# The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers 

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#### Abstract

The future distribution of river fishes will be jointly affected by climate and land use changes forcing species to move in space. However, little is known whether fish species will be able to keep pace with predicted climate and land use-driven habitat shifts, in particular in fragmented river networks. In this study, we coupled species distribution models (stepwise boosted regression trees) of 17 fish species with spe-cies-specific models of their dispersal (fish dispersal model FIDIMO) in the European River Elbe catchment. We quantified (i) the extent and direction (up- vs. downstream) of predicted habitat shifts under coupled "moderate" and "severe" climate and land use change scenarios for 2050, and (ii) the dispersal abilities of fishes to track predicted habitat shifts while explicitly considering movement barriers (e.g., weirs, dams). Our results revealed median net losses of suitable habitats of 24 and 94 river kilometers per species for the moderate and severe future scenarios, respectively. Predicted habitat gains and losses and the direction of habitat shifts were highly variable among species. Habitat gains were negatively related to fish body size, i.e., suitable habitats were projected to expand for smaller-bodied fishes and to contract for larger-bodied fishes. Moreover, habitats of lowland fish species were predicted to shift downstream, whereas those of headwater species showed upstream shifts. The dispersal model indicated that suitable habitats are likely to shift faster than species might disperse. In particular, smaller-bodied fish (<200 mm) seem most vulnerable and least able to track future environmental change as their habitat shifted most and they are typically weaker dispersers. Furthermore, fishes and particularly larger-bodied species might substantially be restricted by movement barriers to respond to predicted climate and land use changes, while smaller-bodied species are rather restricted by their specific dispersal ability.


## KEYWORDS

barriers, climate change, edge populations, habitat shift, land use change, River Elbe, species distribution modeling, species range shift

## 1 | INTRODUCTION

Climate and land use change have become two dominant drivers of global biodiversity change (Oliver \& Morecroft, 2014; Pimm et al., 2014; Sala et al., 2000). There is no doubt that both drivers will severely impact the future distribution of species, as already shown for plants (e.g., García-Valdés, Svenning, Zavala, Purves, \& Araújo, 2015; Theurillat \& Guisan, 2001), mammals (e.g., Brodie, 2016; Trisurat, Kanchanasaka, \& Kreft, 2014), birds (e.g., Bateman et al., 2016; Jetz, Wilcove, \& Dobson, 2007), insects (e.g., Forister et al., 2010; Régnière, 2009), and aquatic organisms (e.g., Collen et al., 2014; Dudgeon et al., 2006). In particular, riverine ecosystems, which are among the most diverse systems on our globe, are considered especially threatened by future global environmental changes (Palmer et al., 2008; Vörösmarty et al., 2010). Climate and land use change are expected to alter rivers by modifications to their flow, temperature, sediment regimes and water quality (e.g., Allan, Erickson, \& Fay, 1997; Meyer, Sale, Muiholland, \& Poff, 1999) with ultimate consequences for the distribution of river fishes (Comte, Buisson, Daufresne, \& Grenouillet, 2013; Markovic et al., 2014; Radinger et al., 2016). Moreover, it has become clear that the interaction of climate and land use changes (cf. the review by Oliver \& Morecroft, 2014) will have severe effects on future biodiversity in general (Mantyka-Pringle, Martin, \& Rhodes, 2012) and on fish assemblages and diversity in particular (Radinger et al., 2016).

Changes to climate and land use conditions will force species to move in space (Loarie et al., 2009), which is associated with habitat losses in some areas and habitat gains in other areas. These changes might lead to an overall expansion or contraction of suitable habitats and/or a shift in the spatial distribution of habitats in up- or downstream direction (Comte \& Grenouillet, 2013; Lenoir et al., 2010). For example, a recent study on climate change effects on fish found mean shifts of species ranges in French rivers of 13.7 m and 0.6 km per decade toward higher elevations and upstream, respectively (Comte \& Grenouillet, 2013). In addition, habitat shifts may be further shaped by changes in precipitation, the interaction of climate and land use changes, and the geographical orientation of river networks. This might result in habitat shifts that diverge from simplified upstream and poleward range expansions (Gillings, Balmer, \& Fuller, 2015; Settele et al., 2014). The pace of climate change may actually exceed the capacity of many species' to track their suitable habitats, in particular in heavily fragmented landscapes (Devictor, Julliard, Couvet, \& Jiguet, 2008; Loarie et al., 2009) such as many river networks. Anthropogenic barriers to movement (e.g., weirs, dams) and the related loss of connectivity constitute one of the largest threats to river ecosystems (Vörösmarty et al., 2010) and may prevent fish from keeping pace with future environmental changes (Settele et al., 2014). In particular, the spatial location of barriers in relation to species occurrences co-determines to what extend barriers affect fish dispersal and the (re)colonization of habitats (Radinger \& Wolter, 2015). Therefore, it is of particular interest to know how fast and to what extent suitable habitats will move in space as a consequence
of combined changes in climate and land use, and whether species will be able to track shifting habitats.

Recently, quantifying and modeling fish dispersal in rivers gained much attention (Radinger \& Wolter, 2014, 2015; Rodríguez, 2002). In a global meta-analysis on the movement of freshwater fishes, Radinger and Wolter (2014) identified leptokurtic dispersal as an intrinsic attribute of fish populations. Fish populations consist of stationary individuals that only show small-scale movements and mobile individuals that are characterized by long-distance dispersal that is crucial for tracking shifting habitats (Radinger \& Wolter, 2014). Leading edge populations, i.e., populations at the limits of a species' current distribution in spatial proximity to the potentially new suitable habitats, are particularly relevant for tracking shifts of suitable habitats (Kühn et al., 2013).

While the impacts of climate and land use changes on the distribution of river fishes are increasingly studied (Comte \& Grenouillet, 2013; Comte et al., 2013; Radinger et al., 2016), the interaction with species-specific dispersal abilities and movement barriers have not yet been evaluated. Therefore, we coupled distribution models of 17 fish species with spatially explicit models of their dispersal in a large European river network while explicitly considering movement barriers. In particular, we analyzed (i) the direction and extent of predicted habitat shifts under coupled climate and land use change for 2050. Moreover, we assessed (ii) the species-specific dispersal abilities of fishes to track predicted habitat shifts under consideration of movement barriers (e.g., weirs, dams).

We hypothesize that (i) the predicted direction and extent of habitat shifts are highly variable among species, differ between headwater and lowland fishes and will be more pronounced for severe than for moderate environmental change (combined scenarios of climate and land use change), and (ii) the abilities of species to keep pace with environmental change will be jointly determined by spe-cies-specific dispersal abilities and the extent of environmental change, and limited by movement barriers.

## 2 | MATERIALS AND METHODS

## 2.1 | Environmental data

### 2.1.1 | Study river network

The study region consists of the River Elbe and its tributaries (Figure 1) that form a major European catchment (148,250 $\mathrm{km}^{2}$ ). The catchment of River Elbe covers parts of four European countries (Germany 65.5\%, Czech Republic 33.7\%, Austria 0.6\%, and Poland $0.2 \%$ ) and discharges on average $711 \mathrm{~m}^{3} / \mathrm{s}$ to the North Sea. The total length of the River Elbe main stem is $1,094 \mathrm{~km}$. This study focused on the Elbe River network upstream the weir Geesthacht (lat: $53^{\circ} 25^{\prime} 29^{\prime \prime} \mathrm{N}$, long: $10^{\circ} 20^{\prime} 12^{\prime \prime}$ E), because the downstream reaches are tidally affected. The model river network was extracted from a digital elevation model (EU-DEM in ETRS89-LAEA coordinate reference system, EPSG code: 3035, http://www.eea.europa.eu/data-and-maps/data/eudem) at a spatial raster resolution of 250 m . For an improved


FIGURE 1 Overview on the River Elbe, its main tributaries, and currently impassable barriers. Filled circles refer to barriers presently impassable ( $n=599$ ). Barriers which are presently partly or fully passable $(n=256)$ are not displayed [Colour figure can be viewed at wileyonlinelibrary.com]
representation of the river especially in topographically flat areas, the CCM2 river network (River and Catchment Database, version 2.1, http://ccm.jrc.ec.europa.eu, De Jager \& Vogt, 2010) was burned into the DEM before extraction (cf. Radinger et al., 2016). The extracted river network comprised 24,284 grid cells corresponding to a total length of approx. $6,100 \mathrm{~km}$. The tools r.stream.order and r.cost of GRASS GIS (Jasiewicz \& Metz, 2011; Neteler, Bowman, Landa, \& Metz, 2012) were used to extract Strahler stream order, Shreve stream order (Knighton, 1998), and distance from mouth. In addition, r.slope.aspect was used to calculate average slope and average absolute curvature (i.e., slope heterogeneity) for single stream segments.

