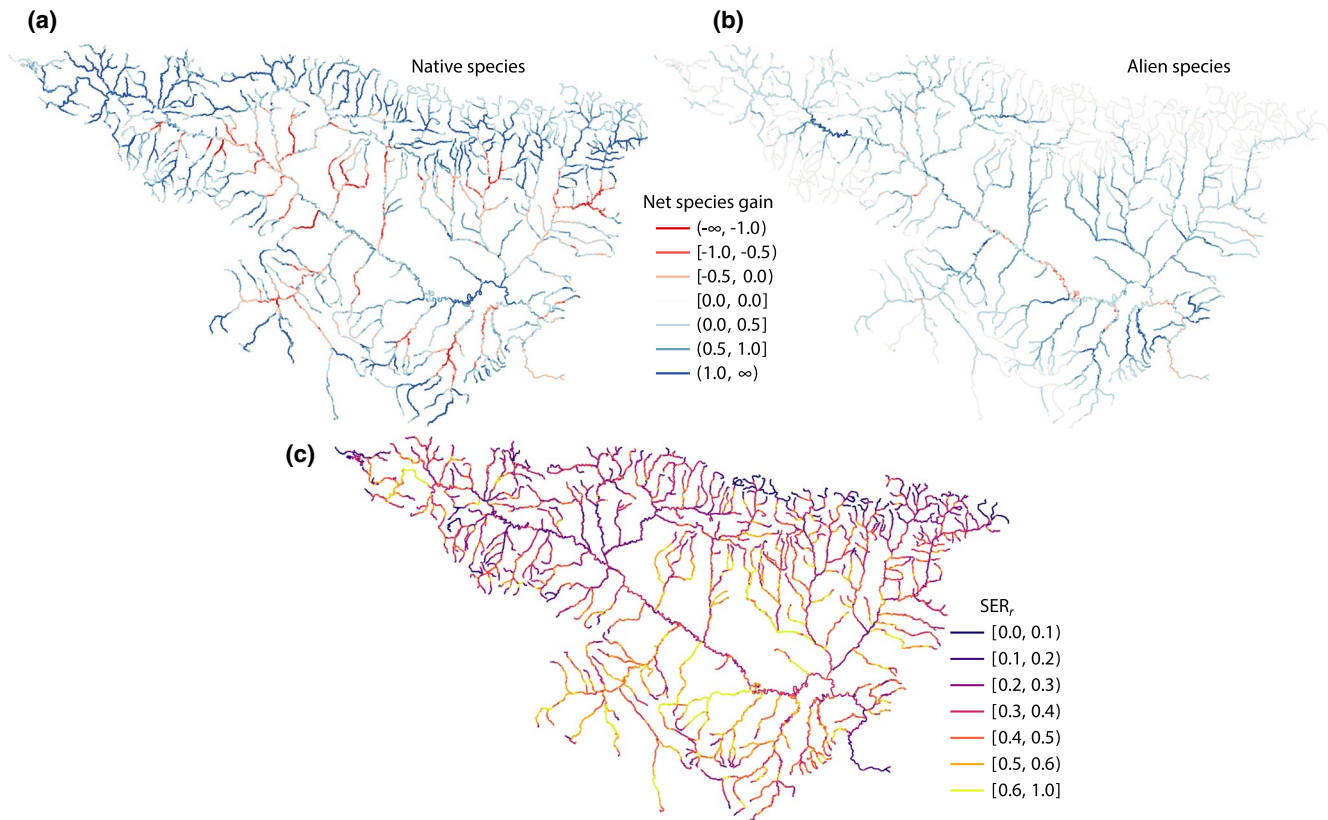
FIGURE 4 Net gain and loss of suitable habitats for the modelled (a) native and (b) alien fish species in the Ebro River study catchment and (c) associated species turnover (i.e. changes in β-diversity) measured by the richness-based species-exchange ratio (SER_r). Maps show the mean difference between the baseline and the future climate change scenarios. The SER_r quantifies the gross change in species composition with larger values indicating higher turnover

4 | DISCUSSION

4.1 | Climate-related habitat shifts of native and alien fishes

This study is aimed at improving our understanding of the joint effects of climate change and restricted river connectivity on the distributions of native and alien fish species in a large Mediterranean river. In general, the extent of projected climate change-induced habitat shifts in the Ebro River was highly variable among species, with approximately 70% of the modelled species projected to gain habitats and 30% to rather loose climate suitable habitats. Similar complex patterns of habitat shifts related to climate change have been reported in previous studies of freshwater fish (e.g. Grenouillet & Comte, 2014; Markovic, Freyhof, & Wolter, 2012; Radinger et al., 2017) and other species groups (e.g. Domisch, Jähnig, & Haase, 2011; Fulton, 2011; Tayleur et al., 2016). For example, 47% of fishes in the European River Elbe (Radinger et al., 2017) and 63% of fishes in French rivers (Grenouillet & Comte, 2014) were modelled to undergo or have already exhibited range expansions, respectively, while the other species showed rather range losses. We note that such differences in climate-induced habitat shifts might result, for example, from

differences in climate change velocities over time and for different geographic areas (e.g. Loarie et al., 2009) or differences in species-specific ecological requirements (e.g. Graham & Harrod, 2009). Previous studies suggested that in particular the interaction of climate change and other anthropogenic drivers contribute to the complex spatial patterns of species responses towards ongoing global change (Heino, Virkkala, & Toivonen, 2009; Olden et al., 2010; Radinger et al., 2016). Here, in particular, hydrologic alteration, habitat degradation or land use as well as their subordinate effects on stream habitats, water quality and flow conditions are important in the Ebro River system (Almeida et al., 2017; Colin, Villéger, Wilkes, de Sostoa, & Maceda-Veiga, 2018; Radinger, Alcaraz-Hernández, et al., 2019).

