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The role of river connectivity in the distribution of fish in an anthropized watershed

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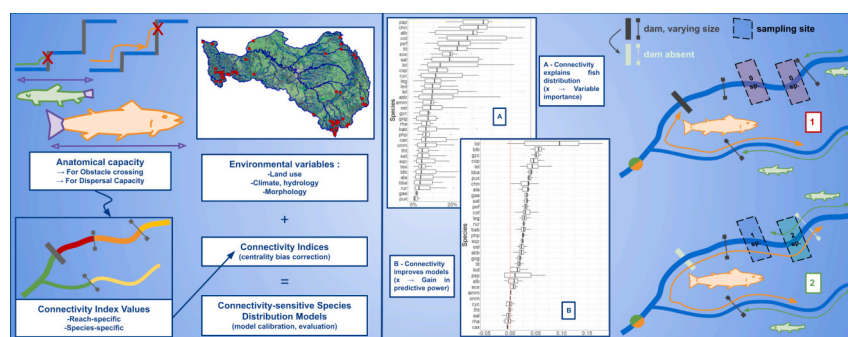
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HIGHLIGHTS

- Fish Species Distribution Models are improved by adding new connectivity indices.
- Barriers and dispersal limitation shape non-diadromous fish distribution.
- For most species, high connectivity is linked to higher probability of presence.
- Indices accounting for ecological zonation are relevant for all but two species.

GRAPHICAL ABSTRACT



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ABSTRACT

The ongoing biodiversity crisis is especially severe in freshwater habitats. Anthropized watersheds, such as the Seine-Normandie basin in France, are particularly affected by human interference. The study of fish species distribution in watersheds often relies on environmental drivers such as land use or climate. Yet, fish are also exposed to river connectivity constraints, such as dams, that are understudied despite their potential impact on fish dispersal. For this study, we investigated the role of local and whole-basin longitudinal connectivity in fish distribution. We designed connectivity indices based on river network characteristics and specific mobility for 33 species and included these indices in species distribution models, taking into account habitat suitability, to quantify their role in species distribution. Keeping the best index for each species, an average of 29% – and up to 57% – of explained fish distribution, depending on species, was tied to connectivity. We found that high connectivity often had a significant and positive linear effect on species presence probability. Using a scoring system across multiple indices, we found connectivity indices that took local context into account (e.g. the ecological zonation of the river) performed consistently better than others. Indices that took only dispersal limitation into account scored higher for 12 species, while barriers, alone, were the most important constraint for 10 species, the

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remaining 11 being associated with both. This work points to fragmentation as a cause for lower likelihood of presence for many non-diadromous river fish species. It highlights the importance of considering both physical and functional connectivity constraints in fish distribution and provides additional insights for river management and restoration.

Abbreviations

ACI	Adjusted Connectivity Index
DS, MS, US, HW	Downstream, Midstream, Upstream, Headwaters
RCI	Reach Connectivity Index
SDM	Species distribution model
ZCI	Zonation-sensitive Connectivity Index

1. Introduction

Freshwater ecosystems, especially watercourses, are among the most diverse ecosystems in terms of species richness (Dudgeon et al., 2006). However, they are also among the most threatened (Collen et al., 2014; Costa et al., 2021), jeopardized by anthropic pressures such as flow modification, habitat destruction or water pollution (Dudgeon et al., 2006). These alterations indirectly lead to the modification of nitrogen and carbon cycles (Vitousek et al., 1997) and riverscapes (Haidvogel, 2018), causing overall shifts, and often declines, in composition and richness of freshwater communities (Alric et al., 2021; Tison-Rosebery et al., 2022).

An important pressure put on watercourses, linked to human interference, is the spatiotemporal modification of connectivity (Zeigler and Fagan, 2014; Crook et al., 2015) – where connectivity is defined as the uninterruptedness of rivers. In riverine ecosystems, connectivity is generally considered along four dimensions: longitudinal (i.e., along the trajectory of watercourses), lateral (i.e., from the limit of the floodplain to the middle of the channel), vertical (i.e., from atmosphere to groundwater) and temporal - through seasonal and multi-year variation (Ward, 1989). Human activities impact all four dimensions (Birnie-Gauvin et al., 2020). Connectivity loss and habitat fragmentation are associated with extinction debt and loss in riverine ecosystem functions (Haddad et al., 2015) and have been linked to lower fish density and richness in rivers (Borthagaray et al., 2020; Radinger and Wolter, 2015). They are a limiting factor for fish distribution (Manfrin et al., 2020; Trigel and Degerman, 2015). Longitudinal connectivity in particular can be understood at different geographic scales, from a single reach to a whole drainage basin, leading to multiple conceptual frameworks for the conception of connectivity metrics in river networks (Amoros and Borrette, 2002; Cote et al., 2009; Pascual-Hortal and Saura, 2006).

Crucially, fish communities are especially negatively influenced by the loss of longitudinal connectivity (Shao et al., 2019) due to the presence of human-made barriers, such as weirs, dams, navigation infrastructures and power plants (Barbarossa et al., 2020; Sun et al., 2022). Other barriers include water pollution phenomena, like deoxygenation, linked to industrial activities and discharges from wastewater treatment plants (Dickey, 2021). Barrier infrastructures are widespread in European basins (Belletti et al., 2020; Duarte et al., 2021), leading to highly disconnected rivers with changes in sediment transport, flow and river depth (Schmutz and Moog, 2018), and available habitats (Horváth et al., 2019). The River Continuum Concept (Vannote et al., 1980) predicts a continuous longitudinal zonation of rivers, reflecting a gradient of physico-chemical conditions which shapes fish communities (Huet, 1954; Verneaux, 1977). This continuum is further impacted by the interruption of natural sediment transport dynamics, jeopardizing

riverine ecosystems (Mergou et al., 2012).

Another distinction can be made between structural connectivity, which is concerned with physical obstacles and networks, and functional connectivity, which takes into account the interaction between species functional traits and their environment (Mimet et al., 2013). Fish dispersal is limited by specific functional capacity for dispersal (Radinger and Wolter, 2014; Skalski and Gilliam, 2000) and circumscribed by the dendritic structure of rivers regarding upstream or downstream movements (Fagan, 2002). High dendricity multiplies dispersal opportunities (Altermatt, 2013), consequently, it is often used as a proxy to measure connectivity in rivers (Cote et al., 2009; Perkin and Gido, 2012). Barriers especially represent major structural hurdles for dispersal, as they hinder longitudinal connectivity, alter fish communities and cause species extirpations, for example by preventing access to breeding and feeding grounds and preventing recolonization (Barbarossa et al., 2020; Fagan, 2002; Granzotti et al., 2018). Both capacity for dispersal and crossing of obstacles are linked to fish size and observable anatomical characteristics (Radinger and Wolter, 2014), as well as related behavioral traits, such as spawning migration (Brönmark et al., 2014; Comte and Olden, 2018).

The influence of barriers on fish distribution in rivers is prominently discussed with diadromous species since obstacles block upstream migration to suitable breeding grounds and have a tremendous impact on species preservation in watersheds (Merg et al., 2020). Non-diadromous species are comparatively less studied. Yet, these fish constitute the overwhelming majority of freshwater species - about 109 fish species in France dwell in freshwater, and only 18 of them are diadromous (Keith et al., 2020). Including non-diadromous species in our understanding of the role of connectivity on river fish distribution is thus essential if we are to protect fish biodiversity in anthropized watersheds.

Niche modeling within fish species distribution models (SDMs) usually relies mainly on hydrological, physicochemical and meteorological gradients and riparian land use characteristics (Bucklin et al., 2015; Foley et al., 2005), since these are crucial aspects of habitat suitability (Ai et al., 2013). This approach ignores the effects of dispersal limitation and the potential role of longitudinal connectivity constraints in fish distribution (Bruneel et al., 2018), which are likely to impact non-diadromous fish distribution.

Our goal is to assess the relative contribution of connectivity in the explanation of non-diadromous fish species distribution compared to an environmental niche modeling approach that is agnostic to dispersal limitation and connectivity. Our specific aims are to: (i) develop and test a set of connectivity indices that take into account physical barriers, species-specific mobility characteristics and geomorphological local and whole-basin context of rivers, (ii) quantify the relative importance of connectivity in fish species distribution compared to habitat-related effects, and (iii) understand the relationship between connectivity constraints and fish distribution across different species and geographical scales. To address these aims, we built species distribution models for 34 fish species in the Seine basin (France) and nearby coastal rivers, in response to habitat-related variables and to a set of connectivity indices designed to study various connectivity constraints, both physical (e.g. obstacles, locks) and functional (i.e. linked to phenological traits).