### 2.1.2 | Current environmental conditions

To model current species distributions, we used current climate and land use conditions for each raster cell of the River Elbe network. In particular, we derived 19 bioclimatic variables (Table S1) representing
the period 1950-2000 from worldclim.org (Hijmans, Cameron, Parra, Jones, \& Jarvis, 2005). We used the land-cover classes of CORINE 2000 (http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-raster-2, spatial resolution: 25 ha) to characterize current land use. To match the categories of the future land use scenarios, the CORINE classes were aggregated to six thematic classes: built-up areas, arable land, permanent crops (e.g., vineyards, orchards), grasslands, forests, and others (e.g., sparsely vegetated areas, inland water bodies and wetlands, bogs, and marshes). For each river cell we calculated average percentages of each of these six land use classes (i) for the entire catchment upstream the respective river cell and (ii) for the sub-catchment of the stream segment where the respective cell belongs to.

### 2.1.3 | Future environmental change scenarios

To model future species distributions, we constructed a moderate and a severe future environmental scenario that combined the
range of potential climate and land use change trajectories until 2050.

For the moderate and severe future climate change scenarios, we selected the IPCC-scenarios RPC2.6 and RCP8.5 (Moss et al., 2010) that yield average global temperature increases by $0.4-1.6^{\circ} \mathrm{C}$ and $1.4-2.6^{\circ} \mathrm{C}$, respectively, by 2050 (IPCC, 2013). Analogous to the current conditions, 19 bioclimatic variables for 2050 (spatial resolution: 30 arcsec) obtained from a downscaled global circulation model (MPI-ESM LR, Max-Planck Institute Earth System Model, Giorgetta et al., 2013) were downloaded from worldclim.org. For the River Elbe catchment, this model projects average temperature increases of $1.3^{\circ} \mathrm{C}$ (RCP2.6) and $2.2^{\circ} \mathrm{C}$ (RCP8.5).

The projected land use changes by 2050 are based on statistically downscaled aggregated land use projections (Dendoncker, Bogaert, \& Rounsevell, 2006; Dendoncker, Rounsevell, \& Bogaert, 2007) following the scenarios of the ALARM project (Spangenberg et al., 2012). In this study we considered i) a moderate ("business-as-might-be-usual," BAMBU) scenario assuming continuation of current socioeconomic and policy strategies with moderate changes in land use, and (ii) a severe ("Growth Applied Strategy," GRAS) scenario implying economic growth with maximum changes in land use. Analogous to the current land use, we calculated average percentage of each of the six land use classes in 2050 for the entire catchment upstream each river cell and for each sub-catchment of a stream segment.

Finally, for the moderate environmental change scenario, we combined moderate changes in climate (RCP2.6) with moderate changes in land use (BAMBU). For the severe environmental change scenario, we combined severe changes in changes in climate (RCP8.5) with severe changes in land use (GRAS).

### 2.2 Species data

A dataset of 1,762 fish samplings collected between 1990 and 2014 was collated for this study. Data were provided by the River Basin Community Elbe (FGG Elbe), the Czech University of Life Sciences in Prague (CULS), the Institute of Inland Fisheries in Potsdam-Sacrow (IFB), the Leibniz-Institute of Freshwater Ecology and Inland Fisheries in Berlin (IGB), and local authorities in the River Elbe and its major tributaries. Fish abundance data were mostly collected by electro fishing. In the main stem of the River Elbe, additional complementary sampling methods were applied, e.g., stow nets, drift nets, gillnets. The sampling data were transformed into binary format (species presence/absence) for each site. Sites with a geographical distance $>100 \mathrm{~m}$ from the river network (i.e., sites located in smaller tributaries and backwaters not represented by the model river network) were excluded. Samples were spatially and temporally pooled (separately for tributaries and main stem) using a cluster algorithm (centroid method) based on geographical distance to ensure a minimum distance of $2,500 \mathrm{~m}$ between the pooled sites ( $n=122$ ). Rare species with less than eight occurrences were excluded from further analyses.

## 2.3 | Species distribution models for current and future conditions

We used boosted regression trees (BRTs) to model the species distributions. BRTs additively combine and average (boosting) many simple single regression trees to a collective model of improved predictive performance (De'ath, 2007; Elith, Leathwick, \& Hastie, 2008). BRTs effectively select relevant variables, identify variable interactions and avoid overfitting (Elith et al., 2008). We used a four-step analytical framework in the statistical software R based on the general guidelines on BRTs recommended by Elith and Leathwick (2013) and already described in detail in a previous study (Radinger et al., 2016): First, we randomly split the occurrence (presence/absence) data for each species into a dataset for model fitting ( $80 \%$ of the sites) and a dataset for model validation ( $20 \%$ of the sites). Second, we built for each species an initial BRT global model ( R package dismo, gbm.step) using the selected occurrence data for model fitting (Bernoulli distribution) and all 36 predictor variables (19 bioclimatic variables, 12 land use variables, 5 stream topological variables, Table S 1 ). Third, we applied an automatized stepwise backward selection of predictor variables (gbm.simplify) to simplify the global model by eliminating variables that did not improve the model (based on model-internal crossvalidation and an assessment of changes in a models' predictive deviance, see Hijmans, Phillips, Leathwick, \& Elith, 2014). Fourth, we calculated a final BRT model (gbm.step) based on the reduced set of predictor variables and validated it using the withhold data from the first step. For each BRT model, tree complexity and learning rate was set to 4 and 0.001 or smaller, respectively, to achieve the recommended number of more than 1000 regression trees (Elith et al., 2008). All other model settings were set to default or were automatically adjusted by the boosting algorithm. We repeated these four steps 10 times to obtain 10 models for each species. Subsequently, we used the 10 species-specific models to map the probability of each species' occurrence for baseline conditions (current climate and land use) and for the moderate (RCP2.6-BAMBU) and severe (RCP8.5-GRAS) future environmental change scenario.

To decrease the predictive uncertainty of the single models, the 10 probability maps for each species were averaged to a consensus model for each species and environmental change scenario using the models' AUC quality (area under the receiver operating characteristic curve) as a weighing factor (Marmion, Parviainen, Luoto, Heikkinen, \& Thuiller, 2009). Finally, we transformed each species-specific consensus probability map into a presence/absence map using a threshold that maximizes the sum of sensitivity (true positive rate) and specificity (true negative rate; Liu, Berry, Dawson, \& Pearson, 2005). A few single grid cells that projected species absences although being fully surrounded by cells projecting presences were reclassified to presences as distances of 250 m are typically covered by home range movements of river fish. The final presence/absence maps show species-specific suitable habitats for current and future (2050) environmental conditions. For all subsequent analyses of species'
habitat shifts and dispersal, only native, nonmigratory species with average model AUC > $0.8(n=17)$ were considered.

## 2.4 | Analysis of changes in suitable habitats and connectivity

To analyze changes in suitable habitats as a consequence of predicted future changes in environmental conditions (Figure 2) by 2050, we calculated five spatial indices for each species: (i) $H_{\text {gain }}=$ extent of suitable habitat gain, (ii) $H_{\text {loss }}=$ extent of suitable habitat loss, (iii) $\mathrm{H}_{\text {netgain }}=$ extent of net gain of suitable habitat, (iv) $H_{\text {dist }}=$ spatial distance of newly suitable habitats (i.e., range shifts), and $(v) H_{\text {dir }}=$ direction of range shifts (up- vs. downstream).