As hypothesized, species' suitable habitats shifted in upstream direction. This is in good agreement with many previous studies that projected or observed shifts of fish thermal habitats towards higher altitudes and in upstream direction in response to warming climates (Comte & Grenouillet, 2013; Isaak & Rieman, 2013; Pörtner & Farrell, 2008), although such studies are often limited to cold water species (reviewed by Comte, Buisson, Daufresne, & Grenouillet, 2013). Consistent upstream shifts were, for example, also observed for >65% of 32 French stream fishes between 1980–1992 and 2003–2009 (Comte & Grenouillet, 2013). Our
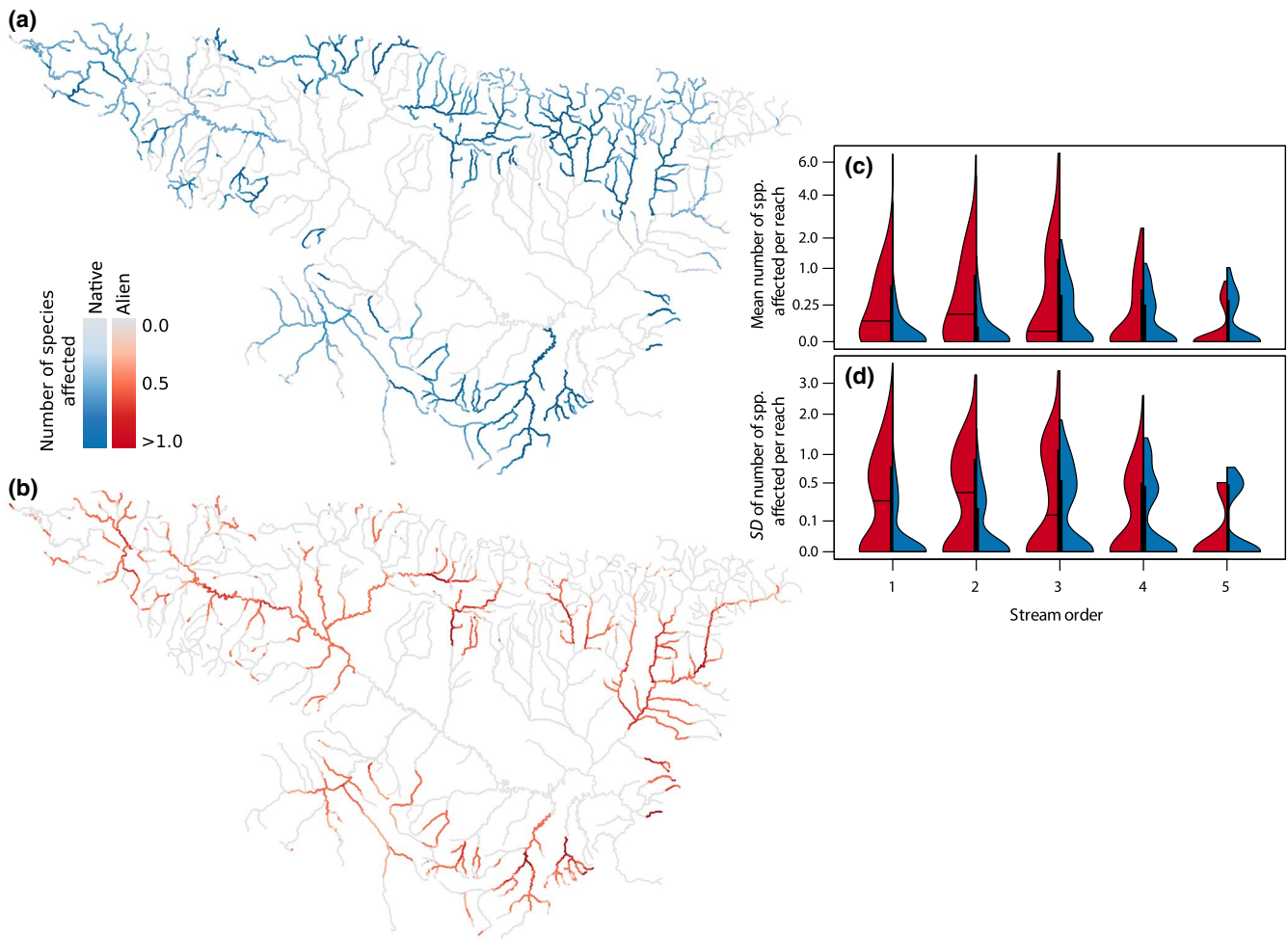
FIGURE 5 Effects of restricted connectivity on the accessibility of suitable habitats for the modelled future climate scenarios. Maps show the mean number of (a) native versus (b) alien species per reach that would find suitable habitats but which are inaccessible because of restricted connectivity. Mean numbers of species are calculated across modelling algorithms and GCM-RCM. Upper violin plots (c) show the distribution of the mean number of native (blue, right half-violins) and alien (red, left half-violins) species per reach of a given Strahler stream order finding suitable but inaccessible habitat; lower violin plots (d) show the distribution of the corresponding standard deviation (*SD*) across modelling algorithms and GCM-RCM. Bold vertical lines indicate the interquartile range between the first and third quartile, horizontal lines show the median

results projected climate-driven upstream shifts at both distributional limits, but with larger shifts at the lower limit compared to the upper limit for most species (Figure 1, compare also with figure 2 in Comte & Grenouillet, 2013). The observed shifts of the downstream limits are in agreement with previous results showing that shifts of the downstream limit were more common than those of the upstream limit (Comte & Grenouillet, 2013). Disparities in the shifts of the up- and downstream limits might potentially be explained by the role of spatial gradients (i.e. stream slopes) in tracking temperature change. In fact, larger longitudinal displacements are commonly required in flatter, downstream areas compared to steeper headwater areas to keep pace with the same rate of temperature change (Loarie et al., 2009). We acknowledge that species of downstream areas are not necessarily limited by warm temperatures since many of them have high preferred temperatures (Shuter, Finstad, Helland, Zweimüller, & Hölker, 2012); however, these species might be still limited by other components of

climate change such as changes in precipitation and hydrology (e.g. Radinger et al., 2017).

