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Prospectives de distribution des poissons dans le bassin Seine-Normandie face aux contraintes de connectivité et de changement global

Thèse présentée et soutenue, le 27 mars 2025 par

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Abstract

Keywords: Global Change – Watershed – Fish Biodiversity – Species Distribution Modeling – Ecological Connectivity - Scenarios

River ecosystems are among the most species-diverse in the world. Global change, coupled with anthropization of watersheds and fragmentation of riverscapes, jeopardize river fish communities and put their future conservation in peril. There is an urgent need for knowledge to inform the design of the operations necessary to the conservation of freshwater ecosystems and fish species. However, the influence of watershed management, river fragmentation and land use on fish distribution and conservation is still poorly understood. This thesis aimed to address this knowledge gap by investigating the role of watershed management and fragmentation on fish species distribution in a warming 21st century, in order to provide information in support of river management and produce tools to better approach this issue. We first studied longitudinal connectivity and its influence on river fish communities, then we built watershed management scenarios which we integrated into species distribution models to study the influence of climate change and watershed management on potential future fish communities, before studying the spread of uncertainty between these two components.

The Seine-Normandie basin, a highly anthropized watershed in Northern France, was selected for this study. A dataset comprising over 2,000 study sites was compiled for the analysis of longitudinal connectivity. Novel connectivity indices were developed, based on functional traits of fish and river fragmentation, some indices accounting for local context (e.g. river size and river centrality within the basin). We were able to assess the relative importance of connectivity in fish distribution via species distribution modelling, indices which included local context performing especially well. We found that dams play a pivotal role in shaping fish distribution.

In order to model future fish distribution, four climate projections were selected across two time horizons, 2050 and 2100. In addition, we constructed four management scenarios to describe different future political orientations with respect to riverscape management. We were able to produce several prospects of species distribution through ensemble modeling. Most species were found to exhibit a decline in range over time due to climate change, management scenarios producing more complex outcomes. Scenarios linked with limited environmental restoration led to high rates of extirpation while scenarios with more ambitious prospects often resulted in enhanced survival rate. These responses exhibited wide variation across species, hindering the identification of a single scenario fitting the whole community.

Finally, we highlighted the relative importance of uncertainty linked to climate change and territorial management across eight species. We found that in most cases climate change carried more uncertainty than watershed management. However the portion of uncertainty carried by territorial management was still important, ranging between 6 % and 30 % on average depending on species. Some species (the bleak, roach) tolerant for warm water or environmental stressors associated with climate change were more impacted by territorial management in specific sites.

Through this PhD we provided insights into the role of connectivity on the composition of river fish communities as well as the influence of management and climate change on future river ecosystems. We were also able to provide new practical clues for future management and new methodologies for assessing connectivity in river networks and integrating it into modeling approaches. We produced plausible futures for river fish distribution, allowing us to assess the importance of climate change and territorial management on fish species conservation. We believe many of these approaches can be applied in similar contexts and contribute to the creation of knowledge necessary to implement the urgent measures required to safeguard river ecosystems in future decades.

Résumé

Mots clés : Changement global – Bassin hydrographique – Biodiversité Ichthyologique – Modélisation de la distribution des espèces – Connectivité écologique - Scénarios

Les écosystèmes dulcicoles sont parmi les plus riches en espèces au monde. Le changement climatique, l'anthropisation et la fragmentation des rivières, mettent en péril les communautés de poissons et leur conservation future. Malgré un besoin urgent de connaissances sur la conservation des écosystèmes d'eau douce et des poissons, l'influence des stresseurs anthropiques sur la répartition et la conservation des poissons est encore mal comprise. Cette thèse visait à combler ce manque de connaissances en étudiant le rôle de la gestion des bassins versants et de la fragmentation sur la répartition des espèces de poissons au 21ème siècle dans un contexte de changement climatique, afin de fournir des informations et outils à l'appui à la gestion des rivières. Pour ce faire, nous avons étudié la connectivité longitudinale et son influence sur les communautés de poissons fluviaux, et construit des scénarios de gestion des bassins versants que nous avons intégrés dans des modèles de distribution des espèces pour étudier l'influence du changement climatique et de la gestion des bassins versants sur les futures communautés de poissons, avant d'étudier la répartition de l'incertitude entre ces deux composantes.

Le bassin Seine-Normandie a été choisi comme point focal de cette étude. Un ensemble de données comprenant plus de 2 000 sites d'étude a été compilé pour l'analyse de la connectivité longitudinale. Des indices de connectivité informés par les caractéristiques fonctionnelles des poissons ont été développés, certains intégrant des aspects locaux. Nous avons pu évaluer l'importance relative de la connectivité dans la distribution des poissons, les indices qui incluaient le contexte local étant les plus performants, et constaté que les barrages jouent un rôle central dans la détermination de la distribution des poissons.

Afin d'explorer les scénarios futurs possibles, quatre projections climatiques ont été sélectionnées sur deux horizons temporels, 2050 et 2100. Nous avons construit quatre scénarios de gestion pour décrire différentes orientations politiques futures en matière de restauration et de gestion des rivières. Les multiples perspectives de distribution des espèces ainsi obtenues grâce à des ensembles de modèles ont montré un déclin des communautés de poissons lié au changement climatique. Les scénarios de restauration limitée étaient liés à des taux élevés d'extirpation tandis que les scénarios avec des perspectives plus ambitieuses entraînaient un taux de survie accru de nombreuses espèces. Une grande variabilité selon les espèces a néanmoins empêché l'identification d'un scénario idéal.

Enfin, nous avons constaté que dans la plupart des cas, le changement climatique contribuait à une plus grande part d'incertitude. La part portée par la gestion territoriale était néanmoins importante, variant entre 6 % et 30 % en moyenne selon les espèces. Certaines espèces (l'ablette, le gardon) plus tolérantes aux facteurs de stress environnementaux associés au changement climatique étaient plus impactées par la gestion territoriale dans des sites spécifiques.

Grâce à cette thèse, nous avons apporté des éclairages sur le rôle de la connectivité sur la composition des communautés de poissons de rivière ainsi que sur l'influence de la gestion et du changement climatique sur les futurs écosystèmes fluviaux. Nous avons également pu fournir des pistes pratiques pour la gestion future et de nouvelles méthodologies pour évaluer la connectivité dans les réseaux fluviaux et l'intégrer dans les approches de modélisation. Nous avons produit des futurs plausibles pour la distribution des poissons de rivière, nous permettant d'évaluer l'importance du changement climatique et de la gestion territoriale sur la conservation des espèces de poissons. Nous pensons que bon nombre de ces approches peuvent contribuer à la création des connaissances nécessaires à la mise en œuvre des mesures requises pour préserver les écosystèmes fluviaux dans les décennies à venir.

Special Thanks

This short tidbit before we start entering more serious subjects is no easier for me to write. I find myself overflowing with gratitude, and a wish to redirect this flow toward all the, let's be honest, hundreds of people who contributed to make this project what it is. I am paralyzed at the idea of forgetting someone, and hope this will not happen too many times, but, knowing it will, please know that my guilt is immense and my apologies are soon to come. I will pretend to bring structure to my gratitude and start with the professional, bleed into the personal, finishing with the silly, but of course many of the names in the following sentences were both very helpful in a professional way, and deeply unserious people outside of work - so please bear with this mess.

I wish to thank the innumerable people who contributed to this thesis, but of course the greatest thanks go to Aliénor, for your ever present help and advice, positive and encouraging attitude, astounding culture and lightning-fast thinking, and because you had to bear with me for 42 months. I thank you for helping me steer this ship the many times it went slightly off-course, lifting it up when it threatened to sink, and bringing it to safer shores. I thank you for your tireless support, minutious attention and the many lessons you imparted onto me. My introduction to the research world was certainly a smooth one, and your contribution to this soft approach is undeniable. I wish you and your family all the best and more, hoping that this project coming to fruition will allow you to rest easier for a little while. Thank you.

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I am deeply grateful for the funding, resources and help in conducting this thesis that me and my supervisors received from INRAE, via the Biosefair program, for which I must thank Sylvie Vanpeene, Marc Deconchat, Christine Argilier, Thierry Caquet and Isabelle Maillet - I deeply appreciated our workshops, and what they allowed me to see of what collaboration in research can look like - as well as the Seine-Normandie Water Agency, through Marie-Pierre Pinon and Luc Pereira-Ramos. I must also thank those in HYCAR who trusted me to prolong this thesis six extra months, including chiefly Aliénor, who fought tooth and nail to obtain the funds, as well as Vazken and Charles for their patience and understanding. I also must extend my thanks to the SEVAB doctoral school, among them Ms. Dominique Pantalacci, who answered my incessant questions with remarkable steadfastness and patience, and all the people with whom I was lucky to cross paths during recaps and missions on videoconference and in Toulouse, as well as Jacques-Eric Bergez for his guidance and occasional chats.

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My arrival in HEF and the welcoming attention I received from all of you, and I do not say this lightly, were the greatest gift a PhD student could receive in my opinion. This great little ecosystem in which I was able to find my place for three and a half years was one of friendliness, tolerance, cakes, cheese and laughter. There is something in the HEF waters that is difficult to describe, an attitude of positivity and understanding which I understand to be quite rare. One cannot help but swim in its crystalline waters. One sees a tench, bringing pain d'épices and other delicacies, expressing light discontent in delightfully Southern ways, bringing sunlight to the dreary corners of the Parisian basin, I am of course talking about Evelyne. Thank you. Next to the tench are Jérôme, the barbel, and Virginie, the stonefly, and Valentin, the spunky dace bringing empathy and light sarcasm to our table of chums. Céline, the sturgeon, brings her own touch of joy, and cheese, to our little assembly, while Aliénor, the tree frog and Alexandre the water frog, roam the pond. To Alexandre in particular I must express a profound expression of friendship. Your presence among us was a genuine delight, and your passion, drive and singular mind carved in unexpected ways make you a gem unlike all others. I believe the fact that our PhDs happen to end on roughly the same date is no coincidence. I mention here our outings, in Orléans, Lyon, highlights of my PhD, and of course our insane conference week in Newcastle-upon-Tyne, between bland foods and crowded pubs - Aliénor, and Laura, the Atlantic salmon who still to this day visits our shores, can testify. Thank you. In a faraway reach of our ecosystem, subject to vastly different thermal conditions, are Rémy the beaver and Coline the trout, late arrivals in the basin, but precious ones nonetheless, bringing their joyous constitution, political ramblings and precious experiences, calming my nerves. Coline I must thank you for the conversations, advice, laughter and the metric tons of food we shared in such a short span of time. Mikel, I hesitate to knight you as a shad or an Adour minnow, both seemed equally fitting, but your composed attitude, profound kindness, and insane skill at board games, will be remembered. I also cherish the moments spent with the interns that found their way to us, some of them staying a bit longer, Tim, the sculpin, who brought tarot back, Elena, the stickleback, who was almost as bird crazy as I was, Romane the pumpkinseed, Julien the catfish, Aurélien the carp, who are now living other adventures on distant shores. I must not forget Marilyne, Aaron S., Marie, Mathieu F., Mathieu G. and Amandine, who migrated to other reaches to thrive elsewhere. Finally, I wished to thank Aaron B., the burbot who spent a moment in our river, settling nearby, with whom I and many spent so many joyous lunches and board game soirées.

Above our flowing waters, Artemhys tests the leaching rains. I wished to thank Leo, who took the mantle of "PhD representative" with grace, Maxime for his sympathetic chats, friendliness and moviegoing hijinks, Romane, Cécile, Soren and Fatima, Jérémy for their conversation, and

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The number of people I would need to mention out of my civilian life to truly capture the amount of company I relied on for these three-point-five years is staggering, so I may forget a few. Chronologically, I wish to thank my father, my mother, who stands tall, my brother, aunt, uncle, for their patience and interest, the rest of my family, as well as Julia, Tilale, Henri, Joseph, Mélanie, Suzanne, Camille, Solène, Alice, Antoine, Maëlle, Thomas, Mathilde, Oriane, Aude - many of you finished your PhD during mine - Sonia, Fleur, Raphaëlle, Marie, Betty, Alix, Clémence, Edouard, Juliette, Tania, all of whom I was thrilled to see at least once or twice during this time of Francilian isolation, as well as all the strangers, ivory gulls, minke whales and storm petrels I found in Scotland and Svalbard, in windswept moors, roaring seas and flowers over permafrost, and the squirrels and parakeets that glided past my office window. The few people whom I have had the privilege of seeing many times from 2021 onward are owed special thanks for bearing with my increasingly chaotic ravings, Célia & Léon, as well as Meriadoc, whom I had the pleasure of cat sitting, Ruikang, to whom I wish the best of luck, Jules, whose travels inspire me, Lucile, whose PhD preceded mine, Zhaoyi, whose letters will soon become spoken words as I reach Shaanxi, Benjamin, with whom I have simmered through the dusty aisles of forgotten museums in search of rare names, Marine, a rare soul, a turnip, infinitely nice, a dear friend, whom I always wish to see again as soon as she leaves, Estelle, a twisted spirit whose company I enjoy immensely and cannot get enough of, Guillaume, who introduced me to Magic The Gathering, many other things, and starts his own doctoral adventure this year and Anna, whose passions and fixations never cease to fascinate me. I must thank Adiel, who introduced us to so many new things, as well as Aiganym, Nurdana, Rasto and Anastasia, for taking care of a certain someone. Most of all, I must thank Gabriel, who grew as I grew, faced it all, stayed close, and gave me so much. I can't wait to see the ways colors will keep on shifting under the waning and waxing of the moon. Thank you.

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Thank you all,

Swann.

Foreword

The SEINARIOS PhD project, which was created for this thesis, spanned three and a half years between October 2021 and March 2025 and benefitted from funding by 1) the Seine-Normandie Water Agency, 2) the Biosefair research metaprogram sponsored by INRAE (National Research Institute for Agriculture, Food and Environment) and 3) the HYCAR (Hydrosystèmes Continentaux Anthropisés – Ressources, Risques, Restauration, eng: Anthropized Continental Hydrosystems - Resources, Risks and Restoration) INRAE Research Unit. All work was conducted within INRAE's Antony site (1, rue Pierre Gilles de Gennes, 92160, Antony, France), in the HEF team (HydroÉcologie Fluviale des bassins anthropisés, eng: River hydroecology of anthropized watersheds), part of the HYCAR research unit. The delimitation of the study area, the Seine-Normandie Administrative Basin (see Chapter II for more information), was determined after consultation of the Seine-Normandie Water Agency, which is tasked with the specific management of infrastructure, and the monitoring of water quality, along with funding of restoration projects and relevant research. It is in this quality that the Seine-Normandie Water Agency funded part of this thesis.

Table of Contents

List of Figures

List of Tables

List of Abbreviations

ACI: Adjusted Connectivity Index

ANOVA: Analysis Of Variance

AESN: Agence de l'Eau Seine-Normandie (Seine-Normandy Water Agency)

BAM: Biotic/Abiotic/Mobility

CMIP: Coupled Model Intercomparison Project

DCI: Dendritic Connectivity Index

FAMD: Factorial Analysis of Mixed Data

GAM: Generalized Additive Model

GBM: Gradient-Boosted Machine

GCM: Global Climate Model

GLM: Generalized Linear Model

HYCAR: Hydrosystèmes Continentaux Anthropisés - Ressources, Risques, Restauration (Anthropized Continental Hydrosystems – Resources, Risks, Restoration)

INRAE: National Research Institute for Agriculture, Food and Environment

OFB: Office Français de la Biodiversité (French Office of Biodiversity)

OPSN: Observatoire des Poissons Seine-Normandie (Seine-Normandie Fish Observatory)

PCA: Principal Component Analysis

PIREN: Programme Interdisciplinaire de Recherche sur l'eau et l'environnement du bassin de la Seine (Interdisciplinary Research Program on the water and environment of the Seine Basin)

RCI: Reach Connectivity Index

RCM: Regional Climate Model

RCP: Representative Concentration Pathway

ROE: Référentiel des Obstacles à l'Ecoulement (Dataset flow obstacles)

SAFRAN: Système d'Analyse Fournissant des Renseignements Adaptés à la Nivologie (System of Analysis Providing Information Adapted to Snow Science)

SSP: Shared Socioeconomic Pathways

SYRAH-CE: Système relationnel d'audit de l'hydromorphologie des cours d'eau (Relational System of Assessment of Watercourse Hydromorphology)

SDM: Species Distribution Model

WFD: Water Framework Directive

ZCI: Zonation-sensitive Connectivity Index

いにしえの
野中の清水
温けれど
元の心を
知る人ぞ汲む
-
inishie no
nonaka no shimizu
nuru keredo
moto no kokoro o
shiru hito zo kumu
-
Springwater once
Flowed from the plain
Though now lukewarm
Those who knew it then
Still draw its waters
-
L’eau qui autrefois
Dans la plaine jaillissait vive
S’est certes attiédie,
Mais ceux qui alors l’ont connue
Vont bien la puiser encore
-
Anonymous
-
古今和歌集 - Kokin wakashū - Collection of Japanese Poems of Ancient and Modern Times (publ. 905)
-
[Poem 887] Translation (fr: Michel Vieillard-Baron)

Chapter 1. Introduction

In this chapter, we introduce the major themes of this thesis, defining the necessary terms and providing ample context to help the reader before diving in. Section 1.1 tackles the theoretical frameworks of ecology this text will come to invoke. Section 1.2 applies these frameworks to point to the general mechanisms behind fish distribution in Western European rivers. Section 1.3 expands on this thought experiment to include anthropogenic impact on European rivers, from river engineering to global changes, and introduces a working definition for river connectivity. Section 1.4 introduces a framework to reflect on future river management. Finally, Section 1.5 brings into focus this thesis' research questions, hypotheses, and the investigative paths that were explored to test them.

1.1 Theory of ecology and species distribution

Ecology as a practice can be described as incredibly ancient considering the sustainable management of lived-in ecosystems by first peoples (Bwambale et al., 2020; Honward, 2023), the knowledge required to perpetuate these management schemata, and the belief systems and frameworks that underpinned their societies. In contrast, ecology as a field can also be described as relatively recent, in the narrower history of academic scientific research (McIntosh, 1986), when compared for example to mathematics or physics.

The concept of species distribution, which can be defined as the totality of locations in which a species can be found, is a central tenet in the field of ecology. This notion is closely related, although somehow different, to that of range, which refers to the geographical extent of a species, and is generally well understood by the public. The work produced for this doctoral thesis is concerned with the mechanisms behind the distribution of river fish, a deceptively simple question hiding multiple layers of assumptions and possible ways to answer, large- and small-scale mechanisms, long- and short-term phenomena, which could never be presented in an exhaustive and digestible manner in a few pages. The relative recency of ecology as an academic field and the complexity of the mechanisms involved led to the rise during the 20th and 21st century of several competing, but not necessarily incompatible, theoretical frameworks to understand the distribution of species and the specific makeup of ecosystems. Here, our aim is to focus on approaches that are broadly used in contemporary research, and especially relevant to understand river fish distribution in Western Europe, which is the focal subject of this thesis.

1.1.1 Niche theories of ecology

The term ”niche theory”, as it is used in ecology in relation to species distribution, can refer to several similar frameworks which rely on a common set of methodological principles. Niche theory aims to understand the presence of a certain species in whichever given ecological context by establishing a series of ecological requirements for their presence, constituting a niche (as in a space or role for the species to occupy). The concept is generally applied to a species, subspecies or population, but in the case of animals which go through metamorphosis, a more practical use of niche can sometimes be passed down to larval, pupal and adult stages (Ebenman, 1992). A common usage of ”ecological niche”, less relevant to this study and corresponding to the ”impact niche” or historical Eltonian definition of niche, equates the niche to a specific role within a network of interactions between different species or groups and usually lends itself well to synthetic qualifiers (e.g. primary, secondary consumer, decomposer) (Hale, 2002; Letten, 2017). The qualifiers themselves are useful tools to describe river fish as well as any other taxa in certain contexts, and this text will likely contain many. Although most of them will carry no explicit reference to Eltonian niches, they should be understood as such.

In contrast, the definition most relevant to the following work, focuses on environmental parameters and requirements for species to feed and spawn. First established as a concept by

Grinnell and theorized more thoroughly by Hutchinson, Hutchinsonian niche theory posits that ecological niche can be defined as the breadth of environmental conditions within which a species can exist indefinitely, reaching a specific maximal capacity within a given space, regulated by resource availability and predation. This ”indefinite existence” and the presumed stability of the studied ecosystem and environmental conditions is a core feature of niche theory. The Hutchinsonian niche is described within an n-dimensional environmental hyperspace consisting in n environmental gradients as an n-dimensional hypervolume which is a section of that space (Hutchinson, 1957). Hutchinsonian niches assume that all environmental parameters relevant to a species’ requirements can be expressed in gradients, and often that species response to one environmental gradient can be expressed through a normal distribution of suitability, centered around a single optimal value. Arithmetization of ecological niche, gradient by gradient, also allows for the quantification of the importance of each gradient to the shape of the hypervolume. Under Hutchinson’s paradigm, no two species can have the exact same niche in a stable state, since resulting competition would result in one species’ extinction. Thus, Hutchinsonian niche theory introduces a critical distinction between fundamental niche, understood as the theoretical niche a species could potentially inhabit, while its realized niche, often called ”requirement niche”, is understood as an adjusted hypervolume of lesser breadth that takes into account inter-species competition, other biotic factors. Asymmetric competition leads to competitive exclusion, either resulting in extinctions or niche partitioning, while symmetric competition leads to sharing of resources and cohabitation in smaller numbers (see Fig. 1). We should note that although the concept of niche partitioning does not explicitly involve speciation processes, it is often evoked when describing mechanisms of speciation leading to sympatric taxa (Petalas et al., 2021; Salton et al., 2024; Scriven et al., 2016; Vellend, 2010). The use of the concept of requirement niche as we defined it above has spanned the latter half of the twentieth century and beyond and led to the birth of numerous subsequent applications from contemporary bioindication tools for ecosystem quality assessment to niche-based species distribution modeling.

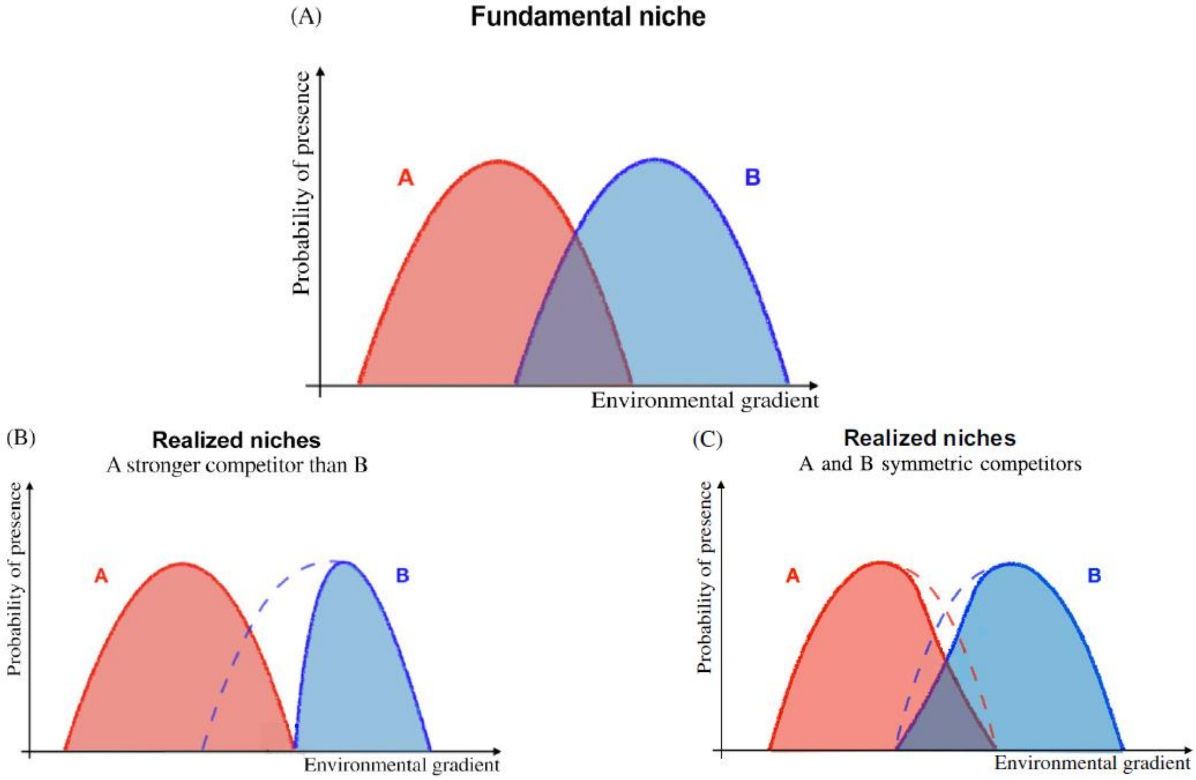

Figure 1: Representation of the difference between fundamental and realized niche for symmetric and asymmetric competitors*. Representations showcasing phenomena of competitive exclusion in a context of asymmetric competition and scramble competition in case of symmetric competitors. Adapted from Poggiato et al. (2021), a case study on joint species modeling.*

Despite its numerous applications in ecology, niche theory remains bound by a few limitations. Some of these limitations are directly concerned with the translation of niche theory into field data analysis and research, where variable acquisition is often perfectible, qualitative, or obtained at low spatial resolutions. Additionally, there is a necessary gap between ideal Hutchinsonian niches, which are defined within a theoretical environmental space which describes the environment with precision, and the reality of information acquisition, which has much more to do with financial and modeling efficacy than completeness. A broader limitation, which will be elaborated on in the next section, is an inherent hypothesis of stability over time, which often is not realized in the field (Hutchinson, 1957).

Finally, a major limitation of niche modeling has to do with stochasticity. Depending on the spatial scale at which a study is conducted, niche suitability and species presence patterns may be mismatched due to various effects from dispersal and its limitations, and more generally all phenomena that might influence species composition without directly involving niche partitioning. In fact, potential distribution of one species obtained through the mapping of favorable conditions on a study area, even considering realized niche obtained through careful study of niche partitioning phenomena, which is often called fundamental range, may yield renderings with limited resemblance to its true realized range due to random dispersal events and local extirpations. On a large scale, a species that inhabits a specific niche within area A may be unable to reach area B, regardless of whether area B offers suitable conditions for existence or not, because of functional limitations to its dispersal, or disappear from an area as a result of a stochastic event disconnected from stable environmental conditions. Thus, the link between species distribution and requirement niche, though interesting, requires precaution (Pagel et al., 2019; Pulliam, 2000), and consideration of these events.

This is why, in practice, niche theory is generally used in combination with careful consideration of expected range, and assumes no major stochastic events. To this end, a few heuristic approaches were proposed, among them the BAM diagram (Soberón & Peterson, 2005) (for Biotic, Abiotic, Mobility), a helpful Venn diagram, we choose to display in Fig. 2 to give a visual overview of these concerns. The diagram showcases abiotic suitability (A, the fundamental niche), biotic niche (B), and zone of potential dispersal (M), and most importantly its intersections ($A \cap B$ being the realized niche and $A \cap B \cap M$ the actual species distribution). The M,A,B components of BAM diagrams can be roughly equated, in this order, to the theory of environmental filters (Kirk et al., 2022; Poff, 1997), a more applied approach to species distribution theory, which similarly describes the way dispersal and accessibility put a first filter on which species can be present in a given context, followed by an abiotic filter, and finally a biotic filter, which gives the actual community composition. These filters are applied from a regional pool of species, and become important at successively smaller geographic scales. This succession of scale-dependent filters is widely observed in sessile and low mobility organisms - and trees in particular (Chase, 2014; Viana & Chase, 2019), but less obvious with mobile organisms, for which dispersal is less predictable (Cardador et al., 2014; Elith & Leathwick, 2009; Emmet et al., 2021), and complementary approaches may be needed.

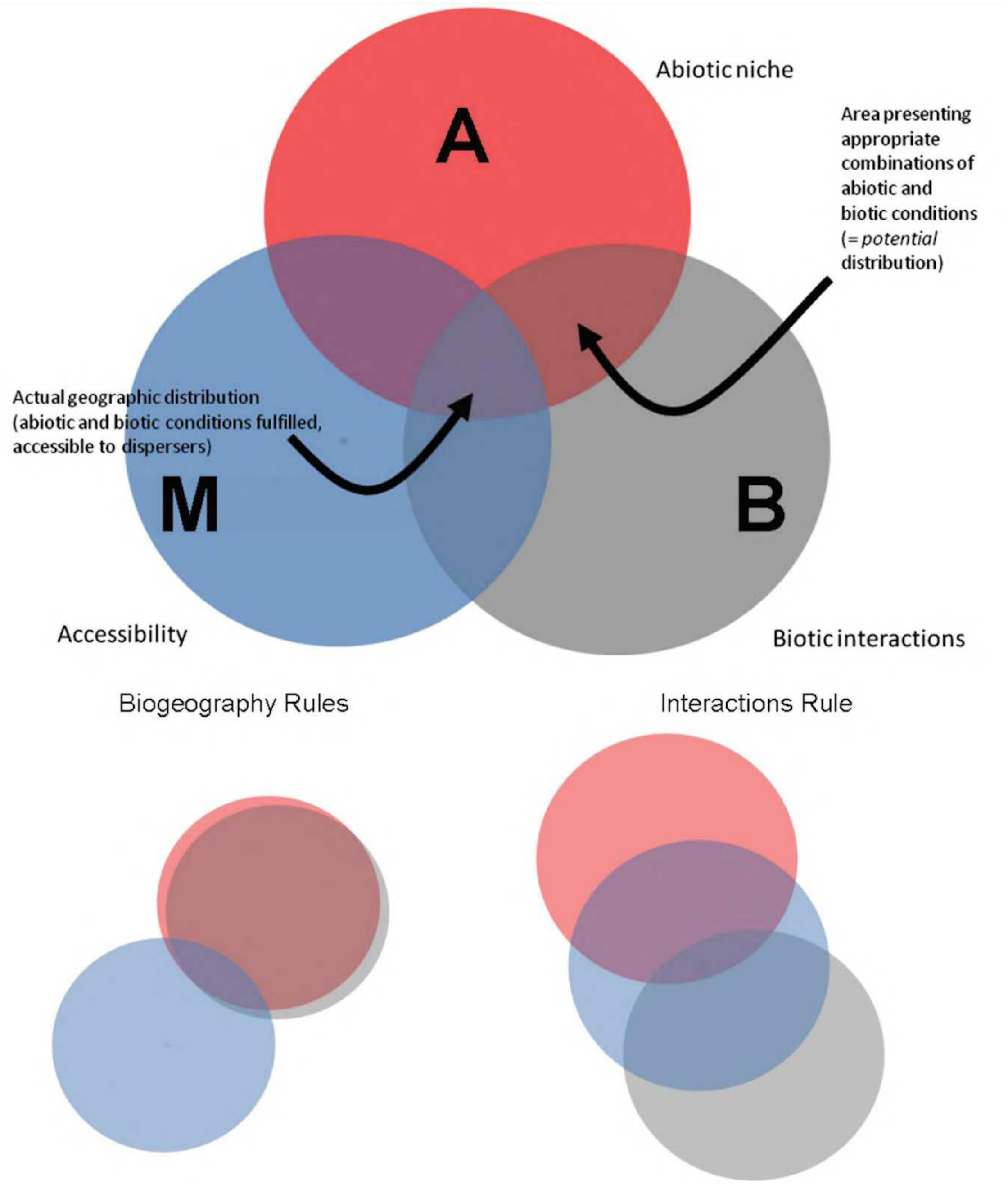

Figure 2: Presentation of the BAM diagram*. Theoretical hypervolumes A (fundamental niche), B (biotic niche), M (effective accessible zone) and their unions. Two specific situations are displayed below: i) limitations in accessibility are the most limiting (obvious examples at large spatial scale - oceans crossings etc.) and ii) biotic interactions prevent the presence of species in a large part of its theoretical niche. Adapted from Peterson (2009), an informative paper on species distribution.*

1.1.2 Neutral theories of biodiversity and biogeography

Whereas niche theory of ecology focuses on environmental variables and their relationship to species presence, the many neutral theories of ecology focus mostly or solely on stochastic effects and describe ecosystems in detail through the lens of migration, extinction or extirpation, and on a long enough time frame, speciation (Kadowaki, 2022). They are thus related to the M component of the BAM diagram shown above. This contemporary theoretical framework originates partly from the discipline of biogeography, the study of the variation of the distribution of species and species assemblages through time and space, with the notable example of insular biogeography theory. Despite its name, this specific theory concerns not only islands but all geographical units which are for one reason or the other, cut off for some time and for some species from a source unit (e.g. islands vs. landmass, lakes, forest patches, mountains). Insular biogeography studies the influence of patch size, distance from source and duration of isolation on species diversity, and on longer time frames, speciation and endemism. It states that increased size, distance and duration of isolation is directly linked to higher diversity (Brown, 1978).