Specifically, $\mathrm{H}_{\text {gain }}$ and $\mathrm{H}_{\text {loss }}$ refer to the number of model grid cells that are projected to become suitable or unsuitable by 2050. The number of cells was converted to river kilometers by multiplying it with the raster cell resolution of the model grid ( 250 m ). $\mathrm{H}_{\text {netgain }}$ refers to the net difference between habitat gains and losses (i.e., $\mathrm{H}_{\text {gain }}-\mathrm{H}_{\text {loss }}$ ). Accordingly, positive and negative $\mathrm{H}_{\text {netgain }}$ indicate whether a species is considered a habitat winner or loser in light of future environmental change. $\mathrm{H}_{\text {dist }}$ describes the distance between the edge of the current distribution and the midpoint of the gained areas. It is calculated as median distance of all suitable cells that will be gained to the closest current edge population. Here, edge populations refer to the outermost cells of the current distribution of suitable habitats of a species (Figure 1). To obtain the direction of range shifts, $\mathrm{H}_{\text {dir }}$, we calculated the difference between the mean Strahler
stream order (Strahler, 1957) of cells of the future distribution of a species and its distribution for current conditions. Accordingly, negative and positive $H_{\text {dir }}$ refer to the extent of upstream and downstream distributional shift, respectively.

We used two-sample Wilcoxon signed-rank tests to compare $H_{\text {gain }}$ versus $H_{\text {loss }}$ and to compare $H_{\text {gain }}, H_{\text {loss }}, H_{\text {dist }}$ and $H_{\text {dir }}$ between the moderate and the severe future environmental change scenario. We used one-sample Wilcoxon signed-rank tests to assess whether $H_{\text {dir }}$ was significantly different from zero. We calculated Spearman rank correlations to assess the relationships between species-specific fish lengths and net habitat gains ( $H_{\text {netgain }}$ ), the distance ( $H_{\text {dist }}$ ), and direction ( $\mathrm{H}_{\text {dir }}$ ) of species habitat shifts. Spearman rank correlations were also calculated to assess whether $H_{\text {dist }}$ and $H_{\text {dir }}$ are related to the species-specific association with a longitudinal fish region (IFR, Index of Fish Region, Dußling, Berg, Klinger, \& Wolter, 2004), i.e., whether headwater species are differently affected than downstream species. The IFR ranges from 3 to 8, where low values indicate headwater species and high values indicate low land species (Dußling et al., 2004).

## 2.5 | Modeling dispersal compensation

### 2.5.1 | Fish dispersal model

To assess the species-specific fish dispersal potentially compensating for predicted habitat shifts, we applied the open source GIS-based fish dispersal model FIDIMO (Radinger, Kail, \& Wolter, 2014; Figure 2). The model calculates species dispersal as leptokurtic diffusion


FIGURE 2 Conceptual scheme of predicted changes in suitable habitats and associated shifts in species ranges of river fish. Predicted future changes in climate and land use cause habitats to shift in space, leading to losses ( $H_{\text {loss }}$ ) and gains ( $\mathrm{H}_{\text {gain }}$ ) in the amount of suitable habitats (quantified in river kilometers) compared to the current conditions. Edge populations at the limits of a species' current distribution are considered particularly important as source for colonizing newly suitable habitats. $\mathrm{H}_{\text {dist }}$ refers to the median distance of newly suitable habitats to the closest current edge population, i.e., the median distance to track by dispersal movements. Dispersal is modeled using the fish dispersal model FIDIMO (Radinger et al., 2014) based on species-specific leptokurtic dispersal kernels and edge populations as source populations [Colour figure can be viewed at wileyonlinelibrary.com]
from source points described by a double-normal probability density function (i.e., dispersal kernel, equation 1). The dispersal kernel accounts for the stationary and mobile component of a fish population where dispersal probabilities are highest close to source and decline with distance $x$ following:

$$
\begin{equation*}
f(x)=p \times \frac{1}{\sqrt{2 \pi \sigma_{\text {stat }}^{2}}} \times e^{-\frac{(x-\mu)^{2}}{2 \sigma_{\text {stat }}^{2}}}+(1-p) \times \frac{1}{\sqrt{2 \pi \sigma_{\text {mob }}^{2}}} \times e^{-\frac{(x-\mu)^{2}}{2 \sigma_{\text {mob }}^{2}}} \tag{1}
\end{equation*}
$$

where $\sigma_{\text {stat }}=$ mean movement distance of the stationary component, $\sigma_{\text {mob }}=$ mean movement distance of the mobile component, and $p=$ share of the stationary component of the population. Spe-cies-specific values for $\sigma_{\text {stat }}$ and $\sigma_{\text {mob }}$ to parameterize the dispersal kernel were obtained from a multiple regression model (Radinger \& Wolter, 2014). This regression model predicts $\sigma_{\text {stat }}$ and $\sigma_{\text {mob }}$ from fish length, aspect ratio of the caudal fin, stream size (stream order), and time. For the calculation of the regression model, we used (i) species-specific common total fish lengths, (ii) species-specific aspect ratios of the caudal fin both reported in fishbase.org (Froese \& Pauly, 2016), and (iii) local stream order extracted from a river network map at each source location. The share of the stationary component ( $p$, equation 1) was set to 0.67 , a mean value described in a previous meta-analysis of movement patterns of 62 river fish species (Radinger \& Wolter, 2014).

The dispersal model was calculated for each species separately using the cells at the edges of their current distribution (i.e., edge populations) as source points for dispersal. The dispersal models were calculated for five time steps of ten years each ( 50 model years). For the consecutive model runs, the output per time step (i.e., a raster map of the probability of each raster cell to become occupied) was used as input for the subsequent time step. Thus, in addition to the initial edge populations for the first model run, we also set those grid cells projected to become occupied after a dispersal model run as source points for the subsequent dispersal model run.

### 2.5.2 | Movement barriers

To account for effects of restricted longitudinal connectivity on species dispersal, we integrated movement barriers (e.g., weirs, dams) in the dispersal model FIDIMO. In the dispersal model, barriers restrict a certain ratio of fish (barrier-specific passability rate ranging between 0 = impassable and 1 = fully passable) from moving upstream (Radinger et al., 2014). A dataset of 855 barriers in the River Elbe network (Figure 1) and basic information on their current passability in upstream direction were provided by the FGG Elbe and the CULS in Prague. Only barriers located within the model river network were considered.

We distinguished between two scenarios of longitudinal connectivity: First, we modeled a reference scenario of full longitudinal connectivity ( $\mathrm{B}_{\mathrm{ref}}$ ) with all barriers considered as fully passable in both directions. Second, we modeled a present scenario ( $\mathrm{B}_{\text {pres }}$ ) where all barriers currently considered at least as partly passable, e.g., those
equipped with a (partly) functioning fish pass, were considered fully passable (passability rate $=1, n=256$ ); all other barriers were considered impassable in upstream direction (passability rate $=0$, $n=599$ ) but passable in the downstream direction. Thus, $B_{\text {pres }}$ represents a best-case scenario of current longitudinal connectivity.

The output of the fish dispersal model for a given species and scenario of longitudinal connectivity is a raster map indicating the probability of each raster grid cell getting reached within the modeled time frame ( $5 \times 10=50$ years). Subsequently, we quantified the river sections that (i) are projected to become suitable habitats (i.e., habitat gains) for the moderate and severe environmental change scenario, respectively, and (ii) concurrently show a dispersal probability $>0$ for a given scenario of longitudinal connectivity. This allows determining an index of species-specific dispersal compensation, $\mathrm{H}_{\text {dispersal:gain }}$, by calculating the proportion of gained habitats that can be reached by dispersal. Furthermore, we calculated the difference between the river kilometers gained and river kilometers lost after dispersal limitation at full connectivity (i.e., without barriers), $H_{\text {netgain }}(D)$, and the analogous difference while accounting for dispersal and barrier limitation, $H_{\text {netgain }}$ ( $D+B$ ). We used two-sided Wilcoxon signed-rank tests to test for differences in $H_{\text {dispersal:gain }}$ between the two scenarios of longitudinal connectivity. We calculated Spearman rank correlations to assess the relationship of $H_{\text {dispersal:gain }}$ with the spatial distance of newly suitable habitat $\left(H_{\text {dist }}\right)$, the direction of habitat shifts $\left(\mathrm{H}_{\text {dir }}\right)$, and the fish length as a speciesspecific proxy for dispersal ability.