Large upstream shifts were projected for the group of alien species (e.g. *G. holbrooki*, *S. glanis* and *C. carpio*), which showed distinct patterns of climate change responses compared to native species (Figures 1 and 3). This suggests that alien species in the Ebro River, which are currently dominating the main stem (Radinger, Alcaraz-Hernández, et al., 2019), might further spread into the upstream tributaries in response to changing climates. In general, our results indicated spatially variable patterns of species gains and losses with gains often dominating over species losses—a pattern that has previously been detected in other river systems (e.g. Buisson & Grenouillet, 2009; Radinger et al., 2016). As a consequence of the projected habitat shifts, species assemblages are predicted to change with most pronounced species turnover (i.e. temporal β-diversity) in the down- and midstream reaches of larger Ebro tributaries where the current community comprising several native species

is expected to convert to an increasingly alien-dominated community. Surprisingly, species gains and losses as measured by net gain were only weakly associated with SER$_r$. A lack of coherence between the temporal change in assemblage α-diversity (e.g. number of species) and temporal β-diversity (i.e. change in species composition) has been noted in previous studies (e.g. Magurran et al., 2018). Thus, even at river reaches with little evidence for pronounced changes in species richness, the compositional effects might be much more prevalent, hence emphasizing the importance of adequate measures of temporal species turnover to capture the consequences of climate change induced species shifts. Such changes might be even more pronounced at the level of local abundances of single species (Shimadzu, Dornelas, & Magurran, 2015) and might express in changes of the interaction among and within species within these new communities (Montoya & Raffaelli, 2010; Walther, 2010). For example, Erős et al. (2020) recently revealed that, at the reach scale, alien species destabilized the dynamics of riverine fish communities and increased in the variability of native populations. This further suggests that new biotic interactions can be expected, that is, indicating potential interactive effects of alien species spread and climate change.

Climate-related range shifts of alien species are increasingly studied, with partly variable outcomes (reviewed by Bellard et al., 2018; Smith et al., 2012). The studies focusing on alien fish suggest that their establishment or spread would be enhanced by increasing temperatures, particularly those of the relatively warm water alien species, such as *C. carpio*, *S. glanis* or *Micropterus* spp. (e.g. Bae, Murphy, & García-Berthou, 2018; Britton et al., 2010; Sharma & Jackson, 2008). However, we note that alien species responses to climate change are likely to be complex, potentially involving other interrelated human-mediated environmental changes such as habitat impairment or hydrological alteration (Britton et al., 2010).

4.2 | Effects of restricted connectivity

Our results re-emphasize that restricted longitudinal connectivity caused by dams is impacting fishes' abilities to keep pace with future climate-induced habitat shifts as indicated in previous studies (e.g. Radinger, Hölker, et al., 2018). The share of suitable habitats in the Ebro River that is inaccessible due to dams is likely to increase under future climate scenarios and varies among species (Figure 2). However, differences between alien and native species were rather small. Substantial impacts of barriers on river fishes' abilities to track future habitat shifts have been reported previously with larger bodied species particularly being impacted by physical barriers while smaller species being rather restricted by their dispersal ability (Radinger et al., 2017; Radinger, Hölker, et al., 2018). Not surprisingly, species with projected large shifts in our study were exceptionally affected by dams. For example, for species such as *S. fluviatilis* or *S. laietanus*, more than 30% of their projected suitable habitats in future are inaccessible, that is, located upstream of dams relative to their current occurrence.

Our results illustrate the dilemma of restoring longitudinal connectivity and the antithetical role of movement barriers in areas prone to alien species: Dams in the Ebro River clearly impact native species by fragmenting and isolating their habitats and preventing them from adjusting their distributions in response to global change. However, enhanced river connectivity may also foster the further spread of alien species. This dilemma has been repeatedly warned in previous work (Fausch et al., 2009; Kirk et al., 2018; Rahel & McLaughlin, 2018). With the spatially explicit modelling framework, we could for the first time reveal the spatially variable impacts of dams on native versus alien species that can help to prioritize river connectivity management (see Figure 5). Thereby, we identified river reaches where restricted connectivity mainly negatively affects native species versus river reaches that are likely conflict-prone in regard to the spread of alien species given full river connectivity. In this context, we also note recent efforts in assessing the selective fragmentation of aquatic systems, such as approaches to allow desirable species pass upstream while preventing or greatly reducing passage by undesirable, for example, alien species (Rahel & McLaughlin, 2018). However, completely selective fish passage systems are rather unlikely or methodologically or economically currently barely feasible (Rahel & McLaughlin, 2018) and their applicability in systems with larger numbers of alien species, such as the Ebro River, remains unclear.

The potential impediment of the active spread of alien species by barriers should not hide the manifold detrimental effects of dams on fish (Fuller, Doyle, & Strayer, 2015; Olden, 2016), of which many even promote the spread of alien species. In fact, the establishment of alien fishes is often facilitated by the changed flow and habitat conditions that result from damming rivers (Gido et al., 2013; Johnson et al., 2008; Liew et al., 2016; Radinger, Alcaraz-Hernández, et al., 2019). Consequently, given the connectivity between reservoirs and other streams of the same catchment, reservoirs might act as 'stepping-stone' habitats and thereby contribute to an increased likelihood of the continued spread of alien species (Johnson et al., 2008; Liew et al., 2016). In this vein, dam reoperation to mimic the natural flow regime (instead of dam removal) has gained increasing interest among practitioners (Poff, 2018).