Temperate-stream fish in the study area constitute a morphologically and ecologically diverse group of organisms (Keith et al., 2020). Smaller species tend to be more sedentary and incapable of overcoming some obstacles to dispersal, as do more bottom-dwelling species. Bigger individuals are more mobile (Radinger and Wolter, 2014), and some potamodromous species move along river networks over long distances.

We hypothesize that connectivity generally plays an important role in fish species distribution and that individual species may respond differently to connectivity, as shown by Van Puijbroek et al., 2021, doing so depending on specific functional characteristics. For instance, highly potamodromous species might be highly sensitive to fragmentation; inversely, some more sedentary species, less likely to require longitudinal movement during their life cycle, might respond poorly to longitudinal connectivity in models. Additionally, we expect species to respond differently to our indices depending on the properties of these indices. For example, species with high dispersal capacity might respond more strongly to indices which include barriers because these structures might affect their life cycles, often preventing feeding or breeding from occurring. We designed a set of connectivity indices that account for connectivity at different geographical scales: the indices that align with scales closest to the species' home range size are expected to perform better than the others. We hope to highlight precise ways in which the bespoke design of connectivity indices might help improve the understanding and prediction of fish distribution.

2. Methods

2.1. General context

2.1.1. Study area

The Seine-Normandie administrative basin in Northern France (Fig. 1) includes the Seine basin (about 80 % of the 95,000 km² surface area) and coastal rivers in Normandy. Inhabited by 18.5 million people, 13 million (70 %) of them within the Parisian Metropolitan Area, the region is mostly composed of lowlands (Fig. 1a). The current climate in the area is classified as Cfb – oceanic climate with warm summers – under the Köpper-Geiger Climate Classification (Kottek et al., 2006) over the whole basin (Strohmeier et al., 2024), with annual rainfall between 590 and 1300 mm. The Seine basin has been subjected to several works of agricultural drainage (Derex, 2001), channelization and construction of barriers. Several large-size dams located in the upstream part of the Seine watershed (the Grands Lacs de Seine) were built to limit the impact of major floods in the Paris urban area and sustain minimal discharges during droughts (Agence de l'Eau Seine-Normandie, 2019).

2.1.2. Network and barrier data

We used the single-strand PIREN-Seine river network for spatial processing (Silvestre, 2024). The ROE database - Référentiel des Obstacles à l'Écoulement (eng: Database of Flow Obstacles) (OFB, 2024), collected by the French Government Office for Biodiversity, provided information on obstacles (dams, weirs, sluices). Over 13,000 obstacles have been identified in the area (Fig. 1b). Heights for these obstacles were informed for 65 % of the obstacles in the ROE database. We estimated the height of the remaining 35 % by random forest regression (Breiman, 2001) using barrier type, state of deterioration, geographical factors, and river characteristics as predictors (see Appendix A). With an explained variance of 27.7 %, the quality of height information is thus less precise for one-third of known obstacles. It appeared better to use these estimates than removing these obstacles from our dataset.

2.1.3. Fish data

Fish data were retrieved from electrofishing sampling conducted between 2000 and 2020 (Observatoire des Poissons Seine-Normandie). Each sample was associated with a study site, date of sampling, and species count of individuals. The dataset is spread across 2145 study sites (Fig. 1c), for an average sampling density of one study site per 18 km of river and includes 5056 sampling events. Thirty percent of sites have been sampled at least twice, and up to 22 times. The observations were aggregated in study sites (Fig. 1c) so that detection in at least one sample is counted as a presence. We proceeded this way to increase the likelihood of non-detections being true absences (when multiple

samples were linked to the same study site) and to prevent pseudo-replication in predictor datasets. The basin is among the most intensely sampled in Europe (Rodríguez-Rey and Grenouillet, 2022) and counts 59 species of fish. For the purposes of this study, 34 species were selected (see Appendix B for a full list and selection criteria). We should note that one species (*Telestes souffia*, Risso, 1827) was later excluded from analysis due to unreliable model outputs, as explained in Section 3.1. Electrofishing was conducted following different protocols: i) either by boat or on foot - depending on river size; ii) to the full extent of planned depletion (i.e. population estimate by retaining fish after electrification, see Harris et al., 2016) or partially; and iii) through a single or multiple-pass depletion. We used a factor of sampling intensity to account for this disparity in sampling effort (see Appendix C for details).

2.2. Species distribution model predictors

Environmental predictors, used to provide a baseline descriptor of fish distribution in our models, were mainly related to hydroclimatology, river morphology, land-use, and riparian characteristics (Radinger et al., 2017) (full list available in Appendix C). We used seasonal air temperature and precipitation averages from the France-wide SAFRAN atmospheric reanalysis (Vidal et al., 2010), available on an 8 by 8-km regular grid, which were subsequently aggregated, from 2000 to 2020. Thermal peak - or the mean water temperature of the 30 hottest consecutive days - was estimated by 100 random forest regressions based on climatic, hydrologic and watershed characteristics following Beaufort et al. (2022) (average explained variance of 77.7 % - see Appendix D). Hydrological regimes and annual minimal monthly discharge with a 5-year return period were obtained from inverse distance weighted geographical interpolations of daily river streamflows retrieved from the HydroPortail (Leleu et al., 2014). Pluriannual average of oxygen, nitrate and ammonium concentration were obtained through simulations produced by the pyNuts-Riverstrahler model for 2017–2021 (Renaud et al., 2024).

We described land use using the THEIA land cover data (Thierion et al., 2021; Fig. 1b), using QGIS version 3.22.3 (QGIS Development Team, 2024). We did so across two complementary scales: 1) sub-catchment and 2) local (Sliva and Dudley Williams, 2001). Subcatchment scale land use was obtained through subcatchment shapefiles from the Seine-Normandie water agency, and intersected with THEIA land use cover categories in the following groups: Impermeable Surfaces (Urban) - Water Surface - Semi-Natural Vegetation (Forests) - Grasslands, Annual Crops, Vineyard and Orchards (Agriculture). Riparian vegetation and floodplain lentic freshwater cover were obtained by intersecting strip-shaped buffers (100-m wide, not counting river width, 3-km long, 500 m downstream and 2500 m upstream). The covariates related to reach characteristics (River straightness, Elevation, Catchment area, Slope) were obtained from the SYRAH-CE (Valette et al., 2012) and PIREN-Seine hydrographic network datasets (Silvestre, 2024). We applied a Principal Component Analysis (PCA) on all the quantitative environmental covariates except for connectivity indices and used five PCA axes (summing up to 85 % of the covariates variation) as distribution model predictors (see Appendix C for details).

2.3. Constraints to longitudinal connectivity

2.3.1. Fish traits and capacity for movement

Obstacle crossing and dispersal events of fish occur due to spawning, migratory and feeding behavior within biological cycles. Both obstacle-related and dispersal-related components of connectivity constraints depend on anatomical characteristics of fish, namely average length (L) and caudal aspect ratio ($AR = h^2/s$, see Fig. 2). Data on average body length was obtained from Baudoin et al. (2014), Keith et al. (2020), and complementary material (see Appendix B). Caudal fin aspect ratio was calculated from photographs taken from fishbase.org (Froese and Pauly, 2023) and the French National Museum of Natural History website