All spatial analysis were carried out in GRASS GIS (version 7.1svn, GRASS Development Team, 2012) using the r.stream toolset (Jasiewicz \& Metz, 2011) for extracting Strahler stream order and r.fidimo (Radinger et al., 2014) for modeling fish dispersal. All statistical analysis were conducted in R (version 3.2.5, R Development Core Team, 2016) using the package dismo (version 1.0-5, Hijmans et al., 2014) for BRT model building, package raster (version 2.3-0, Hijmans, 2014) and rgdal (version 0.9-1, Bivand, Keitt, \& Rowlingson, 2014) for the handling of spatial data in R and package vioplot (version 0.2 , Adler, 2005) for generating violin plots.

## 3 | RESULTS

The distributions for 17 selected fish species native to the River Elbe catchment were modeled using BRTs with good to excellent model quality (AUC $>0.8$, Table 1). The overall mean AUC for all species was $0.86(S D=0.03)$. The modeled species belong to eight families and include typical headwater species (e.g., Salmo trutta) as well as lowland species (e.g., Abramis brama).

From all environmental predictor variables, on average 9.2 (of 19) climatic, 8.0 (of 12) land use and 3.6 (of 5) topological variables were selected in each species-specific model (Table S2). Specifically, "mean temperature of the warmest quarter" and "other land use upstream each cell" were the most frequently selected, i.e., in 13 and 14 (of 17) models, respectively. Across all species, precipitationrelated variables (BIO12-BIO17) were relatively more often selected

TABLE 1 Seventeen modeled fish species in the River Elbe network. IFR describes the species-specific Index of Fish Regions (Dußling et al., 2004), and L is the common species-specific total length (fishbase.org; Froese \& Pauly, 2016) as used in the fish dispersal model. Only native species with a mean quality of the species distribution model and AUC $>0.8$ (area under the receiver operating characteristic curve) were selected for modeling species-specific habitat shifts and dispersal. Mean AUC and the corresponding standard deviation (SD) were obtained from 10 cross-validated boosted regression tree models

| Species name | Scientific name | Family | L [mm] | IFR | Presence/absence | Mean AUC | SD AUC |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Common bream | Abramis brama | Cyprinidae | 250 | 7.00 | 66/56 | 0.86 | 0.09 |
| Bleak | Alburnus alburnus | Cyprinidae | 150 | 6.58 | 89/33 | 0.85 | 0.06 |
| Asp | Aspius aspius | Cyprinidae | 550 | 6.75 | 54/68 | 0.84 | 0.08 |
| Stone loach | Barbatula barbatula | Nemacheilidae | 120 | 5.25 | 13/109 | 0.83 | 0.12 |
| White bream | Blicca bjoerkna | Cyprinidae | 200 | 7.00 | 48/74 | 0.88 | 0.05 |
| Bullhead | Cottus gobio | Cottidae | 100 | 4.17 | 9/113 | 0.82 | 0.15 |
| Northern pike | Esox lucius | Esocidae | 400 | 6.58 | 77/45 | 0.85 | 0.08 |
| Ruffe | Gymnocephalus cernuus | Percidae | 120 | 7.58 | 48/74 | 0.83 | 0.04 |
| Ide | Leuciscus idus | Cyprinidae | 300 | 6.83 | 74/48 | 0.95 | 0.05 |
| Burbot | Lota lota | Lotidae | 400 | 6.17 | 37/85 | 0.86 | 0.09 |
| European perch | Perca fluviatilis | Percidae | 250 | 6.92 | 90/32 | 0.85 | 0.08 |
| River gudgeon | Romanogobio belingii | Cyprinidae | 100 | 6.58 | 17/105 | 0.86 | 0.09 |
| Roach | Rutilus rutilus | Cyprinidae | 250 | 6.83 | 76/46 | 0.84 | 0.07 |
| Brown trout | Salmo trutta | Salmonidae | 200 | 3.75 | 24/98 | 0.84 | 0.1 |
| Pikeperch | Sander lucioperca | Percidae | 500 | 7.25 | 39/83 | 0.82 | 0.08 |
| European catfish | Silurus glanis | Siluridae | 1500 | 6.92 | 26/96 | 0.87 | 0.07 |
| Chub | Squalius cephalus | Cyprinidae | 300 | 5.83 | 75/47 | 0.89 | 0.09 |

(3.4 of 6 variables on average) than temperature-related climatic variables (BIO1-BIO7 and BIO10-BIO11; 4.5 of 9 variables on average).

Across all species, the comparison of current and projected future distributions indicated a median predicted species-specific habitat gain, $\mathrm{H}_{\text {gain, }}$ of 223 km for the moderate and 206 km for the severe environmental change scenario (Table 2). The median spe-cies-specific predicted habitat loss, $\mathrm{H}_{\text {loss }}$, was 268 km for the moderate and 231 km for the severe scenario (Table 2). Across all species, $H_{\text {gain }}$ was not significantly different from $H_{\text {loss }}$ at both scenarios (two-sided Wilcoxon signed-rank test, moderate: $V=85, p>.1$; severe: $V=84, p>.1)$. Furthermore, both $\mathrm{H}_{\text {gain }}(V=72, p>.1)$ and $H_{\text {loss }}(V=57, p>.1)$ were not significantly different between the moderate and severe environmental change scenario. The median net habitat gain $H_{\text {netgain }}$ (i.e., $\mathrm{H}_{\text {gain }}-\mathrm{H}_{\text {loss }}$ ) was -23.5 km for the moderate and -94.3 km for the severe environmental change scenario (Table 2). At both environmental change scenarios, eight species were net habitat winners ( $\mathrm{H}_{\text {netgain }}>0$ ) and nine were net habitat losers $\left(\mathrm{H}_{\text {netgain }}<0\right)$. For both scenarios, Barbatula barbatula and Cottus gobio represented the outright "winners" $\left(\mathrm{H}_{\text {netgain }}>500\right.$ river km ) and A. brama and Aspius aspius the outright "losers" ( $H_{\text {netgain }}<-500$ river km ). $\mathrm{H}_{\text {netgain }}$ was negatively correlated with fish length (moderate: Spearman $r_{\mathrm{S}}=-.51, p=.04$; severe: $r_{\mathrm{S}}=-.48, p=.05$; Figure 3a).

The median distance of predicted habitat gains from the closest current edge population, $\mathrm{H}_{\text {dist }}$, was 14 km for the moderate and 16 km for the severe environmental change scenario. $\mathrm{H}_{\text {dist }}$ was
highly variable among species (see Table 2) ranging from 4 to 73 km for the moderate and from 7 to 96 km for the severe environmental change scenario. The largest distances, $\mathrm{H}_{\text {dist, }}$, were detected for C. gobio ( $\mathrm{H}_{\text {dist }}>70 \mathrm{~km}$ ) and S. trutta ( $\mathrm{H}_{\text {dist }}>40 \mathrm{~km}$ ). $\mathrm{H}_{\text {dist }}$ was significantly higher for the severe than for the moderate environmental change scenario (one-sided Wilcoxon signed-rank test; $V=5$, $p<.001$; Figure 4).

The differences in $\mathrm{H}_{\text {dist }}$ between both scenarios were most pronounced for S. trutta (moderate: 42 km , severe: 96 km ). For both future environmental change scenarios, $\mathrm{H}_{\text {dist }}$ decreased with fish length; however, correlations were marginally insignificant (moderate: $r_{\mathrm{S}}=-.43, p=.08$; severe: $r_{\mathrm{S}}=-.42, p=.09$; Figure 3b). We detected a weak negative trend between $\mathrm{H}_{\text {dist }}$ and the Index of Fish Regions, IFR, of a species (Figure 5a); however, correlations with the IFR were not significant (moderate and severe: $r_{\mathrm{S}}=-.32, p>.1$ ).