In this study, we considered only along-channel movement of fish and how dams restrict species spread. However, previous studies clearly showed the potential relevance of human-mediated dispersal and multiple introductions in allowing alien fish to cross barriers and reach future suitable but inaccessible regions (e.g. Bullock et al., 2018; Johansson et al., 2018). In fact, impoundments created by dams are considered important introduction points for several alien species. Human-mediated dispersal of alien fish across barriers such as deliberate releases of (ornamental) fish (e.g. goldfish) from aquaria or bait buckets (e.g. bleak) not only counteract measures to prevent the further invasion of alien species but might also blur the spatial patterns of restricted species spread found in this study. Here, effective fish monitoring programmes (Radinger, Britton, et al., 2019) to early detect new or secondary introductions of alien species in reservoirs and adjacent river reaches are essential.

There are some limitations that may influence our modelling results. In this study, we only considered the larger dams in the Ebro River catchment (approx. 300) that constitute impassable barriers for the upstream movement of fish. However, we acknowledge that in addition, more than 2,100 smaller sized weirs (Radinger, Alcaraz-Hernández, et al., 2018) fragment the river network and of which many potentially restrict fish movement and alter habitat and flow conditions of the up- and downstream reaches. Thus, our results might be considered rather conservative estimates in regard to habitat fragmentation and the accessibility of suitable habitats.

Furthermore, we acknowledge that the predicted spread of alien species will cause manifold detrimental impacts on the native community (Ribeiro & Leunda, 2012), potentially causing abundance declines or even extirpations of native species (Clavero & García-Berthou, 2005; Hermoso, Clavero, Blanco-Garrido, & Prenda, 2011; Pyšek, Blackburn, García-Berthou, Perglová, & Rabitsch, 2017). However, here we neither modelled species abundances nor did we consider temporal dynamics and biotic interactions between native and alien species as drivers of distribution patterns. A previous study of the same area, however, indicated that biotic interactions were of less importance compared to environmental factors in shaping joint species distributions (Radinger, Alcaraz-Hernández, et al., 2019).

We acknowledge that the distributions of spreading alien species are by definition in a non-equilibrium state and are structured by both the species' environmental tolerances and dispersal constraints (Chapman et al., 2019). This might limit SDMs due to their assumption of equilibrium that is likely to be violated during the invasion process (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012). In our models, we address this concern following an approach proposed by Chapman et al. (2019) that uses prior knowledge of species' requirements to define the unsuitable background for modelling, while also considering accessibility. Nevertheless, we explicitly note that (a) our SDMs were calibrated using a spatially restricted data set that does potentially not capture the full range of environmental conditions found across species (native) ranges, that is, distributional information outside the Ebro region was not included; (b) some introduced species might not yet have fully colonized all potentially suitable locations within the Ebro (colonization credit, e.g. Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017); and (c) alien species might show niche shifts in novel environments of introduced regions (e.g. Tingley, Vallinoto, Sequeira, & Kearney, 2014). Moreover, although having good spatial coverage of sampling sites, we cannot fully exclude any bias in our models resulting from the fish sampling data that were originally collected for monitoring programmes. This all could have influenced the estimation of species response curves and our modelling results on species-specific shifts of their ranges and upper and lower limits (Thuiller, Brotons, Araújo, & Lavorel, 2004). Thus, we encourage future studies to investigate the rarely considered effects of climate change on the transport, introduction success and spread of alien species (Bellard et al., 2018), how climate change shapes biotic interactions and how this in turn will affect native species communities.

In summary, our results predict variable responses to climate change among fishes in the Ebro River, with the majority of species gaining habitats and shifting their range in upstream direction. A distinct upstream spread was especially projected for several alien fish species and most pronounced distributional changes (i.e. losses of native species and gains of alien species) and compositional changes might be expected in the lower and mid reaches of larger tributaries. The role of anthropogenic barriers in this context is highly uncertain but rather unfavourable, as they not only restrict native fishes from tracking shifting habitats but also alter stream habitats and flow conditions. Consequently, effective conservation of fishes in the Ebro River should focus on the restoration of habitats and the natural flow regime, improvements of connectivity for native species and the control of alien species, particularly the prevention of further introductions (Radinger, Alcaraz-Hernández, et al., 2019). To this end, we could identify several river reaches where the connectivity trade-off in the context of climate change is particularly relevant. These first important insights should be further complemented by mechanistic modelling approaches (Tonkin et al., 2019) and accompanied by continued monitoring efforts (Radinger, Britton, et al., 2019) to further improve our understanding and forecasting of the often interrelated effects that climate and ecosystem change, riverine connectivity and alien species are expected to impose on river fish communities.

DATA AVAILABILITY STATEMENT

Environmental and fish data that support the findings of this study are available in figshare at https://doi.org/10.6084/m9.figsh are.12814634. Original environmental data are openly available in the public domain: CHE geoportal (Confederación Hidrográfica del Ebro, http://iber.chebro.es/geoportal/); E-OBS data of current climatic data via the European Climate Assessment & Dataset project (ECAD, https://www.ecad.eu/); EURO-CORDEX data of future climate projections via the Earth System Grid Federation infrastructure (ESGF, https://esgf-index1.ceda.ac.uk/search/corde x-ceda/); CORINE Land Cover 2000 (https://land.copernicus.eu/pan-european/corine-land-cover/clc-2000); European digital ele-

vation model (https://land.copernicus.eu/pan-european/satellite-derived-products/eu-dem/eu-dem-v1.1/). Analyses scripts of this study are available from the corresponding author upon reasonable request.