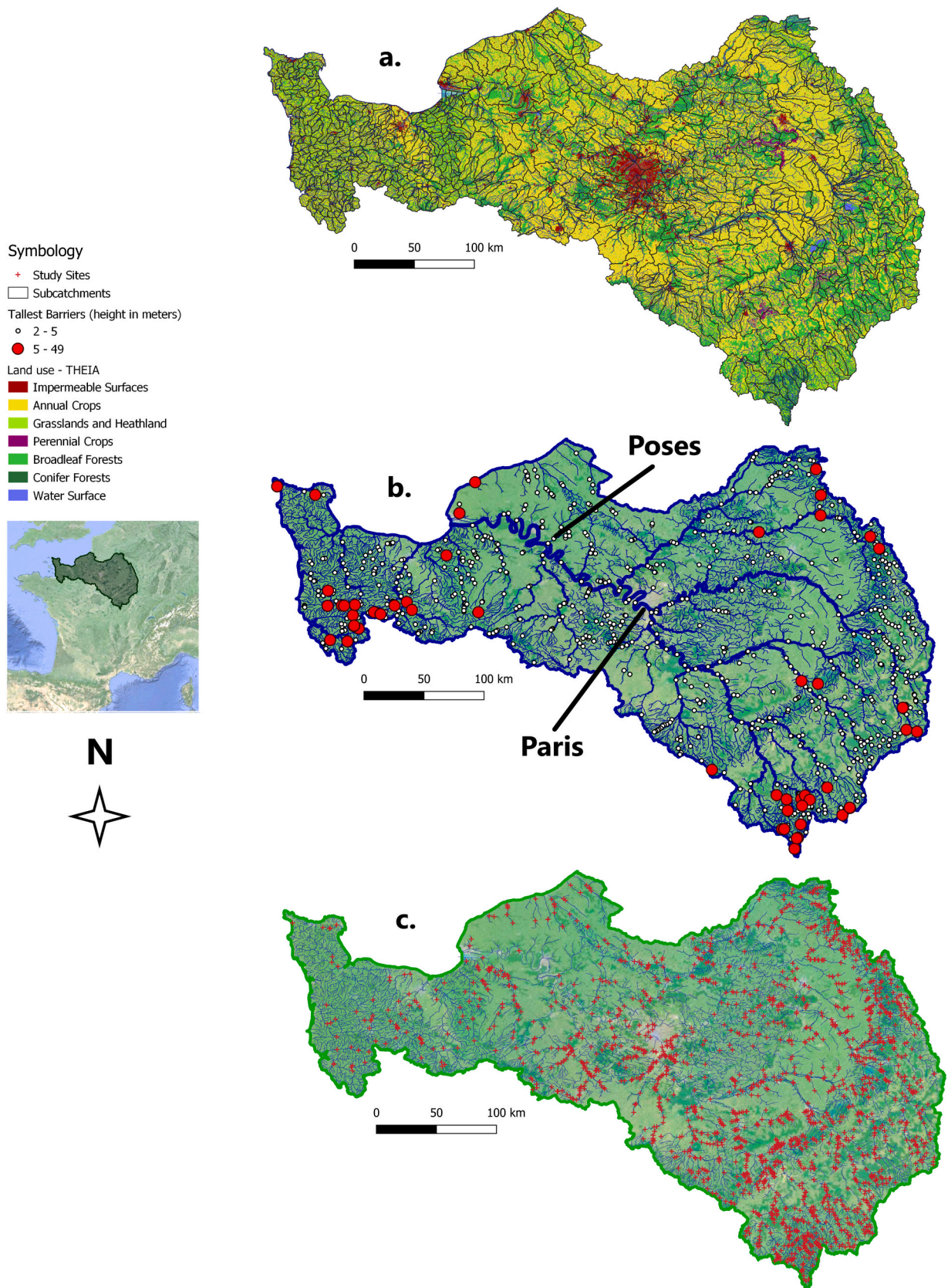
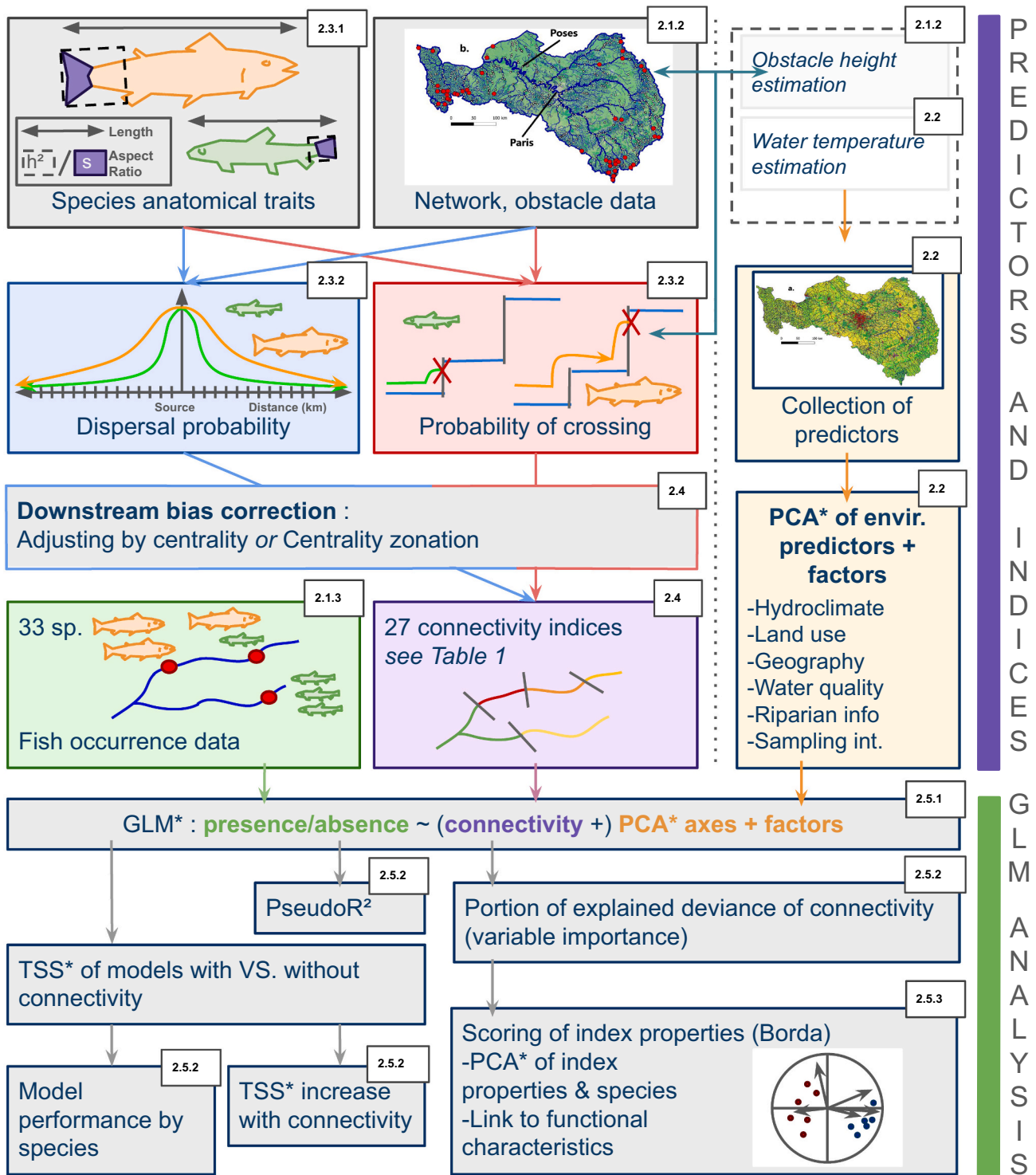


Fig. 1. Study area, the Seine-Normandie basin. A: Subcatchments and land use on the basin; B: The Seine-Normandie river network and its tallest dams (>5 m); C: Spread of the 2145 study sites. Source of land cover data and imaging: THEIA dataset (Thierion et al., 2021).



*GLM : Generalized Linear Models; PCA : Principal Component Analysis; TSS : True Skill Statistic

Fig. 2. Graphical summary of the method used for connectivity index calculation and model analysis. Presentation of modeling steps from anatomical characteristics to obstacle crossing and dispersal kernels, and their integration into reach-specific connectivity indices, to TSS gain and variable importance associated to connectivity. Dispersal kernels based on [Radinger and Wolter \(2014\)](#), index calculation based on [Baldan et al. \(2022\)](#). On the top-right corner of each box is the section number in which additional information can be found.

(Muséum national d’Histoire naturelle, 2021) processed through a freeware raster graphics editor (paint.NET 4.3.1, latest version available <https://www.getpaint.net/>). We used these measurements to estimate jumping height and capacity for dispersal for each species ([Radinger and Wolter, 2014](#)). A graphical summary of the methodological steps to the

calculation of connectivity constrains and their integration in connectivity indices can be found on [Fig. 2](#).

2.3.2. Obstacle permeability and fish dispersal

We considered obstacle crossing asymmetrically (upstream and

downstream) and determined crossing probabilities for each obstacle and species. For upstream crossing, we relied on jumping height as expressed in Meixler (2021), compared to obstacle height, to determine obstacle crossing. We followed Baudoin et al. (2014) both for functional grouping of fish with respect to obstacle crossing and for information on downstream crossing. A full explanation of obstacle crossing probability calculation can be found in Appendix E.

To model the dispersal capacity of fish, we opted for leptokurtic kernels for their closeness to the natural dispersal patterns of fish (Skalski and Gilliam, 2000), through a distribution function F of distance d (in m) from the source population (Eq. (1) below) (Radinger and Wolter, 2014):

$$F(d) = 0.66 \cdot \frac{1}{\sqrt{2\pi\sigma_{stat}^2}} \cdot e^{-\frac{d^2}{2\sigma_{stat}^2}} + 0.33 \cdot \frac{1}{\sqrt{2\pi\sigma_{mob}^2}} \cdot e^{-\frac{d^2}{2\sigma_{mob}^2}} \quad (1)$$

with σ_{stat} and σ_{mob} two standard deviation parameters within normal distributions, calculated through the {fishmove} R package (Radinger and Wolter, 2014), which represent the static and mobile components of fish populations and depend on caudal fin aspect ratio, specific average body length (L), Strahler stream order and the time frame considered for dispersal (Radinger and Wolter, 2014). The time frame was fixed for all species at seven years (Radinger and Wolter (2014) preconize the use of leptokurtic dispersal kernels for very long durations).