Analysis of the directional shift of species habitats, $\mathrm{H}_{\text {dir }}$, indicated a weak overall downstream shift for the moderate (median $\mathrm{H}_{\text {dir }}$ over all species $=0.05$ ) and severe (median $\mathrm{H}_{\text {dir }}=0.04$ ) environmental change scenarios (Table 2); however, $\mathrm{H}_{\text {dir }}$ was not significantly different from zero for both environmental change scenarios (two-sided Wilcoxon signed-rank test, moderate: $V=94, p>.1$, severe: $V=84$, $p>.1$ ). For both scenarios, $\mathrm{H}_{\text {dir }}$ was positively correlated with fish length (i.e., suitable habitat tended to shift downstream for larger fish; moderate: $r_{\mathrm{s}}=.46, p=.06$; severe: $r_{\mathrm{s}}=.64, p=.005$; Figure 3c). Nevertheless, we note that for a given fish length, some species would need to move upstream while others would need to
TABLE 2 Spatial indices of habitat shift of 17 modeled fish species in the River Elbe network for a moderate and a severe environmental change scenario, respectively

| Species | Moderate |  |  |  |  |  |  | Severe |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \mathrm{H}_{\text {gain }} \\ & {[\mathrm{km}]} \end{aligned}$ | $\begin{aligned} & \mathrm{H}_{\text {loss }} \\ & {[\mathrm{km}]} \end{aligned}$ | $\mathrm{H}_{\text {netgain }}$ [km] | $\begin{aligned} & \mathrm{H}_{\text {dist }} \\ & {[\mathrm{km}]} \end{aligned}$ | $\mathrm{H}_{\text {dir }}$ <br> [ $\Delta$ Strahler] | $\mathrm{H}_{\text {netgain }}$ <br> (D) $[\mathrm{km}]$ | $\begin{aligned} & \mathrm{H}_{\text {netgain }} \\ & (\mathrm{D}+\mathrm{B})[\mathrm{km}] \end{aligned}$ | $\begin{aligned} & \mathbf{H}_{\text {gain }} \\ & {[\mathrm{km}]} \end{aligned}$ | $\mathrm{H}_{\text {loss }}$ <br> [km] | $\mathrm{H}_{\text {netgain }}$ [km] | $\begin{aligned} & \mathrm{H}_{\text {dist }} \\ & {[\mathrm{km}]} \end{aligned}$ | $\mathrm{H}_{\text {dir }}$ <br> [ $\Delta$ Strahler] | $\mathrm{H}_{\text {netgain }}$ <br> (D) $[\mathrm{km}]$ | $\begin{aligned} & \mathrm{H}_{\text {netgain }} \\ & (\mathrm{D}+\mathrm{B})[\mathrm{km}] \end{aligned}$ |
| Abramis brama | 18.00 | 560.25 | -542.25 | 4.05 | 0.54 | -542.25 | -542.75 | 36.25 | 613.25 | -577.00 | 6.58 | 0.61 | -577.00 | -577.50 |
| Alburnus alburnus | 114.00 | 523.00 | -409.00 | 12.00 | 0.33 | -453.00 | -469.50 | 1106.00 | 97.25 | 1008.75 | 16.50 | -0.33 | 415.00 | 240.75 |
| Aspius aspius | 23.50 | 808.25 | -784.75 | 14.26 | 0.78 | -784.75 | -784.75 | 59.00 | 750.75 | -691.75 | 13.72 | 0.78 | -691.75 | -692.25 |
| Barbatula barbatula | 994.75 | 98.75 | 896.00 | 24.95 | -0.11 | 68.25 | 51.75 | 886.25 | 212.50 | 673.75 | 28.43 | -0.19 | -69.25 | -83.00 |
| Blicca bjoerkna | 223.25 | 317.25 | -94.00 | 8.72 | 0.32 | -95.50 | -122.50 | 205.75 | 352.00 | -146.25 | 10.47 | 0.35 | -150.00 | -187.00 |
| Cottus gobio | 1746.00 | 20.00 | 1726.00 | 72.78 | -1.18 | 153.75 | 127.50 | 2309.75 | 0.25 | 2309.50 | 83.54 | -1.24 | 187.25 | 158.50 |
| Esox lucius | 544.00 | 416.00 | 128.00 | 16.75 | -0.03 | 54.00 | -189.25 | 308.25 | 920.50 | -612.25 | 24.95 | 0.06 | -707.25 | -806.25 |
| Gymnocephalus cernuus | 339.25 | 43.75 | 295.50 | 22.19 | -0.18 | 44.50 | 23.25 | 136.50 | 230.75 | -94.25 | 36.75 | 0.04 | -210.75 | -288.75 |
| Leuciscus idus | 646.50 | 34.50 | 612.00 | 14.05 | -0.14 | 430.00 | 288.50 | 466.75 | 38.25 | 428.50 | 13.67 | -0.07 | 279.50 | 208.00 |
| Lota lota | 126.25 | 389.25 | -263.00 | 5.29 | 0.08 | -269.00 | -305.00 | 117.50 | 397.75 | -280.25 | 9.54 | 0.09 | -285.25 | -298.75 |
| Perca fluviatilis | 25.50 | 445.00 | -419.50 | 11.29 | 0.06 | -424.25 | -424.25 | 55.25 | 282.00 | -226.75 | 16.15 | 0.05 | -231.50 | -231.50 |
| Romanogobio belingii | 164.25 | 67.75 | 96.50 | 45.58 | 0.05 | -14.75 | -14.75 | 164.50 | 83.00 | 81.50 | 45.71 | 0.02 | -30.50 | -30.50 |
| Rutilus rutilus | 503.25 | 207.75 | 295.00 | 7.97 | -0.06 | 208.50 | 98.50 | 806.25 | 135.00 | 671.25 | 12.74 | -0.17 | 435.75 | 280.75 |
| Salmo trutta | 812.00 | 52.00 | 760.00 | 42.21 | -0.10 | 278.75 | 221.00 | 223.00 | 186.75 | 36.25 | 96.43 | -0.21 | -113.50 | -145.00 |
| Sander lucioperca | 86.00 | 193.25 | -107.25 | 15.80 | 0.16 | -107.25 | -113.00 | 87.00 | 193.25 | -106.25 | 15.80 | 0.16 | -106.25 | -112.00 |
| Silurus glanis | 215.75 | 460.75 | -245.00 | 14.76 | 0.17 | -245.00 | -346.75 | 1197.50 | 324.75 | 872.75 | 38.95 | 0.11 | 872.75 | 276.00 |
| Squalius cephalus | 244.25 | 267.75 | -23.50 | 5.52 | 0.02 | -36.75 | -89.00 | 120.25 | 561.25 | -441.00 | 8.85 | 0.03 | -467.50 | -494.50 |
| Median | 223.25 | 267.75 | -23.5 | 14.26 | 0.05 | -36.75 | -113.00 | 205.75 | 230.75 | -94.25 | 16.15 | 0.04 | -113.50 | -145.00 |
| IQR | 430.00 | 377.25 | 558.5 | 13.47 | 0.27 | 337.25 | 398.50 | 588.75 | 262.75 | 951.5 | 24.02 | 0.28 | 472.50 | 457.25 |

$\mathrm{H}_{\text {gain }}=$ habitat gain in river kilometers, $\mathrm{H}_{\text {loss }}=$ habitat loss in river kilometers, $\mathrm{H}_{\text {netgain }}=$ net habitat gain in river kilometers, $\mathrm{H}_{\text {dist }}=$ median distance of gained habitats to the closest current edge population, $H_{\text {dir }}=$ direction of the habitat shift (negative values = upstream, positive values = downstream), $H_{\text {netgain }}(\mathrm{D})=$ net habitat gain with dispersal limitation and without barriers, and $H_{\text {netgain }}(\mathrm{D}+\mathrm{B})=$ net habitat gain with dispersal limitation and barriers.


FIGURE 3 Fish length in relation to (a) the net habitat gain $H_{\text {netgain }}$ (i.e., difference $H_{\text {gain }}-\mathrm{H}_{\text {loss }}$ ), (b) the median distance of newly suitable habitats to the closest current edge population $\mathrm{H}_{\text {dist }}$ (c) the direction of habitat shifts $\mathrm{H}_{\text {dir }}$, and (d) the species-specific dispersal compensation $\mathrm{H}_{\text {dispersal:gain }}$ (i.e., proportion of newly suitable habitats that can be reached by dispersal) for the moderate (white) and severe (gray) environmental change scenario in 2050
move downstream (Figure 3c). Furthermore, $\mathrm{H}_{\text {dir }}$ was significantly positively correlated with the IFR for the severe ( $r_{\mathrm{s}}=.63, p<.01$ ) but not for the moderate ( $r_{\mathrm{S}}=.35, p>.1$ ) scenario (Figure 5b).