ORCID

Johannes Radinger (iD) https://orcid.org/0000-0002-2637-9464
Emili García-Berthou (iD) https://orcid.org/0000-0001-8412-741X

REFERENCES

Abdi, H., Williams, L. J., & Valentin, D. (2013). Multiple factor analysis: Principal component analysis for multitable and multiblock data sets. *WIREs Computational Statistics*, 5(2), 149–179. https://doi.org/10.1002/wics.1246

Almeida, D., Alcaraz-Hernández, J. D., Merciai, R., Benejam, L., & García-Berthou, E. (2017). Relationship of fish indices with sampling effort and land use change in a large Mediterranean river. *Science of the Total Environment*, 605–606, 1055–1063. https://doi.org/10.1016/j.scitotenv.2017.06.025

Altermatt, F., Seymour, M., & Martinez, N. (2013). River network properties shape α-diversity and community similarity patterns of aquatic insect communities across major drainage basins. *Journal of Biogeography*, 40(12), 2249–2260. https://doi.org/10.1111/jbi.12178

Bae, M.-J., Murphy, C. A., & García-Berthou, E. (2018). Temperature and hydrologic alteration predict the spread of invasive Largemouth Bass (*Micropterus salmoides*). *Science of the Total Environment*, 639, 58–66. https://doi.org/10.1016/j.scitotenv.2018.05.001

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bellard, C., Jeschke, J. M., Leroy, B., & Mace, G. M. (2018). Insights from modeling studies on how climate change affects invasive alien species geography. *Ecology and Evolution*, 8(11), 5688–5700. https://doi.org/10.1002/ece3.4098

Britton, J. R., Cucherousset, J., Davies, G. D., Godard, M. J., & Copp, G. H. (2010). Non-native fishes and climate change: Predicting species responses to warming temperatures in a temperate region. *Freshwater Biology*, 55(5), 1130–1141. https://doi.org/10.1111/j.1365-2427.2010.02396.x

Buisson, L., & Grenouillet, G. (2009). Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. *Diversity and Distributions*, 15(4), 613–626. https://doi.org/10.1111/j.1472-4642.2009.00565.x

Buisson, L., Thuiller, W., Lek, S., Lim, P., & Grenouillet, G. (2008). Climate change hastens the turnover of stream fish assemblages. *Global Change Biology*, 14(10), 2232–2248. https://doi.org/10.1111/j.1365-2486.2008.01657.x

Bullock, J. M., Bonte, D., Pufal, G., da Silva Carvalho, C., Chapman, D. S., García, C., … Delgado, M. M. (2018). Human-mediated dispersal and the rewiring of spatial networks. *Trends in Ecology & Evolution*, 33(12), 958–970. https://doi.org/10.1016/j.tree.2018.09.008

Büttner, G., Feranec, J., & Jaffrain, G. (2002). *Corine land cover update 2000 – Technical guidelines*. Copenhagen, Denmark: EEA.

Carvajal-Quintero, J. D., Januchowski-Hartley, S. R., Maldonado-Ocampo, J. A., Jézéquel, C., Delgado, J., & Tedesco, P. A. (2017). Damming fragments species' ranges and heightens extinction risk. *Conservation Letters*, 10(6), 708–716. https://doi.org/10.1111/conl.12336

Chapman, D., Pescott, O. L., Roy, H. E., & Tanner, R. (2019). Improving species distribution models for invasive non-native species with biologically informed pseudo-absence selection. *Journal of Biogeography*, 46(5), 1029–1040. https://doi.org/10.1111/jbi.13555

Clavero, M., & García-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, 20(3), 110. https://doi.org/10.1016/j.tree.2005.01.003

Colin, N., Villéger, S., Wilkes, M., de Sostoa, A., & Maceda-Veiga, A. (2018). Functional diversity measures revealed impacts of non-native species and habitat degradation on species-poor freshwater fish assemblages. *Science of the Total Environment*, 625, 861–871. https://doi.org/10.1016/j.scitotenv.2017.12.316

Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58(4), 625–639. https://doi.org/10.1111/fwb.12081

Comte, L., & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, 36(11), 1236–1246. https://doi.org/10.1111/j.1600-0587.2013.00282.x

Cornes, R. C., van der Schrier, G., van den Besselaar, E. J. M., & Jones, P. D. (2018). An ensemble version of the E-OBS temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123(17), 9391–9409. https://doi.org/10.1029/2017JD028200

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695

Davey, C. M., Devictor, V., Jonzén, N., Lindström, Å., & Smith, H. G. (2013). Impact of climate change on communities: Revealing species' contribution. *Journal of Animal Ecology*, 82(3), 551–561. https://doi.org/10.1111/1365-2656.12035

Domisch, S., Jähnig, S. C., & Haase, P. (2011). Climate-change winners and losers: Stream macroinvertebrates of a submontane region in Central Europe. *Freshwater Biology*, 56(10), 2009–2020. https://doi.org/10.1111/j.1365-2427.2011.02631.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182. https://doi.org/10.1017/S1464793105006950

Elvira, B., & Almodóvar, A. (2001). Freshwater fish introductions in Spain: Facts and figures at the beginning of the 21st century. *Journal of Fish Biology*, 59(Suppl. A), 323–331. https://doi.org/10.1006/jfbi.2001.1753

Erős, T., Comte, L., Filipe, A. F., Ruhi, A., Tedesco, P. A., Brose, U., … Olden, J. D. (2020). Effects of nonnative species on the stability of riverine fish communities. *Ecography*, 43(8), 1156–1166. https://doi.org/10.1111/ecog.04985

Fagan, W. F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, 83(12), 3243–3249. https://doi.org/10.1890/0012-9658(2002)083[3243:CFAERI]2.0.CO;2

Fausch, K. D., Rieman, B. E., Dunham, J. B., Young, M. K., & Peterson, D. P. (2009). Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology*, 23(4), 859–870. https://doi.org/10.1111/j.1523-1739.2008.01159.x