Works by Bell (Bell, 2000), followed by Hubbell (Hubbell, 2001), at the beginning of the 21st century, took inspiration from insular biogeography to define a unified neutral theory of biodiversity, conceived in part to bring an explanation to some documented cases of two species with apparently identical niches coexisting in the same area. This new framework considers species presence solely in terms of random stochastic phenomena (e.g. migration and colonization, speciation, mortality or extinction, see Fig. 3), assuming no significant influence of ecological differences on the likelihood of the aforementioned phenomena (Gotelli & McGill, 2006). At the metacommunity scale, where metacommunity is defined as a number of communities linked by dispersal dynamics, neutral theory considers speciations and extinctions, occurring at identical rates for all species, as the drivers of diversity, while at the local community scale, dispersal from and into the community also have to be considered, often integrating the metacommunity (i.e. an ensemble of dispersal-tied communities).

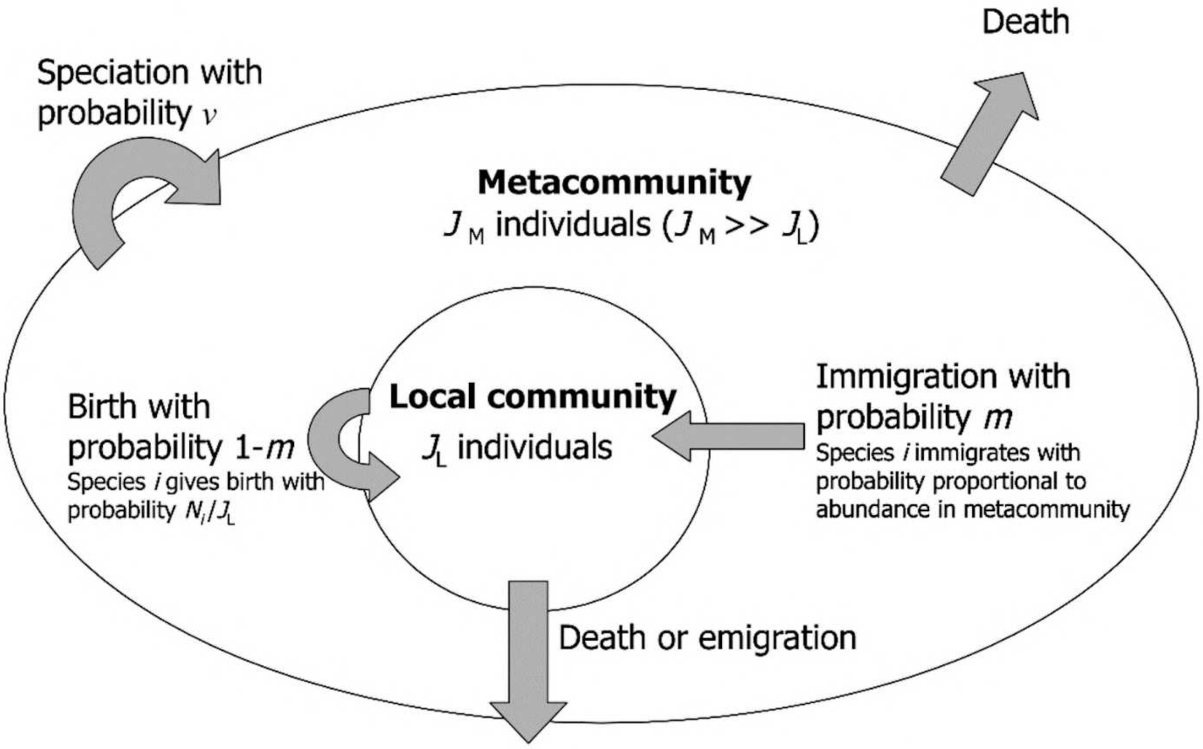

Figure 3: Display of all phenomena included within neutral theory, according to Hubbel's theory, placed at the level of a local community within a larger metacommunity. *All individuals are equivalent under this paradigm and so probabilities of migration and speciation are proportional to species abundance. Adapted from Etienne & Alonso (2007).*

Neutral theory, because it is agnostic of abiotic and biotic components, is bound to be limited in its explanation of species distribution, and has often been falsified, yet it has been revealed to be a good explainer of species distribution in certain methodological contexts such as short-term fluctuations, tropical trees of reef-associated fishes (Alzate et al., 2019; Kalyuzhny et al., 2015; Volkov et al., 2005), and to have inherent value as a stochastic theory (Alonso et al., 2006; Rosindell et al., 2012; Volkov et al., 2003). Within this thesis, neutral theory will be mainly used as a limited framework to elaborate on fish distribution and naturalistic dispersal within a more general niche theory framework, yet explaining its origins and concept will show itself to be necessary in the following Chapters which apply these frameworks in explaining the mechanisms of river fish distribution.

Each theory of biodiversity is to be considered not as attempts to describe the exact mechanisms that determine species distribution and community compositions, but as coherent frameworks which allow one to model and predict useful approximations and place the many mechanisms that shape species distribution within broadly understood systems of thought.

1.2 The determining mechanisms of European river fish distribution

This document focuses specifically on non-diadromous river fish, and consequently this section will describe the mechanisms pertaining specifically to the explanation of river fish distribution, doing so while invoking previously established theoretical frameworks. Unless mentioned otherwise, further exposition will center on Europe, and more specifically Western Europe, as all subsequent chapters will focus on the Seine-Normandie basin within which our study area is nested.

1.2.1 River oddity and ecological implications

Marine, terrestrial, soil and lacustrine contexts answer up to a certain point to similar geometric rules and offer several points of comparison with each other. Between patches, within patch dynamics and landscape ecology (Pickett & White, 1985), dispersal can occur in all directions on a two-dimensional plane, within two-dimensional dispersal kernels (Koch et al., 2020). These relatively simple geometric constraints allow for direct application of niche and neutral theory with little or no caveats needed. The argument can be made that for very small scales, adapted for studying macroinvertebrates, the lateral and longitudinal axes of watercourses are on similar scales, and terrestrial-like assumptions about dispersal and patch dynamics can be true. However, when focusing on larger animals such as fish, watercourses are, for lack of a better word, very odd structures compared to other ecosystems. Frameworks like patch dynamics can be applied to them in certain contexts like whole floodplains (Pringle et al., 1988), within a different geometry and paired with geometrically relevant analyses (Erős & Lowe, 2019). The study of river fish who can disperse along rivers over distances that can reach hundreds of kilometers, and so where active longitudinal dispersal is so much more consequent than invertebrates or sessile organisms, requires an adapted framework. Relatedly, a recurring issue in the disciplines that concern this thesis is the overwhelming predominance of works conducted in terrestrial environments, under assumptions that are simply untrue when working with watercourses and fish. A few of these geometric particularities of rivers include:

1) They are organized in dendritic networks that can be compared to fractal structures (Mandelbrot, 1983). Dispersal along rivers networks for obligate freshwater species such as fish is thus restrictive, shaping communities much more than regional effects (Brown & Swan, 2010; Campbell Grant et al., 2007; Tonkin et al., 2018). Consequently, river fish dispersal is most often expressed though the use of one-dimensional dispersal kernels for longitudinal dispersal (Skalski & Gilliam, 2000).

2) Contrarily to terrestrial ecology, where patch dynamics translate into habitats and corridors, these notions are much more complicated to parse in rivers, where fish, depending on viewpoint, usual habitat can stretch kilometers under paradigms like the River Continuum Concept (see section 1.2.3 and Vannote, 1980), or restricted to usual domain, spawning grounds, or feeding grounds.

3) The longitudinal structure of rivers means that habitats can stretch along rivers for long distances while constituting relatively small surfaces locally, and that dispersal of fish along the longitudinal axis involves much larger distances than along the lateral axis. This particularity has direct consequences on consideration of connectivity (see section 1.3.3).

4) The unidirectional flow of water leads to asymmetric dispersal along rivers, with a much easier downstream movement (Jones et al., 2021).

These unique characteristics have direct consequences on the way ecosystems and communities are structured in watercourses, and greatly influence the distribution of fish species. The geometric, dendritic structure of rivers have led to the creation of multiple metrics to qualify global and total branching complexity. The most widespread in use is the Strahler stream order (Strahler, 1957), which counts headwater streams with the number 1 and adds 1 every time the stream meets a same-order value stream (see Fig. 4).

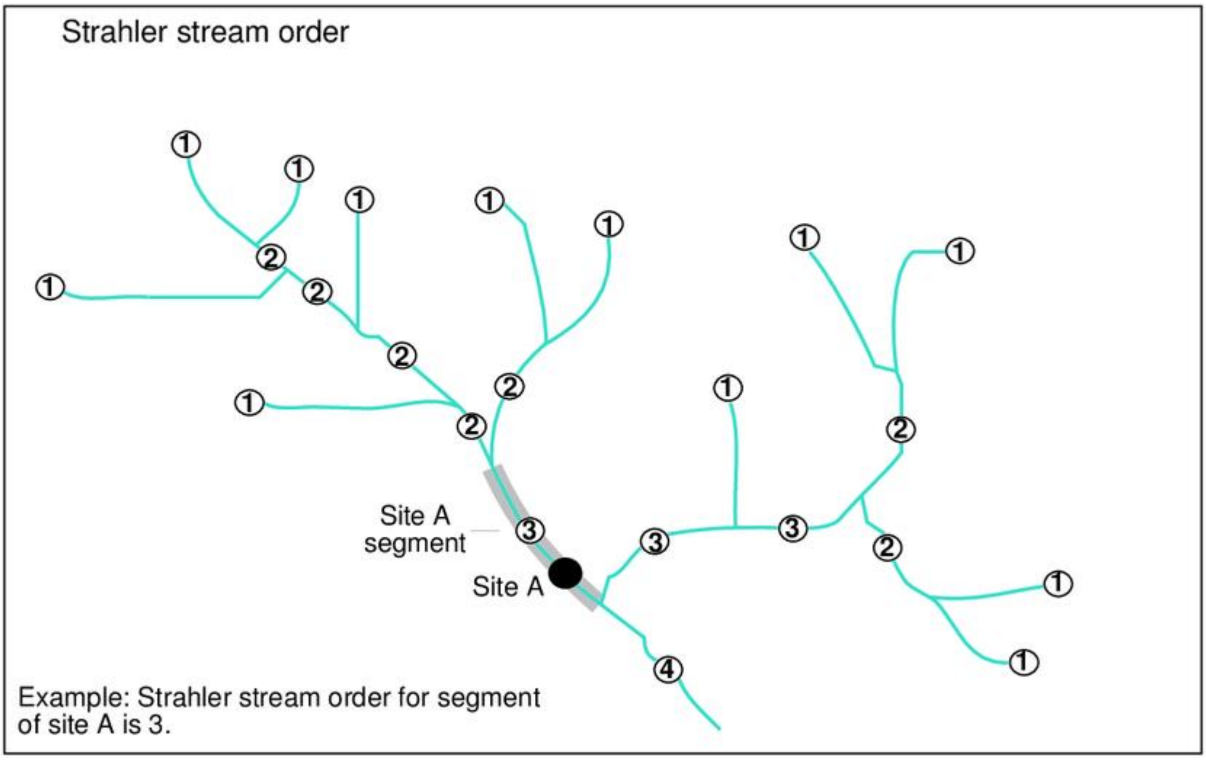

Figure 4: Strahler order illustrated on a simplified river network. *Adapted from Fitzpatrick et al. (1998).*

Rivers flow from small upstream brooks to large lowland rivers and into larger bodies of water. The principles involved into the way flowing water shapes landscapes, carving river valleys, carrying sediment downstream, joining with other streams to form larger rivers, are mostly physical and depend mostly on bedrock weatherability, topology, sediment granulometry, seasonality, and so the general aspect of watercourses is similar in most contexts.

Stream slope is often higher upstream than downstream, leading to higher flow velocity and larger possible sizes for suspended solids and higher granulometry for substrates, higher oxygenation, lower temperatures (Castelltort & Yamato, 2024). In contrast, closer to the estuary, rivers tend to have higher discharge, and carry more sediments in larger and deeper channels. This continuum of gradually shifting abiotic factors, available habitats and hydromorphological properties, essentially environmental gradients, has been observed to create a corresponding continuum or succession of habitats and ecosystems. Thus, predominant environmental gradients shaping requirement niches of freshwater organisms vary mostly longitudinally along rivers. This observation extends to river fish, which were in fact the main reason why Huet defined a succession of ichthyofaunal zones for French rivers (Huet, 1954) based on indicator species (the trout zone above the grayling zone, then barbel zone, then bream zone). Similarly, Illies and Botosaneanu (1963) create a similar classification for benthic invertebrates. These discrete approaches were gradually replaced by finer zonation based on a typology of communities in relation with several ecological gradients, such as Verneaux (1977), then by continuous approaches such as the seminal River Continuum Concept theorized by Vannote (1980), which relies on a more synthetic gradient, i.e. primary productivity, which increases downstream, and shifting functional traits of macroinvertebrate communities.

The dendricity of river networks leads to a multiplication of isolated, or distant, areas within a given catchment. Additional barriers at larger scales that include water salinity or natural obstacles like waterfalls impede some freshwater fish from swimming from one basin or area to the next, increasing this natural fragmentation of freshwater ecosystems. The variety of environmental conditions caused by the River continuum concept, as well as the lateral differentiation of habitats (from the floodplain and banks to the benthos and the water column), also lead to a high diversity of habitats, and potential ecological niches (Lévêque et al., 2008). These characteristics are due to encourage allopatric and sympatric speciation as specified by insular biogeography theory. Consequently, at least 38 % of fish species identified as of 2023 live in freshwaters, also amounting to 26 % of vertebrate species while freshwater habitats constitute approximately 1 % of planetary water cover (Froese & Pauly, 2023). The River Continuum Concept and geometry of rivers are essential concepts to the understanding of the diversity of fish communities and are intrinsically linked to the ecological gradients and neutral theory mechanisms that shape river fish distribution (Vannote et al., 1980).

1.2.2 Theories of paleogeography and European freshwater fish

Complementary to a river structure approach to the understanding of the shaping of freshwater communities, regional factors rooted in palaeogeogrphy. Contrarily to North America, where mountain ranges (Rocky Mountains, Appalachians) and rivers (Mississippi and tributaries) are directed North to South, Europe's landscape features are broadly East-West (rivers like the Danube, Loire and Seine and Mountains like the Alps and Pyrenees). In times of fluctuating glacial periods, North American species were able to migrate in order to remain within their preferred niche while European species were often extirpated (Davis, 1983; Roberts & Hamann, 2015). North America currently hosts around 1000 species of freshwater fish while Europe counts around 550, a large portion of which are either non-native or exclusive to Western Russia (Froese & Pauly, 2023). Receding sea levels and growing ice caps in colder periods (the last glacial period running from 115,000 to 11,700 BP) led to changing riverine ecosystems, and the exclusion of all but the most cold-tolerant species like chars and whitefishes, who inhabit arctic and montane rivers today. As climate warmed up again, potamodromous and resident fish species regained their range slowly, through river captures and rare stochastic events, while euryhaline species gradually returned to more Northern watersheds via the sea. This implies that most fish species currently present in Northern watersheds, like the Seine-Normandie basin at the center of this thesis, have continuously inhabited these watersheds for at most two hundred thousand years (Keith et al., 2020).

1.2.3 River fish in their environment

Freshwater fish species fill a wide array of Eltonian niches, vary widely in size, habitat occupancy, feeding and spawning strategy. Nonetheless as freshwater organisms, these species spend at least a large part of their life in freshwater. Consequently, a wide array of environmental gradients most important to segregate each species' fundamental niche come down to physical and chemical properties of the freshwater column they inhabit. Following the River Continuum Concept explained above, environmental gradients vary along a longitudinal axis and are conceptually inextricable from the River Continuum Concept; these environmental gradients are further described below. Developing them separately in this section is in no way an effort to divorce them from this larger framework, but a key to understanding a few ways in which fish species react differently to their environment.

A first essential gradient when describing the ecological niche of a river fish species is salinity (from brackish estuaries to far inland headwaters). River fish species can be categorized into several suitability profiles with respect to salinity (Keith et al., 2020): i) Euryhaline fish are generally physiologically able to handle both seawater and freshwater, sequentially or interchangeably, and thus tolerate a large range of salinity, with ii) Marine stenohaline species, and iii) Freshwater stenohaline fish, which rarely visit even brackish habitats. A second gradient, related to elevation and correlated to river size, is water temperature. Some species, as for salinity, can accommodate wide ranges of temperature with no impact on breeding and feeding, while others prefer colder or warmer environments and decrease in fitness when out of range. The main families of freshwater fish occurring in Western Europe, as we hinted in the Paleogeography section, exhibit distinct suitability profiles when it comes to water temperature. At the cold end of the spectrum, whitefish (Coregonidae), graylings (Thymallidae) and salmonids (Salmonidae) can be found in montane lakes and streams and arctic rivers (the Arctic char *Salvelinus alpinus* can be found above the 80th parallel North in Svalbard and Greenland

(Gulseth & Nilssen, 2001)). Some stenotherm species like the brown trout (*Salmo trutta*) and some whitefish (*Coregonus spp.*) struggle above 15-18 °C waters. Some eurytherm species like the Eurasian carp and European eel (Cyprinus carpio and Anguilla anguilla) can live in very cold and warm waters while others like the pike (Esox lucius) are at peak fitness around 19-21 °C. A third environmental gradient, water oxygenation, is directly linked to flow velocity (oxygen saturation is highest in small, highly agitated streams) and water temperature. Salmonids are generally oxyphilic, found in highly oxygenated waters, while some species like the Eurasian carp (*Cyprinus carpio*) or Catfish (*Ameiurus melas*) are generally euryoxyphilic. We should note that the sensitivity of river fish to environmental conditions can also vary along developmental stages, from egg to breeding adult, this is especially true of species which migrate significantly to breed and spawn. The BAM approach and the niche theory inform us that within dispersal capabilities, specialist species (e.g. stenohalines, stenotherms) will be distributed in habitats that fit narrower requirements. These are the mechanisms that allow for the formation of the typological communities like the ones described in Huet (1954), which then led to the theorization of the River Continuum Concept. These specialist species coexist with generalist species (e.g. euryhalines, eurytherms). Their presence will be determined by dispersal and competitive exclusion mechanisms.

1.2.4 River fish in motion

Gathering information on environmental predictors of fish distribution is essential to the building of niche modeling approaches which aim at understanding the patterns in species distribution. Similarly, understanding the behavior of fish with respect to dispersal and migration is useful to the integration of these phenomena in modeling, a major goal of this thesis. Although dispersal limitation processes generally lack in species distribution modeling approaches, dispersal of river fish along rivers is essential in determining their distribution in river basins. Capacity for dispersal in river networks indeed determines the accessibility of vacant areas by river fish. On one hand, rivers and riverscapes – defined as all landscape elements in and around watercourses (Torgersen et al., 2022) - constitute obstacles to the dispersal of fish. Excessively long distances between suitable habitats, or opportunities for successful spawning and feeding may preclude fish dispersal to said habitats (Barbarossa et al., 2020; Fagan, 2002; Granzotti et al., 2018). More directly, physical obstacles (like waterfalls) and chemical obstacles (like zones of high salinity or low oxygen saturation) may act as total or partial barriers to dispersal (Urbanski & Nogueira, 2024). Similarly, low plunge pool depth, whether constant or linked to a drought, may impede obstacle crossing, while high flow velocity may prevent some species from moving upstream (McKay et al., 2013; Rincón et al., 2017).

These obstacles to dispersal are to be evaluated in tandem with the inherent capacity of each species for dispersal, which can be broadly linked to a few traits which can be classified as behavioral or anatomical. 1) Behavioral traits are linked to migratory behavior: euryhaline diadromous fish species migrate from sea to rivers, and the opposite, to feed and spawn, which necessary leads to long-distance migration, while potamodromous species migrate on shorter distances, and resident species mostly do not migrate. Skalski and Gilliam (Skalski & Gilliam, 2000) show that not all fish within a given population will disperse along the river axis; a large proportion of fish disperse on short distances and a few individuals disperse on longer distances, leading to a probability of dispersal described best by a leptokurtic dispersal kernel (i.e. a density law built by adding two normal distributions, one for the static component and one for the mobile component). 2) Fish capacity for dispersal, beyond behavioral traits, is determined by a few anatomical traits among which the most important are body length and caudal aspect ratio (Radinger and Wolter, 2014). Body shape also influences swimming speed and efficacy, and diverse morphologies adopt relatively different swimming techniques to reach feeding and spawning grounds (Atkinson, 2020; Reinhardt et al., 2008). Although behavioral and anatomical traits often agree (e.g. large fish also tend to be potamodromous) some fish species do not obey this rule, for example the Eurasian Carp, which is very large and generally resident.

1.3 Human presence and river fish

It is safe to assume that as soon as a permanent human populations established themselves durably on European soil (the debate as to when this event happened, and even what should be considered human occupation, is beyond the scope of this text), all phenomena pertaining to the distribution of fish increasingly became inextricably linked to human activity (Malhi, 2017). The Seine-Normandie basin makes no exception. Thus, in qualifying the mechanisms that influence fish distribution, it is simply impractical to attempt to make a distinction between so-called ”natural” and purely anthropogenic processes. In order to take into account this necessary lack of qualification, theoretical frameworks for species distribution used in ecology, such as those presented in section 1.1, were conceived to be applicable to various spatial and temporal scales and do not explicitly differentiate anthropogenic influences on environment and population dynamics from pseudo-natural ones. However it is trivial to note that human activity affects all the processes which determine fish distribution, from environmental variables to obstacles to dispersal. The study of the ichthyofauna of anthropized rivers and watersheds requires an in-depth study of human interference on ecosystems, and the way this interference leads to change into environmental parameters and ecosystem morphology relevant to river fish. This section exposes the noteworthy practices of human societies with respect to river fish habitats and ecology, linking them to the determining mechanisms of river fish distribution exposed in the previous section.

1.3.1 The Commodification of River Fish

River fish are relatively inconspicuous in daily life, nonetheless they have constituted a source of nutrition for humans for millennia (Hu et al., 2009). Their primary cultural imprint on human societies have thus revolved around food security, as well as subjects of artistic expression (Moyle & Moyle, 1991). However, with the appearance of modern and contemporary societies, the general commodification of natural resources have led to new relationships between humans and the animals with which they share their space.

The treatment of river fish as commodities led to the creation and upkeep of social networks revolving around river fish, from associative and professional fishing, in-land fisheries to culinary experimentation, which have significant ramifications in river fish population management (culling and releases) and environmental management (Manning, 2011; Pister, 2001). Many species in European rivers are regularly fished, some of them consumed, while others are only valued as sports fishing prizes or not at all. These cultural representations are a first aspect to contemporary representations of river fish, which give them a prominent place in some social structures. A second aspect is their more academic instrumentalization as objects of study placed within the ecosystem. In addition to their value as concrete subjects in biological research, anatomy, phylogenetics, and occurrence data for projects such as this one, river fish are valued as integrated elements in conceptual frameworks of nature. Beyond talks of the intrinsic value of living organisms, human research tends to evaluate their contribution to ecosystem functioning, as well as the services they fulfill for human societies, such as their involvement in bio-geochemical cycles or their value as cultural objects and as commodities (Driessen, 2013; Pownkumar et al., 2022; Villéger et al., 2017). All these representations around river fish as well as the watercourses in which they dwell are inherently present in all reflections with respect to the management of fish and rivers, with a focus for example on rarer, native species for conservation. These representations have in part guided past and present human behavior around rivers, but also differential treatment of existing taxa, with categorical constructs like non-native/native, migratory/sedentary, edible/not edible, rare/abundant leading both management and research on river fish. A notable example is the emphasis placed on diadromous fish in European basins due to both their recent decline and their high intrinsic value as commodities (Merg et al., 2020). Salmon, shads, eels, sea trouts are all highly valued for their rarity, leading to increased focus in research and river management, as well as their use as consumable products, considered in Western Europe as superior delicacies to most non-diadromous species. The pervasiveness of these societal constructs being what it is, this thesis cannot pretend to fully disenthrall itself from these biases but will strive to minimize their impact on produced work.

1.3.2 Infrastructures of human activity and anthropized rivers

The fulfilling of essential needs of human societies and its increased essential and non-essential demand for consumer goods and services have led to an increasing mutation of natural landscapes (Bhagwat, 2014; Haidvogl, 2018; Mander & Jongman, 1998). The use of land for agriculture has caused the historical reduction of woodland surface in Western Europe, accelerating from the Middle Ages onward (Kaplan et al., 2009). Since forest root systems are essential for soil retention, increased deforestation has led to increased runoff, erosion, and the increased turbidity in freshwater in many European rivers (de la Paix et al., 2013; Posada-Marín & Salazar, 2022) including the Seine. In more recent times, the widespread use of pesticides and fertilizer in post-WW2 conventional agriculture has led to the leaching of these compounds from agricultural soils into nearby rivers (Holvoet et al., 2007; Rani et al., 2021). Concurrently, growing need for urban development and industry has led to the sealing of soils on an unprecedented scale, hampering soil absorption of rainwater (Tobias et al., 2018). The release of industrial wastewater, sewage, fertilizer-laden agricultural runoff, has led to the recurring presence of various micro and macro-pollutants in rivers, leading to decreased fitness for river fish, as well as organic matter, nitrates and phosphates (Jones, 2013). Similarly, nitrates and phosphates boost the growth and reproduction of algae, bacteria and certain plant species, leading to decreased oxygen, and occasional hypoxia, and a consequential decrease in diversity and abundance of fish communities, in a process called eutrophication (Hilton et al., 2006; Kelly & Whitton, 1998). Watercourses previously considered oligotrophic (low nutrient content) were occasionally converted into mesotrophic and eutrophic systems, leading to consequential restructuring of ecosystems, favoring euryoxyphilic species over oxyphilic ones, and more generally favoring generalist species with wide requirement niches, more resilient to change. Events of hypoxia in rivers occurred regularly in the Seine basin, causing impoverished fish communities, and eventually leading to the construction of water oxygenation stations around Paris (SIAAP, 2011). Deforestation is especially damaging to fish communities when riparian forests are cleared, since they provide a last barrier to water contamination, regulate water temperatures and provide specific habitats to certain species (Studinski et al., 2012). More generally, the overall homogenization of freshwater ecosystems favor generalist species over specialist species, leading in turn to more homogenous and less diverse communities (Cheng et al., 2018; Clavel et al., 2010). Now more aware of these adverse effects, legislating bodies have taken steps to reduce them, from regulating fertilizer use, curbing soil artificialization and generalizing the treatment of wastewater to encouraging more responsible agricultural and industrial practices (Lawton, 2007; Ludwig et al., 2001), as well as broader initiatives of restoration of riverscapes, which in our study area were formalized by the Water Framework Directive (WFD, see directive 2000/60/CE, 2000, JORF). These initiatives have proven effective to a point, reducing hypoxia events in rivers, sometimes with the help of oxygenation stations, and partially slowing down eutrophication (Thyssen, 2001).

Human practices concerning the extraction and introduction of fish in watercourses, intrinsically linked to their perceived values as consumer goods and resources, greatly shape fish communities in European rivers (Copp et al., 2005; Gozlan et al., 2010). The practice of fishing, though in decline, likely contributed to the extirpation and reduction in populations of several species, especially large, diadromous species like eels, salmon, shads, sturgeons, although habitat destruction also contributed (Jonsson et al., 1999). Concurrently, the needs of people who practice angling led to the introduction of non-native fish species with potential for fishing (Carpio et al., 2019). However, fishing was not the only impetus for the introduction of exogenous fish in rivers: an older, prevailing view in the nineteenth and early twentieth century led to the introduction of tens of American and East European fish species in Western European rivers, with the explicit goals to ”enrich” fish communities (Cowx, 1997). To this day, interest groups linked to these domains of activity and schools of thought conduct heavily regulated releases of fish in rivers to maintain stocks of desirable species. To these voluntary, traceable introductions, we must add more discreet introductory events for certain species, which were either to a certain degree illicit, or accidental. The increase of waterway transport, leading to the taking and release of ballast water, and the sustained practice of building parallel and connecting canals increases the probability of introductions from waterway to waterway, with a few confirmed instances, such as the round goby (*Neogobius melanostomus*) in some European rivers (Copp et al., 2005). Not all exogenous introductions lead to perennial populations, a combination of environmental requirements and competitive exclusion selecting for ecologically-suited species nonetheless. Generalist exogenous species, however, are often successfully introduced in new watersheds, for example the black bullhead catfish (*Ameiurus melas*), a North American species which is euryoxyphilic and eurytherm and thus can inhabit many different river habitats (Leunda et al., 2008).

Because rivers represent a source of freshwater and a means of transport for people and merchandise, human populations have tended to concentrate around major river axes and coastlines (Haidvogl, 2018). Of the top 50 cities in Europe by population, 33 were built along large rivers (OECD, 2020). Agriculture and industry often rely on regular taking of water from rivers and water bodies. These practices are especially damaging in times of drought (Bourzac, 2013). Additionally, navigation and flood protection have historically led to the alteration of river hydromorphological characteristics. The transformation of rivers into waterways, regulation of flow, channel width and depth can be achieved through the modification of the length of watercourses, the straightening of meandering rivers into navigation channels, and the dredging of riverbeds (Brooker, 1985; Julien, 2018). The embankment of rivers is also commonly employed to impede the natural modification of watercourse trajectory and stabilize waterways to allow for the navigation of larger vessels. These infrastructural projects can heavily transform riverscapes (see Fig. 5) and tend to reduce the diversity of habitats in riverbanks and in rivers and the leveling of channel depth reduces the lateral differentiation in habitats (Ward & Stanford, 1995). Both these effects lead to the disappearance of feeding and spawning grounds for fish and thus reduces diversity while navigation itself can be damaging to freshwater communities through regular vessel-induced waves (Jeliazkov et al., 2024[1]; Wolter, 2001). The straightening of waterways leads to the increase of flow velocity, increasing bank incline and reducing the available surface for river fish. The needs of navigation, flood control and the need for reservoirs also lead to the construction of thousands of obstacles like dams, weirs and locks, which are known to alter channel depth and width, reduce river slope, modify sediment transport, oxygenation, causing an accumulation of fine sediments above dams (Abbott et al., 2022; Haddad et al., 2015; Shih et al., 2022). The slowing of flow and widening of the channel creates in some cases, like large hydroelectric dams, quasi-lentic environments susceptible to eutrophication and favorable to generalist species (Prchalová et al., 2009). The difficulty for some animal species to cross these obstacles when moving upstream

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[1] This collaborative work of bibliographic analysis received contributions from the author (Swann Felin) and is featured in the Appendices of this manuscript.