2.4. Connectivity indices

2.4.1. Reach connectivity index family (RCI)

To obtain build a set of 27 connectivity indices that combined different connectivity constraints (see Table 1 below), we adapted functions from the R package {riverconn} (Baldan et al., 2022) on R version 4.3.1 (R Core Team, 2023), which allowed for the use of leptokurtic dispersal kernels (R codes available upon request). {riverconn} uses a graph created from a directed river network (Erős et al., 2012) composed of N vertices (confluences, barriers, springs and estuaries) and N-1 edges with assigned permeability and weights (w_i). The package calculates factorized probabilities of connectedness I_{ij} , based on Rodeles et al. (2021) between every couple of reaches i and j (Eq. (2)):

$$I_{ij} = c_{ij}B_{ij} \quad (2)$$

where c_{ij} is the obstacle permeability (i.e., probability of crossing) and B_{ij} , the raw dispersal probability based on dispersal kernel calculation, between reach i and reach j. This method allows us to create three

Table 1

List of the 27 connectivity indices built and used in this paper with their properties depending on the connectivity constraints considered (whether physical barriers alone, or functional dispersal limitation alone, or both), and of the notations used for our longitudinal zonation strategy.

Index Notation	Family of indices	Properties	Zonation strategy	Corresponding hypothesis
RCI-D	Reach (3 indices)	barriers	none	Connectivity is best expressed at a whole-basin scale
RCI-L		dispersal		
RCI-LD		both		
ACI-D	Adjusted (3 indices)	barriers	$ACI = \frac{RCI}{\log(C+1)}$ (where C is Centrality)	Connectivity is most usefully described when adjusted to centrality
ACI-L		dispersal		
ACI-LD		both		
ZCI-D	Zonation-sensitive (3 × 7 indices)	barriers	Seven Zonations (see Appendix F) used as a weights factor in RCIs	Connectivity is best understood within the longitudinal zones of the watershed
ZCI-L		dispersal		
ZCI-LD		both		

For ZCI.

Seven zones: DS1/2-MS1/2-US1/2-HW.

DS = Downstream / MS = Midstream / US = Upstream / HW = Headwaters.

different types of indices, depending on if they take i) both constraints into account, ii) only dispersal ($I_{ij} = B_{ij}$) or iii) only obstacles ($I_{ij} = c_{ij}$). Reach Connectivity Indices (RCIs, Eq. (3)) correspond to the probability of connectedness between all edge pairs:

$$RCI_i = \sum_{j=1}^{n-1} I_{ij} \frac{w_j}{W} \quad (3)$$

where I_{ij} are the probabilities of connectedness from reach i to reach j, and W is the sum of custom weights w_j that allow accounting for habitat suitability differences of the receptor reach j. In the case of RCI indices, w_j are considered constant across all reaches.

2.4.2. Adjusted connectivity index family (ACI) and zonation-sensitive connectivity index family (ZCI)

The RCI naturally favors the largely undammed downstream reaches that are directly connected to many parts of the network leading to a spatial bias in the study of headwater species. To compensate for this bias, we calculated a set of adjusted indices. The downstream to upstream gradient was approached using Betweenness Centrality (Freeman, 1977) of reaches, a value independent of fish species, noted as C_i . For every reach i, betweenness centrality is the number of shortest paths passing through said reach in a graph, which in the case of dendritic networks, exponentially increases with downstreamness (see Appendix F for a visual representation of the centrality bias in base RCI). We first calculated an Adjusted Connectivity Index (ACI, Eq. (4)) as follows:

$$ACI_i = \frac{RCI_i}{\log(C_i + 1) + 1} \quad (4)$$

In order to investigate connectivity within a natural longitudinal zonation of the river, we then created a set of Zonation-Sensitive Connectivity Indices (ZCI) centered around seven zones, mimicking the seven Strahler order values in the network. These zones (Downstream 1 and 2, Midstream 1 and 2, Upstream 1 and 2, and Headwaters) are intended to reflect even categories of upstreamness within the river network, linked to successive biotic communities within a river continuum. We replaced the constant RCI weights w_j (see Eq. (3)) by a choice of seven lognormal and exponential functions of betweenness centrality (see Appendix F for an example, and curves related to betweenness centrality categories).

2.5. Species distribution model analysis

2.5.1. Building GLMs

To test the effect of connectivity indices on fish distribution while accounting for environmental effects, we used binomial generalized linear models (GLMs; R package {stats}, R Core Team (2023)) for each of the 33 species and 17 index types (i.e. 891 models) an ran cross-validations with ten subset-train-test sequences – 75 % of sites devoted to training. Linear and quadratic effects were tested. To characterize the role of individual connectivity indices on fish species, we also retrieved GLM coefficients and p-values of raw linear and quadratic terms of connectivity indices and classified the significant relationships as: i) positive linear effect; ii) negative linear effect; iii) quadratic effect.

2.5.2. Model performance and importance of connectivity

We assessed model performance with two criteria: the True Skill Statistic (Allouche et al., 2006) and Mc Fadden’s Pseudo-R-squared (Smith and McKenna, 2013). Threshold for presence and absence in predicted sets was determined through the maximization of TSS values (Manel, 2001). We calculated the gain in TSS of models that included connectivity compared with those that did not and tested the significance of the difference through Wilcoxon one-sample tests (‘wilcox.test()’ function in {stats} R package) with a p-value threshold of 0.05. TSS and PseudoR² were considered simultaneously to gather information

both on model skill and explanatory power, which are not necessarily correlated. PseudoR² values scale between 0 and 1 and are considered satisfactory above 0.2 and very good above 0.4. We also assessed the relative importance of our connectivity indices and other predictors based on the percentage of deviance explained by individual predictors (McCullagh and Nelder, 1999) as calculated by the function ‘importance.glm()’ from the R package {tornado} (Carnell, 2023). For a graphical overview of our analyses, please refer to Fig. 2.

2.5.3. Index properties and species functional response

In order to investigate functional relationships between index properties and species response, we relied on the Borda preferential scoring system (Reilly, 2002). Through the ranking and scoring of indices for each species in terms of explained deviance, we obtained information about the performance of index properties. The resulting values were analysed through PCAs (separated between significant positive, negative and polynomial relationships) to highlight groups of