Fletcher, D. H., Gillingham, P. K., Britton, J. R., Blanchet, S., & Gozlan, R. E. (2016). Predicting global invasion risks: A management tool to prevent future introductions. *Scientific Reports*, 6(1), 26316. https://doi.org/10.1038/srep26316

Freeman, L. C. (1978). Centrality in social networks conceptual clarification. *Social Networks*, 1(3), 215–239. https://doi.org/10.1016/0378-8733(78)90021-7

Fuller, M. R., Doyle, M. W., & Strayer, D. L. (2015). Causes and consequences of habitat fragmentation in river networks. *Annals of the New York Academy of Sciences*, *1355*(1), 31–51. https://doi.org/10.1111/nyas.12853

Fulton, E. A. (2011). Interesting times: Winners, losers, and system shifts under climate change around Australia. *ICES Journal of Marine Science*, *68*(6), 1329–1342. https://doi.org/10.1093/icesjms/fsr032

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models – How violating the equilibrium assumption can create new insights: Beyond the equilibrium assumption of SDMs. *Global Ecology and Biogeography*, *21*(11), 1126–1136. https://doi.org/10.1111/j.1466-8238.2012.00768.x

Gido, K. B., Propst, D. L., Olden, J. D., & Bestgen, K. R. (2013). Multidecadal responses of native and introduced fishes to natural and altered flow regimes in the American Southwest. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(4), 554–564. https://doi.org/10.1139/cjfas-2012-0441

Gido, K. B., Whitney, J. E., Perkin, J. S., & Turner, T. F. (2016). Fragmentation, connectivity and fish species persistence in freshwater ecosystems. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 292–323). Cambridge, UK: Cambridge University Press.

Graham, C. T., & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, *74*(6), 1143–1205. https://doi.org/10.1111/j.1095-8649.2009.02180.x

Grenouillet, G., & Comte, L. (2014). Illuminating geographical patterns in species' range shifts. *Global Change Biology*, *20*(10), 3080–3091. https://doi.org/10.1111/gcb.12570

Harrell, F. E. (2015). *Regression modeling strategies*. Cham, Switzerland: Springer International Publishing.

Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, *84*, 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x

Hermoso, V., Clavero, M., Blanco-Garrido, F., & Prenda, J. (2011). Invasive species and habitat degradation in Iberian streams: An analysis of their role in freshwater fish diversity loss. *Ecological Applications*, *21*(1), 175–188. https://doi.org/10.1890/09-2011.1

Herrera-R, G. A., Oberdorff, T., Anderson, E. B., Brosse, S., Carvajal-Vallejos, F. M., Frederico, R. G., … Tedesco, P. A. (2020). The combined effects of climate change and river fragmentation on the distribution of Andean Amazon fishes. *Global Change Biology*, in press. https://doi.org/10.1111/gcb.15285

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). *dismo: Species distribution modeling*. Retrieved from http://cran.r-project.org/package=dismo

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., … Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, *55*(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hothorn, T., Hornik, K., van de Wiel, M. A., & Zeileis, A. (2008). Implementing a class of permutation tests: The coin package. *Journal of Statistical Software*, *28*(8), 1–23. https://doi.org/10.18637/jss.v028.i08

IPCC. (2013). Summary for policymakers. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 3–30). Cambridge, UK: Cambridge University Press.

Isaak, D. J., & Rieman, B. E. (2013). Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Global Change Biology*, *19*, 742–751. https://doi.org/10.1111/gcb.12073

Jager, H. I., Chandler, J. A., Lepla, K. B., & Winkle, W. V. (2001). A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes*, *60*, 347–361.

Jarić, I., Lennox, R. J., Kalinkat, G., Cvijanović, G., & Radinger, J. (2019). Susceptibility of European freshwater fish to climate change: Species profiling based on life-history and environmental characteristics. *Global Change Biology*, *25*, 448–458. https://doi.org/10.1111/gcb.14518

Jiménez-Valverde, A., Lobo, J. M., & Hortal, J. (2008). Not as good as they seem: The importance of concepts in species distribution modelling. *Diversity and Distributions*, *14*(6), 885–890. https://doi.org/10.1111/j.1472-4642.2008.00496.x

Johansson, M. L., Dufour, B. A., Wellband, K. W., Corkum, L. D., MacIsaac, H. J., & Heath, D. D. (2018). Human-mediated and natural dispersal of an invasive fish in the eastern Great Lakes. *Heredity*, *120*(6), 533–546. https://doi.org/10.1038/s41437-017-0038-x

Johnson, P. T. J., Olden, J. D., & Vander Zanden, M. J. (2008). Dam invaders: Impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment*, *6*(7), 357–363. https://doi.org/10.1890/070156

Kano, Y., Dudgeon, D., Nam, S., Samejima, H., Watanabe, K., Grudpan, C., … Utsugi, K. (2016). Impacts of dams and global warming on fish biodiversity in the Indo-Burma hotspot. *PLoS One*, *11*(8), e0160151. https://doi.org/10.1371/journal.pone.0160151

Kirk, M. A., Rosswog, A. N., Ressel, K. N., & Wissinger, S. A. (2018). Evaluating the trade-offs between invasion and isolation for native brook trout and nonnative brown trout in Pennsylvania streams. *Transactions of the American Fisheries Society*, *147*(5), 806–817. https://doi.org/10.1002/tafs.10078

Lasne, E., Sabatié, M.-R., Jeannot, N., & Cucherousset, J. (2015). The effects of dam removal on river colonization by sea lamprey *Petromyzon marinus*. *River Research and Applications*, *31*(7), 904–911. https://doi.org/10.1002/rra.2789

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR : An R package for multivariate analysis. *Journal of Statistical Software*, *25*(1), 1–18. https://doi.org/10.18637/jss.v025.i01

Legendre, P., & Legendre, L. (2012). *Numerical ecology* (3rd Engl. ed.). Amsterdam, Netherlands; Oxford, UK: Elsevier.