(more so than downstream) also leads to the fragmentation of habitats and populations (see next section, which discusses connectivity) and the shift of communities (Jones et al., 2021).

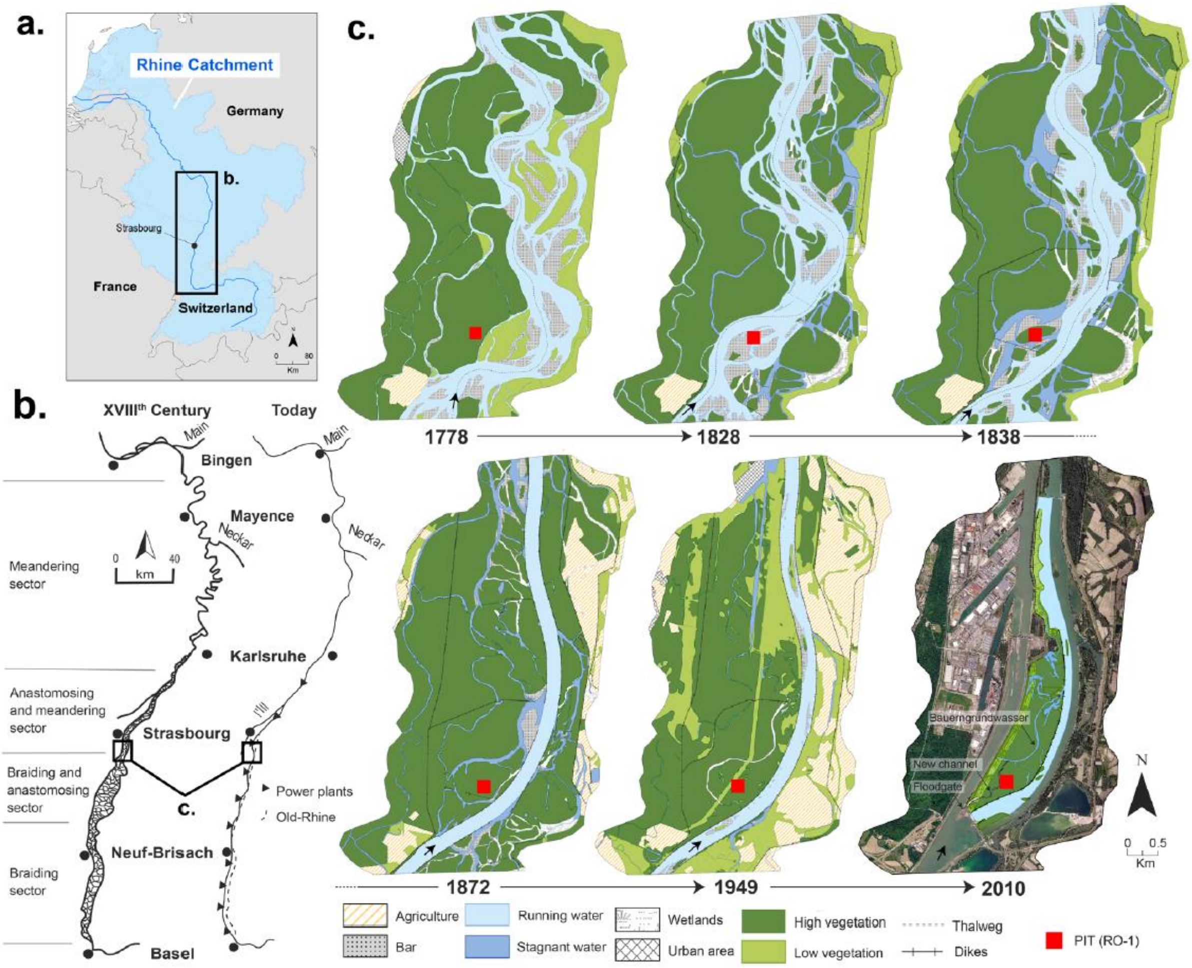

Figure 5: Visual example of the extent of the impact of river engineering on riverscapes - the Rhine in Strasbourg, France. *a) Overview of the River Rhine catchment with the location of Strasbourg. b.) Comparison of the Upper Rhine system before and after river engineering works in the 19th and 20th century. c.) Historic development of a smaller area from AD 1778 until 2010: we note the draining of floodplains, channelization and deviation of the river, building of an inland port. Adapted from Preusser et al. (2016).*

1.3.3 Defining connectivity for riverscapes

As shown above, human interferences on aquatic habitats are complex, wide-ranging, and especially impactful in heavily anthropized areas. They modify river fish communities and trophic webs in ways that are sometimes difficult to parse. In particular, some river engineering operations impede the movement of fish and other organisms along rivers, or from bank to channel. These issues are a matter of connectivity, they are central to this thesis and will be discussed in this section.

The concept of connectivity in ecology arose from terrestrial landscape ecology and could be defined as the ”uninterruptedness” of a given system or unit of space. In terrestrial ecology, connectivity is generally defined on a two-dimensional plane (Baguette et al., 2013). It provides a framework to study both structural connectivity, or the configuration of patches of suitable habitat and their distances to one another, and functional connectivity, or the ability of species to cross unsuitable spaces between patches and overcome obstacles to dispersal. Connectivity is thus a useful tool to discuss the potentiality for dispersal and the accessibility of ”patches” in the framework of neutral theory. It is generally absent in niche modeling (Bruneel et al., 2018). A series of approaches exist for bridging this gap, which is also a challenge of this thesis (see Chapters 2 and 3). In river ecology, the singular dimensionality of studied space leads to additional terms to approach connectivity in watercourses. River connectivity is divided into four subconcepts (see Fig. 6) with very different phenomena attached (Ward, 1989): longitudinal connectivity, which describes interactions along the river axis, lateral connectivity, which describes interactions between the floodplain, river and banks, vertical connectivity, which refers to connection between surface water and the water table, and temporal connectivity, which describes interactions between different points in time (e.g. seasonal variations in flow, communities of freshwater organisms etc.). In this thesis, longitudinal connectivity will be the main focus, while lateral connectivity will be often included and discussed in modeling and ecological contexts. Temporal connectivity will appear only a few times in larger discussions. Finally, vertical connectivity is out of the scope of this work. Thus, for the sake of brevity, the use in the rest of this manuscript of the term ”connectivity” without an epithet will always mean longitudinal connectivity.

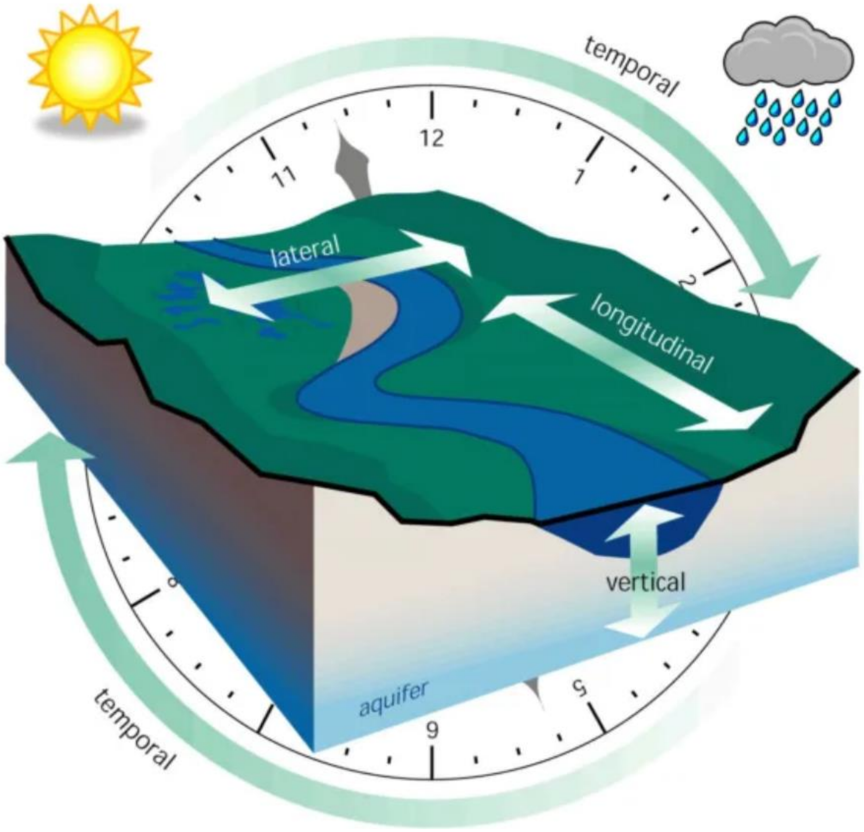

Figure 6: Illustration of the four axes of river connectivity. *Adapted from a report from the Federal Interagency Stream Restoration Working Group (1998).*

Embankment, channelization and riparian habitat destruction directly impact lateral and vertical connectivity, while extreme punctual events like hypoxia of pollution with pesticide can disrupt temporal connectivity. Longitudinal connectivity, which is extremely relevant to river fish dispersal due to the shape of river networks and specific migratory behaviour (Benitez et al., 2018; Rodeles et al., 2020, 2021), is greatly impacted by the construction of dams, weirs and locks along the longitudinal axis of rivers (Duarte et al., 2021). They are the most widespread cause of habitat fragmentation in watercourses and have immediate consequences on fish communities (Rodeles et al., 2021; Barbarossa et al., 2020). The ecological importance of river connectivity has been repeatedly highlighted (Pringle, 2003). Connectivity loss and habitat fragmentation have been proven to reduce biodiversity in freshwater ecosystems, sometimes leading to species extirpations (Kominoski et al., 2017), while dam removal has been found to increase community resilience and ecosystem biodiversity (Catalano et al., 2007; Duda et al., 2021; Stanley & Doyle, 2003). Potamodromous fish populations with large domains are sometimes diminished by the reduction of accessible space when stuck between large dams. The creation of an important contrast in river morphology between upstream and downstream sections of a dam also contributes to fragmentation by breaking the continuum. Less obvious obstacles can also be considered when discussing longitudinal connectivity: localized hypoxia, absence of essential resources or pollution can constitute a challenge for the crossing of fish despite the absence of a dam (Urbanski & Nogueira, 2024). Longitudinal connectivity, due to downstream flow of rivers, is often considered asymmetrically, indeed, downstream movement and dispersal are generally considered to be more achievable than upstream movement for some types of obstacles; additionally, fish larvae, which do not have enough strength to carry themselves against river flow in many cases, may be carried downstream over an obstacle, reinforcing this asymmetry of dispersal (Baudoin et al., 2014), in some cases leading to community shifts by separating individuals according to morphological traits (Jones et al., 2021).

1.4 The coming decades

This thesis is concerned with prospective distribution of river fish in the Seine-Normandie basin. As such, it requires dealing with environmental and methodological challenges particular to the near future, bringing with them necessary added context: anthropogenic climate change and future watershed management.

1.4.1 Anthropogenic climate change in Europe

Beyond the direct consequence of human activity on rivers through agriculture, industry and urbanization, a more global threat to freshwater ecosystems is climate change. Now thoroughly proven, caused by human burning of carbon-rich fossil fuels, deforestation and livestock farming, anthropogenic global climate change is the main challenge of our century, and is met with the widespread and enduring procrastination and sluggishness of decision-makers. Atmospheric CO_2 has increased from less than 280 ppm in pre-industrial times to approximately 426 ppm today (Mauna Loa Observatory, 2025), the consequences of climate change on ecosystems, global cycles and human societies are already observed today, and are likely to be catastrophic in the near and further future. Global consequences of global change include the melting or continental ice shelves and subsequent sea level rise, endangering coastal cities and likely to cause a seeping of saltwater in coastal aquifers (Masterson & Garabedian, 2007). Changes in climate would affect different landmasses in different ways. Europe in particular is warming at a faster pace than average (Copernicus, 2024). In Northern France, these changes would also concern precipitation intensity and distribution, as well as the intensity and frequency of extreme climate events such as heat waves and floods. A combination of the effects of climate changes and extreme events on Earth are due to bring loss of capital and life. It is thus crucial to develop tools to predict these events and mobilize the means necessary to protect populations and ecosystems.

The situation of Western Europe with respect to climate changes is a singular one, with a Northern half affected by cold spells, long floods compared to a much more drought and flash-flood prone Southern half. The contrasts between Northern and Southern halves are generally predicted to be accentuated by future climate change, with a wetter Northern Europe and a drier Southern Europe, bringing new challenges to water management and ecosystem conservation. While drier periods may result in an increase in occurrence of intermittent rivers in some watersheds, causing disruption of temporal connectivity and causing great harm to all obligate aquatic organisms, increased precipitation and more intense rainy episodes may lead to increased runoff, erosion and discharge. Increased water temperature as a result of air temperature going up may also lead to an increase in primary production, and general eutrophication of watercourses (Nazari-Sharabian et al., 2018), as well as the progressive shift of ranges for mobile species as a result of requirement niche shifts, a phenomenon already observed in current rivers for some fish species, with range shifts observed upstream, poleward, and to higher altitudes (Comte et al., 2013, 2013; Grenouillet & Comte, 2014; Maire et al., 2019). The more general disruption of environmental gradients in rivers is also due to wreak havoc in fish communities, which is theorized to favor generalist species over specialists, especially stenotherms, in many contexts a recurrent pattern in contexts of mass extinctions and rapid change like the one currently affecting freshwater ecosystems (Daufresne & Boët, 2007).

1.4.2 Watershed management scenarios

The multitude of elements developed above give a general idea of the drivers of present fish distribution. However, when discussing future events in general and change in watershed management in particular, one has to deal with a complex web of interactions between climate change, existing environmental conditions in constant mutation, and the positive or negative contribution of human activity, which all contribute to biotic, abiotic and stochastic phenomena which will determine the composition of future river fish communities. A first approach to discussing future events is the prescriptive approach used by regulatory bodies seeking to emit guidelines for the behavior of states and management entities. A collection of injunctions, objectives and recommendations, prescriptive texts are less interested by what may happen than by what should be made to happen. However, in the context of a study of possible futures and prediction modeling, completely prescriptive approaches are impractical. A better framework to explore the future without overstepping would be to remain in the realm of thought experiments, leading to systematic modeling approachesand anticipatory prediction (Maris et al., 2018) . The IPCC did as such, formulating scenarios, relying on socioeconomic and physical factors before imputing these ”stories” into calibrated models. The use of watershed management scenarios in particular is well-suited to exploring the potential distribution of river fish, when future management, despite existing prescriptive and predictive literature, remains unknowable: an array of contrasting stories about future management of watersheds, studied simultaneously, allows researchers to cover more ground than a simple educated guess about the most likely future. Their development will be explained in Materials and Chapter 4 of this thesis.

1.5 The purpose of this thesis: understanding the influence of watershed management on fish distribution in a context of fragmentation and global change

We have shown that river fish communities are incredibly species-rich and diverse. They are also uniquely sensitive to human activity and its consequences on riverscapes, both because of the historical proximity of dense human urban centers and associated infrastructure to rivers and because river water often becomes the final receptacle of pollutants. River ecosystems are fragile, uniquely threatened, and so understanding how to best preserve freshwater fish communities requires studying connectivity, climate change and management constraints that may altogether determine the potential futures of these communities. Current state of niche modeling for freshwater tends to use primarily environmental gradients to explain fish distribution, shying from information on migration and colonization, preventing the field from estimating their relative importance in the explanation of species distribution compared to more classical environmental gradients.

For the river fish of the Seine-Normandie drainage basin, these stochastic processes include their capacity for dispersal in a context of significant anthropogenic connectivity constraints, and can be classically expressed through the use of connectivity indices. To study the potential distribution of river fish in future contexts and thus understand the influence of management decisions on fish distribution and ensure their preservation, the main challenge is the establishment of future conditions in a modeling context, which necessitates the use of management scenarios and climate projections which are to be compared, and their impact on fish communities assessed.

The objectives of this thesis are the following:

- **To create an approach to assess longitudinal connectivity loss on a large drainage basin whilst taking functional traits of fish into account**
- **To investigate the influence of connectivity loss on potamodromous and resident fish of the Seine-Normandie watershed**
- **To construct management scenarios for the Seine-Normandie watershed adapted to riverscapes**
- **To understand the influence of climate change and management decisions on potential future fish distribution**
- **To parse the portion of uncertainty linked to climate projections and scenarios in the future distribution of fish**

As explained in section 1.3.3, we expect connectivity to play a significant role in current fish distribution in addition to the environment (first hypothesis). As exposed in sections 1.4.1, we further expect climate change to greatly influence future fish distribution (second hypothesis) and we expect watershed management decisions on connectivity and land use to impact future fish distribution (third hypothesis). Finally, we expect climate projections and watershed management scenarios to both provide uncertainty to future fish distribution and for climate change to represent a larger share (fourth hypothesis).

The following manuscript is articulated following six steps. Chapter II presents the study area and the material and data used in this thesis. Chapter III tests our first hypothesis, presenting the study assessing the influence of longitudinal connectivity on fish distribution through novel connectivity metrics and connectivity-sensitive distribution models (article published). Chapter IV tests our second and third hypothesis, presenting the study that investigated the respective influence of climate change and management scenarios on fish future distribution and range shifts in the coming century. Chapter V deepens the question of the relative contribution of climate change projections and management scenarios through a reflection on uncertainties, testing our fourth hypothesis. Finally, Chapter VI offers a general discussion of the overall results of the thesis and brings a final conclusion and a few perspectives for future work.

Chapter 2. Materials

Further development and all following chapters will concern only the Seine-Normandie Administrative basin described below. This Materials section will present a general geographical, climatic and hydrologic context for the basin in Section 2.1, going into details about the method of acquisition of current climate and hydrological data. Section 2.2 will present the anthropogenic occupation and transformation of the basin and explains how obstacle and land use data were obtained. Section 2.3 will detail fish community composition in the basin and present our fish dataset. Section 2.4 will present the theoretical framework and limitations of Species Distribution Models. Section 2.5 will give a state of the art of connectivity and connectivity indices, in relation with river networks. Finally, Section 2.6 will focus on the challenges and methodological requirements of futurology as it pertains to this thesis, mainly detailing future climate projections and management scenarios.

2.1 Geographical and hydroclimatic Context

2.1.1 General geography of the Seine-Normandie basin

The French State manages the rivers that flow within its borders through a system of special districts which do not follow traditional administrative borders (French “régions”, see Fig. 8, and “départements”), instead keeping major drainage basins whole and forming large territorial units by following ridge lines. Six Water Agencies are tasked with managing 7 administrative basins within hexagonal France and Corsica, see Fig. 7, while smaller Water Offices were formed for Overseas départements.

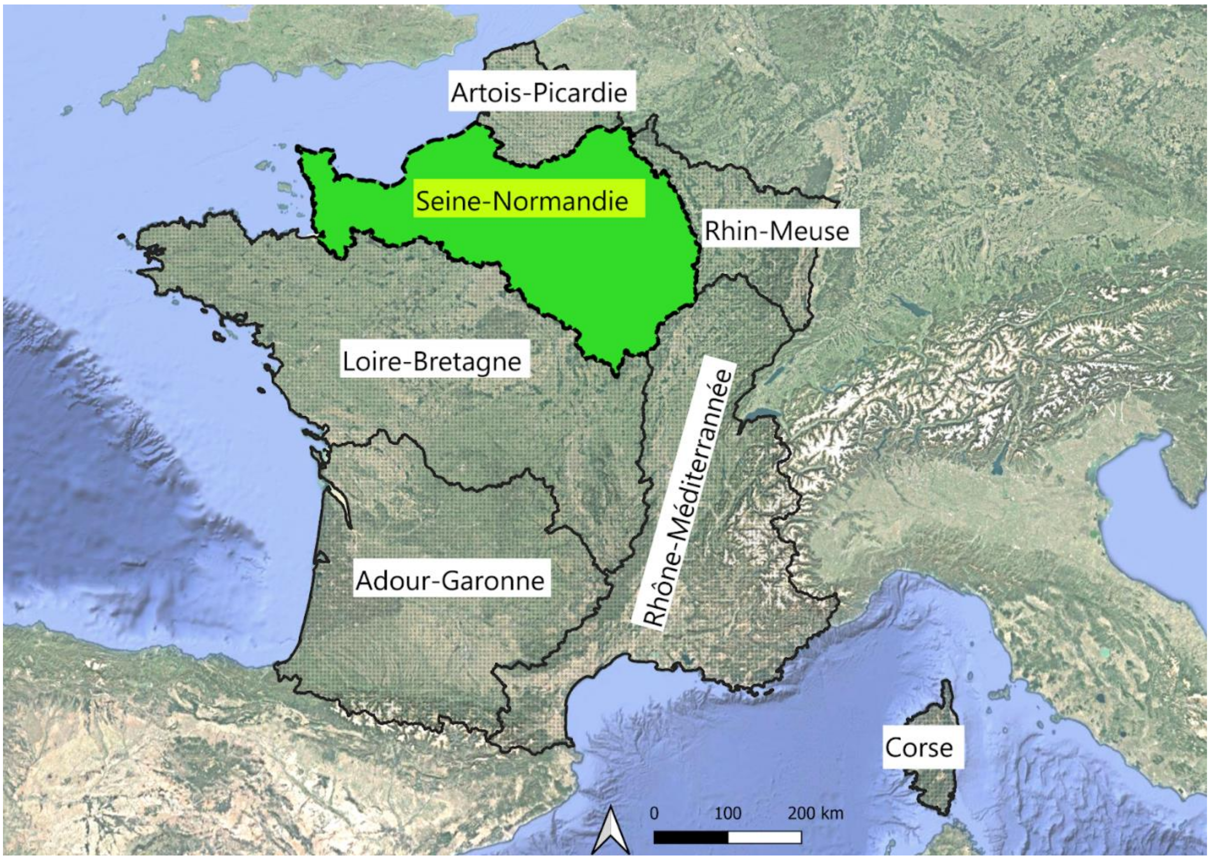

Figure 7: The Seine Normandie basin among the Administrative Basins of Hexagonal France. *The basin is connected to all its neighbors through an extensive network of canals.*

The Seine-Normandie administrative basin is located in Northern France and spans 95,000 km². The Seine drainage basin covers 83 % of the basin surface, while the rest of the basin is composed of the coastal rivers of Normandy (the Orne, Vire and Dives being the three largest watersheds among them). Our study area spans several administrative regions of France but retains its territorial unity when it comes to water management.

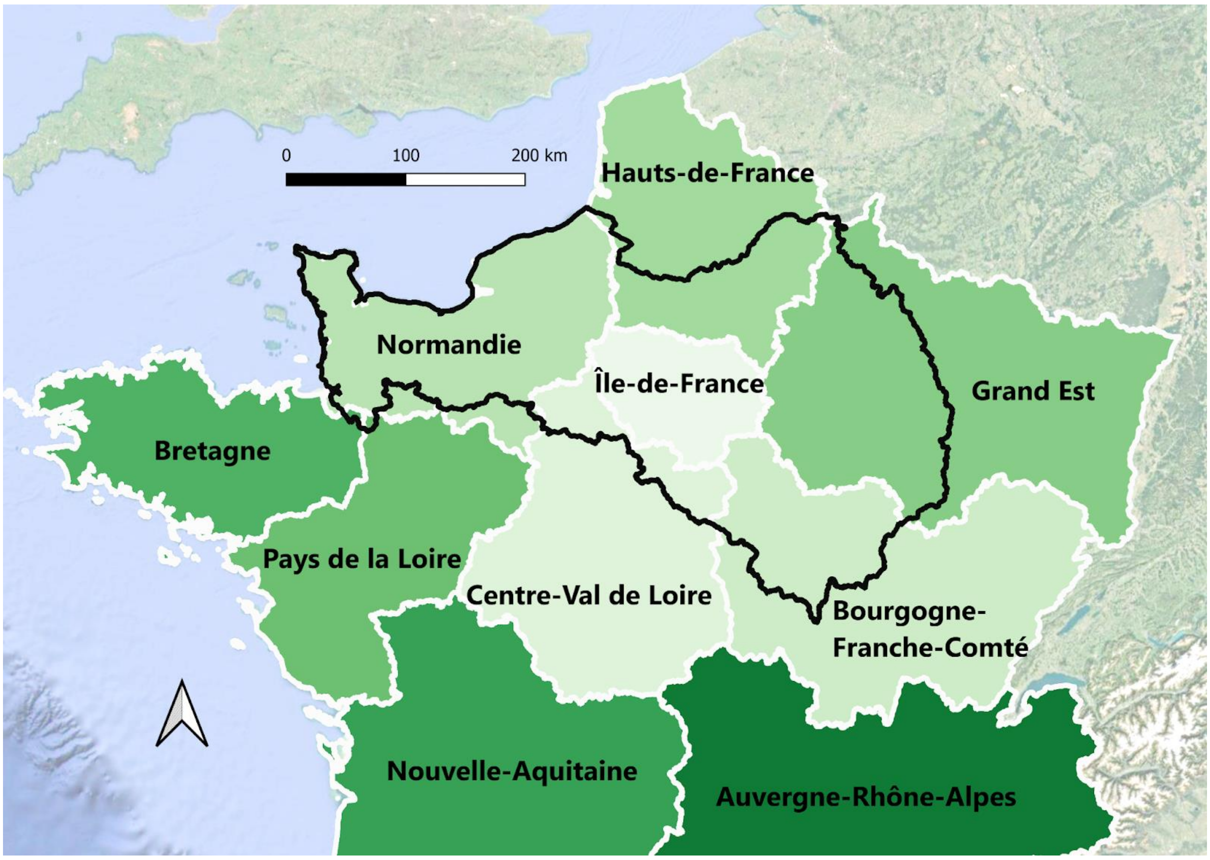

Figure 8: Administrative divisions of Northern France and overlap with the Seine-Normandie administrative basin.

It is mostly composed of lowlands, with the exception of the Morvan Massif to the Southeast, which culminates at 901 m (Haut-Folin). Outside of this massif, elevation rarely exceeds 400 m. The basin is geologically defined by the Paris Basin - composed of mesozoic and cenozoic sedimentary rocks of various porosity, from chalk to limestone, influencing river network complexity. Outside of the Basin are the edges of the Palaeozoic Armorican Basin in Normandy and Morvan massif in Burgundy, made of plutonic rock (see Fig. 9).

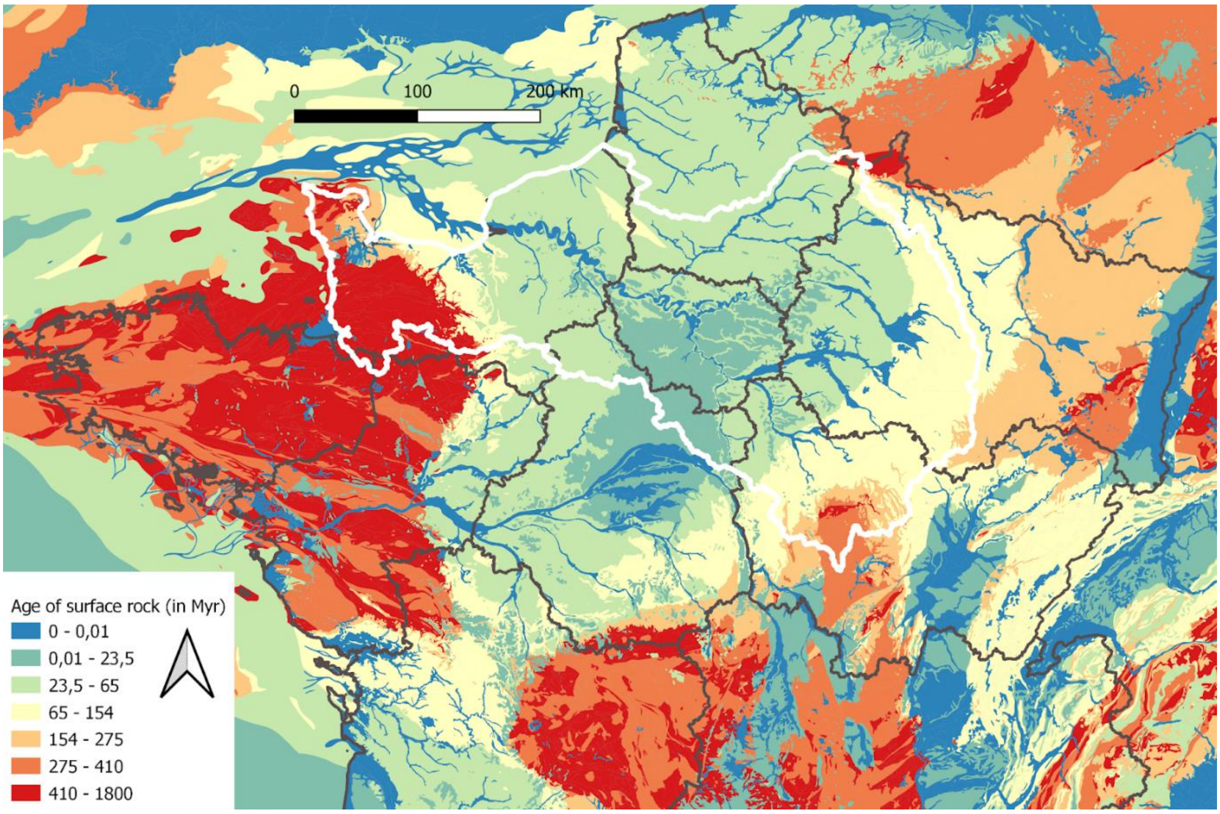

Figure 9: Geological map of Northern France and overlap with the Seine-Normandie administrative basin. *The Morvan Massif to the Southeast and Armorican Massif to the West are highlighted as older rocks.*

Geological subregions of the basin, which we will refer to as hydroecoregions in the rest of the text, were defined following local geological, geomorphological and climate properties and have been extracted for use in this work as geographical factors. Two levels of complexity exist for this differentiation of subregions, and the most precise (Hydroécorégion de niveau 2, see Fig. 10) was kept for this thesis (Wasson et al., 2004).