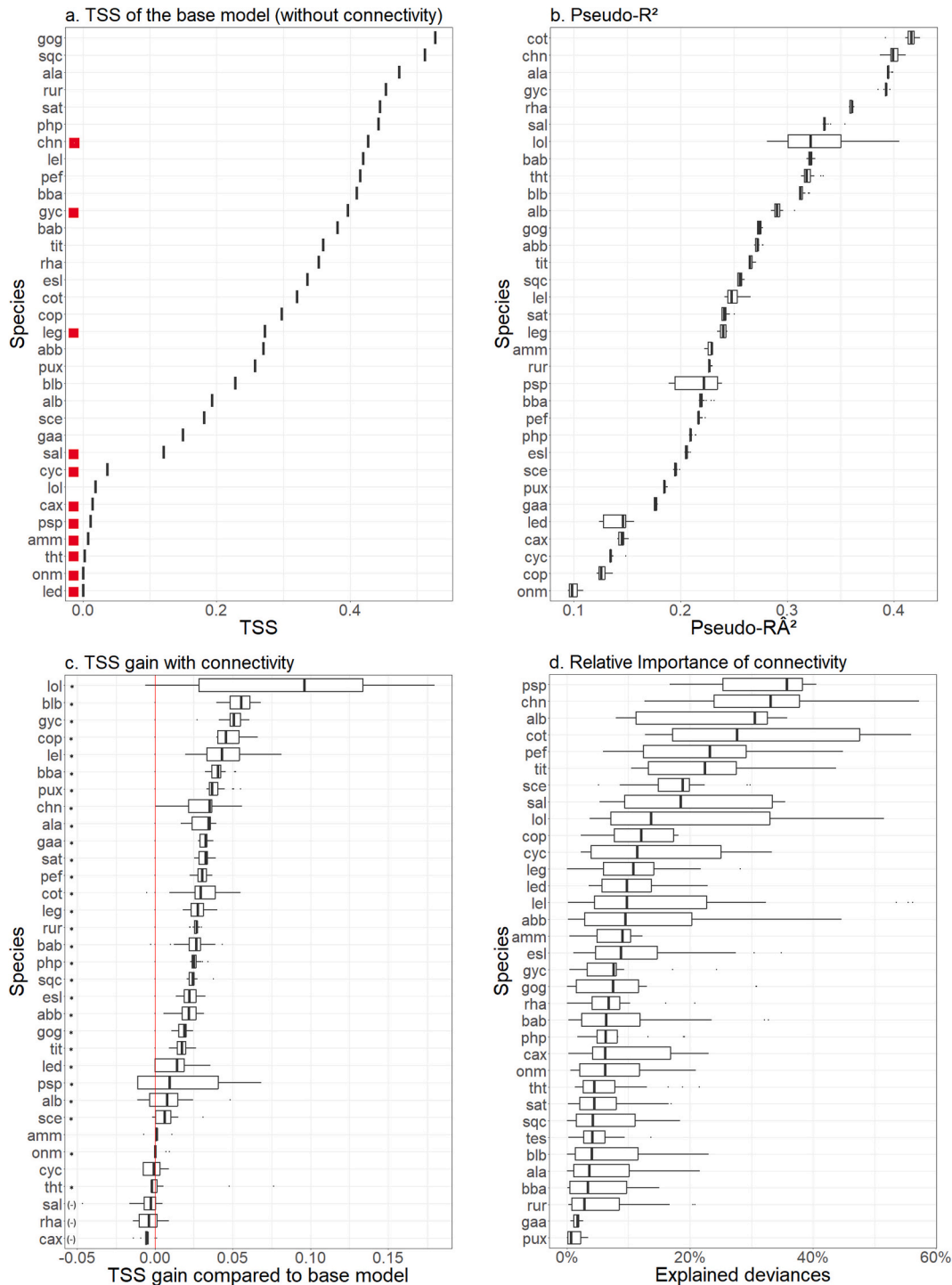


Fig. 3. Model and index performance. a: Boxplot of base model SDM TSS values for all species; red squares show non-native species. b: Boxplot of PseudoR² values across connectivity indices for all species. c: Boxplot of TSS gain due to connectivity indices (TSS of connectivity-sensitive SDMs - TSS of base SDM) across indices for all species; * indicates connectivity-sensitive models with significantly higher TSS values (p -value < 0.05, see Appendix I for full values); (-) indicates significantly negative values; blank is non-significant. d: Boxplot of values of connectivity relative importance (explained deviance) across indices for all species.

common carp, bitterling (rha), zander (sal) and Prussian carp. Including connectivity in our models caused an average gain of 0.023 TSS (0.043 when keeping the best indices) and up to 0.180. We found an increase in TSS of at least 0.020 for all species except six (catfish, carps, rainbow trout, bitterling and zander), and an increase of at least 0.05 for eleven species.

3.3. Importance and effects of connectivity across fish species and indices

3.3.1. Relative importance and significance of connectivity indices

The relative importance of connectivity indices compared to other predictors varied according to species and index type but were above zero for all species (Fig. 3c). For the nase, spined loach, dace and burbot, some indices explained over 50 % of explained deviance, whereas for three-spined sticklebacks, the best-performing indices explained at best 2.7 % of deviance. Across fish species, an average of 29 % – and from 2.7 % up to 57 % – of explained fish distribution, was tied to the best-performing connectivity index (see Fig. 3d) versus other predictors. Overall, out of 891 index-species distribution relationships, 364 were significant. Linear and quadratic term significance for connectivity indices differed across species (Fig. 4a; see Appendix H for a full table of significance), but linear effects described the relationship between connectivity and fish presence more consistently. For six species, the spined loach (cot), nase (chn), bullhead, burbot, schneider (alb) and dace (lel), >20 out of 27 indices had significant effects, while the ruffe and common carp had no index with significant effect.

3.3.2. Performance of the different connectivity indices

Overall, the ACI index family (Adjusted Connectivity Index) performed the best, each index significantly explaining more species than all others. Additionally, these adjusted indices significantly explained the distribution of 23 species (Fig. 4b) and presented the best-scoring indices for 8 species (Fig. 5). The ZCI index family (Zonation-sensitive Connectivity Index; see Section 3.3.4) significantly explained the

distribution of 30 species and presented the best indices for 26 species, across 21 indices with the most downstream and upstream zonations performing the best (both 9 species). The RCI family indices (i.e., non-adjusted Reach Connectivity Indices) presented the best indices in terms of importance for two species, the bleak (ala) and perch (pef) and significantly contributed to the distribution of 18 species in total. However, RCI did not rank first for any species in terms of Borda Scoring.

3.3.3. The influence of connectivity on the probability of fish presence

Across indices and fish species, effects of connectivity on fish presence, when significant, were mostly positive (Fig. 4b), with 32 % of positive effects (against 5 % of negative effects and 3 % of polynomial effects, the remaining being non-significant). Negative effects were found especially for the pumpkinseed (leg), stone loach (bba), rainbow trout, roach (rur), ninespine stickleback and tench (tit). Polynomial effects occurred in 14 species, including the zander (sal), for which it is the only significant relationship found. Very few species responded to only one index type, rather responding to multiple index families and indices within families.

3.3.4. Relationship between fish species response and connectivity index properties

Overall, we found no significant difference in importance between indices that took barriers into account (17.5 % average), and those that did not (18 % average). Similarly between indices that took dispersal into account (18 %) and those that did not (17 %). Indices that included only barriers scored better for nine species (e.g. bream [abb], bleak, barbel [bab]) (Fig. 5). Those that included only dispersal scored better for twelve species (e.g. stone loach, carps, pike), the remainder responding better to indices that took both constraints into account. The performance of the different zonation-sensitive indices across species often followed the fish ecological zonation from the source to the estuary with headwater and upstream ZCI (HW, US) performing best for some headwater species (e.g. three-spined stickleback, gudgeon, minnow) and

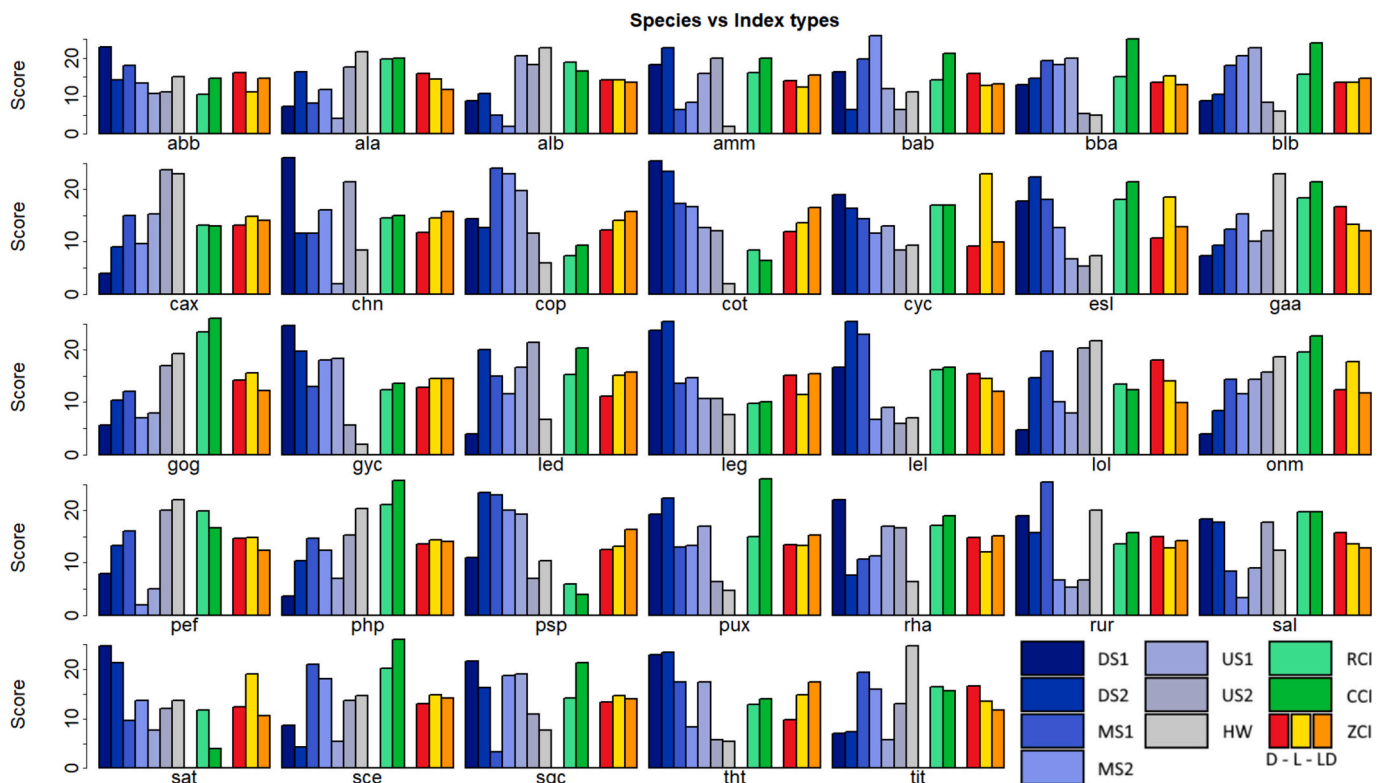


Fig. 5. Scoring of all index properties on all index-species combinations. Grouped by species, scaled bar plots, legend of index properties on the bottom right (DS1 to HW: ZCI zonations; D: Dams taken into account, not dispersal; L: Dispersal taken into account, not dams; LD: Dams and dispersal taken into account).

downstream ZCI (DS1, 2) performing best for some large river species (e.g. pike, bream, ruffe).