The fish dispersal model revealed that whether projected newly suitable habitats can be reached by dispersal (i.e., dispersal compensation, $\mathrm{H}_{\text {dispersal:gain }}$ ) strongly varies among species and depends on the scenario of longitudinal connectivity and future environmental conditions (Figure 6, Table S3). The highest median $\mathrm{H}_{\text {dispersal: }}$ gain $=0.83$ was detected for a scenario of full longitudinal connectivity ( $\mathrm{B}_{\text {ref }}$ ) and moderate environmental change; the lowest median $\mathrm{H}_{\text {dispersal:gain }}=0.52$ was identified for present longitudinal connectivity ( $\mathrm{B}_{\text {pres }}$ ) and severe environmental change. $\mathrm{H}_{\text {dispersal:gain }}$ was significantly different between $B_{\text {ref }}$ and $B_{\text {pres }}$ for the moderate (median difference in $\mathrm{H}_{\text {dispersal:gain }}=0.07$, two-sided Wilcoxon signed-rank test, $V=105, p<.005$; Figure 6) and severe environmental change scenario (median difference in $\mathrm{H}_{\text {dispersal:gain }}=0.13$, $V=120, p<.001$; Figure 6), indicating that barriers limit species dispersal induced by future environmental change. After accounting for dispersal limitation, a positive $H_{\text {netgain }}$ (D) was detected for only seven and five (of 17) species at the moderate and severe scenario,
respectively. After accounting additionally for barrier limitation, $H_{\text {netgain }}(D+B)$ generally decreased and was positive for only six and five species, respectively. For the scenario of full longitudinal connectivity ( $\mathrm{B}_{\text {ref }}$ ), $\mathrm{H}_{\text {dispersal:gain }}$ was significantly negatively correlated with $\mathrm{H}_{\text {dist }}$ (moderate: $r_{\mathrm{S}}=-.61, p<.01$, severe: $r_{\mathrm{S}}=-.61, p<.01$; Figure 7a) and significantly positively correlated with $\mathrm{H}_{\text {dir }}$ (moderate: $r_{\mathrm{S}}=.78, p<.001$; severe: $r_{\mathrm{S}}=.85, p<.001$; Figure 7b) and fish length (moderate: $r_{\mathrm{S}}=.83, p<.001$; severe: $r_{\mathrm{S}}=.80, p<.001$; Figure 3d). In other words, the proportion of newly suitable habitats that can be reached by dispersal, $\mathrm{H}_{\text {dispersal:gain, }}$, was highest for larger fish with shorter distance to newly suitable habitats that are located in the downstream direction.

## 4 | DISCUSSION

In this study, we combined analyses of distributional changes and dispersal of 17 fish species in the European River Elbe catchment. We provide new insights on how river fish can keep pace with projected habitat shifts as a consequence of climate and land use


FIGURE 4 Median distance of newly suitable habitats to the closest current edge population, $\mathrm{H}_{\text {dist }}$, for the moderate (white) and severe (gray) environmental change scenario in 2050. Circles and corresponding lines refer to direct comparisons of $\mathrm{H}_{\text {dist }}$, for specific species ( $n=17$ ). Violin plots show the probability density of the data over all species for the respective environmental conditions; bold vertical lines indicate the interquartile range between the first and third quartile and horizontal lines show the median. $\mathrm{H}_{\text {dist }}$ was significantly higher for the severe than for the moderate environmental change scenario (one-sided Wilcoxon signed-rank test; $V=5, p<.001$ )
change and how this is related to species-specific dispersal abilities and barriers to movement.

## 4.1 | Future habitat winners and losers

Predicted global changes affected all 17 modeled fish species in the River Elbe catchment. Specifically, the extent of habitat loss compared to habitat gain was highly variable among species. For both environmental scenarios, some species were identified as net habitat winners (e.g., B. barbatula, C. gobio) while others were identified as net habitat losers (e.g., A. brama, A. aspius; Table 2, Figs S1-S17). This is not surprising, as the response of (fish) species to environmental change is typically complex and will vary according to their environmental tolerances (Graham \& Harrod, 2009; Heino, Virkkala, \& Toivonen, 2009; Shuter, Finstad, Helland, Zweimüller, \& Hölker, 2012). Analogous to our study, a variable pattern of global change losers and winners has been previously observed, across species within e.g., birds (Tayleur et al., 2016), marine fish (Hiddink \& ter Hofstede, 2008), and freshwater macroinvertebrates (Domisch, Jähnig, \& Haase, 2011) as well as across entire species groups, e.g., in marine ecosystems (Fulton, 2011) and standing freshwater bodies (Rosset \& Oertli, 2011). Moreover, in a meta-analysis of climate change effects on 273 species, Gibson-Reinemer and Rahel (2015) found that range shifts measured in multiple geographical areas might be inconsistent even within the same species highlighting how other factors as biotic interactions and local, nonthermal abiotic conditions (e.g., land use) might supersede effects of changing climate.

Here, we modeled habitat shifts of fishes for combined climate and land use change scenarios. Our results revealed that in addition


FIGURE 5 Index of Fish Regions (IFR) in relation to (a) the median distance of newly suitable habitats to the closest current edge population $\mathrm{H}_{\text {dist }}$ and (b) the direction of the habitat shift, $\mathrm{H}_{\text {dir }}$ (negative values $=$ upstream, positive values $=$ downstream) for the moderate (white) and severe (gray) environmental change scenario in 2050, respectively
to temperature, precipitation and land use are also relevant drivers of fish distributions (Table S2). Thus, the interplay of multiple drivers as well as the topological location within the river network determines the fate of a species' habitat. In fact, for many species-in particular lowland species (e.g., A. brama)-precipitation seasonality (i.e., hydrological variation within a year) was a major climatic driver and negatively related to species presence. Accordingly, those species might be negatively affected by changes in precipitation (i.e., more pronounced contrast between wet and dry periods and regions) as predicted for mid-latitudes (IPCC, 2013). In contrast, headwater species (e.g., S. trutta) were almost unaffected by precipitation seasonality. From the land use variables, specifically the class "other" including inland water bodies and wetlands was most relevant and


FIGURE 6 Differences in species-specific dispersal compensation $H_{\text {dispersal:gain, }}$ between two scenarios of longitudinal connectivity: $\mathrm{B}_{\text {ref }}=$ reference scenario of full longitudinal connectivity, $\mathrm{B}_{\text {pres }}=$ present scenario with 599 impassable barriers. Circles and corresponding lines refer to direct comparisons of $\mathrm{H}_{\text {dispersal: gain }}$, for specific species $(n=17)$. Violin plots show the probability density of $\mathrm{H}_{\text {dispersal:gain }}$ for $\mathrm{B}_{\text {ref }}$ and $\mathrm{B}_{\text {pres }}$ and for the moderate (white) and severe (gray) environmental change scenario in 2050, respectively; bold vertical lines indicate the interquartile range between the first and third quartile and horizontal lines show the median. $\mathrm{H}_{\text {dispersal:gain }}$ was significantly different between $\mathrm{B}_{\text {ref }}$ and $\mathrm{B}_{\text {pres }}$ for both environmental change scenarios (two-sided Wilcoxon signed-rank tests, $p<.005$ )


FIGURE 7 Species-specific dispersal compensation $\mathrm{H}_{\text {dispersal:gain }}$ (i.e., proportion of newly suitable habitats that can be reached by dispersal) in relation to (a) the median distance of newly suitable habitats to the closest current edge population $\mathrm{H}_{\text {dist }}$ and (b) the direction of the habitat shift $\mathrm{H}_{\text {dir }}$ (negative values $=$ upstream, positive values = downstream) for the moderate (white) and severe (gray) environmental change scenario in 2050
commonly positively related to species presence (Table S2). This is in close agreement with other studies emphasizing the relationships between riverine habitats and connected inland and floodplain water bodies that promote in particular lowland fishes (Schiemer, Zalewski,

## \& Thorpe, 1995).

Furthermore, our results also stress the high complexity that contributes to the observed species-specific responses toward multiple environmental drivers: First, boosted regression trees allow for nonmonotonic and discontinuous, threshold-dependent responses toward single variables. Second, the environmental variables might interact with each other and jointly buffer or amplify species
responses. Third, although the applied future land use scenarios follow a gradient of human intervention (Baseline < BAMBU < GRAS), the changes in single land uses vary regionally and between the scenarios (see Figs S2-S5 in Radinger et al., 2016). For example, arable land is predicted to decrease in the northeastern areas and to increase in western areas of the catchment; Grassland in the River Elbe catchment is only predicted to decrease at the moderate scenario, but not at the extreme scenario. These multiple sources of complexity might also contribute to the observed diverging projections of suitable habitats for four species (Esox lucius, G. cernuus, Alburnus alburnus, Silurus glanis) between the moderate and the
severe scenario (Table 2). We could not detect a single common variable or single interaction between variables related to the opposing pattern of gains and losses between both scenarios for these species. However, species-specific analyses of variable interactions and nonmonotonic responses, as well as determining environmental tipping points and how these interact with spatially nonuniform changes in land use was beyond the scope of this study.