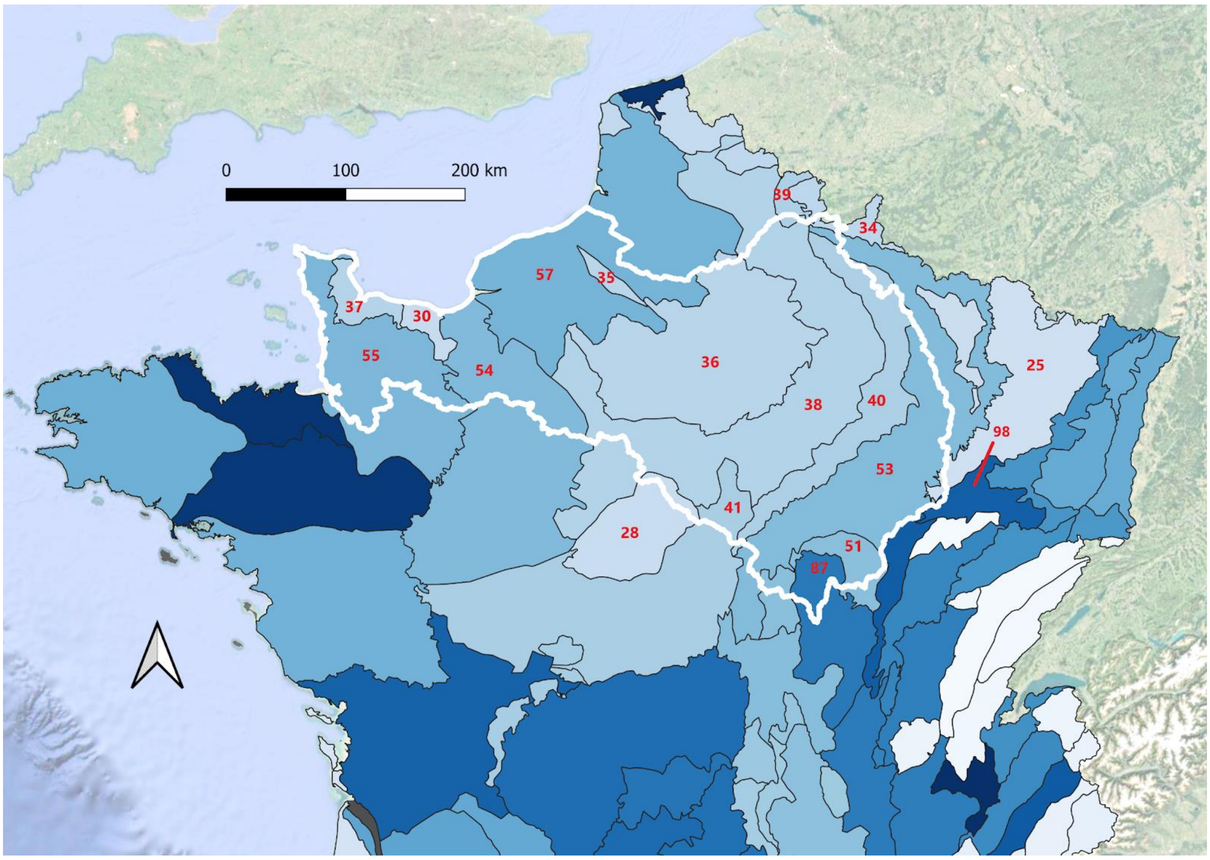

Figure 10: Hydroecological regions of Northern France and overlap with the Seine-Normandie administrative basin. *25: Plateau Lorrain; 28: Sologne - Forêt d'Orléans; 30: Plaine de Caen; 34: Ardennes; 35: Pays de Bray; 36: Bassin Parisien; 37: Cotentin Est; 38: Auréole Crétacé; 39: Thiérache; 40: Champagne humide; 41: Tables Calcaires Sud Loire; 51: Bazois Auxois; 53: Côtes Calcaires; 54: Nord Loire - Perche; 55: Massif Armoricain Nord-Est; 57 Haute-Normandie Picardie; 87: Morvan-Charollais; 98: Collines sous-vosgiennes.*

2.1.2 Climate and hydrology

The Seine-Normandie basin is located in Northwestern Europe and as such falls entirely into the climate category Cfb – oceanic temperate climate with warm summers under the Köppen-Geiger Climate Classification (Kottek et al., 2006; Strohmenger et al., 2024). It is characterized by even precipitation during the year, low temperature amplitude, mild winters and cool summers. Within this broadly defined climate type, the basin displays a relative diversity of climates. Annual precipitation ranges from 588 mm in the Beauce agricultural region to 1261 mm in the Morvan Massif and continental Western Normandy (Vidal et al., 2010). Figure 11 features precipitation data across the Seine-Normandie basin (also see Fig. 13 for seasonal variations).

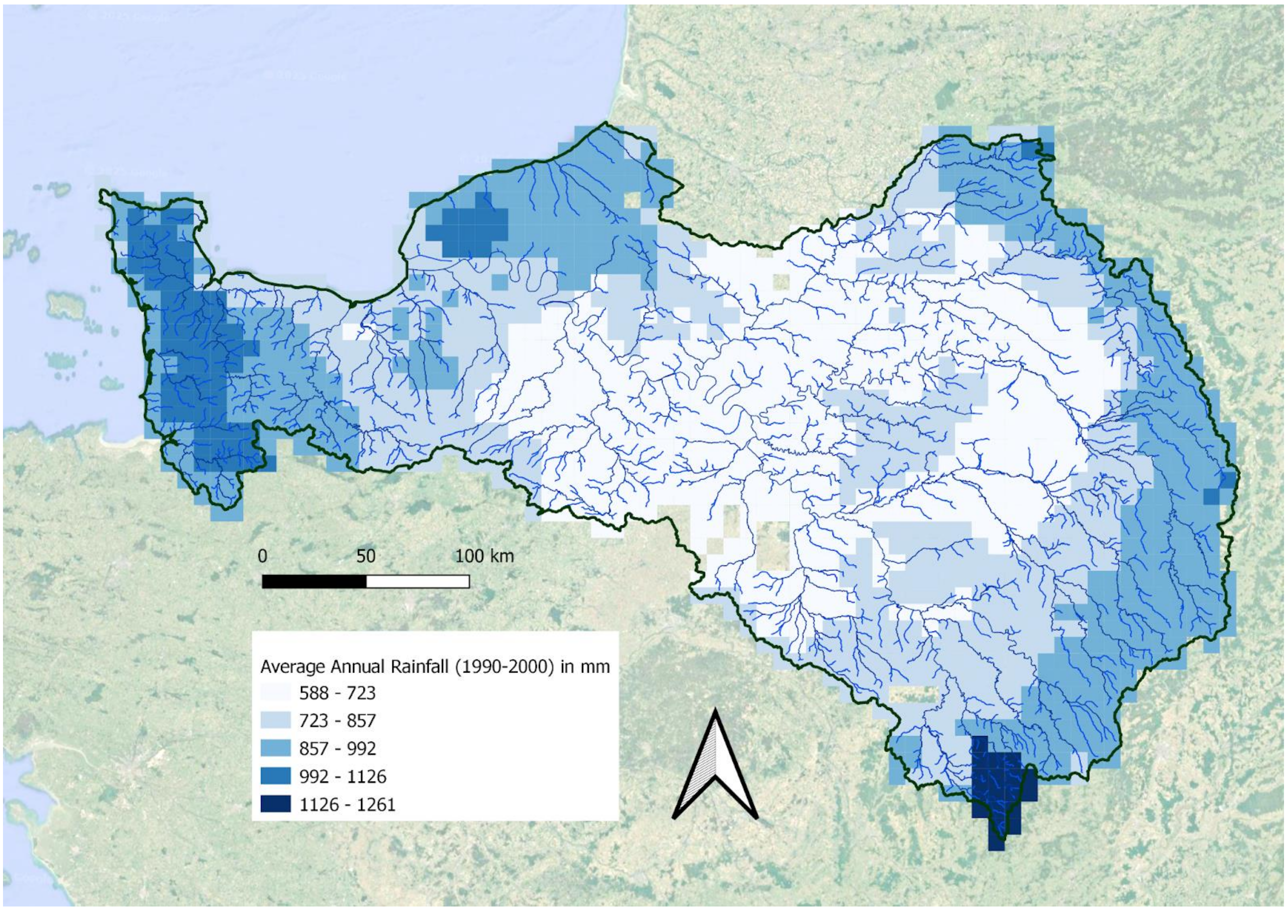

Figure 11: Average annual precipitation over the Seine-Normandie Basin (1990-2000), in mm, data originating from the SAFRAN grid dataset (Vidal et al., 2010). *The Morvan massif and Western Normandy are visibly the rainiest areas in the basin. We show the variations which are regrouped within the Cfb oceanic climate (Kottek et al., 2006; Strohmenger et al., 2024).*

Similarly, coastal Western Normandy sees average January temperatures around 6 °C (while certain parts of Champagne sees 3 °C averages), and 16.5 °C July averages (while Paris sees 20.9 °C averages, see Fig. 12 for a broader overview of the basin and Fig. 13 for seasonal variations).

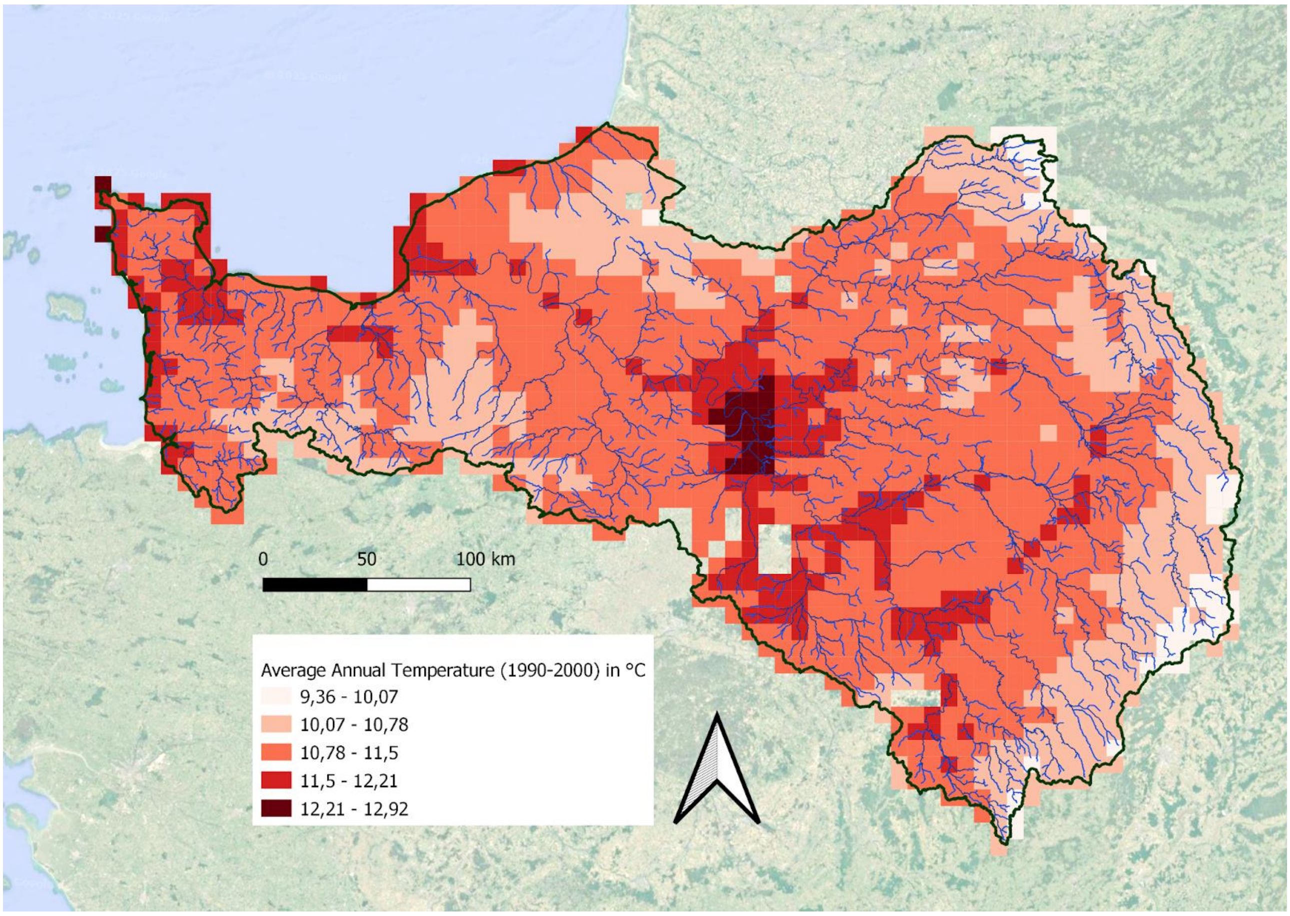

Figure 12: Average annual temperature over the Seine-Normandie Basin (1990-2000), in °C, data originating from the SAFRAN grid dataset (Vidal et al., 2010). *The Parisian region is warmer on average due to urban heat island, while Western Normandy is exposed to more pronounced oceanic regulation, leading to warmer winters.*

The Seine-Normandie basin counts approximately 55,000 km of watercourses and flows into the English Channel. The Seine river, being the main river in the study area, oscillates around 550 m^3s^{-1} at its estuary (see Fig. 13 for a seasonal profile of discharge), occasionally reaching 1500 m^3s^{-1} (in comparison to e.g. the Rhine with 2,900 m^3s^{-1} average discharge or, further, the Volga with 8,380 m^3s^{-1} average discharge).

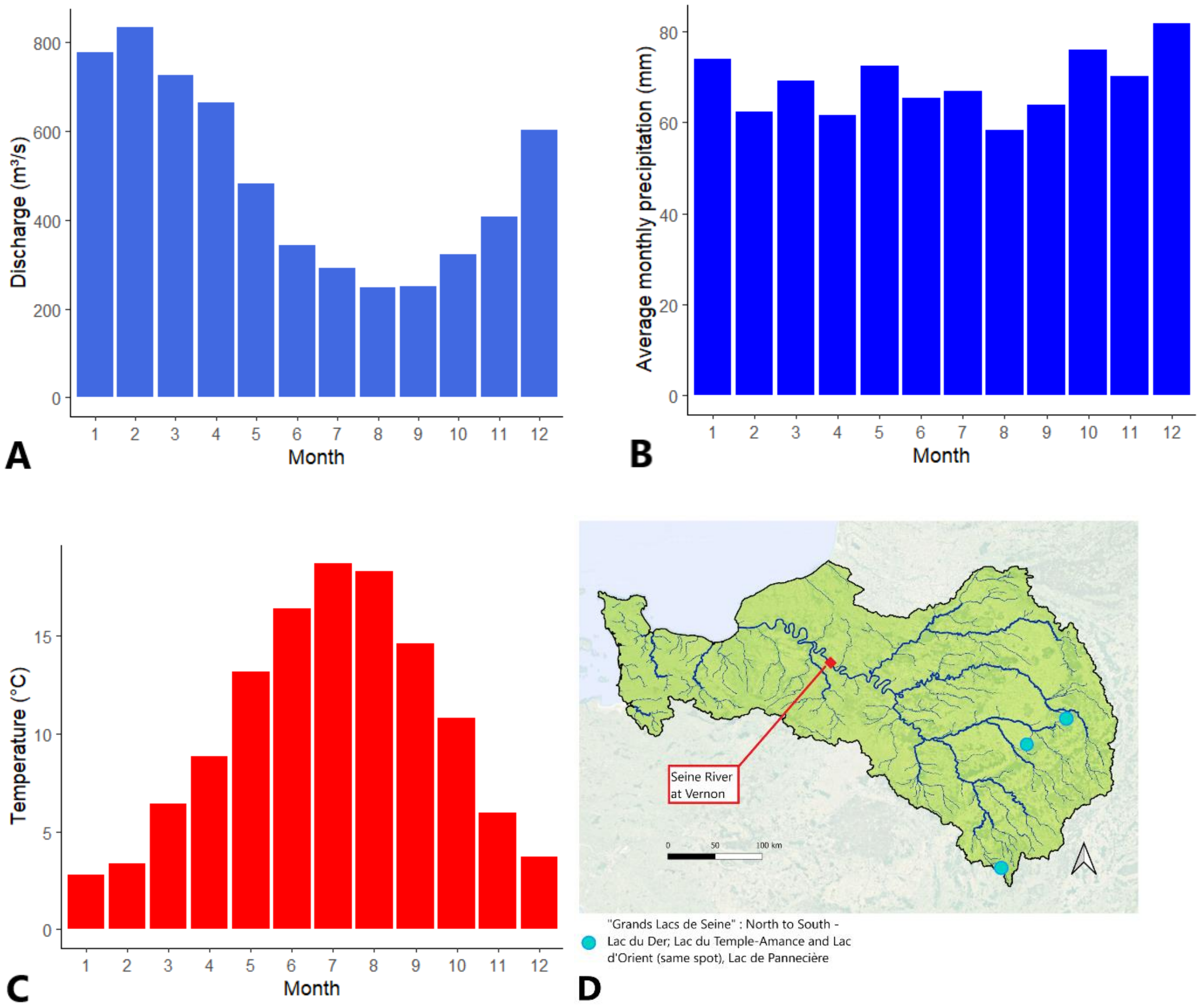

Figure 13: Climate and hydrological data for the Seine River at Vernon (data: 1976-2005). *A: Average discharge for each month (m^3s^{-1}), lowest values in August, highest values in February (Leleu et al., 2014). B: Average monthly precipitation (mm), relatively homogeneous spread (Vidal et al., 2010). C: Average temperature for each month (°C), peak in July, lowest values in January (Vidal et al., 2010). D: Location of data extraction station.*

The Seine takes its traditionally accepted source in Burgundy, flowing Northwest toward the Channel. Its main tributaries, the Yonne, Marne and Oise rivers, each provide approximately 100 m^3s^{-1} of discharge. Coastal rivers of Normandy included in the administrative basin can be divided between i) the Seine-Maritime rivers, which flow straight with little to no dendricity, heading North on Cretaceous chalk and into the English Channel (e.g. the Varenne, the Bresle and the Veules, the shortest non-tributary river in France) and ii) the Lower Normandy rivers, among which the Orne river is the largest, with an average discharge shy of 28 m^3s^{-1}. Hydrological regime in the basin, defined as the shape of the distribution of flows year-round, is almost uniformly pluvial - no river in the basin is connected to a mountainous area high enough to allow for nival regimes. A more precise typology of regimes for France (Beaufort et al., 2022) shows a certain variation in regime in the basin, with subsoil properties having a clear influence - connection with a water table allowing for a regulation of flow.

Whe should note that, in order to reduce the chances of flooding in Paris, in reaction to the especially intense flooding in 1910, a set of large lakes as water storage systems were installed in the Yonne, Aube, Seine and Marne upstream basins. Called the “Grands Lacs de Seine”, these lakes (the Der-Chantecoq, Temple-Amance, Orient and Pannecière, as well as a new project on the Bassée river, see Fig. 13) were made through damming and canal building from 1949 onward, and are used to mitigate droughts and floods, therefore modify discharges in larger rivers from the Seine basin.

2.1.3 Collection of data on hydrology and climate

Meteorological data was obtained from the SAFRAN dataset (Vidal et al., 2010), a meteorological reanalysis provided by Météo-France, the French weather institute. In parallel, daily streamflows were obtained through inverse distance weighted geographical interpolations of the HydroPortail (Leleu et al., 2014), from which sundry hydrological indicators were obtained (see Chapter 3). Water temperatures, expressed as thermal peak - or the mean water temperature of the 30 hottest consecutive days - were obtained through machine learning extrapolation of available data following methods presented in Beaufort et al. (2022). Finally, water quality data (oxygen, nitrate and ammonium concentration) were obtained through simulations produced by the pyNuts-Riverstrahler model for 2017-2021 (Renaud et al., 2024).

2.2 Human presence and anthropization

2.2.1 Demographics and land use

Human occupation in our study area is highly heterogeneous. The total population within the basin as of 2023 was around 18.5 million people. It is thus the most populous administrative basin in France while being the fourth largest in terms of surface. 70 % of the basin's population is located within the Paris Metropolitan Area (about 20 % of the basin's surface area). In contrast, one of the least densely populated départements in France (Haute-Marne) is located mostly within the basin. Major urban areas, populations and watercourses are featured in Fig. 14. Human occupation in the region dates from the Pleistocene, but urban settlements developed in the gallo-roman era. Agriculture spread in favorable regions through progressive land clearance and deforestation, wetlands were put through widespread drainage, while less suitable areas were turned into pastures and bocage. Current land use in the basin is spread between highly agricultural regions (dominated by wheat, rapeseed and sugar beets) and pasture-dominated landscapes in Western Normandy and parts of Champagne.

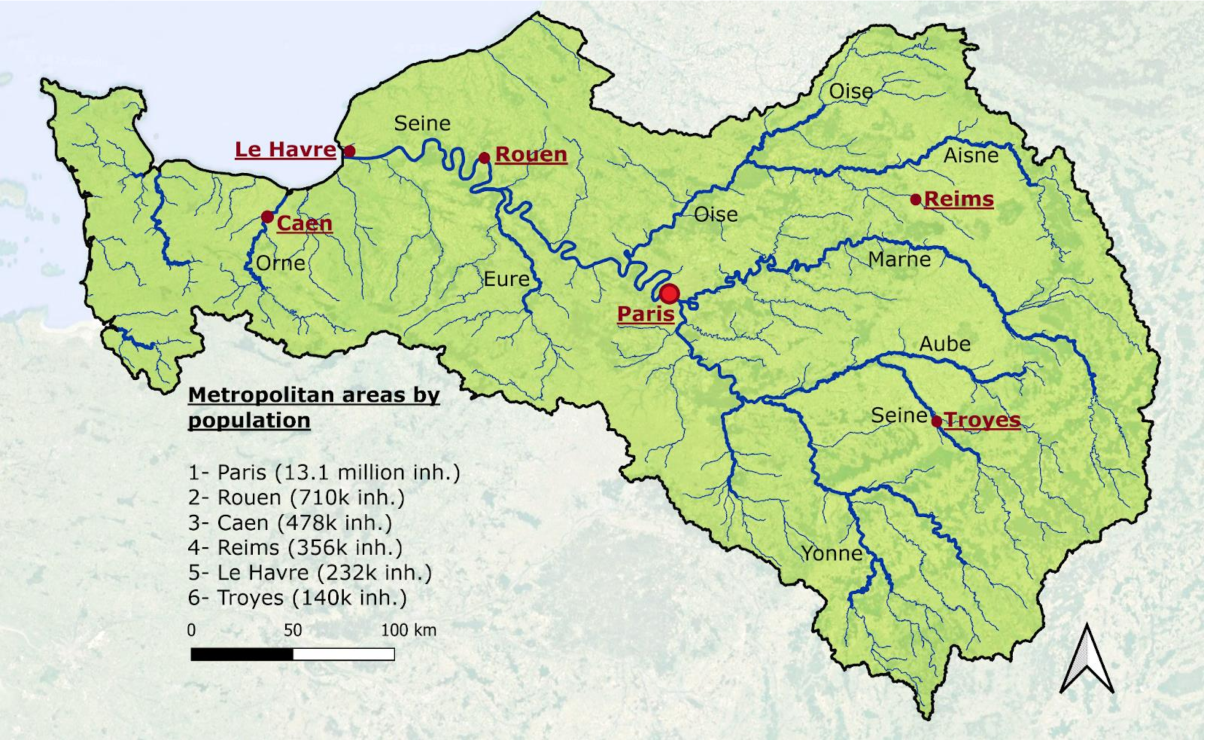

Figure 14: Map of the Seine-Normandie basin, including major rivers, major urban areas and population. *Parisian macrocephaly in the basin leads to a 18x ratio between its population and the next most populous urban area.*

For the purpose of this thesis, land use was obtained through the THEIA land use database (Thierion et al., 2021), acquired from interpretation of satellite photography. THEIA uses 23 precise land use categories. The land use categories currently present in the basin are illustrated in Figures 15 through 17.

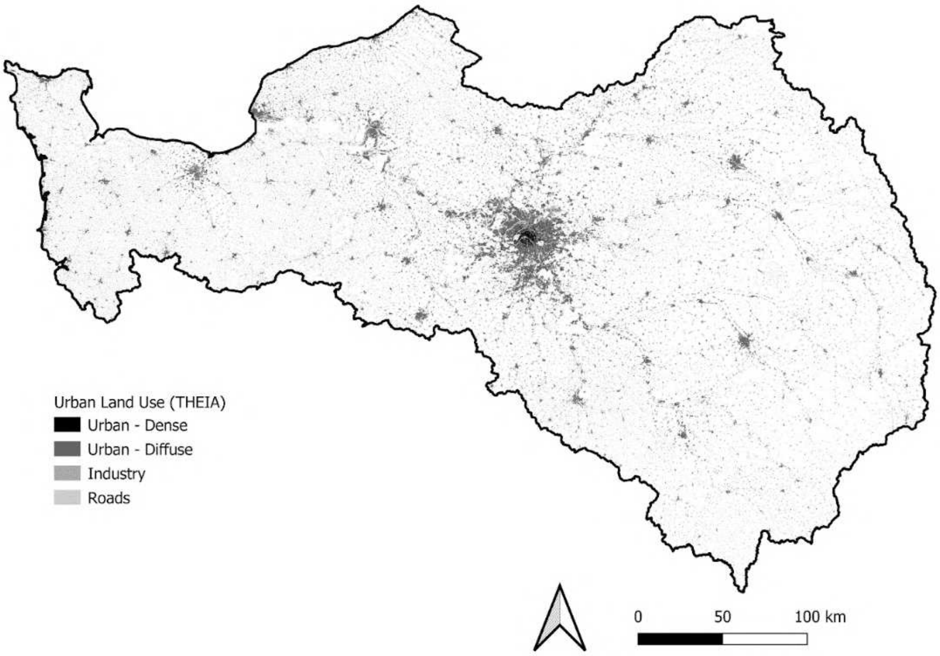

Figure 15: Map of THEIA urban land cover in the Seine-Normandie basin, color coding in legend. *The Parisian agglomeration, as well as Caen, Le Havre, Rouen, Reims and Troyes are plainly visible.*

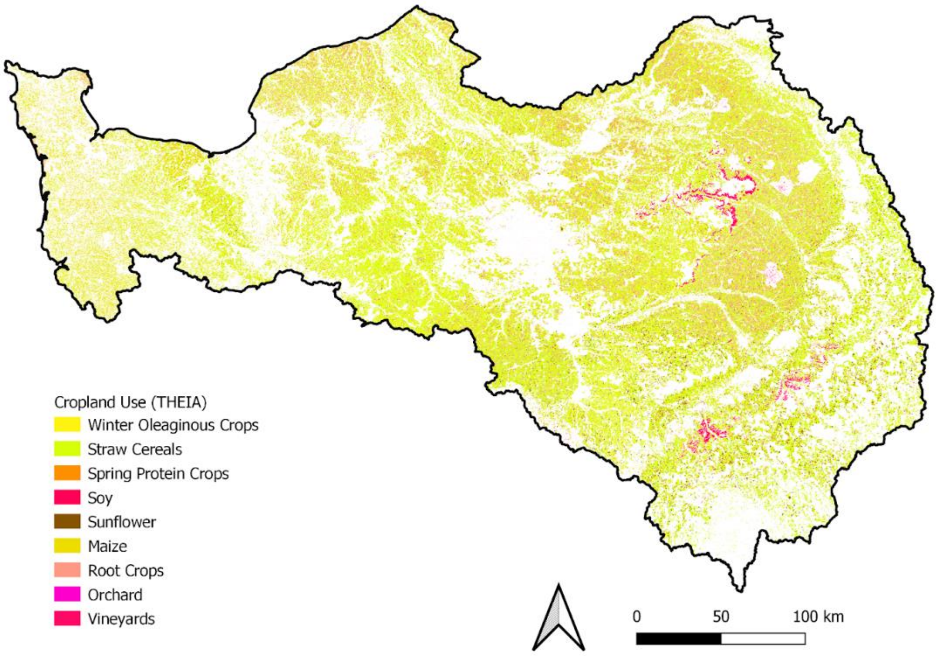

Figure 16: Map of THEIA agricultural land cover in the Seine-Normandie basin, color coding in legend. *Wine-producing regions in Champagne and Burgundy are plainly visible, while agriculture in general is widespread.*

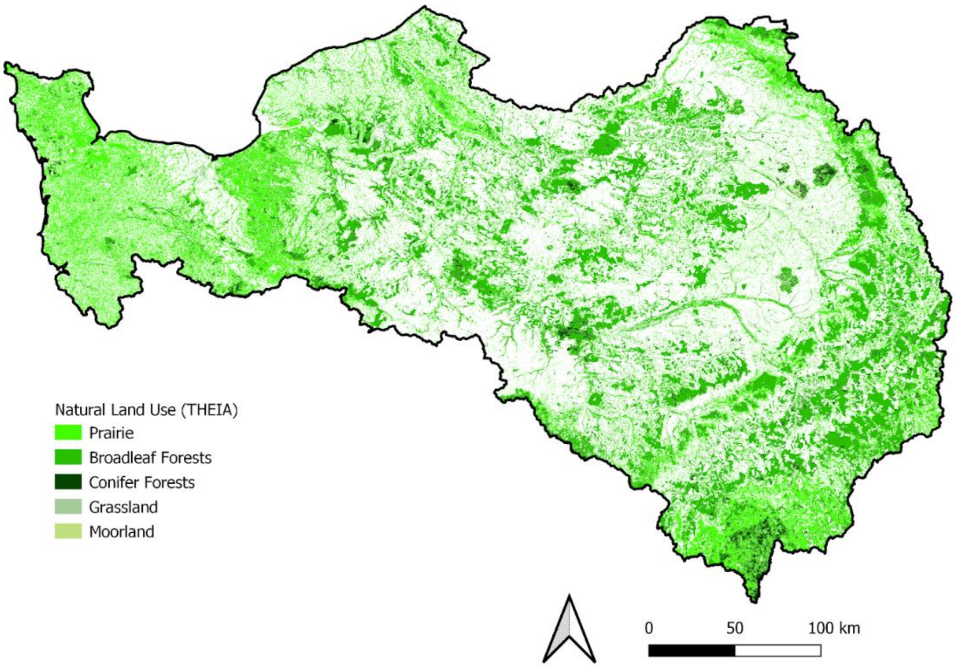

Figure 17: Map of THEIA pseudo-natural land cover in the Seine-Normandie basin, color coding in legend. *Prairies in grassland are widespread in the West while broadleaf forests are widespread. Conifer forests, often planted, can be found in some managed forests and in the Morvan Massif to the South.*

These land use categories were collapsed into four: urban land (impermeable surfaces), semi-natural land (forests, grassland), water cover and agricultural cropland for the purpose of terrestrial land use (see Fig. 18 for a whole-basin categorical mapping of land use). Grasslands and forests were grouped together due to the relatively extensive nature of prairies, their extreme diversity compared to standardized cropland practices and potential to provide environmental and agricultural services (Michaud et al., 2013). We put grassland and forests in sharp contrast to annual crops and vineyards/orchards in terms of chemical inputs and habitat disturbance. We chose to highlight water cover in land use to portray dynamics of lateral connection and local practices of water pumping for agriculture, and impermeable surfaces to highlight these often high disturbance areas (pollution, navigation, river engineering etc.).