Twenty-seven fish species responded linearly and positively to connectivity indices and were used for PCA (see biplot in Fig. 6). This PCA, displaying the shape and strength of the responses of fish to index properties, allowed us to identify mainly four groups of fish with respect to their responses. Fish reacted to indices which included barriers (LD and D) differently than to those that did not (L), and so the first group, consisting of the crucian carps, burbot, spined loach, bullhead and topmouth gudgeon was driven by L indices as well as MS1-2, and US1-2 zonations. The second group, consisting of the barbel, nase, dace, minnow, trout, chub, grayling, schneider and catfish was mainly driven by D and LD indices as well as DS1-2 and HW zonations. A third group, mainly driven by RCI and ACI indices instead of ZCI, consisting of the stone loach, three-spined stickleback, pike, silver bream, perch, pumpkinseed and sunbleak, and a fourth one, driven by midstream ZCI and, to a certain extent, L indices, consisting of the bream, rudd, gudgeon, bitterling and rainbow trout. Nine species responded linearly and negatively to connectivity indices and strictly polynomial relationships were found for fourteen species (the corresponding PCA graphs can be found in Appendix J).

4. Discussion

4.1. Base distribution models and species-specific responses

Ignoring connectivity, we showed that fish distribution was mostly driven by Strahler order, hydrological region and elevation. Strahler order and elevation are regularly retrieved as a good predictor of fish distribution (Gonzalez-Ferreras et al., 2016; Markovic et al., 2012) as Strahler order allows for distinction of river size categories, and elevation is linked to a broader climatic gradient to which some fish are sensitive (Buisson et al., 2008). In the case of this particular study area, hydrological region and elevation are tied to basin geography and geomorphology. Fish species associated with the best model prediction performance were often the most widespread species in the basin because more occurrences allow for a more precise definition of the niche (Hernandez et al., 2006). Conversely, poorer model performance was mostly associated with non-native species, a persistent challenge in predicting non-native species distribution and expansion through SDMs (Rodriguez-Rey, 2019). This is in part due to the relative recency and localized nature of exotic introductions and the generalist ecology of many successfully introduced non-native species (Clavel et al., 2010). In fact, the prevalence of non-native fish in anthropized rivers like the Seine can be linked to a historical tendency for the release of non-native species (Lyach, 2022), which is to be contrasted with current practices

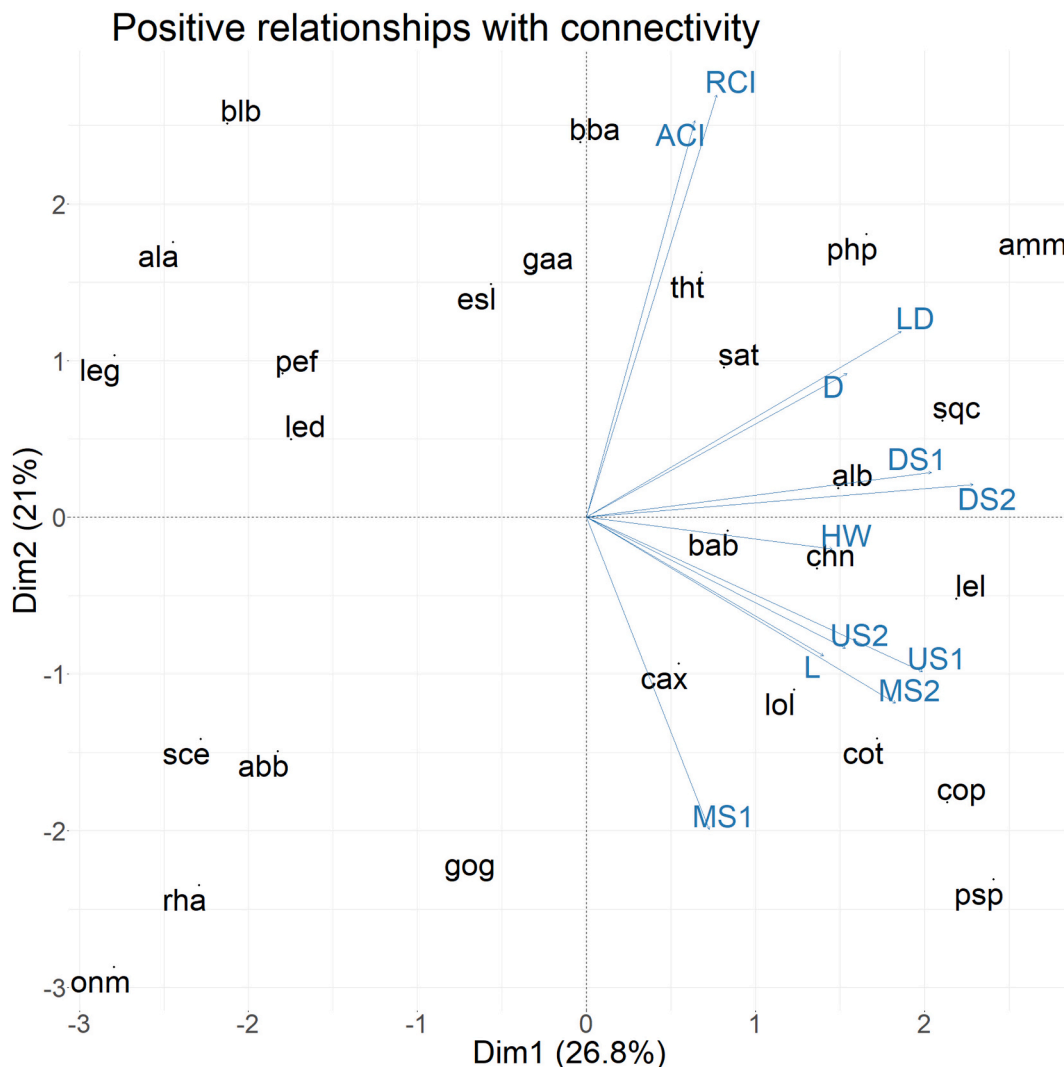


Fig. 6. PCA biplot of importance scorings across connectivity index properties and fish species (positive relationships only, 27 species).

which focus on species that are already present, a point discussed in Section 4.4.