Corresponding to our results, Comte and Grenouillet (2013) found a highly variable pattern of range expansions and contractions among stream fishes in French rivers from 1980 to 2009. While they found an overall trend of habitat contractions, habitat expansions were particularly prevalent at the downstream range limit for several upstream and midstream species (Comte \& Grenouillet, 2013). By comparison, both habitat gains and losses projected in our study were apparently located at the upper range limits (see Figs S1-S17).

Despite the variable response to projected global environmental change, we found a negative relationship between predicted net gains of suitable habitats ( $\mathrm{H}_{\text {netgain }}$ ) and fish body size. In particular, the extent of suitable habitats was projected to expand for smallerbodied fishes, whereas that of larger-bodied fishes was projected to contract (Figure 3a). A similar trend has already been observed previously for fish of the North Sea where smaller fish increased their geographical range, whereas the range of larger fish decreased, which has been partly attributed to climate change (Hiddink \& ter Hofstede, 2008). In regard to this relationship and supported by their own empirical data, Daufresne, Lengfellner, and Sommer (2009) suggested Bergmann's rule (Bergmann, 1847) as a potential ecological theory underlying this pattern. Bergmann's rule states that warm regions tend to be inhabited by relatively smaller-bodied species than cold regions, which has also been evaluated in fish (e.g., Atkinson, 1994; Blanchet et al., 2010; Rypel, 2014). Although the mechanisms underlying a body size-temperature relationship in ectotherms have remained controversial (e.g., Belk \& Houston, 2002; Walters \& Hassall, 2006), it has been related to the size at maturation, which is larger for organisms raised in cold temperatures than for organisms raised at warmer temperatures (e.g., Atkinson, 1994). Accordingly, with increasing temperature and thus with a spatial expansion of relatively warmer habitats, smaller-bodied species should benefit and also increase their range sizes. Thus, Bergmann's rule might be partly reflected also in our results. However, as we did not exclusively investigate temperature effects on species habitat shifts but also changes in precipitation and land use, the attribution of the detected body size-range relationship solely to Bergmann's rule might be compromised. Moreover, larger-bodied, warm-water species (e.g., A. brama, Sander lucioperca) particularly responded to summer temperatures (BIO10, Table S2). Increasing temperatures (and thus elevated evapotranspiration) combined with decreasing precipitation in summer as predicted for the River Elbe catchment will lead to reductions in summer discharge. It is hypothesized that reductions in discharge constitute rather a limiting factor for larger-bodied species especially in relatively smaller tributaries, causing their habitats to contract at their uppermost distributions (i.e., leading to a relative downstream shift of the "center of distribution"). In accordance, for
a small lowland river, Guse et al. (2015) showed that the impacts of climate change-induced reductions in discharge on fish habitat suitability scales with body size where larger species (e.g., Leuciscus leuciscus) were more negatively affected than smaller species (e.g., Phoxinus phoxinus). Thus, changes in temperature and precipitation as well as consequent (seasonal) changes in discharge might constitute a further explanation of the detected relationship between habitat gains and losses and fish body size.

## 4.2 | Habitat distribution shifts

In addition to projected changes in the extent of suitable habitats, also the direction of habitat shifts was variable across species-with seven species being predicted to shift upstream and ten downstream (cf. Figure 5b). Given the branching characteristic of rivers an unambiguous assignment of habitat shifts to either up- or downstream proves rather difficult (e.g., a tributary might be considered downstream as well as upstream relative to the position within the main stem). Hence, we calculated shifts of the mean stream order (Strahler, 1957) between a species' current and future distribution as a proxy for directional shifts.

The detected downstream shift seems inconsistent with the frequently proposed uphill shift induced by climate warming. However, Lenoir et al. (2010) reported unexpected downhill shifts also for other species groups (e.g., plants, insects). In particular, the interaction of land use and climate change might constitute a potential mechanism for deviations in the direction of habitat shifts, downhill/ downstream versus uphill/upstream (Lenoir et al., 2010), which is also supported by our results. Previous studies mainly focused on the response of cold-water fishes to climate change and here in particular on temperature effects (e.g., stream isotherm shifts, Isaak \& Rieman, 2013) causing upriver shifts with associated habitat losses at the downstream range limit (e.g., Rieman et al., 2007). Our study expands previous works by including cool- and warm-adapted fish species (e.g., many cyprinids), which are not necessarily limited by warming stream temperatures since many of them have high preferred temperatures (Shuter et al., 2012). However, these species may be affected by other factors as changes in land use and/or precipitation patterns (Graham \& Harrod, 2009). For example, the greatest land use changes in the River Elbe catchment between baseline and severe future conditions are projected for the two most dominant land use classes "arable land" (decrease from $46 \%$ to $39 \%$ ) and "forest" (increase from 30\% to 36\%). In particular, the small-bodied species B. barbatula and C. gobio that were positively related to forest and negatively to arable land (Table S2) substantially benefited from projected land use changes.

Interestingly, the results showed that especially lowland fish species (IFR > 6.5) tend to shift downstream, whereas headwater species (low IFR, cold-water species) tend to shift upstream (Figure 5b). As a consequence, at the level of entire species assemblages the IFR is likely to increase especially in headwaters. This is in close agreement with a previous large-scale European study that reported increases in IFR with climate change at the species assemblage level
were most pronounced in headwaters (Pletterbauer, Melcher, Ferreira, \& Schmutz, 2015). We argue that the reportedly more synergistic and additive interactions of climate and land use change in downstream parts (Radinger et al., 2016) as well as (seasonal) changes in flow conditions contribute to the projected downstream shift of lowland species in this study. However, the underlying mechanism of this downstream shift deserves further species-specific analysis, which was beyond the scope of this study. Nevertheless, most of the study species remain in their original longitudinal zonation (within $\pm 0.5$ stream orders compared to the current conditions; Figure 5b). This might also be attributed to Shreve stream order, which was a decisive predictor for most species, thus contributing to the continuance at a specific longitudinal region. Thus, our results suggest that global environmental change is not likely to override general associations of fishes to a specific longitudinal region within a river network (i.e., Index of Fish Regions, Dußling et al., 2004).

## 4.3 | Distance of habitat shifts and dispersal compensation

We found that the abilities of species to track environmental change were jointly determined by both, species-specific dispersal and the extent of predicted habitat shifts. Here, the distance between source populations (Radinger, 2015)-in particular populations at the edge of current distributions-and newly suitable habitats appears decisive for potential future colonizations. The modeled species have to disperse on average 15 km ( $\mathrm{H}_{\text {dist }}$ by 2050) to keep track with future habitat shifts, i.e., to reach future suitable habitats. Interestingly, the differences in the distances to newly suitable habitats (i.e., habitat shifts) between the moderate and severe scenario were rather marginal, yet significant (median: 14 km vs. 16 km ).

Moreover, the distances from current edge populations to newly suitable habitats were larger for headwater species (low IFR, Figure 5a) than for lowland species. One likely explanation for this pattern is the dendritic characteristic of rivers (Peterson et al., 2013). Specifically, newly suitable habitats of headwater species might be gained in streams in close proximity (short Euclidian distance) to their current distribution; however, these habitats might be topologically distant as fish are typically constrained to disperse along river corridors (Altermatt, 2013; Fagan, 2002).