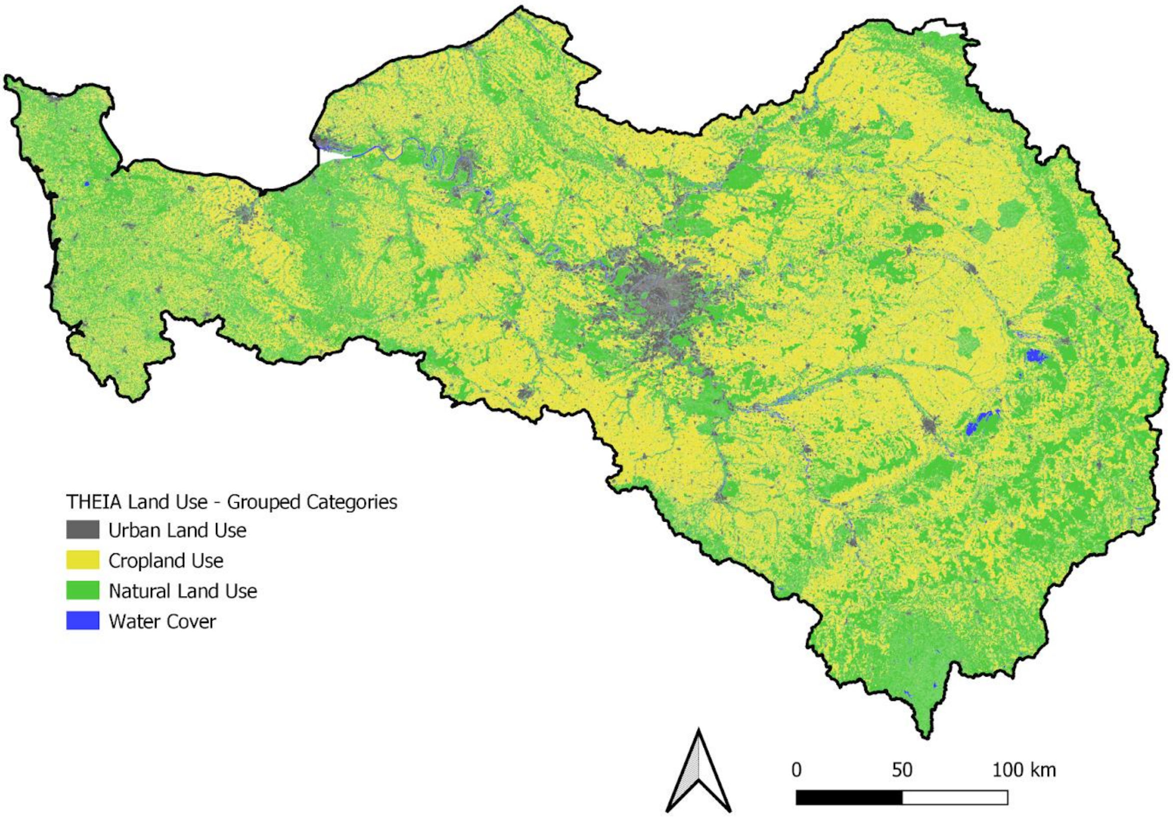

Figure 18: Map of THEIA land use, collapsed into four categories - urban, agricultural, semi-natural and water cover.

Land use variables were extracted with two approaches, one for overall land use, created to cover general land use in the neighboring area, and the other specifically for riverbank use, as it can be markedly different from overall land use (e.g. a river with extensive riparian forest cover, contrasted with highly agricultural land use in the area). We should note that forested areas were considered separately from any other land use categories for riverbank land use, as in the precise context of riverbank management riparian forests distinctly critical for riverscape conservation in the relative absence of wetlands (Riis et al., 2020). Overall land use was obtained from land use proportions within standard subcatchments of the Seine-Normandie basin, divided on major confluences and ridge lines, provided by the Seine-Normandie Water

Agency. Riverbank use was obtained through strip-shaped buffers (100-m wide, not counting river width, and 3-km long, 500 m downstream and 2500 m upstream, with compensation at sources for a conservation of sampling area) were created for each study site, and forest cover, which we equated with natural land use within floodplains, and water cover, which we identified with potential lateral connectivity sources in high flow values, were calculated within these buffers.

2.2.2 Human activity, infrastructure and obstacles

As agricultural and industrial activity in the basin generated an increasingly larger need for navigation, as well as protection from floods and droughts, a series of infrastructural projects were endeavored to accommodate these new needs. Large river axes were stabilized through the dredging of sediments, creation of embankments, channelization of courses, as well as the draining of floodplains. Smaller rivers were channelized and straightened for flood protection, taken out of their natural course and de-meandered in certain cases, greatly transforming landscapes and, coupled with the draining of wetlands, opening real estate for new uses and sometimes increasing the flow and velocity of rivers (Flipo et al., 2021). This process of channelization is still ongoing, with the projected recalibration of the upstream Seine (see the Décret du 22 juillet 2022, JORF - in French). In parallel, with increasing demand for river interconnectivity in the past centuries for boat traffic, several locks were put on major axes to regulate water level and render navigation easier and canals were dug between major watersheds, linking the Seine to the Mediterranean Sea via the Rhône and to the Atlantic Ocean and North Sea through the Loire, Escaut and Rhine. Under increased demand for densification of inland transport (European Commission, 2021), these projects continue to be greenlit to this day, with the Seine-Nord Canal expected to be navigated by the 2030s (see the Ordonnance n° 2016-489 du 21 avril 2016 relative à la Société du Canal Seine-Nord Europe, 2016). Dams and weirs of varying size were also progressively installed, either to support mills, regulate flow, store water or allow for the passage of vehicles. Some of them were retrofitted to produce electricity, especially locks, but large hydroelectric dams, typical of mountainous areas, remain rare on the basin.

2.2.3 Network resources and variable extraction

Around 12,000 obstacles, and counting, were identified on the basin and stored within the ROE database (Référentiel des Obstacles à l'Ecoulement, eng: Database of Flow Obstacles, see Fig. 19), made available by the French Office for Biodiversity (OFB, 2024), which we relied on for this thesis. To assess obstacle crossing by fish in the context of connectivity index calculation (see section 2.5), obstacle heights were needed in this thesis. However, they were not always known (65 % complete). This implied developing a statistical model to extrapolate the unknown obstacle height to be used in our connectivity modeling (see Chapter 3 and appendices). To study the Seine-Normandie basin, we chose the single-strand PIREN-Seine river network (Silvestre et al. 2024), displayed in all maps found in this thesis and used in all approaches involving network analysis in further sections. Single-strand and clean networks allow for simpler study of dendritic networks and longitudinal connectivity (e.g. through the absence of loops and minimal disconnections). We also used the SYRAH-CE network (SYstème Relationnel d'Audit de l'Hydromorphologie des Cours d'Eau, eng: Relational System Audit for Watercourse Hydromorphology) network (Valette et al., 2012) for complementary information on river straightness (for each reach, the ratio between river length and straight length between the two ends of the reach).

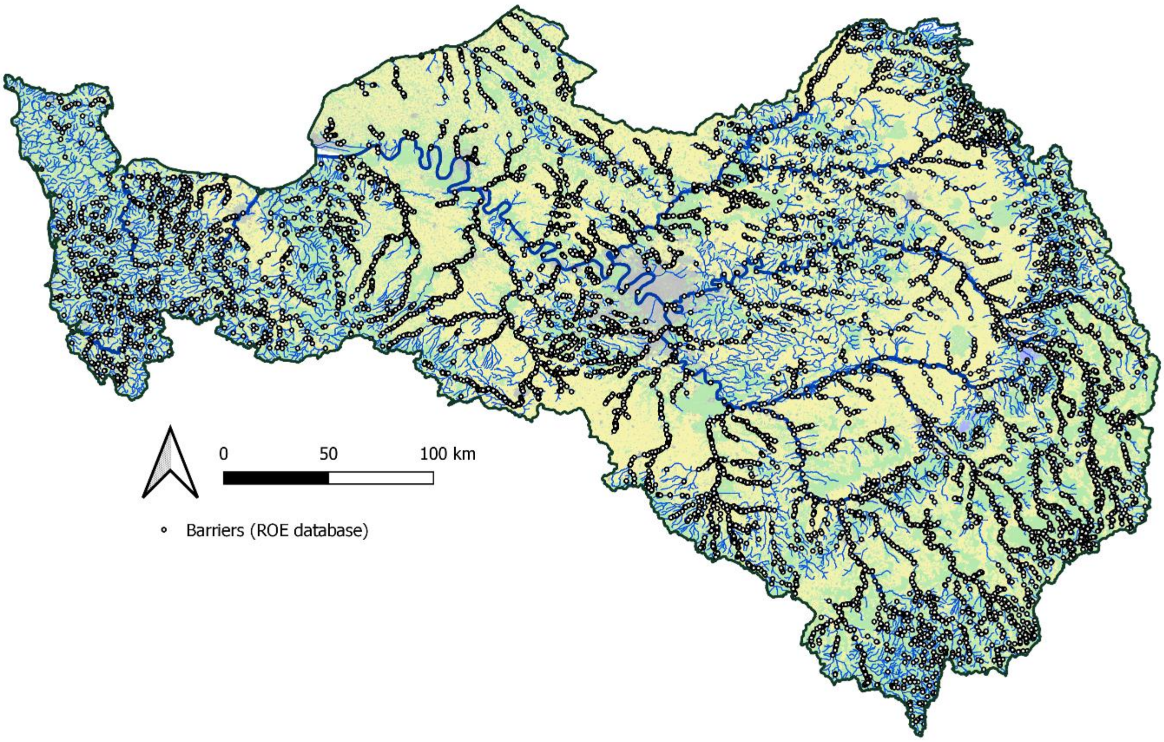

Figure 19: Map of all barriers within the Seine-Normandie basin.

2.3 Fish communities and fish dataset

2.3.1 The ichthyofauna of the Seine-Normandie basin

Given its west coast oceanic climate, frequent rainfall and flat lowland terrain, and its situation in Northwestern Europe, fauna, ichthyofauna and flora in our study area are typical of the Western palearctic, with very few endemic taxa (Keith et al., 2020). The basin's natural vegetation is mostly broadleaf forests of beech (*Fagus sylvatica*) and oaks (*Quercus sp.*), now widely replaced by yearly crops. Terrestrial and aquatic fauna generally belong to families common all over the Palearctic. As for river fish, not accounting for extirpated sturgeons and several estuarine taxa, native species originate from eight orders, two of which (Anguilliformes, Clupeiformes) only include diadromous species - the eel (genus *Anguilla*) and shads (genus *Alosa*). Petromyzontiformes include two diadromous and one resident lamprey (genera *Petromyzon* and *Lampetra*, spread across the Northern Hemisphere), which are elongated jawless fish. Cypriniformes are small to midsize fish; they represent the majority of native fish species in the basin and come in various shapes. All fifteen local native species (among them the breams – genera *Abramis* and *Blicca*, loaches – *Cobitis* and *Barbatula* - and bleak - *Alburnus*) are non-diadromous and are spread in seven families. Salmoniformes are large-sized, highly attractive, often obligate or non-obligate diadromous species, and natively represented in the area by the diadromous atlantic salmon (*Salmo salar*) and non-obligate diadromous trout (*Salmo trutta*). Esociformes, from the rivers of the Northern Hemisphere, and Gadiformes are both represented by one species, the predatory pike (*Esox lucius*), and the burbot (*Lota lota*) only freshwater member of the cosmopolitan order that also includes cod. Perciformes, an extremely specious and morphologically diverse order of freshwater and marine fish, includes sculpins (Cottidae), sticklebacks (Gasterosteidae) and perch (Percidae). To the 23 species of native, non-diadromous freshwater fish present in the area were progressively added through voluntary and accidental introductions a number of species originating from North America, Eastern Europe and Asia. Firmly established Cypriniform species include the sunbleak, souffia, asp, several carps (*Cyprinus* and *Carassius*), nase and ide from other European rivers and the silver and grass carp and the topmouth gudgeon from Eastern Asia. Within Siluriformes, the brown bullhead catfish (*Ameiurus melas*) originates from North America while the wels catfish (*Silurus glanis*) originates from Europe, and is now the largest fish species present in the area by far. Salmoniformes introduced for angle fishing include the brook (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*), and the grayling (*Thymallus thymallus*). Several goby species were introduced accidentally from Eastern Europe via ballast water release; finally, two European Perciformes (the zander, *Sander lucioperca*, and ruffe, *Gymnocephalus cernua*) are now well established in the area, and one Centrarchiform from North America, the pumpkinseed (*Lepomis gibbosus*), which is now invasive in some European rivers, and found in all types of rivers, showing high levels of polymorphy. Most species, both native and introduced, can be found in both the Seine river and coastal rivers of Normandy, except for the bitterling, barbel, schneider, nase, souffia, spined loach, both catfishes, burbot and pumpkinseed, which are only found consistently in the Seine. Studied fish communities are diverse in terms of size, feeding strategy and habitat. We collected information on these fish for multiple purposes, mainly migratory behavior (Teletchea & Teletchea, 2020), average size, as well as caudal fin aspect ratio, a secondary indicator of dispersal capacity. The latter was trickier to find, for available data did not overlap with our species of interest, and for some species, obtained on subpar data. We took the time to create new data for studied species, obtained from pixel analysis of photographic data. Additional information on fish species included in this thesis can be found in Appendix B of Chapter 3.

2.3.2 Electrofishing dataset

Fish sampling data in our study area is obtained through electrofishing. Electrofishing is generally conducted with the help of a cathode and anode delivering a direct current in water, stunning fish and making them surface, facilitating count of fish, collection and identification. The technique is conducted either on foot in small watercourses or on a boat in larger ones. Sampling is ideally conducted through a series of electrofishing depletions (i.e. taking of fish from the river) along a length of watercourse, so as to deplete the area as thoroughly as possible. Electrofishing is generally considered a compromise between method efficacy and destructiveness, allowing for a relatively thorough sampling and minimal, although proven, risk of injury and decreased fitness for sampled fish. Boat sampling of larger rivers will result in less thorough sampling of a chosen site, due wider channel and area.

This thesis used data collected between 2000 and 2020, but this type of data has been collected regularly under similar rigorous methods from the 1980s onward. A large number of study sites were incorporated in a campaign of sampling led by centralized institutions, some of which were kept to this day, leading to an ensemble of sites counting tens of recorded samples. In contrast, some study sites were abandoned later, and some study sites were the result of individual, punctual or operation-related samplings and counted fewer samples, and often a single one. As a result, 2146 study sites were kept for our first study (see Chapter 3), and 2044 in our second and third study due to a lack of sufficient hydrological data available for modeling and fusion of similarly located sites). Our dataset, compiled by the OPSN (L'Observatoire des Poissons du bassin Seine-Normandie, or Observatory of Fish in the Seine-Normandy basin), corresponds to all samples, compiled into geographically coherent study sites.

2.4 Niche theory and distribution modeling

The theorization of ecological niche as developed by Hutchinson and others, since it relies on a series of statistical and mathematical principles, lends itself well to modeling approaches. Correlative species distribution modeling approaches in particular (as opposed to mechanistic models, see. Evans et al., 2015) can be considered like modeling extensions of niche theory although they have evolved independently (Elith & Leathwick, 2009; Hirzel & Le Lay, 2008). The need to apply niche theory principles on concrete environmental data soon arose, and took profit of increasing computing power and available statistical modeling tools. Depending on the tools and environmental data used and the goal of these approaches, they received many names. The term ENM (Ecological Niche Modeling) qualifies, depending on who you ask, either a generic term for all these approaches, or only qualifies models which are focused in their design on the characterization of a species' ecological niche (Peterson & Soberón, 2012). HSM (Habitat Suitability Models) qualify models which explicitly seek to find the potential distribution (or the fundamental niche) of a species (Hirzel & Le Lay, 2008). When focusing on climate predictors, the term CEM (Climate Envelope Models) is used. The goal of CEMs, in that sense, is distribution-oriented (i.e. CEMs are mostly interested in model predictions based on niche theory, either in a different spatial unit, time, or both) (Araújo & Peterson, 2012). A more general approach, SDMs (Species Distribution Models) are similarly distribution-oriented, but integrate several predictors outside of climate predictors. This SDM approach is both the most commonly and broadly used in academic productions in ecology (Miller, 2010), and the one that is conceptually closer to the type of models used during this thesis, and so this term will be used exclusively. They allow the creation of a link between theories of ecology and the empirical study of species distribution, as well as the prediction of potential distribution in new contexts, which will be the central use of these tools in this thesis. However, the use of SDMs requires a few components, all subject to their own limitations described below, which are sometimes difficult to minimize: 1) Environmental predictors, 2) Species presence(-absence) / abundance data, 3) Methods of Analysis to create a niche and predict species probability of occurrence (Elith & Leathwick, 2009).

Environmental data used in SDMs generally include an array of relevant quantitative and qualitative environmental predictors. Their acquisition is generally of limited precision, and potentially impacted by mistakes in measurements or spatialization (erroneous coordinates). In practice, the amount of relevant environmental gradients available in niche modeling is substandard compared to the Hutchinsonian ideal (i.e. n gradients that fully describe an environment) and so niche modeling generally occurs in a lower-dimension hyperspace, producing similarly amputated hypervolumes. This greatly simplified representation of niche theory is much less detrimental than one can expect, since when thinking in statistical modeling terms, a compromise between model simplicity and goodness of fit is much more desirable than completeness (Rochefort-Maranda, 2016). This different paradigm for niche construction leads to a conscious selection of environmental predictors - eventually coming with model selection algorithms or dimensionality reduction methods. Examples of commonly used predictors include the climate envelope, discharge, Strahler order and surrounding land use proportions estimates.

Species occurrence data is found either in the form of presence-only data, presence-absence data or, more rarely, abundance data (Lawson et al., 2013; Waldock et al., 2022). They are generally complicated to obtain in a standardized way, as sampling in a large geographical area generally comes with temporal differences in sampling, different people involved, and in the case of rivers, different river sizes and landscape elements, which influences the method used to sample watercourses and their efficiency (Kennedy & Strange, 1981). For instance, sampling conducted in a brook easily accessible by foot may be more thorough than sampling conducted in the estuary of a large river, especially when electrical fishing cannot reach bottom-dwelling fish.

SDMs rely on either statistical or machine learning analysis methods to detect niche patterns in environmental gradients. Linear and additive models (GLM and GAM) are frequent techniques, while on the machine learning side, Random Forests, Boosted Regression Trees, Neural networks are examples of algorithms used to model species distribution. The growing use of SDMs in multiple contexts has led to the creation of a contingent of tools to increase their accuracy and evaluate their performance. A tool often used to increase model performance is ensemble modeling, where several algorithms are used several times and predictions are averaged to create a final, optimized predicted presence value (Grenouillet et al., 2011). Metrics like the TSS (True skill statistic) (Allouche et al., 2006) and the AUC (Area under the curve) (Elith et al., 2006), which compute the amount of accurate predictions of absences and presences, were developed to evaluate and compare model performance and help in algorithm selection. Specifically when using SDMs to predict species distribution in a new context (space, but especially time), comes with limitations, linked to framework assumptions, some directly transferred from niche theory (Dormann, 2007). They include an assumption that detected patterns in species distribution are transferable in new contexts for prediction (which precludes adaptation or plasticity). Another major limitation of SDMs is, as advocated in the present thesis, the lack of account taken of stochastic processes, which may induce 1) Presences in theoretically non-suitable areas due to rare events or temporary survival (Pulliam, 1988), 2)

Absences in theoretically suitable areas due to dispersal limitations, stochastic extirpation, or unaccounted for competitive exclusion (Velazco et al., 2020), 3) A lack of independence of occurrence data, especially due to spatial autocorrelation, which is very common in SDMs, and especially so in river networks for species who are limited in their dispersal capacity and overall range, leading for example to a localized concentration of occurrences (Mielke et al., 2020).

2.5 Connectivity indices and river fish

2.5.1 Measuring connectivity

Connectivity, whether terrestrial or aquatic, can be understood as a broad concept of uninterruptedness and describes many observable properties of landscapes, as such multiple methods of quantification have been proposed, depending on the needs of the researcher and context of implementation (Keeley et al., 2021). These methods can be implemented either to measure connectivity as a direct expression of interruptedness or to represent connectivity loss and thus integrate some notion of time. Relatedly, they can either rely on observations of individual behavior, population, species and community dynamics, or be built through theoretical representation of dispersal, connection and connectivity loss. Metrics for connectivity can encompass whole landscapes, or patches within these landscapes, and can either be exclusively structural and agnostic of studied species, their functional traits and their range, or integrate functional characteristics of relevant organisms, as well as presence/absence or abundance data for said species. Functional characteristics are especially relevant to the concept of dispersal. Firstly, beyond topological/euclidean distance, the presence of barriers to movement and dispersal, which are specifically considered with respect to fish functional characteristics, incentivizes the researcher to make use of more functional expressions of distance like the concept of cost distance, or the associated landscape resistance, and more precise related concepts like hydrological distance in the case of river networks. Secondly, dispersal capacity of species, whether defined as a threshold or a dispersal kernel function, provide additional information on specific movement and achievable dispersal distances for said species. Regardless of functional integration or integration of presence data, metrics conceived to measure connectivity are intrinsically linked to 1) A geometric framework of representation for studied space and its needed parameters (e.g. patches, with their occupancy/suitability/size; graphs, with the configuration of nodes and edges etc.) and 2) A type of quantity (distance, amount, count, probability etc.).

Separate from other metrics of connectivity in their breadth and methodology, some straightforward measurements of connectivity involve fieldwork or simulation of a restricted number of individuals (Tischendorf & Fahrig, 2000). Those can use effective occupancy of patches through time, or dispersal success from one patch to the next, observed through diverse methods (observation, tracking, tagging of individuals etc.). Similar methods can be employed for genetic material (Storfer et al., 2007). However, most developed metrics rely on theoretical approaches. Simplest metrics of connectivity focus on a patch (or patches) of interest and its relationship to its immediate neighbors. They are determined within a patch dynamics representation of space and are applicable to both terrestrial ecosystems and river networks. They can consider said distance (topological, functional or hydrological) to the nearest patch, with functional notions of patch suitability or occupancy data sometimes specified. They can also consider patch size as a weighting factor, or, in the context of conservation ecology, include protected status as a property for the study of connectivity (in question, for example, the efficacy of a mosaic of neighboring, but not immediately contiguous, protected habitats to the conservation of a species or several). Similar approaches can use predetermined buffers around a patch of interest and measure suitable patch area within the buffer, with an optional weighting by distance from the patch of interest (this is the Proximity Index, see Zeller et al. (2016)). In functional approaches, buffer dimension, as well as the consideration of linkage between patches, can be determined according to a threshold of dispersal or dispersal kernel calculated with knowledge of specific capacity for dispersal (e.g. a group of patches too far away from the rest of patches in a mosaic landscape will not be considered as linked). Although all methods above focus on one patch at a time, the calculation of connectivity values of all patches within a study area, ideally isolated from other suitable patches, allows for the comparison of said values or, via an averaging or weighted averaging of said values for example, to landscape-scale values for connectivity.

Other metrics use graphs as schematic representations of patches and the space in between, with centroids of patches as vertices, associated with properties of patches like size; and links between neighboring patches as edges, associated with a distance value (physical, functional, hydrological). This framework allows for more complex approaches which calculate connectivity values for all patches/vertices (Keeley et al., 2021). The study of connectedness within graphs can work through the evaluation of the immediate neighbors of each node, their interconnections (Clustering coefficient), or their isolation within said graph. Betweenness centrality (which we use as a debiasing factor further in this thesis, see Chapter 3 and Barthélemy (2004), can be defined as a measurement of the number of different shortest paths (from node i to node j) within the network which pass through a specific node. Thus we obtain a value of connectedness within our network. A similar approach, the Integral Index of Connectivity (IIC, see Saura & Pascual-Hortal (2007)), calculates at the scale of the landscape the degree of connectedness, taking into account the length of shortest paths and the size of each patch. The integration of dispersal functions (whether under the shape of thresholds or continuous kernels) in graph approaches allows for a different approach to functional integration in calculation of connectivity. More explicitly related to the scale of the population, they allow for the calculation of a probability of dispersal from one patch to the other (probability of incidence, see Baldan et. al, 2022). An average of probabilities between one patch and all others, weighted by distance, allows for a node/patch-specific value of connectivity as well as information on the importance of each node within a graph to total landscape connectivity, while some approaches allow for landscape-scale connectivity values.

This multitude of options (see Table 1) when considering connectivity must lead to a reflection by the researcher related to study design, overall goals and consequences on index type and choice.

Table 1: List of main connectivity index properties and related options. *Adapted from Keeley et al. (2021).*

Index Properties	**Possible approaches**
General context	• Terrestrial/Marine/Riverine etc. • Anthropized or wild areas
Point of view	• Total connectivity of study area • Local connectivity of patch/vertex/subsection • Contribution of local unit to general connectivity
Methodological basis	• Observation of dispersal behavior and patch occupancy on individual specimens • Study of elected communities or populations • General theory of dispersal and environmental suitability at the species scale
Integration of species traits	• Structural approach (no functional integration) • Functional approach (different levels of complexity) • Both
Reflection on suitability	• No account taken of environmental suitability • Binary / Discrete • Continuous (use of buffers, kernels, SDMs)
Graphical Representation	• Patches, corridors, occupancy and passage • Graphs (vertices and edges) • …
Type of metric	Amount / Density / Distance / Probability etc.
Dispersal	• Use of a threshold of dispersal • Use of dispersal kernels

2.5.2 Longitudinal connectivity metrics in the Seine-Normandie basin

Within large river networks like the Seine-Normandie basin, and when dealing with obligate aquatic species, some aspects of longitudinal connectivity especially, a main concern of this thesis, are constrained by the property of river networks. Their meandering nature precludes the use of euclidean distance as a relevant metric, and so hydrological distance is more appropriately used. Patch dynamics within riverbeds (Pringle et al., 1988), while readily studied within river networks when studying small areas, is less feasible than in terrestrial contexts, for which land use is detectable from satellite imaging. Similarly, approaches which use field measurements are not feasible on such a scale. Therefore, the main elements of cost distance readily available to the researcher are dams and their permeability to river fish. Flow asymmetry necessarily requires different treatments of obstacle permeability for upstream and downstream passage. However, a widespread component within connectivity indices designed for river networks is dispersal kernels and thresholds, which allow for precise consideration of dispersal for studied species. River networks lend themselves well to graph analysis, and in the case of single-strand networks like the one in use for this thesis, produces graphs for which all paths are shortest paths, and which count n+1 vertices for n edges, leading to possible associations between one node and one downstream edge (excluding the estuarine vertex), meaning that we can think of the Seine-Normandie river network graph as a collections of vertex-edge pairs. In this context, the landscape-scale indices are catchment-scale, while node-specific indices are reach-specific. Connectivity indices like betweenness centrality are relevant to river networks, however we argue that approaches that take into account obstacle permeability and dispersal have the potential to be more relevant to the study of species distribution. This requires reach-specific indices, which is why node-specific indices are especially relevant.

Rodeles et al., (2021) and Baldan et al., (2022) built a unified system to understand practical longitudinal connectivity indices for river networks. This system relies on a probability of incidence I_{ij}:

$$I_{ij} = c_{ij}B_{ij} \ (Eq. 2.1)$$

where c_{ij} is a component of dispersal probability (described as structural in Baldan et al., 2022) which accounts for dams and other obstacles and B_{ij} is a component of dispersal probability which accounts for the dendritic configuration of reaches and the functional capacity of fish for dispersal. Reach-specific connectivity RCI_i is thus obtained:

$$RCI_i = \sum_{j=1}^{n} I_{ij} \frac{w_i}{W} \ (Eq. 2.2)$$

where n is the number of reaches, w_i a custom weighting factor (which can be used for environmental suitability) and W is the total weights.

This allows us to retrofit many connectivity indices (see Table 2), in use for river networks before 2021, into a unified framework for river connectivity indices, according to the method used (or lack thereof) for the integration of permeability (binary or symmetric and discrete or continuous) and dispersal. Baldan et al. (2022), while introducing the R package <riverconn>, classifies these indices according to these methods, as well as the type of distance between vertices used, and the type of object for which the index calculates a connectivity value, with catchment-scale indices generalized as CCI, and reach-specific indices generalized as RCI. Among them are the Probability of connectivity and Integral Index of Connectivity mentioned above, applied to river networks, as well as the Dendritic Connectivity Index (DCI) which does not consider dispersal.

Table 2: Examples of connectivity indices which can be obtained through the aforementioned framework. *Adapted from Baldan et al. (2022).*

Index name	**Reference**	**Weight**	**cij**	**Bij**
Dendritic Connectivity Index (DCI)	Cote et al. (2009)	Reach length	Symmetric passabilities	No
Population Connectivity Index (PCI)	Rodeles et al. (2021)	Reach length	Symmetric passabilities	Exponential symmetric dispersal kernel
Probability of Connectivity (PC)	Pascual-Hortal and Saura (2006)	Reach/Habitat Area	No	Exponential symmetric dispersal kernel
Integral Index of Connectivity (IIC)	Pascual-Hortal and Saura (2006)	Reach/Habitat area	No	Binary symmetric dispersal probabilities
Volume-based River Connectivity Index (RCIVOL)	Grill et al. (2014)	Reach volume	Symmetric passabilities	No
River Class Connectivity Index (RCICLASS)	Grill et al. (2014)	Reach volume, unique reach classes	Symmetric passabilities	No
River Migration Connectivity Index (RCIRANGE)	Grill et al. (2014)	Potential number of migratory fish species	Symmetric passabilities	No
Stream Continuity Index (SCI)	Shao et al. (2020)	Stream order, reach length	Symmetric passabilities	No
Dendritic Connectivity Index for diadromous fish (DCId)	Cote et al. (2009)	Reach length	Symmetric passabilities	No
Breeding Area Connectivity Index (BACI)	Rodeles et al. (2019)	Habitat area	Binary passabilities	No
Residual Core Length (RCL)	Fuller et al. (2015)	Reach length	Binary passabilities	No

Catchment Area Fragmentation Index (CAFI)	Jumani et al. (2022)	Barrier upstream area	Symmetric passabilities	No
Catchment Area Rainfall Fragmentation Index (CARFI)	Jumani et al. (2022)	Barrier upstream precipitation	Symmetric passabilities	No

2.6 Future environmental and management conditions

2.6.1 Future climate modeling

Following the sixth report emanating from the IPCC at the start of the 2020s (Calvin et al., 2023), the methodology for producing projections relies on the five coined Shared Socioeconomic Pathways (SSPs). SSPs are intended as scenarios meant to explore the possible attitudes of governments with respect to climate change mitigation and adaptation, including a broad reflection on socioeconomic factors (Calvin et al., 2023). SSPs have succeeded to past Representative Concentration Pathways (RCPs), which focused mostly on the evolution of the concentration of greenhouse gases and were used as a basis to the fifth IPCC report (Stocker et al., 2013). Ultimately, both SSPs and RCPs are scenarized in terms of radiative forcing scenarios. RCPs are still in widespread use while dealing with the study of the impact of climate change to this day, due to the large number of projections available at fine spatial scales. The Coupled Model Intercomparison Project (CMIP) is a collective which aims at improving climate modeling. The agreed-upon process for climate projections under the fifth and sixth installments of the CMIP advocates the coupled use of General Circulation Models (GCMs), in which RCPs or SSPs are input, and Regional Circulation Models (RCMs), along with the necessary bias correction. Good practice is generally to multiply GCM and RCM in order to consider climate modeling uncertainties (Danandeh Mehr & Kahya, 2017; Sørland et al., 2018).

2.6.2. Climate projections

For the purposes of this thesis, we did not produce ourselves climate projections over the Seine-Normandie basin, but instead opted to rely on well-honed datasets like the Explore2 dataset. Indeed, the Explore2 was a national project (2021-2024) whose aim was to provide up-to-date climate and hydrological projections over France up to 2100 to stakeholders and water managers (Marson et al., 2024). This dataset aims at being used as the reference for climate change and future hydrology-based studies nowadays. The Explore2 projections rely on RCPs and the methods within the fifth installment of CMIP. The rationale behind this choice was the large availability of regionalised climate data over France, in opposition to the still under development regionalised climate data related to SSPs. However, knowing the sixth installment was in development, we chose four GCM-RCM combinations leading to climate projections which fell within the 5 to 95 % of projected climate values produced for the sixth installment under the equivalent SSP 5-8.5. These four Explore 2 projections (noted A1, B3, C2 and F9, see Fig. 20 and 21 for a display of all projections available and out general selection process, and Chapter 4 for general descriptors and a breakdown for each selected projection of GCM/RCM used) were also chosen for their coverage of seasonal variation in prediction, and in discussion with AESN agents.