Leprieur, F., Brosse, S., Grenouillet, G., Tedesco, P. A., Beauchard, O., Bigorne, R., … Hugueny, B. (2017). A global database on freshwater fish species occurrences in drainage basins. *Figshare – Dataset*. https://doi.org/10.6084/m9.figshare.c.3739145_D5.v1

Lévêque, C., Oberdorff, T., Paugy, D., Stiassny, M. L. J., & Tedesco, P. A. (2008). Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, *595*(1), 545–567. https://doi.org/10.1007/s10750-007-9034-0

Liew, J. H., Tan, H. H., & Yeo, D. C. J. (2016). Dammed rivers: Impoundments facilitate fish invasions. *Freshwater Biology*, *61*(9), 1421–1429. https://doi.org/10.1111/fwb.12781

Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, *28*(3), 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Lobo, J. M., Jiménez-Valverde, A., & Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, *33*(1), 103–114. https://doi.org/10.1111/j.1600-0587.2009.06039.x

Lurgi, M., Lopez, B. C., & Montoya, J. M. (2012). Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 2913–2922. https://doi.org/10.1098/rstb.2012.0238

Maceda-Veiga, A. (2013). Towards the conservation of freshwater fish: Iberian Rivers as an example of threats and management

practices. *Reviews in Fish Biology and Fisheries*, 23(1), 1–22. https://doi.org/10.1007/s11160-012-9275-5

Magurran, A. E., Deacon, A. E., Moyes, F., Shimadzu, H., Dornelas, M., Phillip, D. A. T., & Ramnarine, I. W. (2018). Divergent biodiversity change within ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 115(8), 1843–1847. https://doi.org/10.1073/pnas.1712594115

Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., … Darwall, W. (2014). Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions*, 20(9), 1097–1107. https://doi.org/10.1111/ddi.12232

Markovic, D., Freyhof, J., & Wolter, C. (2012). Where are all the fish: Potential of biogeographical maps to project current and future distribution patterns of freshwater species. *PLoS One*, 7(7), e40530. https://doi.org/10.1371/journal.pone.0040530

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, 15(1), 59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x

Matsuzaki, S. S., Sasaki, T., & Akasaka, M. (2013). Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography*, 22(9), 1071–1082. https://doi.org/10.1111/geb.12067

Montoya, J. M., & Raffaelli, D. (2010). Climate change, biotic interactions and ecosystem services. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2013–2018. https://doi.org/10.1098/rstb.2010.0114

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., … Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, 463(7282), 747–756. https://doi.org/10.1038/nature08823

Murdoch, D., & Chow, E. D. (2018). *ellipse: Functions for drawing ellipses and ellipse-like confidence regions*. Retrieved from https://cran.r-project.org/package=ellipse

Neteler, M., Bowman, M. H., Landa, M., & Metz, M. (2012). GRASS GIS: A multi-purpose open source GIS. *Environmental Modelling and Software*, 31, 124–130. https://doi.org/10.1016/j.envsoft.2011.11.014

Olden, J. D. (2016). Challenges and opportunities for fish conservation in dam-impacted waters. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 107–148). Cambridge, UK: Cambridge University Press.

Olden, J. D., Kennard, M. J., Leprieur, F., Tedesco, P. A., Winemiller, K. O., & García-Berthou, E. (2010). Conservation biogeography of freshwater fishes: Recent progress and future challenges. *Diversity and Distributions*, 16(3), 496–513. https://doi.org/10.1111/j.1472-4642.2010.00655.x

Olden, J. D., & Poff, N. L. (2003). Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist*, 162(4), 442–460. https://doi.org/10.1086/378212

Palmer, M. A., Reidy Liermann, C. A., Nilsson, C., Flörke, M., Alcamo, J., Lake, P. S., & Bond, N. (2008). Climate change and the world's river basins: Anticipating management options. *Frontiers in Ecology and the Environment*, 6(2), 81–89. https://doi.org/10.1890/060148

Pletterbauer, F., Melcher, A. H., Ferreira, T., & Schmutz, S. (2015). Impact of climate change on the structure of fish assemblages in European rivers. *Hydrobiologia*, 744(1), 235–254. https://doi.org/10.1007/s10750-014-2079-y

Poff, N. L. (2018). Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater Biology*, 63(8), 1011–1021. https://doi.org/10.1111/fwb.13038

Pörtner, H. O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, 322(5902), 690–692. https://doi.org/10.1126/science.1163156

Pyšek, P., Blackburn, T. M., García-Berthou, E., Perglová, I., & Rabitsch, W. (2017). Impact of biological invasions on ecosystem services. In M. Vilà & P. E. Hulme (Eds.), *Impacts of biological invasions on ecosystem services* (pp. 157–175). Springer International Publishing. https://doi.org/10.1007/978-3-319-45121-3

QGIS Development Team. (2018). *QGIS geographic information system. Open source geospatial foundation project*. Retrieved from http://qgis.osgeo.org

Quinn, R. M., Gaston, K. J., & Arnold, H. R. (1996). Relative measures of geographic range size: Empirical comparisons. *Oecologia*, 107(2), 179–188. https://doi.org/10.1007/BF00327901

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Radinger, J., Alcaraz-Hernández, J. D., & García-Berthou, E. (2018). Environmental and spatial correlates of hydrologic alteration in a large Mediterranean river catchment. *Science of the Total Environment*, 639, 1138–1147. https://doi.org/10.1016/j.scitotenv.2018.05.227

Radinger, J., Alcaraz-Hernández, J. D., & García-Berthou, E. (2019). Environmental filtering governs the spatial distribution of alien fishes in a large, human-impacted Mediterranean river. *Diversity and Distributions*, 25, 701–714. https://doi.org/10.1111/ddi.12895