As a consequence of the distance of habitat shifts and the varying species-specific dispersal abilities, the degree to which species can track environmental change ( $\mathrm{H}_{\text {dispersal:gain }}$ ) is variable among species. On average over all modeled species and at full longitudinal connectivity ( $\mathrm{B}_{\text {ref }}$ ), $71 \%-83 \%$ (Table S3) of the future gained habitats can be reached by dispersal. Here, we modeled rather long-term projections of species dispersal ( 50 years). As long-term dispersal typically entails higher predictive uncertainties and might be influenced by stochastic elements of environmental variability (e.g., hydrological extreme events) and individual dispersal (Melbourne \& Hastings, 2009), the interpretation of the results should be cautious and primarily allows for relative comparisons among species. Nevertheless, the dispersal model indicated that certain species are likely to
perform well in tracking predicted habitat shifts $\left(\mathrm{H}_{\text {dispersal:gain }}>99 \%\right.$; e.g., A. aspius), while others will perform considerably poor ( $\mathrm{H}_{\text {dispersal:gain }}<10 \%$; e.g., C . gobio) and thus will presumably not be able to keep pace with environment change even in the long run. In accordance, Comte and Grenouillet (2013) detected a mismatch between climate change velocities and observed range shifts of fishes in French rivers, indicating that the majority of stream fish are not able to keep pace with climate change.

We found that in particular smaller-bodied fish ( $<200 \mathrm{~mm}$ ) were most vulnerable and least able to track future environmental change (Figure 3d), which can be related to two mechanisms: First, the projected habitat shifts (i.e., $\mathrm{H}_{\text {dist }}$ ) were larger for smaller-bodied fish (Figure 3c). Second, smaller-bodied fish are considered weaker dispersers with smaller average dispersal rates. Thus, regarding the latter, the observed relationship is not surprising as fish length is an implicit parameter of the applied dispersal model (Radinger \& Wolter, 2014). Interestingly, the results revealed that downstream shifting species are better in tracking these shifts than those shifting upstream. This might be again influenced by the dendritic structure of river networks where in upstream directions the dispersal probability is split at each confluence (e.g., fish might enter tributaries or remain in the main stem when moving upstream). Previous studies have already emphasized the importance of the network structure of rivers affecting many ecological processes such as dispersal and population dynamics (e.g., Altermatt, 2013; Grant, Lowe, \& Fagan, 2007); however, there is little empirical work that explicitly investigated the role of the dendritic structure of rivers in relation to the biotic response toward future environmental change (e.g., Inoue \& Berg, 2017). Accordingly, we strongly encourage further analysis of how connectivity and the distinct shape of river networks interact with distributional patterns and species dispersal and how this affects the overall capability to keep pace with future environmental change.

Our results showed that fish will be affected by barriers that restrict their movement and thus their capability to track future habitat shifts (Settele et al., 2014). Hence, improvements to the longitudinal connectivity are essential also in the light of environmental change. The results showed that impacts of barriers can be substantial (Figure 6), in particular for larger-bodied species as they exhibit a higher likelihood to encounter a barrier during upstream movement, but some (smaller) species are rather restricted by their dispersal ability. For example, E. lucius shows a net habitat gain of 128 km (Table 2, moderate scenario); however, when accounting for dispersal the net gain is only 54 km and becomes even negative (i.e., net habitat loss; -189 km ) when accounting for both dispersal and movement barriers that limit recolonization. Therefore, coupling a dispersal model considering barriers with predictions of range shifts provides a valuable approach for river management. It allows identifying barriers that have highest impact on river fish and which should be made passable in future. In general, the impact of movement barriers depends on their spatial location relative to the distribution of suitable habitats and on the species-specific dispersal abilities (Radinger \& Wolter, 2015). This study focused on movement barriers as a major cause of fragmentation in rivers. However, we
acknowledge that there are also other factors causing habitat fragmentation such as unsuitable habitats and natural or anthropogenic landscape features (e.g., water withdrawals, waterfalls) that might restrict species' dispersal (Fuller, Doyle, \& Strayer, 2015), which have not been considered in this study.

To our knowledge, this is the first study that explicitly couples projections of species habitat shifts with a spatially explicit dispersal model to simulate and assess the ability of fish to track future environmental change. However, there are several limitations that may influence our results related to (i) the predicted habitat shifts based on future environmental change, and (ii) the predicted dispersal of fishes to compensate for shifting habitats. In this study, we used climate and land use variables to predict suitable habitats; however, the suitability of riverine habitats for fish is influenced by many other factors that were not included such as hydromorphological and hydraulic variables (e.g., flow velocity, depth), bottom substrates or instream and riparian habitats (e.g., large wood, bank structures; Radinger, Wolter, \& Kail, 2015). For example, large habitat gains are predicted for C. gobio (related to projected decreases in arable land use); however, this species strongly depends on coarse substrates (Knaepkens, Bruyndoncx, Bervoets, \& Eens, 2002), which might still constitute a limiting factor in these areas. Furthermore, we only analyzed fishes whose distributions could be modeled with high accuracy based on commonly available climate and land use variables. We assume, by including further hydraulic and hydromorphological predictors, additional species could be modeled with high accuracy, thus providing a much more differentiated overall picture on future habitat shifts. Also the choice of the underlying statistical model and the selection of the climate and land use change data for current and future conditions might influence the results (e.g., Buisson, Thuiller, Casajus, Lek, \& Grenouillet, 2010). Moreover, a key assumption underlying environment-habitat models is that a species' habitat niche remains constant through time. However, it is anticipated that species show phenotypically plastic responses to changing environmental conditions, which might result in evolutionary adaptive responses, i.e., species might be able to adapt to future environmental change, especially those with short generation times (Crozier \& Hutchings, 2014; Merilä \& Hendry, 2014).

Moreover, long-distance dispersal is driven by rare long-range dispersal events, which is not adequately reflected by dispersal kernels that assume average, smooth dispersal patterns (e.g., Hallatschek \& Fisher, 2014). Recently, Wells et al. (2017) evaluated the efficacy of leptokurtic dispersal kernels to predict the dispersal of a river fish (Cottus carolinae) and found that for hydrologically stable conditions empirically observed dispersal patterns were similar to model predictions by Radinger and Wolter (2014). Nevertheless, we acknowledge that the realization of a probabilistic dispersal kernel strongly depends on individual decisions to move which is inherently stochastic (Melbourne \& Hastings, 2009; Radinger et al., unpubl.), and is conditioned by environmental extreme events (e.g., flow pulse) that might disrupt dispersal patterns (Wells et al., 2017). Moreover, we classified one-third of a population as mobile, which corresponds
to a commonly observed mean value among fishes (Radinger \& Wolter, 2014). However, we acknowledge that the mobility of a population, and thus the rate of spread, might be variable depending on e.g., habitat quality (McMahon \& Matter, 2006) and individual behavior (Fraser, Gilliam, Daley, Le, \& Skalski, 2001). Furthermore, we note that long-term projections of species spread are co-determined by the sizes of source populations and population growth "along the road" (Holmes, Lewis, Banks, \& Veit, 1994; Radinger et al., unpubl.), which have not been included in this study. Thus, regarding the limitations of the dispersal model the analyses of this study can be regarded as gross approximations of species dispersal capabilities. Hence, we encourage the further development of process-based models and empirical studies to investigate the mechanistic interplay of habitat suitability, population dynamics, and species dispersal to allow for more profound evaluations of species abilities to track future environmental change.

This study focused on shifts of species' habitats induced by future climate and land use changes and related dispersal movements. However, recent studies emphasized that future environmental change entails ecological impacts that are beyond species' range shifts such as changes in community composition and the loss of biotic interaction among species (Radinger et al., 2016; Valiente-Banuet et al., 2014), effects on demographic rates and population viability (Selwood, McGeoch, \& Mac Nally, 2015), and changes in body sizes and growth rates (Ruiz-Navarro, Gillingham, \& Britton, 2016).

In sum, our results predict an overall future net loss in suitable habitats of the modeled fish species in the River Elbe catchment in response to climate and land use changes by 2050. In particular, the interaction of temperature, precipitation, land use, and spatial location within the river network as well as potential, nonmonotonic species-environment responses contributed to the complex pattern of habitat shifts among species. Furthermore, the coupled fish dispersal model indicated that suitable habitats might shift faster than many species disperse, i.e., species' dispersal ability and movement barriers limit the colonization of future suitable habitats. In general, larger fish had smaller net gains in habitat, but less dispersal limitation overall. This is because they are typically better dispersers and had smaller distances to travel in a more downstream direction. Conversely, small fish had larger net gains in habitat but were rather dispersal limited. Movement barriers will further restrict fishes' ability to respond to climate and land use changes, particularly that of lar-ger-bodied species.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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