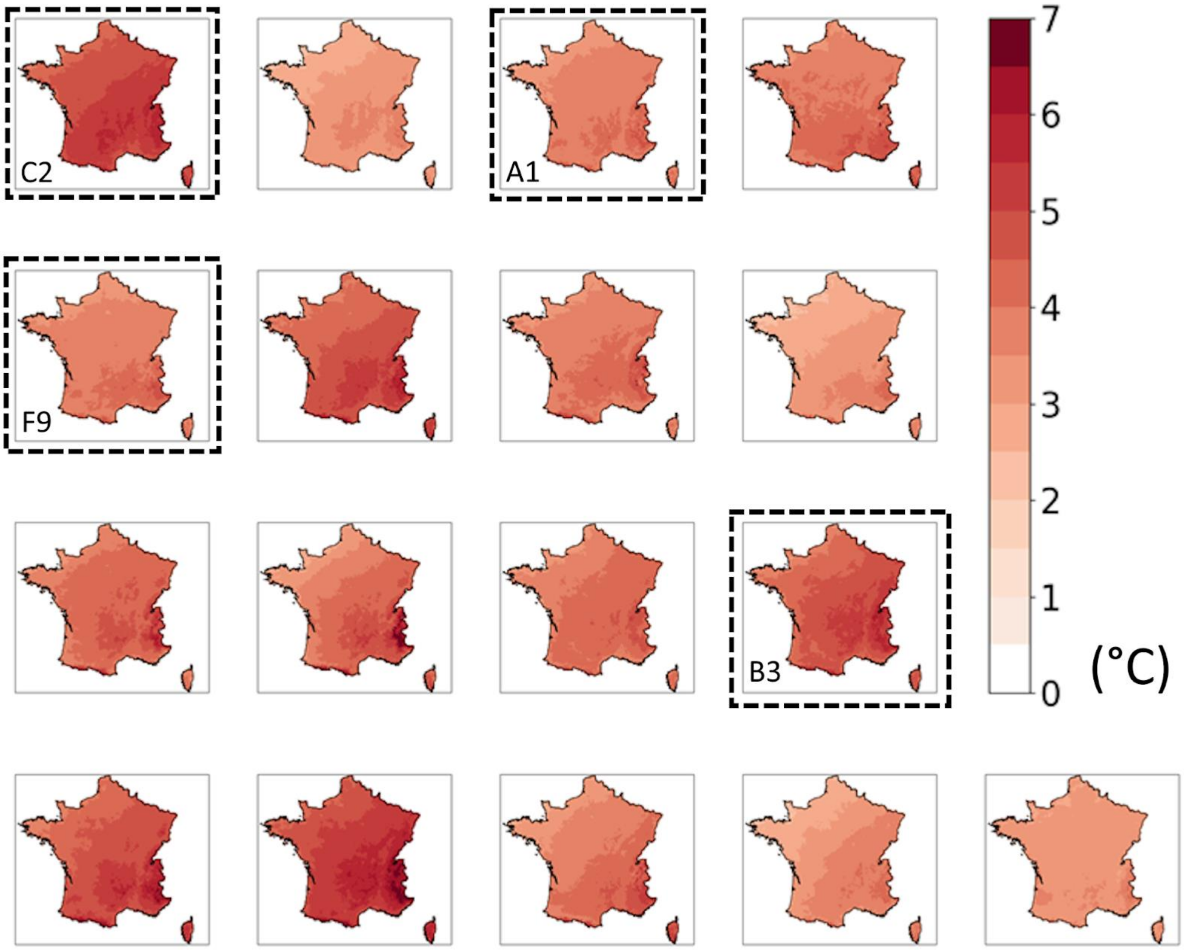

Figure 20: 17 Explore2 projections displaying the evolution of annual average temperature (°C) between (1976-2005) and (2070-2099). *All projections calculated with RCP 8.5. We highlight selected projections: B3 and C2 are visibly warmer than F9 and A1. Adapted from Marson et al. (2024).*

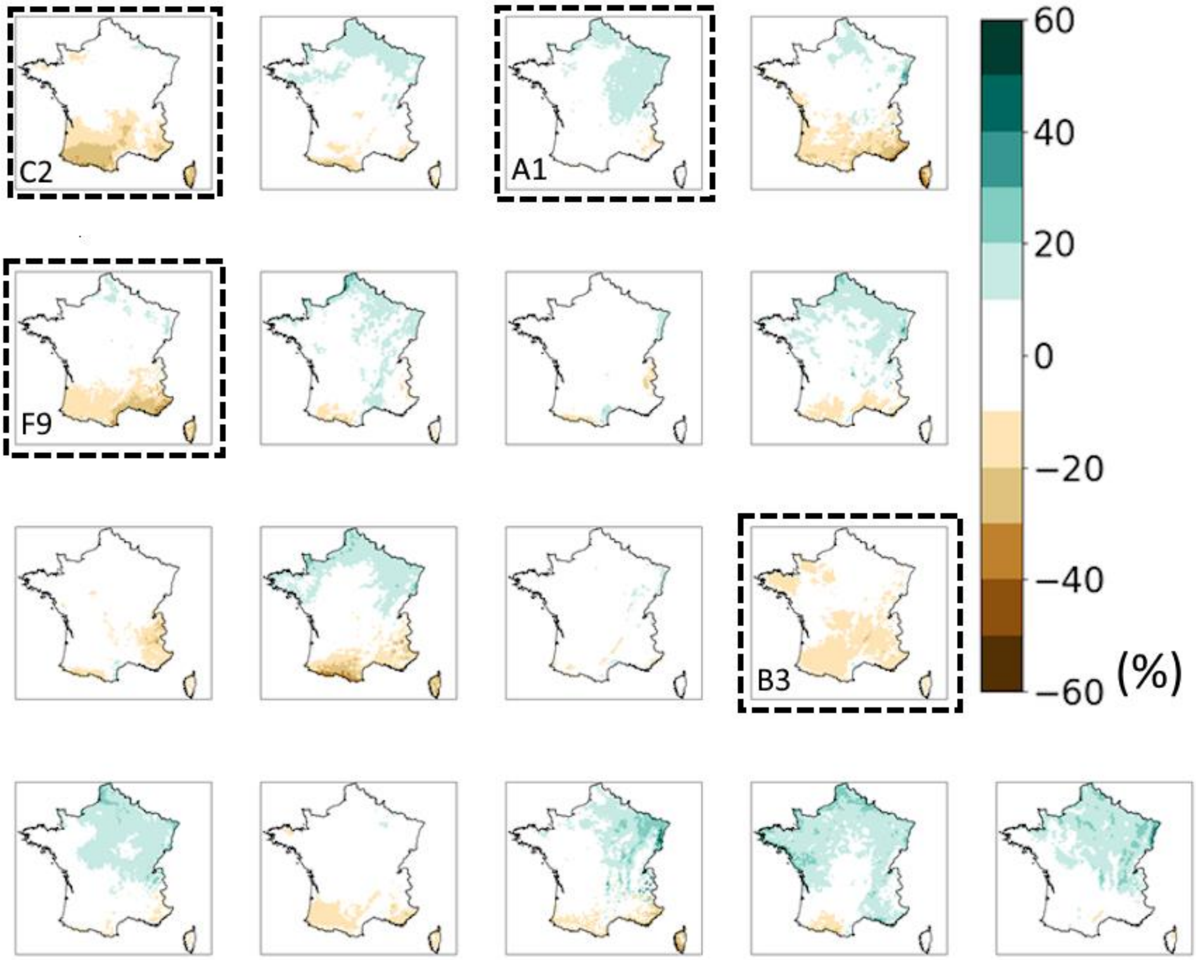

Figure 21: 17 Explore2 projections displaying the evolution of annual precipitation (%) between (1976-2005) and (2070-2099). *All projections calculated with RCP 8.5. We highlight selected projections: in the Seine-Normandie basin, B3 and C2 are drier while A1 is wetter.*

Projected hydrological predictors were obtained through semi-distributed models (see Chapter 4, Coron et al., (2017) and De Lavenne et al. (2019)), for each climate projection, either directly for most study sites, or via projections taking into account of flow regulation by the Grands Lacs de Seine (see section 2.1.1) originating from the IN-WOP project (Dorchies & Ricquier, 2024). Once climate and hydrological data akin to training predictors, data obtained for current datasets (see section 2.1.3), similar methods were used to obtain comparable predictors (see Chapter 4).

2.6.3. Building watershed management scenarios

As developed in our introduction, the need to investigate future land use and practices incites us to formulate management scenarios to cover different futures and to step away from reflections on likelihood of one scenario over the other, which is necessarily contingent on hot-button political discourse and unpredictable decision-making, especially as the timeframe stretches into the future. Although the term "scenario" in the context of futurology and modeling of environmental conditions has no clear, consensual definition, a series of elements can be used to build a practical definition for the purposes of this thesis (March et al., 2012). A scenario will be defined within this manuscript as an internally consistent and plausible story, or set of related internally consistent and plausible stories, set in the future, which were obtained through prospection and/or study of norms and planning documents instead of prediction apparatuses. They may be obtained through a "if … then" type structure of reasoning. This definition is of crucial importance to the futurologist, because the term "scenario" is already used in vernacular language, but with a broader definition. Stories telling completely fictional events, stories extracted from predictive processes, and absolutely certain future events for example, could not be conceived as scenarios in this thesis. An interesting edge case is stories that only focus on a subquestion, for which plausibility needs to be assessed. For example "All (100 %) people leave the city of Paris and relocate in the Haute-Marne département" is implausible but necessitates broad prospective research and modification of many environmental variables. We would not consider this a scenario. Inversely, "Artificialization of riverbanks is criminalized" is plausible, but requires very few modifications of environmental variables. We would consider this a scenario.

A first decision to make when constructing scenarios is between static and dynamic scenarios. Static scenarios recount the future at a single time point whereas dynamic scenarios seek to recount the evolution of environmental conditions from the present to an agreed upon future. Both approaches are not necessarily distinct, but on a spectrum, depending on the amount of resources and documentation invested in a dynamic approach. Scenarios also take many forms depending on the project within which they are built, and to what end. If used as a thought experiment, or within a process of negotiation, concertation or scientific emulation, scenarios need only be stories in plain text using appropriate vocabulary for the intended audience. An example would be a concerted effort among different actors of a single territorial unit, for which the presentation of broad scenarios would help with the unearthing of leverages and stakeholder interactions. However, in a modeling process, simple stories must be interpreted into usable numeric variables and environmental factors.

The type of story that a scenario tells can also vary widely. For example, they can be overarching stories, or single-issue scenarios, provided they are plausible, depending on the intent, a scenario can be conceived as a straightforward continuation of current policy and management trends, or to the contrary act as a contrast through the hypothetical implementation of alternative management decisions. However, in the framework of environmental management where scenarios are often used, a large body of work has allowed Lacroix et al. (2019) - see Fig. 22 - to create a visualisation tool for management scenarios.

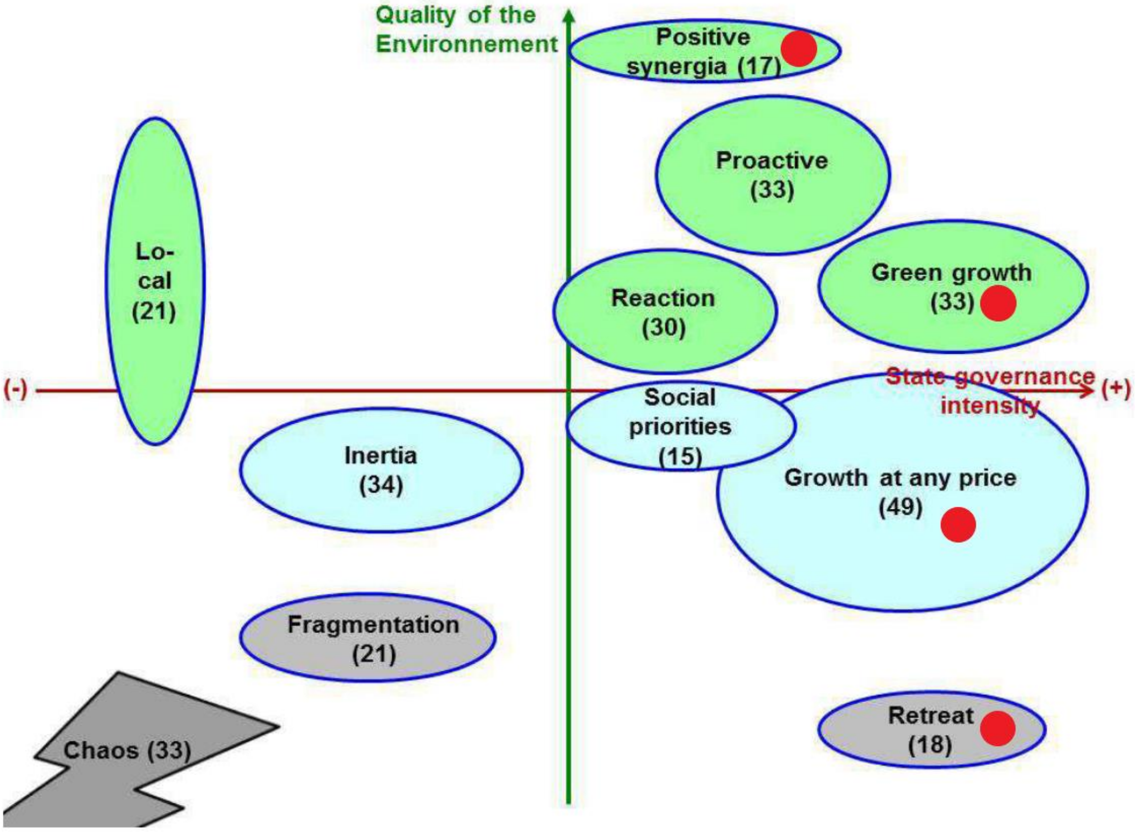

Figure 22: Literature review by Lacroix et al. (2019) displaying its typology of scenarios. *They are categorized on two axes - State governance intensity and Quality of the Environment, leading to eleven distinct categories of scenarios. Each red dot corresponds to a scenario adapted for this thesis.*

On two axes, namely Intensity of State Governance and Quality of the Environment resulting from implied management, large scenario categories are labeled. Each label corresponds to a set of similar stories categorized under both axes. Low governance scenarios, which we chose not to explore during this thesis for multiple reasons (i.e. the difficulty in making simple numeric scenarios from a large sum of local initiatives, and to create coherent and plausible stories this distant from current paradigms). During successive workshops and meetings with members of the Seine-Normandie Water Agency and French Office for Biodiversity from 2022 to 2024, and within a context of growing, topical retreat on environmental messaging from influential institutions due to growing pressure for agricultural sovereignty and financial austerity, the formulation of scenarios changed drastically. Originally, planned scenarios broadly corresponded to a “Green Growth” and “Positive Synergia”, with possibility of subscenarios, a third scenario corresponding to a “Growth at any price” paradigm, while the “Green Growth” scenario was retooled to fit the vision of multiple interlocutors. Finally, a fourth scenario was added to fit a “Retreat” paradigm (see Chapter 4 for details).

In order to produce scenarios for future management, we seek to find a compromise between feasibility and relevance. Roadblocks to the construction of scenarios necessarily encountered during doctoral work are limited time and resources, which can lead to an unseemly gap between the ambition of a scenario when taken as a story, and the breadth of variables available to cover the implied modifications in environment and management. When in possession of larger means, projects like Barles et al. (2024) can fit a story to larger research and thus construct much more elaborate scenarios, including fine geographical analysis of local land use, carbon, nitrogen and energy cycles, agrarian systems and macro/microeconomics. In order to avoid this pitfall, and with the smaller means at our disposal, we opted for modifiers for land use, connectivity and river bank properties (see Chapter 4). This way, we do not overstep our capabilities while producing contrasting and relevant scenarios of land use and river properties. Climate projections were coupled to formulated management scenarios, leading to a number of projection*scenario contexts on which one can predict fish distribution.

Subsequent chapters will make use of connectivity indices and other predictors to shape species distribution models designed to predict fish distributions models, then applied to new conditions of climate and watershed management - relating to land use and connectivity, through projections and scenarios. The multiplication of projections and scenarios guarantees a diversity of studied futures and will finally lead to a study on uncertainty, where scenarios will be the main focal point of discussion.

Chapter 3.

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

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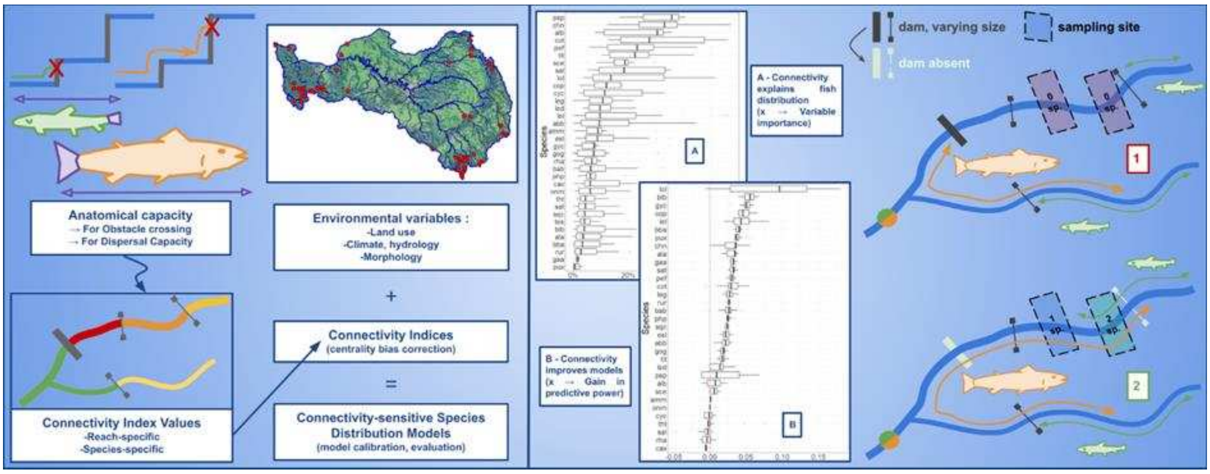
Foreword

This first article, now published in Science of the Total Environment, is concerned with the first methodological and scientific challenge of this thesis, namely the place that could be cavred of longitudinal connectivity in species distribution models. As such, this thesis chapter stands on its own as a complete process, we designed novel connectivity indices informed by functional traits based on support from literature, tested their performance as predictors and fish distribution, and used them to try and characterize the influence of longitudinal connectivity on river fish distribution.

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 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.

Graphical Abstract



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

Keywords

Connectivity; River fish; Barriers; Species Distribution Models; Connectivity indices; Dispersal

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 (Haidvogl, 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 & 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 & Wolter, 2015). They are a limiting factor for fish distribution (Manfrin et al., 2020; Trigal & 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 & Bornette, 2002; Cote et al., 2009; Pascual-Hortal & 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 & 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 & Wolter, 2014; Skalski & 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 & 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 & Wolter, 2014), as well as related behavioral traits, such as spawning migration (Brönmark et al., 2014; Comte & 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 & 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 Puijenbroek 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 (Strohmenger et al., 2024), with annual precipitation 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 et al. 2024). The ROE database - Référentiel des Obstacles à l'Ecoulement (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 & 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).

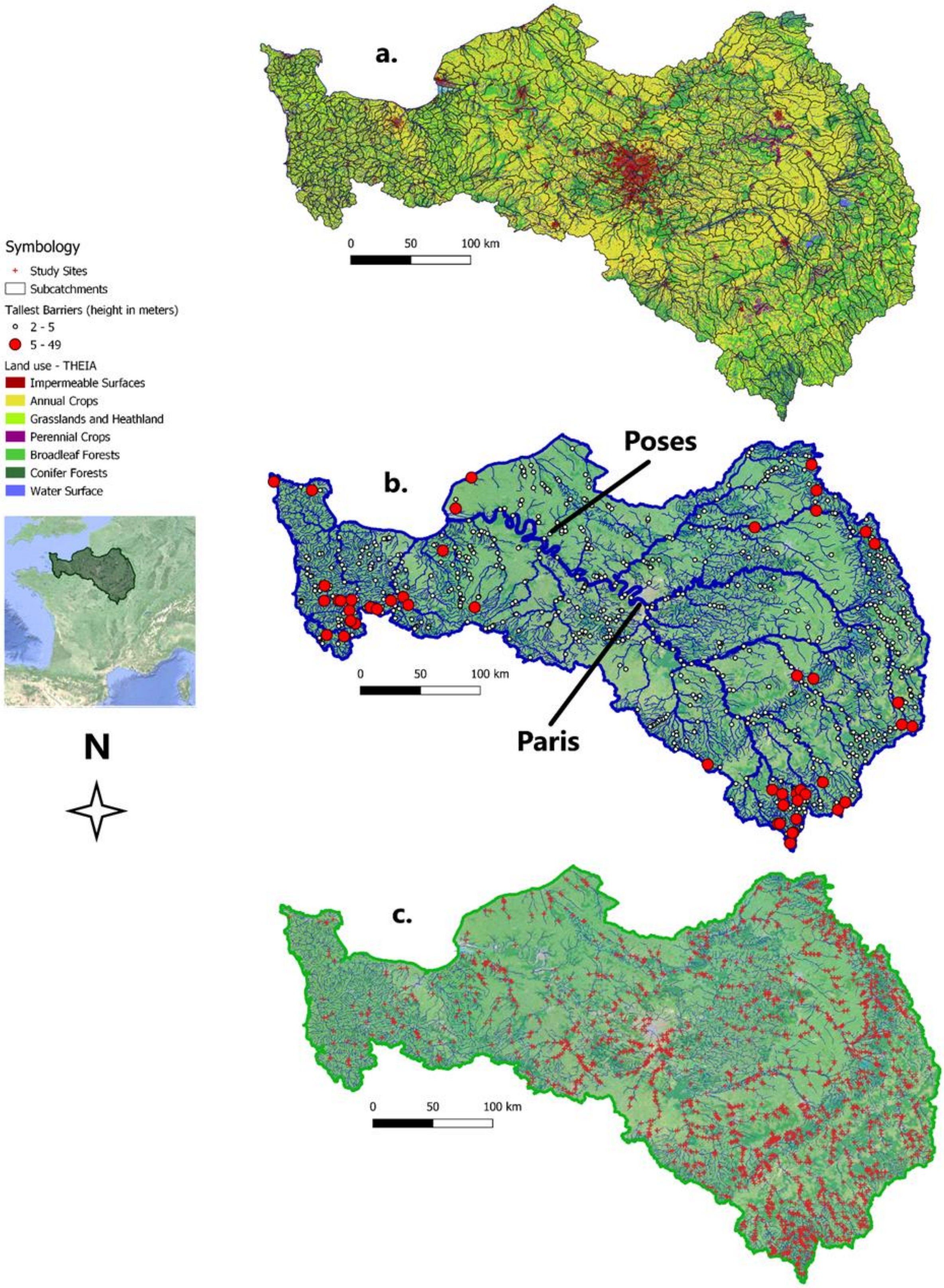

a.
0 50 100 km
Symbology
Study Sites
Subcatchments
Tallest Barriers (height in meters)
2 - 5
5 - 49
Land use - THEIA
Impermeable Surfaces
Annual Crops
Grasslands and Heathland
Perennial Crops
Broadleaf Forests
Conifer Forests
Water Surface
b.
Poses
Paris
0 50 100 km
N
c.
0 50 100 km

Figure 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 (>5m);* ***C****: Spread of the 2145 study sites. Source of land cover data and imaging: THEIA dataset (Thierion et al., 2021).*

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) subcatchment and 2) local (Sliva & 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 et al., 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 & Pauly, 2023) and the French National Museum of Natural History website (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 & 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.

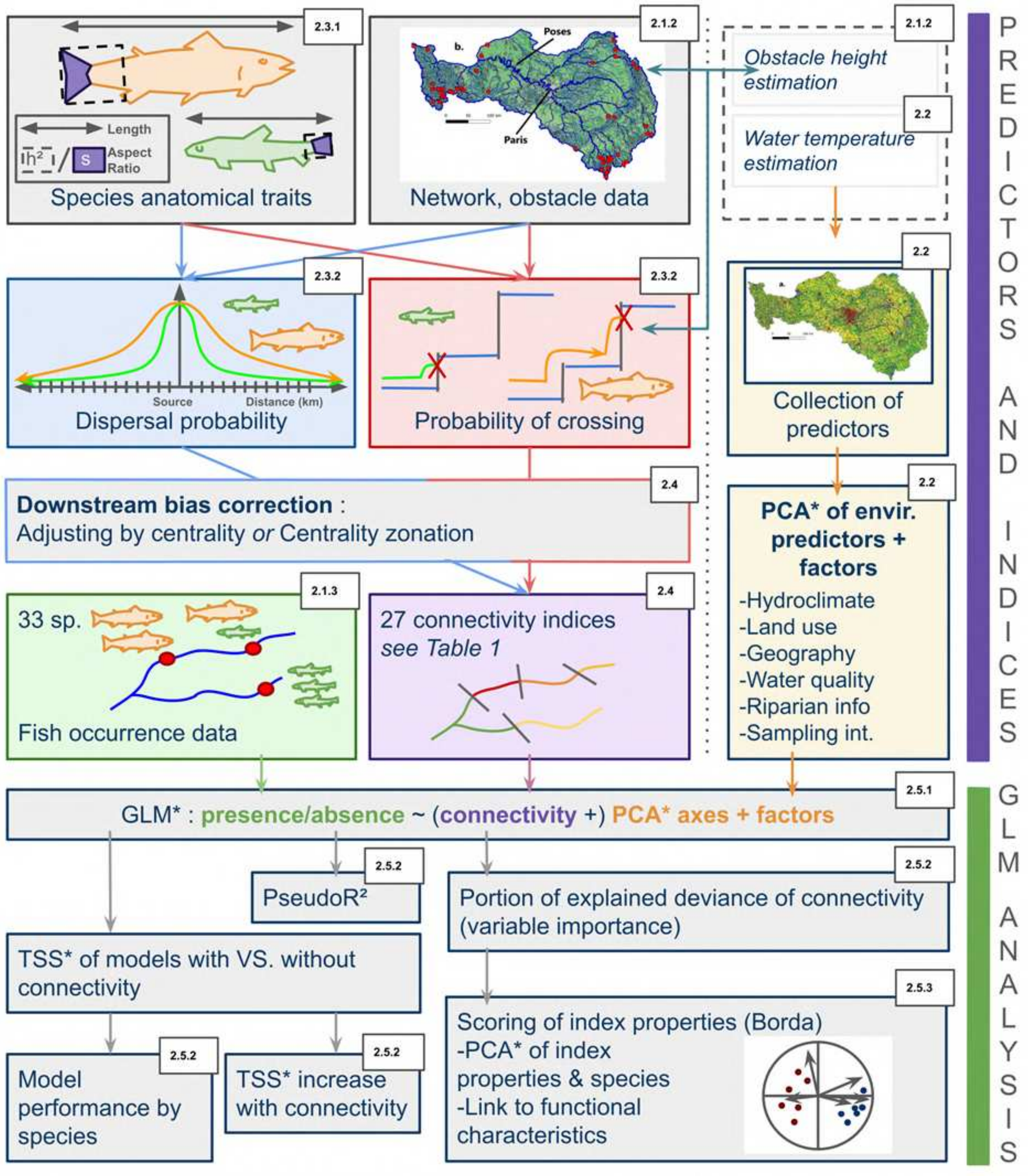
2.3.2. Obstacle permeability and fish dispersal

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 & Gilliam, 2000), through a distribution function F of distance d (in m) from the source population (Eq. 3.1 below) (Radinger and Wolter, 2014):

$$F(d) = 0.66 \cdot \frac{1}{\sqrt{2\pi\sigma_{stat}^2}} \cdot e^{-\frac{d^2}{2\sigma_{stat}^2}} + 0.33 \cdot \frac{1}{\sqrt{2\pi\sigma_{mob}^2}} \cdot e^{-\frac{d^2}{2\sigma_{mob}^2}} \quad (Eq. 3.1)$$

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 & 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).



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

Figure 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.

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. 3.2):

$$I_{ij} = c_{ij} B_{ij} \quad (Eq. 3.2)$$

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 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. 3.3) correspond to the probability of connectedness between all edge pairs:

$$RCI_i = \sum_{j=1}^{n-1} I_{ij} \frac{w_j}{W} \quad (Eq. 3.3)$$

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.

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 only	none	Connectivity is best expressed at a whole-basin scale
RCI-L		dispersal only		
RCI-LD		both		
ACI-D	Adjusted (3 indices)	barriers only	(where C is Centrality)	Connectivity is most usefully described when adjusted to centrality
ACI-L		dispersal only		
ACI-LD		both		
ZCI-D	Zonation-sensitive (3 x 7 indices)	barriers only	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 only		
ZCI-LD		Both		

<u>For ZCI</u>
Seven zones: DS1/2-MS1/2-US1/2-HW
DS = Downstream / MS = Midstream / US = Upstream / HW = Headwaters

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. 3.4) as follows:

$$ACI_i = \frac{RCI_i}{log(C_i + 1) + 1} \quad (Eq. 3.4)$$

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. 3.3) 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 & 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 PseudoR^2 were considered simultaneously to gather information both on model skill and explanatory power, which are not necessarily correlated. PseudoR^2 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 & 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 species with similar response to connectivity and look for ecological and functional explanations (e.g. if the “barrier-sensitive” index property scores well for some species, we can infer a link between barriers and said fish distribution and study these species to find common traits).

3. RESULTS

3.1. Base SDM and species response to environmental predictors

When studying the importance of environmental predictors in base models (i.e. without connectivity), the Strahler index, the altitudinal gradient and hydrological regions showed to be consistently more important than other predictors in most species (Appendix G). The minnow (php) and bleak (ala) were especially sensitive to the riparian vegetation gradient while the water temperature was important for the bleak (ala), burbot (lol) and spined loach (cot). The bullhead (cop) was most sensitive to the ammonium pollution gradient, the chub (sqc) and grayling (tht) to hydrological regime, and the stone loach (bba) and rainbow trout (onm) to minimal discharge. Strahler order, altitudinal gradient and hydrological region accounted altogether for at least 45 % and up to 82 % of the explained variation of species distribution. The sampling bias factor explained an average of 4 % and up to 15 % of the model deviance depending on the species and was most prevalent in the spined loach (cot), sunbleak (led) and pike (esl).

Prediction performance of the base model (i.e., with no connectivity index added) varied widely depending on species (TSS up to 0.53; Fig. 3a). The souffia (code: tes) was not retained further into our analysis because its relative abundance and restricted distribution created unreliable modeling outputs. Species with highest prediction performance were in the majority native to the study area, the gudgeon (gog), chub and bleak (ala), while non-native species tended to be linked to lower performance, especially the grayling (tht), catfish (amm) and rainbow trout. PseudoR² values showed a medium to high goodness of fit, except for sticklebacks (gaa and pux), sunbleak, bullhead (cop), rudd (sce), rainbow trout and carps (cax and cyc), for which it fell below 0.2 (Fig. 3b). Overall TSS and PseudoR² values were weakly correlated (r² ~ 0.14).