4.2. The role of connectivity in the shaping of fish distribution

Connectivity indices improve our understanding of fish distribution. Our findings show that, in 31 species out of 33, longitudinal connectivity, through at least one index, contributes significantly to fish species once usual environmental constraints have been accounted for. This has already been amply demonstrated in diadromous species - eels, salmon, lampreys (Duarte et al., 2021; Nunn and Cowx, 2012). However, to our knowledge, this study enables us to finely demonstrate this relationship on an array of non-diadromous species for the first time: it highlights that river connectivity is a determinant of the distribution of most fish species and has to be considered in SDMs. The benefit of including longitudinal connectivity in species distribution models has been investigated in aquatic contexts, though with different methods for the calculation of connectivity and different geographical frameworks. In Branco et al. (2012), the use of metrics like a count of barriers upstream and downstream led to a minimal and generally non-significant impact of connectivity in non-diadromous fish distribution. However, the present study does corroborate the proportionally greater importance of environmental variables over connectivity indices in terms of importance. Contrastingly, Van Looy et al. (2014) retrieved more significant results by employing both local and large scale dam-density and cumulation metrics, although the study in question used more general bioindication metrics in lieu of fish presence-absence data, preventing specific discussion of connectivity and fish distribution. Additionally, it does not take network structure into account in its conception of longitudinal connectivity (Fullerton et al., 2010). Mahlum et al. (2014), used the Dendritic Connectivity Index as defined by Cote et al. (2009), which is conceptually closer to our indices than to barrier density, and similarly worked on a larger scale. Similarly to Mahlum et al. (2014), we find in most cases that connectivity remains a secondary predictor when compared to core environmental gradients and certain other anthropogenic pressures, although certain models did in fact show a substantial portion of explained variability, leading to a substantial average of 29 % of explained distribution for our best-performing indices across our species, although they did not systematically come with a high increase in prediction performance. Thus, larger-scale approaches to the measurement of connectivity, in contrast to proximity-based indices like local obstacle density, can be valuable, which may in turn render large-scale studies of connectivity more feasible. Lacking from the examples above are both the introduction of specific dispersal capacity and dam permeability as introduced by Rodeles et al. (2021), and the finer account taken of capacity for obstacle crossing and dispersal, which we argue allows us to achieve higher index performance and significance by distinguishing subtler nuances in the variations of longitudinal connectivity. Specifically, this paper used functionally informed (Skalski and Gilliam, 2000; Baudoin et al., 2014) and continuous information for both components, instead of strictly probabilistic - as in Clark et al. (1998), which was conceived for tree seedling dispersal and is often used in river fish as well - or binary, as presented in Baldan et al. (2022) for example. Significant gain in prediction performance was true for all but five species, but remained in the 2 to 5 % range in most cases (rising up to 20 %). These performances surely cement our expectations for connectivity indices as predictors in SDMs as mostly secondary, sometimes exceeding these expectations. However, one should take note that a 5 % increase in prediction performance in a 2000-site dataset can amount to up to an additional 100 study sites correctly predicted: this is considered a notable increase in the context of SDMs (Karger et al., 2023).

Among significant effects of connectivity indices in tested models, a majority were positive, indicating a co-occurrence of high connectivity reaches and increased fish species presence. Previous works studying the impact of river network connectivity tend to corroborate this result both through a modeling approach and on the field, as compiled for example

by Shao et al., 2019. The negative impact of connectivity loss on fish presence is often associated with the impairment of movement for diadromous and potamodromous species, preventing breeding and feeding migrations caused by obstacles (Fullerton et al., 2010; Merg et al., 2020). This may ultimately lead to local extirpations (Fagan, 2002; Kominoski et al., 2017) and changes in community structure. In contrast to potamodromous species, some resident species, less impacted by these phenomena, often had more contrasted responses to connectivity. We found six fish species for which it seemed to consistently impact fish presence negatively - all non-potamodromous except one, the roach, which occasionally engages in seasonal spawning and feeding migration (Brönmark et al., 2014). Investigating the causes of these relationships leads us to discuss a few complementary explanations: i) Methodology: With ZCIs, which accounted for the zonation of rivers, a high connectivity value can be linked to an absence (and vice versa) for species which simply do not dwell in corresponding zones (e.g. the pike, typically found in limnophilic habitats (Keith et al., 2020), is associated with a large amount of positive effects of connectivity for indices associated with zones where pike are often found, and negative effects for indices calibrated for upstream reaches). ii) Fish size: The few species that were associated with good model performance and significant negative effects of connectivity across indices were mostly small-bodied (roach, ninespine stickleback, stone loach, or pumpkinseed). Small size in freshwater fish is generally associated with a small home range size (Minns, 1995), and consequently with a lower likelihood of encountering a barrier given the mean distance between barriers (approximately 2.8 km). iii) Ecological preference: For example, this study recovered the stone loach as consistently negatively impacted by higher connectivity. According to Sun et al., 2022, stone loach populations were found to decrease following barrier removal perhaps due to a preference for fine sediments, which can accumulate close to dams. Inversely, the presence of other upstream small fish like the bullhead, which often dwell in riffle (Keith et al., 2020), is correlated positively to connectivity. Similarly, the ruffe favors eutrophic waters (Gutsch and Hoffman, 2016) and the pumpkinseed is a non-native generalist with important phenotypic plasticity (Keith et al., 2020; Mittelbach et al., 1999), both species may be well-suited to low-connectivity reaches. iv) Stochastic effects: For larger, generalist or non-native species such as the Eurasian carp, positive occurrences in low-connectivity reaches can be linked to intrusions from human-made lentic aquatic habitats such as quarries, fisheries, canals (Britton et al., 2011) or because low-connectivity reaches are a refuge against competition or predation from species with greater connectivity requirements. This has not been consistently verified for river fish in impounded river reaches but has been widely documented both for freshwater fish in other anthropogenic water bodies (irrigation pipes and canals, rice paddies, quarry ponds, see Chester and Robson, 2013). We hypothesize that the very few cases where significant effects of connectivity on fish presence were quadratic may be due to the aforementioned phenomena occurring in subsections of the network leading to parabola-shaped responses for these species.

4.3. Linking connectivity index properties and species-specific response

Correcting for local context improved connectivity indices. The three families of connectivity indices tested in our study, allowed us to test the effect of correction by centrality in index performance in fish distribution models and compensate for a centrality bias in RCI. We bring ample evidence that correction by betweenness centrality, both through a simple adjustment as in ACIs and through longitudinal zonation as in ZCIs, greatly improved connectivity importance (averaging 11 %) and model power (an average of one, and up to seven additional points for the grayling), invalidating our RCI-hypothesis in most cases.

ACIs ranked best overall in terms of significant species coverage and performed well for most species, suggesting that considering the local context of connectivity within the large-scale dendritic network would greatly improve index performance. However, in some cases, ZCIs

performed better than ACIs, especially for the spined loach, bullhead, pumpkinseed and topmouth gudgeon. These species are small, non-potamodromous, and can be found in most river types except the reaches closest to the estuary. They all responded significantly to most indices, but especially downstream and midstream indices. We can hypothesize that ZCIs are especially appropriate for these resident species either because contrarily to larger species, they might find themselves isolated between barriers in midstream reaches and be recovered as mainly midstream species or because the ACI is most useful for upstream reaches. The complementary performances of ACI and ZCI indices show that both a large-scale approach and a small-scale component of connectivity, dendricity and obstacles are needed to study the role of connectivity in fish distribution in diverse communities, although ZCI must be handled with warranted precaution due to their purposefully limited geographical scope. Previous studies generally pointed the importance of local context over large-scale connectivity for river fish (Mahlum et al., 2014; Van Looy et al., 2014) with the first arguing that the importance of connectivity in models is scale-dependent and the second investigating the importance of scale through dam-density metrics designed for different scales, using fish community bioindicators as response variables (Oberdorff et al., 2002), finding local context to be particularly important to understand the importance of connectivity on fish community structure. Our ACIs allow for a large-scale study of connectivity with greater relevance through a correction for the local context.

When examining the relative scoring of indices that do or do not take barriers and dispersal capacity into account, 23 species scored higher with indices that included barriers (either alone or in tandem with dispersal), leading us to conclude that barriers cannot be discarded as shapers in the current distribution of fish in rivers. These findings align with earlier works conducted at different scales that showed barriers as the main drivers of freshwater fish distribution and diversity (Shao et al., 2019; Birnie-Gauvin et al., 2020; Anas and Mandrak, 2021). The Seine-Normandie basin, our study area, happens to be very densely dammed, which makes it especially subject to fragmentation. However, very large dams (over 5 m high) are scarce (72) in the study area and are mostly restricted to specific areas in the basin (Southern Coastal Normandy, Morvan Mountains). As was corroborated in other geographical contexts (Baumgartner et al., 2022), large barriers do not seem to be the main focus of connectivity loss and its impact on fish distribution, implying that approaches taking smaller obstacles are essential to understanding the impact of connectivity constraints on fish distribution. In the process of restoring connectivity through the prioritized and thoughtful removal of barriers in the context of a durable restoration of riverscapes (Basak et al., 2021), small and mid-size obstacles are to be considered outright. Barrier prioritization methods such as the one developed by Baldan et al., 2022 can provide information on the most impactful dams for removal and connectivity restoration. Beyond fish conservation efforts, barrier removal is often linked to increased resilience and the improvement of local environmental conditions (Abbott et al., 2022; Kornis et al., 2015).