Radinger, J., Britton, J. R., Carlson, S. M., Magurran, A. E., Alcaraz-Hernández, J. D., Almodóvar, A., … García-Berthou, E. (2019). Effective monitoring of freshwater fish. *Fish and Fisheries*, 20(4), 729–747. https://doi.org/10.1111/faf.12373

Radinger, J., Essl, F., Hölker, F., Horký, P., Slavík, O., & Wolter, C. (2017). The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Global Change Biology*, 23(11), 4970–4986. https://doi.org/10.1111/gcb.13760

Radinger, J., Hölker, F., Horký, P., Slavík, O., Dendoncker, N., & Wolter, C. (2016). Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. *Global Change Biology*, 22(4), 1505–1522. https://doi.org/10.1111/gcb.13183

Radinger, J., Hölker, F., Horký, P., Slavík, O., & Wolter, C. (2018). Improved river continuity facilitates fishes' abilities to track future environmental changes. *Journal of Environmental Management*, 208, 169–179. https://doi.org/10.1016/j.jenvman.2017.12.011

Radinger, J., & Wolter, C. (2015). Disentangling the effects of habitat suitability, dispersal, and fragmentation on the distribution of river fishes. *Ecological Applications*, 25(4), 914–927. https://doi.org/10.1890/14-0422.1

Rahel, F. J., & McLaughlin, R. L. (2018). Selective fragmentation and the management of fish movement across anthropogenic barriers. *Ecological Applications*, 28(8), 2066–2081. https://doi.org/10.1002/eap.1795

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., … Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. https://doi.org/10.1111/brv.12480

Ribeiro, F., & Leunda, P. M. (2012). Non-native fish impacts on Mediterranean freshwater ecosystems: Current knowledge and research needs. *Fisheries Management and Ecology*, 19(2), 142–156. https://doi.org/10.1111/j.1365-2400.2011.00842.x

Richardson, D. M., Pysek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, 6(2), 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Sharma, S., & Jackson, D. A. (2008). Predicting smallmouth bass (*Micropterus dolomieu*) occurrence across North America under climate change: A comparison of statistical approaches. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(3), 471–481. https://doi.org/10.1139/f07-178

Shimadzu, H., Dornelas, M., & Magurran, A. E. (2015). Measuring temporal turnover in ecological communities. *Methods in Ecology and Evolution*, 6(12), 1384–1394. https://doi.org/10.1111/2041-210X.12438

Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimüller, I., & Hölker, F. (2012). The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences*, *74*(4), 637–657. https://doi.org/10.1007/s00027-012-0274-3

Smith, A. L., Hewitt, N., Klenk, N., Bazely, D. R., Yan, N., Wood, S., … Lipsig-Mummé, C. (2012). Effects of climate change on the distribution of invasive alien species in Canada: A knowledge synthesis of range change projections in a warming world. *Environmental Reviews*, *20*(1), 1–16. https://doi.org/10.1139/a11-020

Solans, M. A., & Poff, N. L. (2013). Classification of natural flow regimes in the Ebro basin (Spain) by using a wide range of hydrologic parameters. *River Research and Applications*, *29*(9), 1147–1163. https://doi.org/10.1002/rra.2598

Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., & Osman, R. W. (2002). Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(24), 15497–15500. https://doi.org/10.1073/pnas.242437499

Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W., & Gravel, D. (2017). Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution*, *1*(7), 0182. https://doi.org/10.1038/s41559-017-0182

Tayleur, C. M., Devictor, V., Gaüzère, P., Jonzén, N., Smith, H. G., & Lindström, Å. (2016). Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species. *Diversity and Distributions*, *22*(4), 468–480. https://doi.org/10.1111/ddi.12412

Tedesco, P. A., Beauchard, O., Bigorne, R., Blanchet, S., Buisson, L., Conti, L., … Oberdorff, T. (2017). A global database on freshwater fish species occurrence in drainage basins. *Scientific Data*, *4*, 170141. https://doi.org/10.1038/sdata.2017.141

Thuiller, W. (2003). BIOMOD – Optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, *9*(10), 1353–1362. https://doi.org/10.1046/j.1365-2486.2003.00666.x

Thuiller, W., Brotons, L., Araújo, M. B., & Lavorel, S. (2004). Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, *27*, 165–172. https://doi.org/10.1111/j.0906-7590.2004.03673.x

Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2020). *biomod2: Ensemble platform for species distribution modeling* (R package). Retrieved from https://cran.r-project.org/package=biomod2

Tingley, R., Vallinoto, M., Sequeira, F., & Kearney, M. R. (2014). Realized niche shift during a global biological invasion. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(28), 10233–10238. https://doi.org/10.1073/pnas.1405766111

Tonkin, J. D., Poff, N. L. R., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., … Lytle, D. A. (2019). Prepare river ecosystems for an uncertain future. *Nature*, *570*(7761), 301–303. https://doi.org/10.1038/d41586-019-01877-1

Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P. A., … Villéger, S. (2018). Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecology Letters*, *21*(11), 1649–1659. https://doi.org/10.1111/ele.13141

Villéger, S., Grenouillet, G., & Brosse, S. (2014). Functional homogenization exceeds taxonomic homogenization among European fish assemblages. *Global Ecology and Biogeography*, *23*(12), 1450–1460. https://doi.org/10.1111/geb.12226

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2019–2024. https://doi.org/10.1098/rstb.2010.0021

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., … Bugmann, H. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, *24*(12), 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Ziska, L. H., & Dukes, J. S. (2014). *Invasive species and global climate change*. Oxfordshire, UK; Boston, MA: CAB International.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Radinger J, García-Berthou E. The role of connectivity in the interplay between climate change and the spread of alien fish in a large Mediterranean river. *Glob Change Biol*. 2020;00:1–16. https://doi.org/10.1111/gcb.15320