3.2. General contribution of connectivity to SDM performance

In terms of TSS, connectivity-sensitive SDMs – i.e., those that included connectivity indices – on average predicted species presence better than the base model (Fig. 3c). Predictive power was significantly higher than for the base model for all species except for the catfish, 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), more than 20 out of 27 indices had significant effects, while the ruffe and common carp had no index with significant effect.

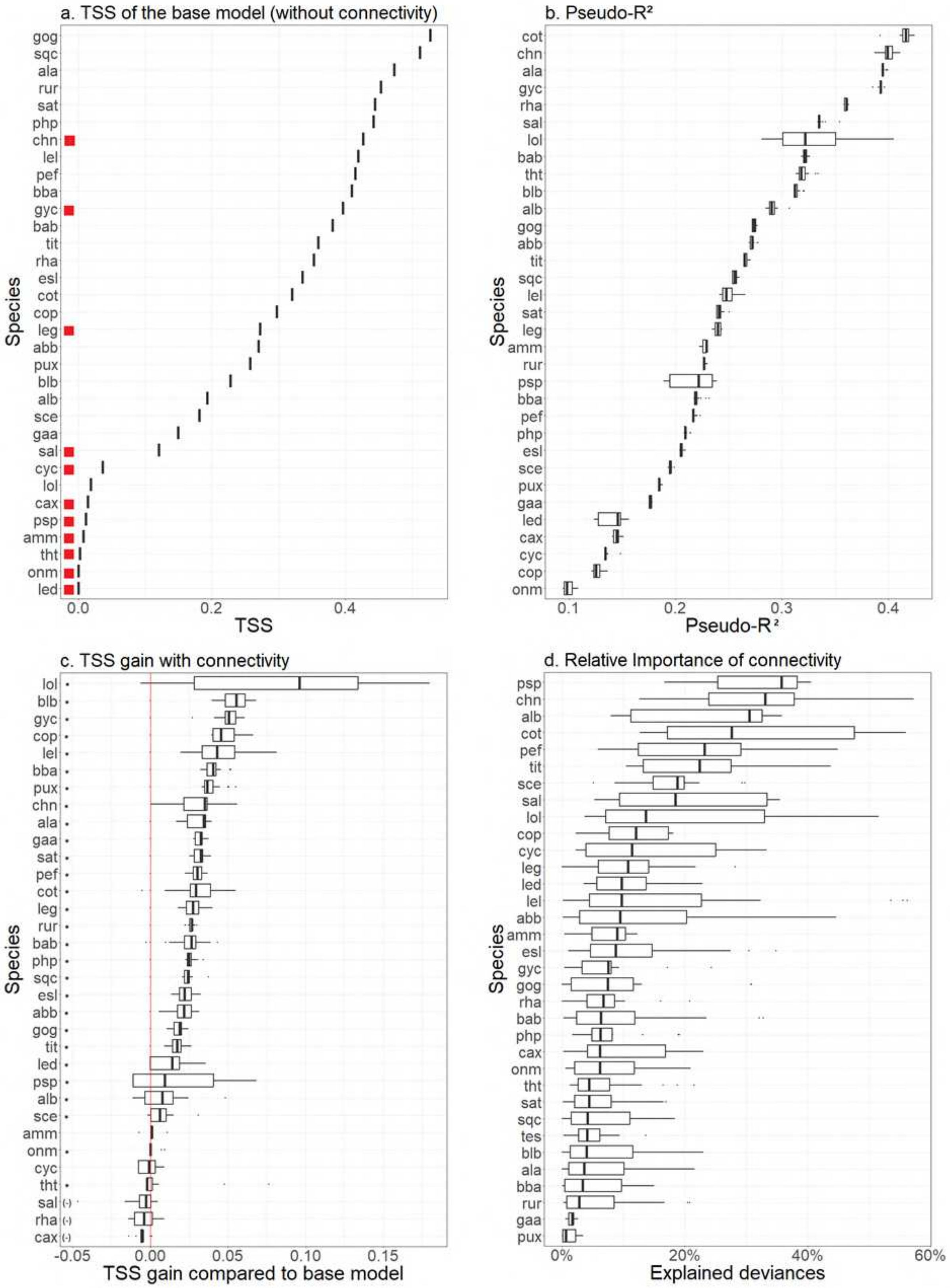


Figure 3. Model and index performance. a: Boxplot of base model SDM TSS values for all species; red squares show non-native species. b: Boxplot of PseudoR² values across

*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.*

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.

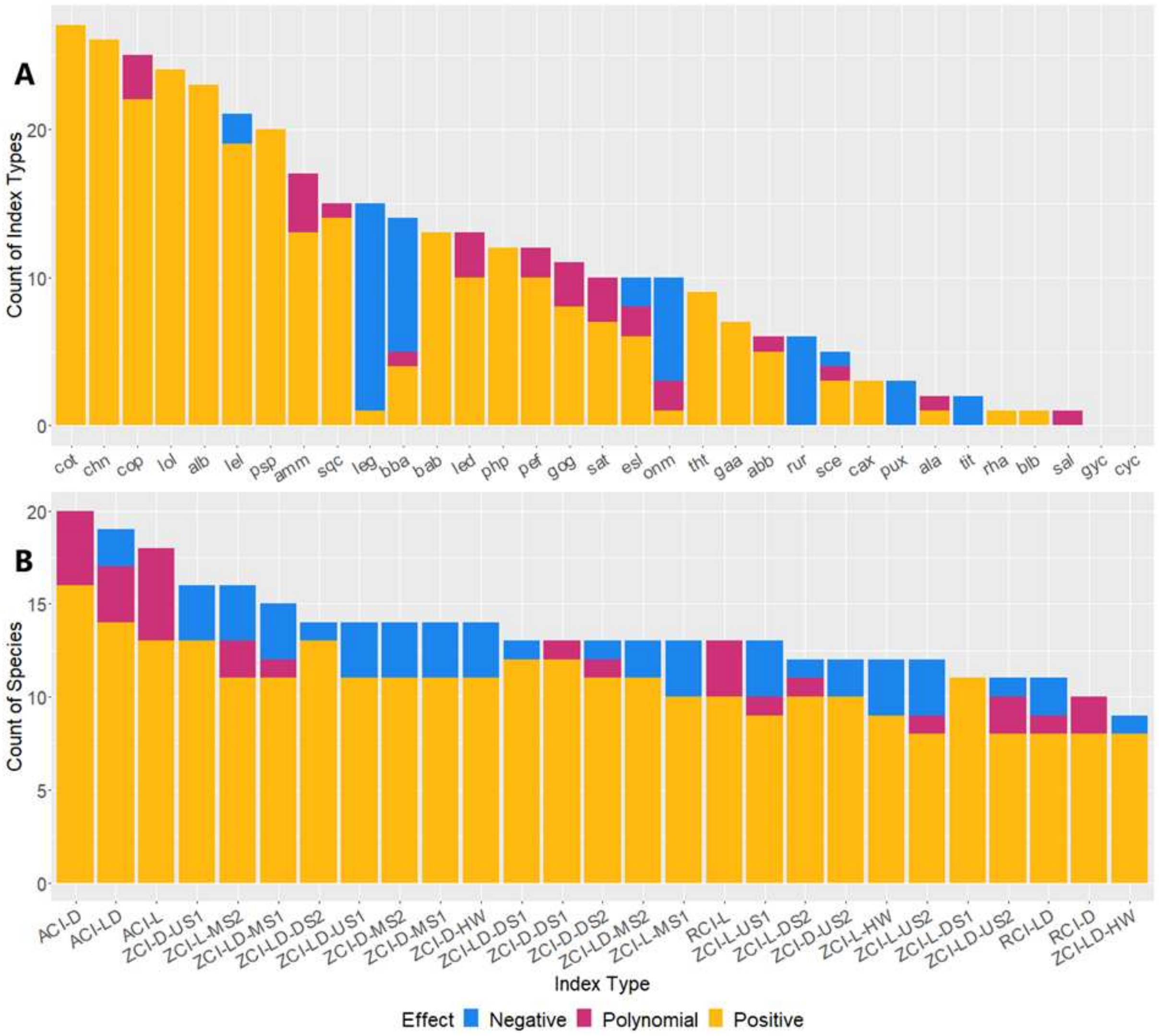


Figure 4. Account of significant effects across species and indices. a: Count of indices (per species) for which significant effects were linear positive, linear negative, or exclusively polynomial (total number of indices is 27); b: Count of species (per connectivity index) for which significant effects were linear positive, linear negative, or exclusively polynomial (total number of species is 33).

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

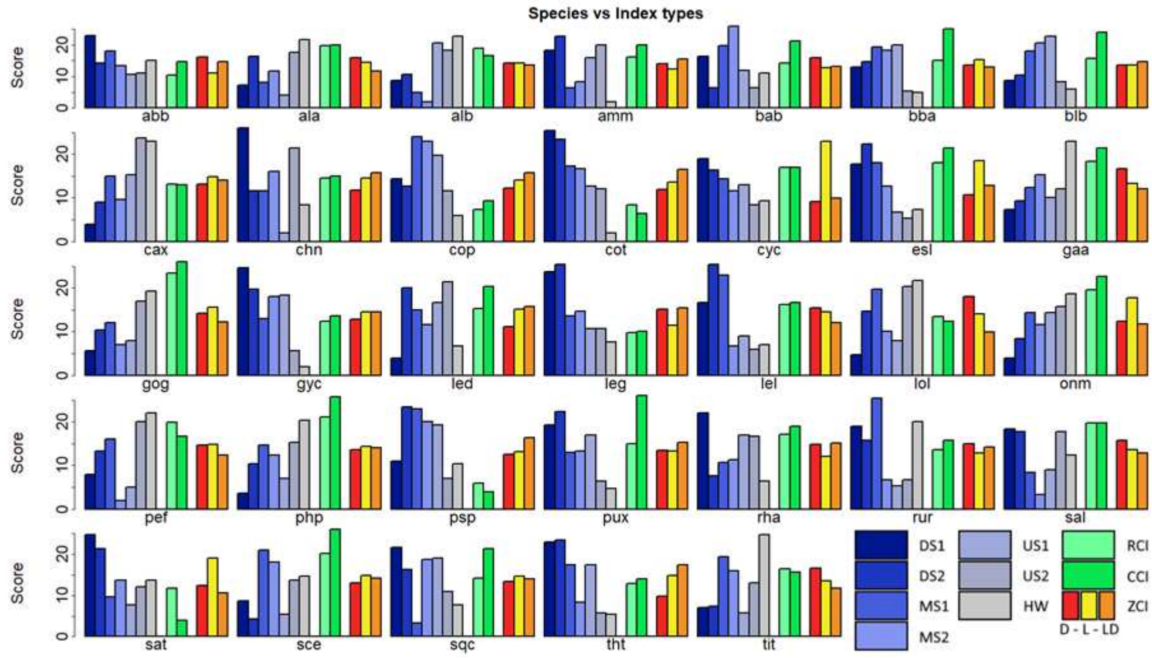


Figure 5: Scoring of all index properties on all index-species combinations. Grouped by species, scaled bar plots, legend of index properties on the bottom right (DS1 to HW: ZCI zonations; D: Dams taken into account, not dispersal; L: Dispersal taken into account, not dams; LD: Dams and dispersal taken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

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).

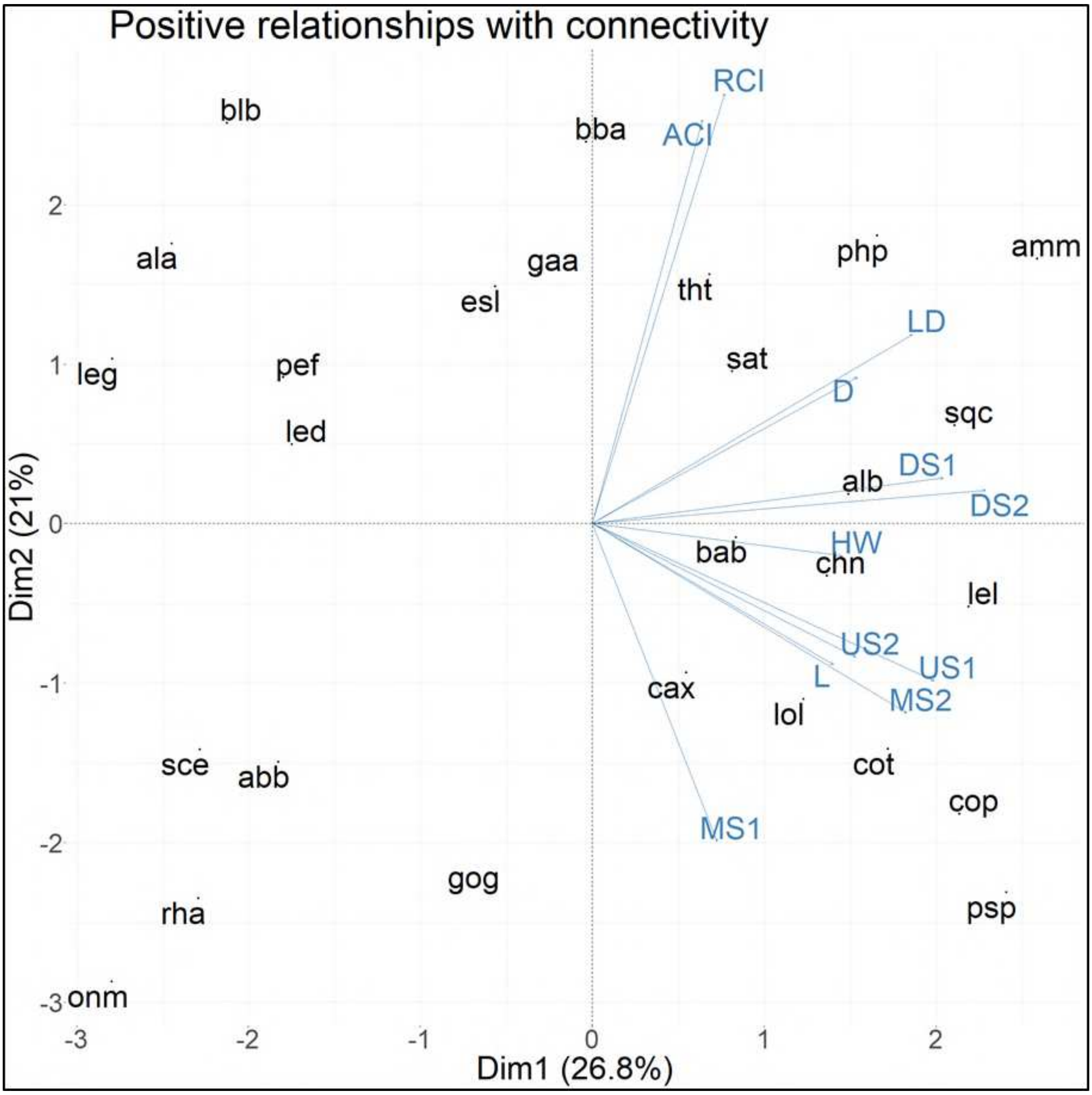


Figure 6: PCA biplot of importance scorings across connectivity index properties and fish species (positive relationships only, 27 species).

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 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 & 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 & 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 et al., 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 be 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 & 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, 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 & 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 & 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 (>1 5 % 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.

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CRediT AUTHORSHIP CONTRIBUTION STATEMENT

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

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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APPENDICES TO CHAPTER 3

APPENDIX A: Obtaining estimates for missing obstacle heights

Random Forest Regression Protocol For The Estimation Of Obstacle Heights

Predictors:

1) *Wasson et al. (2004)*

-Hydrological region (REGION)

2) *Silvestre et al. (2024) - features of PIREN-Seine hydrographic network*

-Strahler order (STRAHLER)
-Average reach width (m) (WIDTH)
-Average slope (°) (SLOPE)
-Average elevation (m) (ELEVATION)
-Drainage basin surface area (km^2) (SBV)

3) *OFB (2024) - ROE dataset*

-Barrier type (large dam - weir - bridge-related structure) (TYPE)
-State of deterioration (in construction, extant, partial destruction) (STATE)

Methodology:

We withdrew the highest obstacles (>20m) from the training dataset to decrease RMSE, similarly, we assumed that larger (>3m) obstacles were well documented, so predicted heights were truncated at this threshold. We set the algorithm at 500 trees and ran 100 random forests on different seeds, averaging predictions. Model cross-validation was done through 80/20% training datasets, 100 runs, and the calculation of Root Mean Square Error (RMSE) and explained variance.

Model Performance:

During Cross-validation, RMSE averaged at 0.79, and explained variance at 27.7%.

Variable Importance:

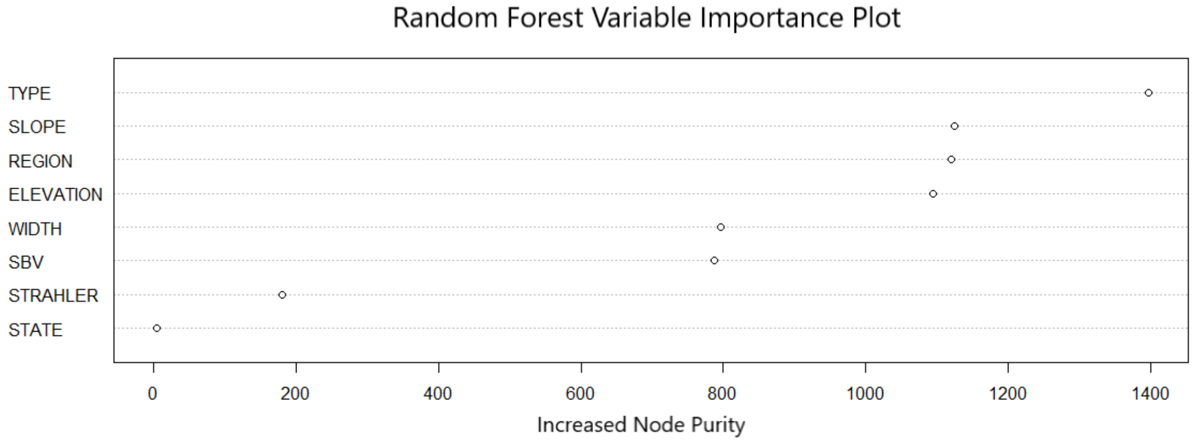

Fig. A.1: Random Forest Variable Importance Plot for the prediction of obstacle heights

Obstacle Height Classes:

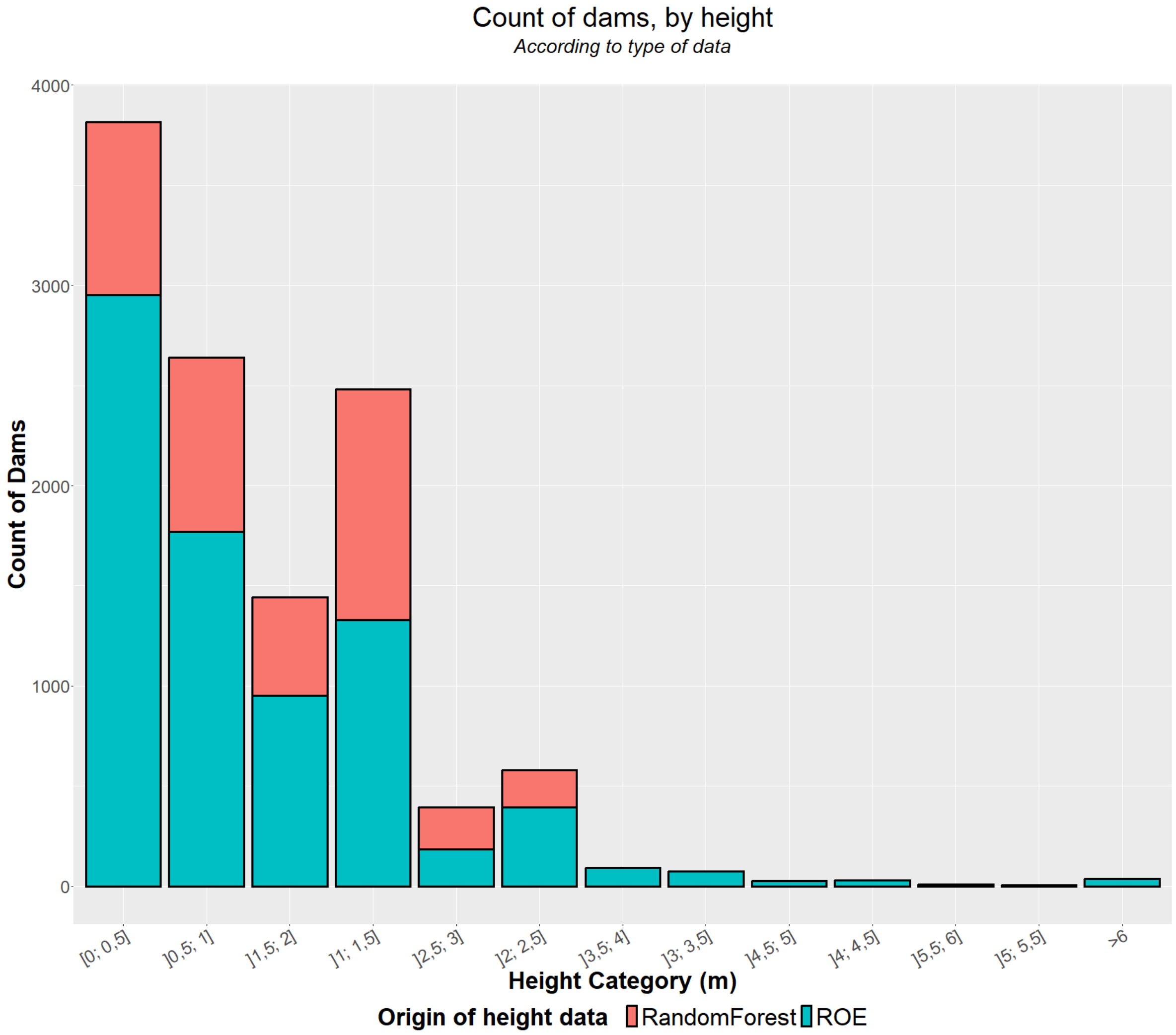

Fig. A.2: Barplot of barrier height categories and count of barriers per category

APPENDIX B (Table B.1.): Fish species and families, species codes and traits

List of species studied in this paper along with their ecological and morphological characteristics: Code = species name abbreviation; **Head =** Presence of the species in headwaters reaches (yes/no), retrieved from dataset (at least 10% of headwater study sites) and (Keith et al., 2020); **Coast =** Presence of the species in coastal rivers of Normandy (yes/no), retrieved from dataset; **Nat =** Native (yes) or non-native (no); **Mov =** Potamodromous (pot) or sedentary (sed), information obtained through (Teletchea & Teletchea, 2020); **L(mm)** = Average length (as defined in Baudoin et al. (2014) as "Lpmoy") - used for dispersal capacity calculations; **Cat** = Barrier crossing subcategories from Baudoin et al. (2014) for categorical lengths from A (brown trout, high jumping ability and swimming speed) to L (bitterling, sticklebacks, minnow, sunbleak, smaller species, rarely jump); **AR** = Caudal Fin Aspect Ratio - see Fig.2. From the 59 species recorded in the study area, the following species were selected to comply with three criteria: 1) They are not diadromous; 2) They are present in at least 40 study sites to allow for species distribution modeling, twice the often quoted low-prevalence break-point (Jiménez-Valverde et al., 2009); and 3) Their body shape is broadly fusiform and thus suitable for the calculation of caudal aspect ratio needed for assessing species dispersal abilities (see section 2.3) (thus excluding the brook lamprey (*Lampetra planeri*, Bloch, 1784) and wels catfish (*Silurus glanis*, Linnaeus, 1758))

Family	**Name**	**Code**	**Head**	**Coast**	**Nat**	**Mov**	**L(mm)**	**Cat**	**AR**
Acheilognathidae	Bitterling[1] *Rhodeus amarus*	**rha**	no	no	yes	sed	80	L	2.72
Gobionidae	Gudgeon[2] *Gobio gobio*	**gog**	yes	yes	yes	sed	130	K	1.76
	Topmouth gudgeon[3] *Pseudorasbora parva*	**psp**	no	yes	no	sed	80 [b]	J	2.52
Cyprinidae	Barbel[2] *Barbus barbus*	**bab**	no	no	yes	pot	550	E	2.26
	Carassius carps[a] Conflation of: 1) Prussian carp[1] *C. gibelio* 2) Crucian carp[2] *C. carassius*	**cax**	no	[a]	no	sed	200	J	1.93

	Eurasian carp[2] *Cyprinus carpio*	**cyc**	no	yes	no	sed	580	F	2.49
Leuciscidae	*Common* bream[2] *Abramis brama*	**abb**	no	yes	yes	pot	400	G	3.18
	Bleak[2] *Alburnus alburnus*	**ala**	no	yes	yes	sed	100	J	1.99
	Schneider[1] *Alburnoides bipunctatus*	**alb**	no	No	yes	pot	140	J	2.68
	Silver bream[2] *Blicca bjoerkna*	**blb**	no	yes	yes	pot	280	H	2.88
	Nase[2] *Chondrostoma nasus*	**chn**	no	No	no	pot	400	E	2.53
	Sunbleak[4] *Leucaspius delineatus*	**led**	no	yes	no	sed	80	L	2.14
	Chub[2] *Squalius cephalus*	**sqc**	yes	yes	yes	pot	450	E	2.06
	Dace[2] *Leuciscus leuciscus*	**lel**	no	yes	yes	pot	250	I	2.34
	Souffia[5] *Telestes souffia*	**tes**	no	No	no	sed	180	J	2.21
	Minnow[2] *Phoxinus phoxinus*	**php**	yes	yes	yes	pot	80	L	1.91
	Roach[2] *Rutilus rutilus*	**rur**	yes	yes	yes	pot	230	J	2.29
	Rudd[2] *Scardinius erythrophthalmus*	**sce**	no	[a]		sed	230	J	2.04
Tincidae	Tench[2] *Tinca tinca*	**tit**	no	yes	yes	sed	400	H	1.92
Cobitidae	*Spined* loach[2] *Cobitis taenia*	**cot**	no	No	yes	sed	100	K	1.5
Nemacheilidae	*Stone* loach[2] *Barbatula barbatula*	**bba**	yes	yes	yes	sed	100	K	1.24
Ictaluridae	Catfish[6] *Ameiurus melas*	**amm**	no	No	no	sed	275[b]	H	1.67
Esocidae	Pike[2] *Esox lucius*	**esl**	yes	yes	yes	sed	700	C	2.17
Salmonidae	*Brown* trout[2] *Salmo trutta*	**Sat**	yes	yes	yes	pot	400	A	2.03
	Rainbow trout[7]	**onm**	no	yes	no	pot	350[b]	B	2.15

	Grayling[2] *Thymallus thymallus*	**tht**	no	yes	no	pot	400	D	3.03
Lotidae	Burbot[2] *Lota lota*	**lol**	no	No	yes	pot	450	H	0.99
Gasterosteidae	*Three-spined* stickleback[2] *Gasterosteus aculeatus*	**gaa**	yes	yes	yes	sed	80	L	1.79
	Pungitius sticklebacks Hybrid population of: 1) Ninespine stickleback[2] *Pungitius pungitius* 2) Smoothtail ninespine stickleback[8] *Pungitius laevis*	**pux**	yes	yes	yes	sed	80	L	1.66
Percidae	Ruffe[2] *Gymnocephalus cernua*	**gyc**	no	yes	no	sed	130	K	2.12
	Perch[2] *Perca fluviatilis*	**pef**	yes	yes	yes	sed	300	H	2.24
	Zander[2] *Sander lucioperca*	**sal**	no	yes	no	pot	600	G	2.2
Centrarchidae	Pumpkinseed[2] *Lepomis gibbosus*	**leg**	no	No	no	sed	80[b]	J	1.96
Cottidae	Bullhead[9] *Cottus perifretum*	**cop**	yes	yes	yes	sed	100	K	1.41
Taxa: 1. Bloch, 1782 **2.** Linnaeus,1758 **3.** Temminck & Schlegel, 1846 **4.** Heckel, 1843 **5.** Risso, 1827 **6.** Rafinesque, 1820 **7.** Walbaum, 1792 **8.** Cuvier, 1829 **9.** Freyhof, Kottelat & Nolte, 2005									
a. Case of the Carassius carps: the Prussian carp is absent from coastal rivers, the Crucian carp is present, in recent years, the Prussian Carp tends to prevail in samples and Case of the rudd: native in the Seine basin and introduced in coastal rivers **b.** For fish not included in Baudoin et al. (2014): Pseudorasbora parva, small fish in the 70-100 mm range with diverging sources on average size in European waters, we assign it an 80 mm average length (like the sticklebacks, bitterling etc.); Lepomis gibbosus, small fish, highly polymorphous, generally smaller in Europe than native populations, which leads us to assign it an 80 mm length (Copp et al., 2004); Rainbow Trout, 350 mm and Catfish, 275 mm, from average range (Keith et al., 2020)									

APPENDIX C: List of environmental covariates or factors and of final predictors used in species distribution models in addition to connectivity indices (see section 2.3)

Covariates (summarized into PCA coordinates)	Definition (source)
Annual Precipitation (mm)	2000-2020 annual average (SAFRAN)
Summer Precipitation (mm)	2000-2020 Jun-Jul-Aug average (SAFRAN)
Fall Precipitation (mm)	2000-2020 Sep-Oct-Nov average (SAFRAN)
Winter Precipitation (mm)	2000-2020 Dec-Jan-Feb average (SAFRAN)
Spring Precipitation (mm)	2000-2020 Mar-Apr-May average (SAFRAN)
Summer Air Temperature (°C)	2000-2020 Jun-Jul-Aug average(SAFRAN)
Fall Air Temperature (°C)	2000-2020 Sep-Oct-Nov average (SAFRAN)
Winter Air Temperature (°C)	2000-2020 Dec-Jan-Feb average, (SAFRAN)
Spring Air Temperature (°C)	2000-2020 Mar-Apr-May average(SAFRAN)
Air Temperature Differential – (July - January) (°C)	2000-2020 average (SAFRAN)
Water Temperature - Thermal Peak (°C)	Average Temperature over the 30 warmest consecutive days. See Appendix C and Beaufort et al. (2022)
Land use: Grassland, Forest, Urban / Agriculture and Water Cover (%)	Proportion of surface area covered by land-uses within whole catchments (THEIA)
Buffer strip land use: Bodies of Water and Riparian vegetation (%)	Proportion of surface area covered by land-uses within strip-shaped buffers (THEIA)
River Straightness	True Reach Length / Straight Reach Length (SYRAH-CE reaches i.e. hydromorphologically homogeneous sections, see Valette et al. 2012)
Slope ($m.km^{-1}$)	Average slope in local reach (PIREN-Seine hydrographic network)
Elevation (m)	Average of maximum and minimum reach elevation (PIREN-Seine hydrographic network) (Silvestre et al. 2024)
QMNA5 ($m^3.s^{-1}$)	Annual minimal monthly discharge with a 5-year return period, obtained from Inverse distance weighting of Hydroportail data (Leleu et al., 2014)

Concavity Index (CI)	Expressed as $(Q_1-Q_{10})/(Q_{10}-Q_{99})$, where Q_p is the daily flow exceeded p% of the time (Beaufort et al., 2022), reach CI value obtained from Inverse distance weighting of Hydroportail data points (Leleu et al., 2014)
Catchment area (km^2)	PIREN-Seine hydrographic network
Pluriannual average O_2 concentration ($mg.L^{-1}$)	Simulations produced by the pyNuts-Riverstrahler model on the scale of the Seine-Normandy basin for the time period 2017-2021 (Renaud et al., 2024)
Pluriannual average NO_3^- concentration ($mg.L^{-1}$)	Simulations produced by the pyNuts-Riverstrahler model on the scale of the Seine-Normandy basin for the time period 2017-2021 (Renaud et al., 2024)
Pluriannual average NH_4^+ concentration ($mg.L^{-1}$)	Simulations produced by the pyNuts-Riverstrahler model on the scale of the Seine-Normandy basin for the time period 2017-2021 (Renaud et al., 2024)
Gradients from the PCA of all environmental quantitative covariates (included in final model)	**Definition (source)**
Elevation gradient (Axis 1: 51.7% of expl. variances)	Positively correlated to Annual Air Temperature, Land use - Urban. Negatively correlated to Rainfall, Elevation, Land use - Forests.
Minimal discharge gradient (Axis 2: 12.5% of expl. variances)	Positively correlated to QMNA5, Bodies of water in buffer strips, Land use - Water cover. Negatively correlated to Land use - Agricultural land.
Air Temperature range gradient (Axis 3: 10% of expl. variances)	Positively correlated to air temperature differential. Negatively correlated to Land use - Agricultural land.
Ammonium gradient (Axis 4: 5.5% of expl. variances)	Positively correlated to NH_4^+ content. Negatively correlated to O_2 content.
Riparian vegetation integrity gradient (Axis 5: 5.1% of expl. variances)	Positively correlated to concavity. Negatively correlated to riparian vegetation in buffer strips.
Factors (included in final model)	**Definition (source)**
STRAHLER Order	Strahler (1957)

Hydroecological Region	Wasson et al. (2004) - 12 homogenous subregions (from 17: factor levels with <10 data points conflated with neighboring regions) with respect to geophysical factors key in the structure of freshwater ecosystems
Hydrological Regime	Mainly pluvial regime groups, labeled 1 through 6 according to classification by Sauquet et al. (2008), obtained from Hydroportail streamflows (Leleu et al., 2014)
Sampling Intensity of electrofishing depletion (see Harris et al., 2016) for each study site. We retain the best Sampling Intensity rating among samples)	1: Partial sampling from a boat 2: Partial sampling by wading 3: Complete sampling by wading, single pass 4: Complete sampling by wading, several passes

APPENDIX D: Obtaining estimates for study site water temperatures (Thermal Peak)

Random Forest Regression Protocol For The Estimation Of Water Temperature

Predictors for thermal peak: Average Temperature over the 30 warmest consecutive days (Beaufort et al., 2022)

1) *Vidal et al. (2010) SAFRAN - Climatic Variables*

- Mean annual precipitation (mm) - 2000-2020 (MAP)
- Mean August precipitation (mm) - 2000-2020 (MSP)
- Mean Annual Snow Accumulation (mm) - 2000-2020 (MSA)
- Mean Summer Air Temperature (July - August) (°C) - 2000-2020 (MST)

2) *Leleu et al. (2014) Hydrologic Variables - Inverse Distance Weighting Interpolation*

- Mean Annual Specific Discharges (L.s^{-1}.km^{-2}) (Qmean)
- Mean Monthly Minimum Specific Discharge - Specific QMNA5 (L.s^{-1}.km^{-2}) (Qmin)
- Concavity Index [-] (CI)
- Hydrological Regime [-] (REGIME)

3) *Silvestre et al. (2024) - features of PIREN-Seine hydrographic network*

- Elevation (m) (ELEVATION)
- Drainage area (km^{2}) (SBV)
- Mean slope of reach (m.km^{-1}) (SLOPE)

4) *Valette et al. (2012) - features of SYRAH-CE reaches*

- Riparian Vegetation Cover (%) (RIP)
- Linear density of upstream obstacles (km^{-1}) (LDEN)
- Areal density of upstream obstacles (km^{-2}) (ADEN)
- Upstream Pond Cover (%) (POND)

Methodology:

We set the algorithm at 500 trees and ran 100 random forests on different seeds, averaging predictions. Model cross-validation was done through 80/20% training datasets, 100 runs, and the calculation of Root Mean Square Error (RMSE) and explained variance.