Through the study of index properties and their scoring, we were able to link index performance to network properties and fish functional traits, understood as specific characteristics of fish which interact with their environment. Dispersal was an essential component of longitudinal connectivity for 25 species. Thus, we show that even in long timespans, functional and behavioral limitations in dispersal are due to shape fish distribution alongside environmental gradients and barriers (Radinger and Wolter, 2015). Referring to our PCA output, we found that fish from the first group (the burbot, bullhead, spined loach, topmouth gudgeon) reacted strongly to midstream and upstream indices, and to indices which only take dispersal into account. These species are indeed found in these reaches (Keith et al., 2020), the burbot is potamodromous, and directly impacted by dams, but already restricted in the study area to a few suitable areas, presumably less disconnected, all other species are small and sedentary, and presumably less impacted by dams. Relatedly,

the second group (barbel, nase, dace, minnow, brown trout, schneider, chub and catfish) was driven by downstream indices as well as all indices that include obstacles. All species listed except the catfish are potamodromous and therefore more likely to be impacted by the presence of dams. This could be explained by the prevalence of heavily dammed rivers or large obstacles in highly downstream or central reaches (e.g. navigational locks) and the least central reaches (e.g. weirs on streams), compared with more intermediary reaches, which is consistent with our study area, though not true in all studied rivers. The third group was correlated to RCI and ACI, suggesting these species are more sensitive to large-scale than small-scale approaches for connectivity.

Both the third and fourth groups, interestingly, were represented by a majority of species which either i) routinely use peripheral habitats for feeding and spawning like the pike, gudgeon, sunbleak, bitterling, and both breams (Tales et al., 1996) or ii) consistently inhabit lentic habitats and backwaters within the floodplain (Keith et al., 2020; Sun et al., 2022) like the pumpkinseed, perch, rudd, bitterling, three-spined stickleback and stone loach. Relatedly, the first and second group species are generally not found in backwaters and use main river channels for spawning and breeding. This pattern has few exceptions (namely the rainbow trout and bleak on one side, and the catfish, topmouth gudgeon and crucian carp on the other). This suggests that species that are laterally and less longitudinally mobile for feeding, breeding or both, as well as those who often dwell in lentic habitats, might be sensitive to longitudinal connectivity in different ways, observable through this kind of analysis. Investigating lateral habitat use in fish species and its links to longitudinal dispersal and response to connectivity was not considered for this study, but might constitute an elucidating complementary study given the impact of lateral connectedness on fish conservation (Manfrin et al., 2020). The current predictors intended to represent lateral connectivity (floodplain forest and water cover), which did not reflect fish species use of peripheral habitats in terms of relative importance, may then have to be redesigned with multiscale and functionally-sensitive properties in mind, akin to longitudinal connectivity indices. An interesting perspective might be to investigate the potential for resilience in the context of anthropized watersheds and its hypothetical links to the ability of fish to exploit peripheral habitats. Functional links to connectivity like lateral habitat use incite us to push for further research on the subject of functional traits. Further analyses of specific responses to connectivity with different datasets would also allow to identify functional groups of dispersal and response to connectivity, potentially useful for instance in metacommunity analyses (Jeliazkov and Chase, 2024).

4.4. Limitations of this study

While converting electrofishing data into a working dataset, a few assumptions were made, namely i) non-detection over repeated samples constituted true absences and ii) a single detection was equated to prolonged presence, despite possible instances of punctual release (e.g. for fishing purposes). Fish species most likely to be released in rivers (e.g. trout, pike and other popular species for angling) are already widespread in the basin. Thus, by selecting only species detected on a large amount of sites, the few voluntary introductions remain less prominent in model training. We assume the unwelcome effects of these presumably rare events, i.e. a falsification of their range in the study area that impacts model results in a significant way, are unlikely to occur. Like any observation data, our dataset has probably been the subject of some sampling bias due to the different protocols used and imperfect detection. The sampling method was highly variable along rivers, as small headwater brooks allow for on-foot electrofishing, which is a much more exhaustive sampling method, whereas larger rivers require the use of a boat and a generally lower realized sampling intensity. However, the depth (over twenty years) and quality of the data collection (with 75 % of the data collected through near exhaustive electrofishing) probably compensated for this error, rarest species were excluded, and our models

took this sampling heterogeneity into account through a bias factor which was recovered as important across species. Similarly, our barrier dataset was the result of intensive data collection which is still ongoing today, which implies no guarantee of the completeness of the dataset, although the highest obstacles were presumed to be already known. Retrieval of other predictors followed several collection pathways, from independent regression (water temperature) to interpolation (hydrological variables) and gathering from several pre-existing datasets. Additionally, we used certain physical and geographical predictors such as elevation and Strahler order. These are not environmental predictors and thus must be considered with caution in niche models, but their use was nonetheless indispensable, as i) the environmental variables they are often proxies for (e.g. stream velocity, primary production) could not be obtained and ii) they represent an important part of explained deviance for most species (>15 % for 25 species for the first PCA axis which includes elevation and 30 species for Strahler order). Some of these predictors were partially or fully correlated with environmental variables, which was successfully taken into account by our PCA analyses. As for our connectivity indices we chose to use average body length and caudal fin aspect ratio as the main factors for obstacle crossing and dispersal. These tools were useful for most species, but lose some accuracy for a few edge cases like small species with high capacity for jumping, which were managed by categorical length averages, and large Eurasian carps, which cannot jump despite their size. Uncertainty linked to individual predictors, not assessed directly in this paper, nonetheless must be kept in mind. The choice of GLMs and the restriction to relatively simple predictors for this paper emerged from a compromise between model complexity (including nine environmental predictors, plus models repeated for 27 indices times 33 species) and model interpretability. If prediction had been the goal, more sophisticated models, machine learning and ensemble modeling, for example, would have led to higher performance and TSS values.

5. Conclusions

The significant impact of connectivity in species distribution models at the scale of a large anthropized watershed points to the importance of barriers, habitat fragmentation, and specific capacity to disperse along dendritic networks as crucial agents in the distribution of a majority of freshwater fish species in the Seine Basin. Our indices, designed to take into account morphological predispositions of fish to barrier crossing and dispersal, provided a significant explanation for fish distribution. Thus, this study presents a reproducible framework for the design and calculation of connectivity indices, which may provide further understanding of the complex relationship between river fish and connectivity constraints in future studies and render large-scale studies of the influence of longitudinal connectivity on fish distribution more feasible. In most species, high connectivity, as defined in these indices, seemed to be linked to a higher likelihood of presence, which seems to corroborate other approaches that highlight the beneficial effect of connectivity on fish and other river organisms. The negative responses of a number of smaller species to higher connectivity values are often explained by specific preferences and traits, and should not be neglected. In any case, major takeaways of this study are: i) retaining both barrier crossing and dispersal capacity should be the default choice in considering longitudinal connectivity constraints for river fish, both when creating reach connectivity metrics within the framework of species distribution modeling and when considering restoration of ecosystem functions and fish communities in direct field applications; ii) taking into account a measure of upstreamness or centrality into connectivity indices when working on watershed scale should be considered— we recommend the use of ACI-like methods (adjusted reach connectivity indices) as they were shown to be relevant for most species studied, and the use of finer local context ZCI-like methods if needed; iii) considering the topical question of connectivity, fish distribution and species conservation, and the mounting proof of its importance in shaping communities, a broader,

multi-scale investigation of the relationship between fish species and connectivity is urgently needed to preclude preventable loss. A better understanding of the complex functional relationship between connectivity constraints and river fish species, for example, body size or the influence of lateral habitat use, may help create practical groupings of species for which conservation and restoration measures may be strategized. Finally, it is important to state that, in a context of rapid climate change, which has already caused (Comte et al., 2013) and is due to cause the move of fish communities under environmental pressure, the conservation of longitudinal connectivity, and its restoration, may be crucial in safeguarding some species from rarefaction and extirpation. Operations, like the prioritized and thoughtful removal of barriers, and the restoration of riverscapes, as recommended for example in the European Water Framework Directive, can represent one of the many operations necessary to minimize the consequences of climate change on freshwater ecosystems (Branco et al., 2014; Thieme et al., 2021). Upstream of these examples of concrete actions, this study explores new tools to assess connectivity loss in rivers, focusing on the conservation of river fish: one can hope these tools may help the broader community of researchers to achieve a better understanding of the vulnerability of fish communities in rivers and, as the window for action against ecological collapse keeps on shrinking, contribute to reduce the severity of its effects.

CRedit authorship contribution statement

Swann Felin: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jérôme Belliard:** Writing – review & editing, Supervision, Methodology, Data curation. **Gaël Grenouillet:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Florentina Moatar:** Writing – review & editing, Resources, Methodology, Data curation. **Céline Le Pichon:** Writing – review & editing, Supervision, Methodology. **Vincent Thieu:** Writing – review & editing, Software, Data curation. **Guillaume Thirel:** Writing – review & editing, Validation, Supervision, Software, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Alienor Jeliakov:** Writing – review & editing, Visualization, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors of this manuscript declare no competing financial or personal interests in the conduction of this study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.178204>.

Data availability

R codes will be made available upon direct request. Data can only be made available upon individual direct request to the authors Swann Felin and Jérôme Belliard.

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