Model Performance:

During Cross-validation, RMSE averaged at 1.87, and explained variance at 77.7%.

Variable Importance:

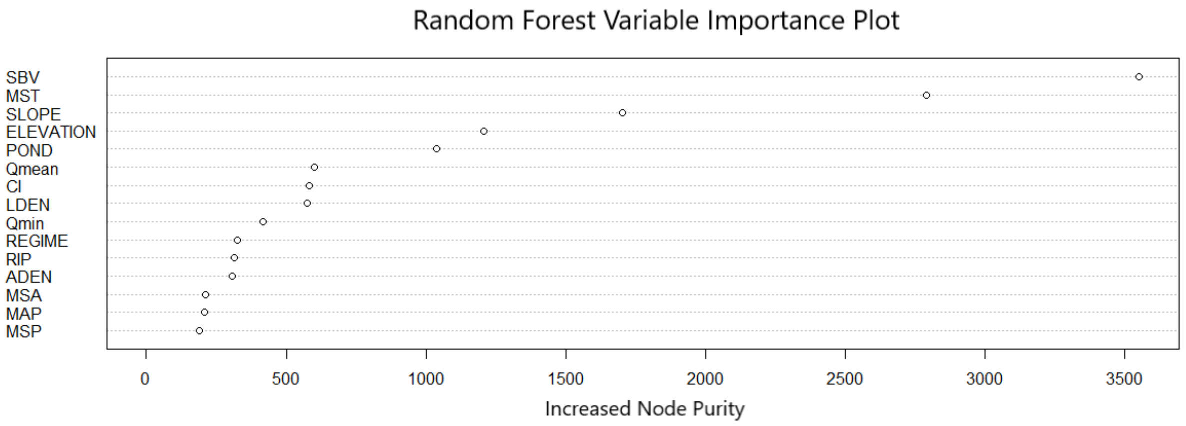

Fig. D.1: Random Forest Variable Importance Plot for the prediction of Thermal Peak (Water Temperature)

APPENDIX E: Full explainer of our method for the calculation of obstacle crossing probability (or permeability)

We considered obstacle crossing asymmetrically (upstream and downstream). According to Meixler (2021), one of the main criteria for the upstream crossing of obstacles is the comparison between jumping height (JH), obtained from fish average length, and obstacle height. We hypothesized there to be sufficient plunge pool depth and velocity on all barriers which are also low enough to be jumped. Jumping height (JH, in m) was obtained from Meixler (2021):

$$JH = \frac{(9L)^2}{2g} \quad (Eq.E.1)$$

with g the gravitational constant set at 9.8 m.s^{-2} (Eq. E.1) and L the fish length (in m). To account for specific functional differences with respect to jumping ability, fish length was averaged across functional fish barrier permeability categories for obstacle crossing, following the Baudoin et al. (2014) ICE protocol (Informations sur la Continuité Écologique - Information on Ecological Continuity, see Appendix B for ICE categories).

To obtain contrasted permeability values (or probability of crossing) between 0 and 1, we compared fixed obstacle heights to jumping heights, obtained through Eq. E.1, with fish length, and thus jumping heights, expressed in the shape of a density function: adult fish length distribution $DL(x, \xi, \omega, \alpha)$ was expressed as a skew normal distribution (Blanchet et al., 2010, see Eq. E.2) as function of x (in m) to reproduce natural fish size assemblages:

$$DL(x, \xi, \omega, \alpha) = \frac{2}{\omega\sqrt{2\pi}} e^{-\frac{(x-\xi)^2}{2\omega^2}} \int_{-\infty}^{\alpha\left(\frac{x-\xi}{\omega}\right)} \left(\frac{1}{\sqrt{2\pi}}\right) e^{-\frac{t^2}{2}} dt \quad (Eq.E.2)$$

with constant parameters ξ=0.75L (location), ω=0.375L (scale), α=4 (skewness), and L categorical average fish length. Using the inverse of Eq. E.1, we expressed the fish length L (m) as the inverse function of jumping height JH (m), see Eq. E.3):

$$JH = \frac{(9L)^2}{2g} \Leftrightarrow L = \frac{\sqrt{2gJH}}{9} \quad (Eq.E.3)$$

Thus, replacing x by $\frac{\sqrt{2gx}}{9}$ we obtained the corresponding skewed jumping height distribution function of x (in m), expressed as density $DJH(x, \xi, \omega, \alpha)$ - see Eq. E.2 and E.3 and Fig. 2. We then calculated the upstream permeability $P_u(H,\xi,\omega,\alpha)$, a value comprised between 0 and 1:

$$P_u(H, \xi, \omega, \alpha) = \frac{\int_H^{+\infty} DJH(x,\xi,\omega,\alpha)dx}{\int_0^{+\infty} DJH(x,\xi,\omega,\alpha)dx} \quad (Eq. E.4) \text{ if no fish pass or lock,}$$

$$P_u(H, \xi, \omega, \alpha) = 0.5(1 + \frac{\int_H^{+\infty} DJH(x,\xi,\omega,\alpha)dx}{\int_0^{+\infty} DJH(x,\xi,\omega,\alpha)dx}) \quad (Eq. E.5) \text{ if fish pass or lock present}$$

with H (m) the height of an obstacle (Eq. E.4 and E.5). When a barrier was associated with a fish pass or lock (4 % of barriers), permeability was adjusted systematically by considering half of the fish as successful (Bunt et al., 2012) in passing obstacles upstream through fish passes. Downstream permeability P_d is linked to survival after crossing. Mortality during downstream movement originates from shocks endured during descent (falling heights for larger fish, faster currents for others), trapping in water pumping stations, predation due to dizziness after descent etc. (Baudoin et al., 2014). The relationship between fish size and height-dependent crossing success and survival being complex and poorly understood, we treated downstream permeability as a linear function of obstacle height, homogenous for all species, with $P_d(H)=1-(H/5)$, to set permeability at 0 when obstacle height exceeds 5 m.

APPENDIX F: Understanding centrality bias in RCI. Fig. F.1. Centrality subcategories, lognormal and exponential distributions of weight factors on logarithmic axis; Fig. F.2. Cartography of base RCI (values for bullhead - cop) highlighting relationship to centrality (high RCI correlated to high centrality); Fig. F.3. Cartography of Betweenness Centrality

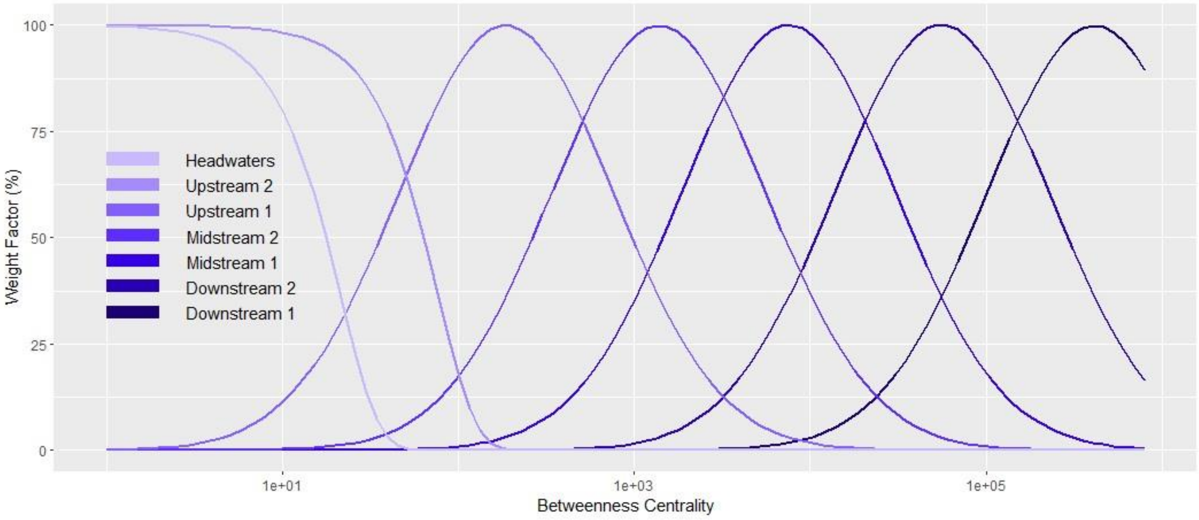

Fig. F.1. Centrality subcategories, lognormal and exponential distributions of weight factors on logarithmic axis

Example of zonation function:

Considering the weighting lognormal function W (Eq. F.1):

$$W(C) = A \cdot \frac{1}{\sigma C\sqrt{2\pi}} \cdot exp(-\frac{(\ln(C) - \mu)^2}{2\sigma^2})\ (Eq. F.1)$$

with C the betweenness centrality and A, σ, μ constant numerical values. With reach centrality values on our river network between 0 and 800000, the US1 zonation weighting factor $W_{US1}(C)$ is equal to W(C) with A=7.05528·10^4, σ=1.4, μ=10.8888, leading to a lognormal curve with a maximum value of 1 for C=7546.

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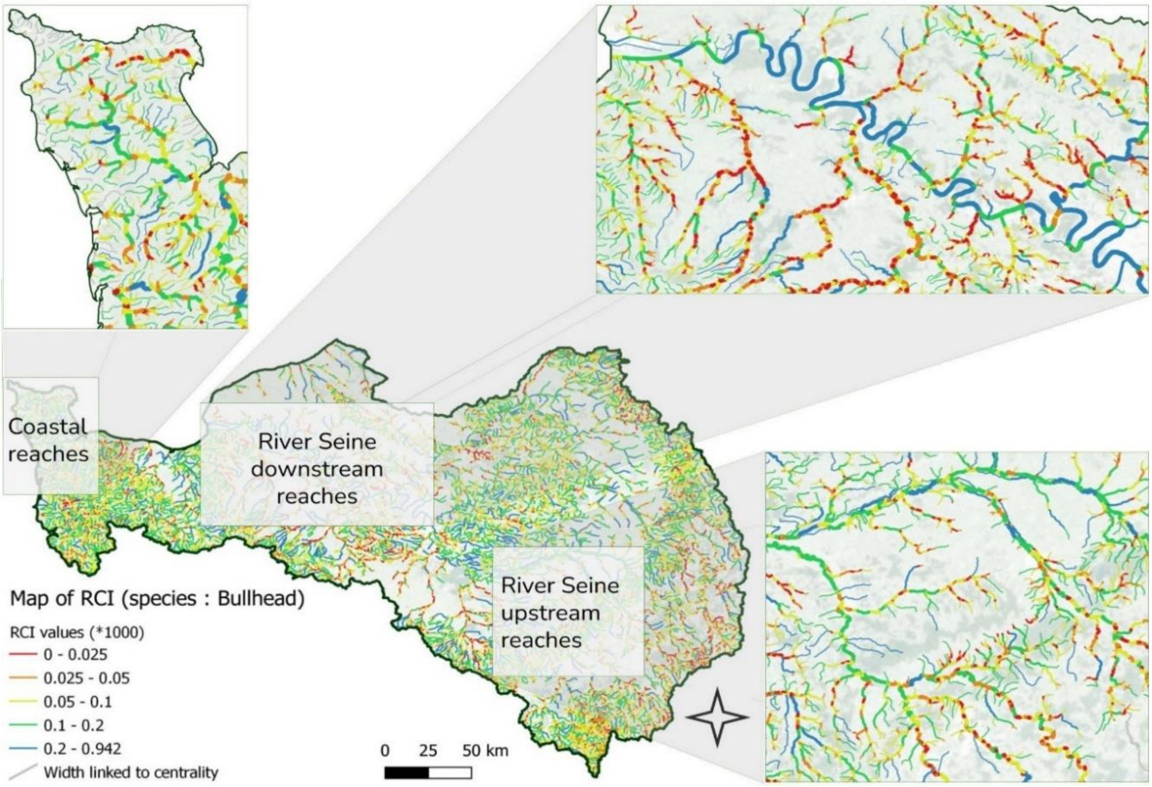

Fig F.2 Cartography of base RCI (values for bullhead - cop) highlighting relationship to centrality (high RCI correlated to high centrality)

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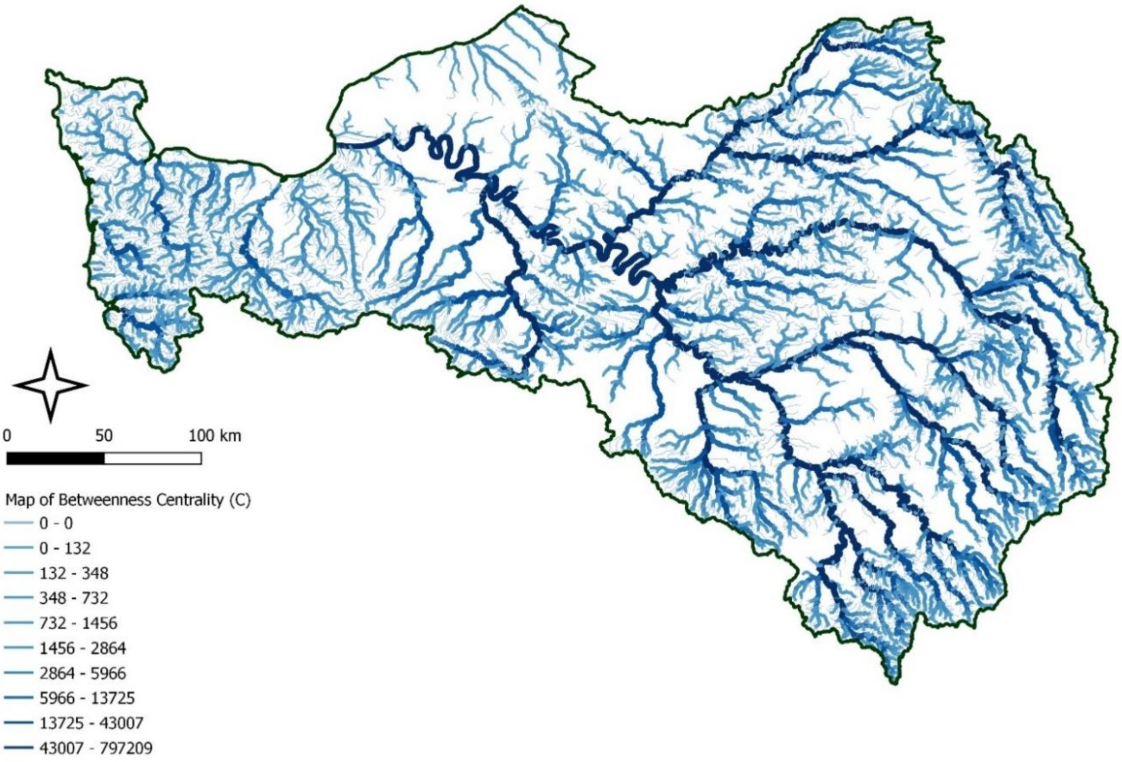
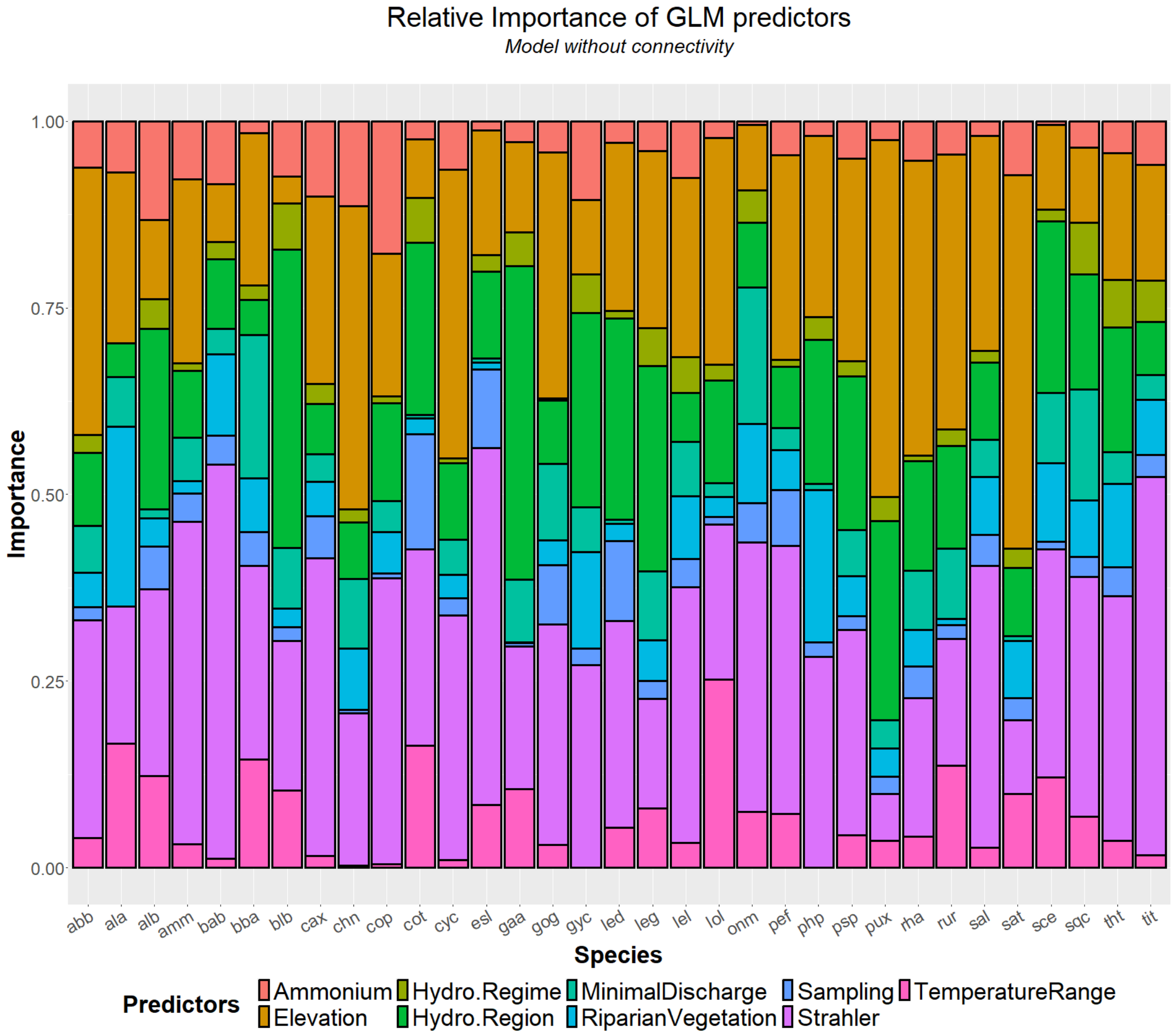


Fig. F.3 Cartography of Betweenness Centrality

APPENDIX G (Fig. G.1.): Relative importance of environmental predictors in base SDMs (without connectivity): Relative importance of predictors in base model (with no connectivity index), predictors ordered by alphabetical name, with Ammonium representing PCA Axis 4, Elevation PCA Axis 1, MinimalDischarge PCA Axis 2, Riparian Vegetation PCA Axis 5, Air Temperature Range PCA Axis 3, as described in Table 1.



APPENDIX H (Table H.1): Table of significance of the effect of connectivity indices on fish distribution (p-values above 0.05 grayed out, positive linear effect in blue, negative linear effect in red, exclusively polynomial effect in orange)

	(LD/D/L) RCI			(LD/D/L) ACI			(LD/D/L) DS1			(LD/D/L) DS2			(LD/D/L) MS1			(LD/D/L) MS2			(LD/D/L) US1			(LD/D/L) US2			(LD/D/L) HW		
abb			🟧										🟦	🟦	🟦		🟦	🟦									
ala					🟦								🟧														
alb	🟦	🟦	🟦	🟦	🟦	🟦	🟦		🟦		🟦		🟦	🟦	🟦	🟦		🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
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APPENDIX I (Table I.1): One-sample Wilcoxon signed-rank test off TSS gain, across 27 indices, compared to base model. “diff” is the difference between the average of 27 connectivity-sensitive models TSS and base model TSS. p-value significance threshold at 0.05. Negative values of diff and above-threshold p-values are in italics.

Species	**diff**	**p-value**	**Species**	**diff**	**p-value**	**Species**	**diff**	**p-value**
rha	*-3.513e-3*	9.71e-3	**led**	0.0125	4.2e-4	**sat**	0.0319	1.49e-8
gog	0.0181	5.82e-6	**sqc**	0.0248	5.92e-6	**onm**	1.397e-3	0.0477
psp	0.021	0.0141	**lel**	0.0451	1.49e-8	**tht**	3.755e-3	0.0445
bab	0.0255	2.98e-8	**php**	0.0259	5.93e-6	**lol**	0.0894	8.29e-6
cax	*-6.277e-3*	3.77e-6	**rur**	0.0263	5.91e-6	**gaa**	0.0321	5.84e-6
cyc	*-1.558e-3*	*0.245*	**sce**	6.418e-3	6.93e-5	**pux**	0.0389	5.67e-6
abb	0.0214	5.92e-6	**tit**	0.0173	5.92e-6	**gyc**	0.0493	5.74e-6
ala	0.0314	5.9e-6	**cot**	0.0309	6.62e-6	**pef**	0.0303	5.93e-6
alb	7.141e-3	0.0147	**bba**	0.04	5.89e-6	**sal**	*-4.870e-3*	1.03e-3
blb	0.0551	5.91e-6	**amm**	*-3.769e-5*	*0.195*	**leg**	0.0275	5.9e-6
chn	0.031	5.93e-6	**esl**	0.0228	1.49e-8	**cop**	0.0486	5.91e-6

APPENDIX J (Fig. J.1) : PCA biplot of importance scorings across connectivity index properties and fish species (negative relationships only, 9 species). Fig. J.2.: PCA biplot of importance scorings across connectivity index properties and fish species (polynomial relationships only, 27 species).

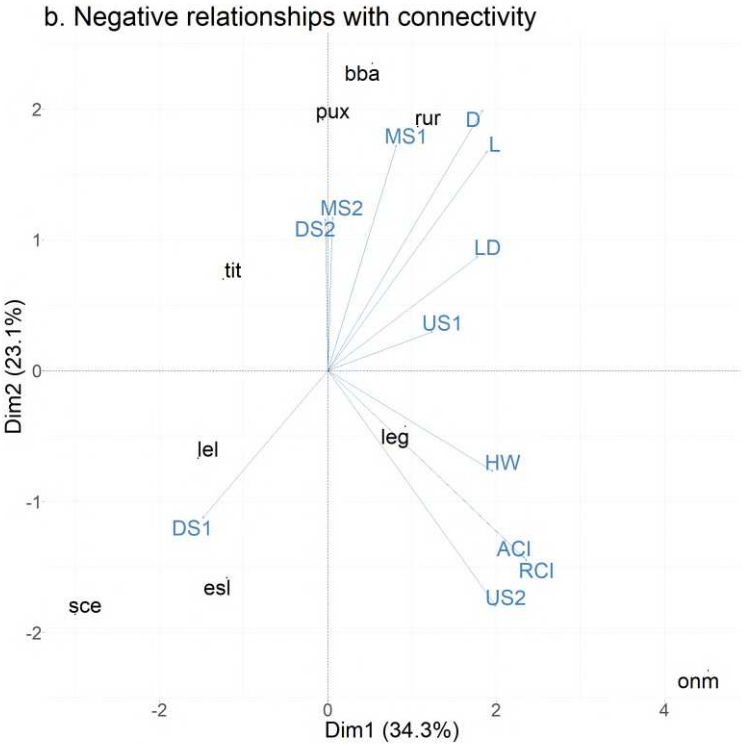

Fig J.1

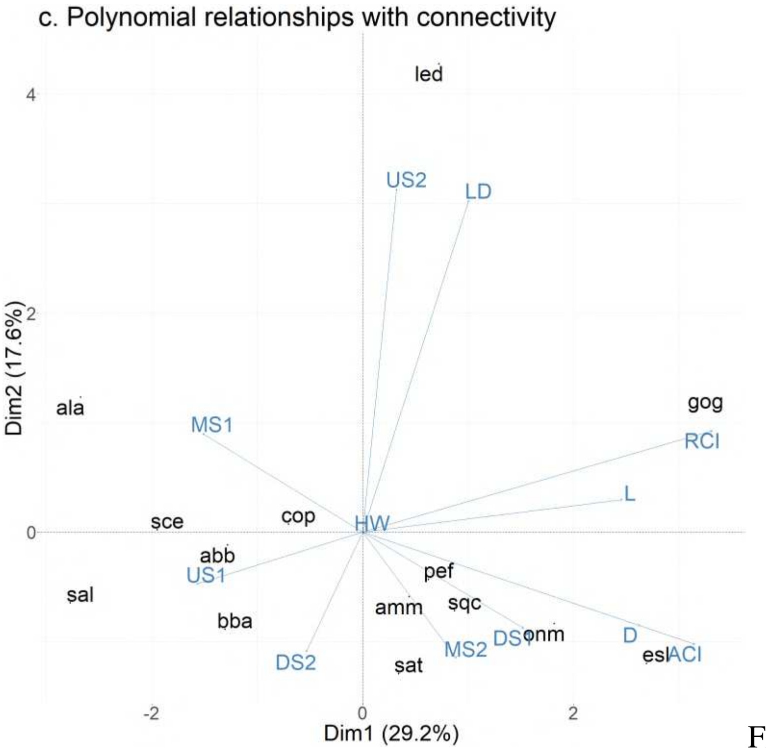

Fig J.2

Chapter 4.

The influence of management scenarios on future fish distribution: the case study of an anthropized watershed

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To be submitted in Global Change Biology

Foreword

This second article, to be submitted shortly as of writing, is concerned with the key hypotheses of this thesis, i.e. the respective influence of climate change and watershed management on potential future fish distribution. The novel results presented in the previous chapter concerning longitudinal connectivity are integrated in this chapter's methods, while focusing on larger issues of riverscape management (including, but not limited to longitudinal connectivity) through a set of scenarios constructed with members of government agencies concerned with riverscape restoration and management.

Abstract

Ongoing anthropogenic global change has begun impacting the diversity and distribution of fish communities in European rivers. River fish in anthropized watersheds like the Seine-Normandie basin are especially vunerable to the impacts of human activity on rivers, from fragmentation to channelization. Inversely, restoration initiatives like dam removals have been proven to have positive consequences on fish communities. Despite this, the impact of watershed management on fish communities in a context of climate change is rarely studied. Through a procedure of ensemble modeling, distribution models were trained on land use, connectivity and hydroclimatic predictors and used to predict potential distribution of eight species selected for their overall performance in models. Future hydroclimatic conditions were obtained through a selection of climate projections while land use and connectivity were expressed through watershed management scenarios. Model predictions showed a predominance of the effects of climate change over management in shaping species distributions, and an overall decline for most species, with individual variations. Differing properties of climate projections and geographic differences showed a sensitivity of fish to

increasingly dry seasons, while management scenarios highlighted an overall preference of fish for scenarios which included restoration of watersheds and higher proportions of semi-natural land use. For example, under projections for which summers were not too dry and scenarios of reasonable to ambitious restoration of watercourses, the perch saw its range expand by up to 70%, while the opposite conditions were predicted to lead to its near-extinction in the basin. Interestingly, the trout showed a surprising affinity for low restoration which could be explained by lower model performance and human interference in its current range. Overall, the bleak climate-driven future of river fish does seem to also be shaped by management to some extent, which should incite stakeholders to investigate the question further and take appropriate action.

1.INTRODUCTION

Anthropogenic climate change is due to put unprecedented pressure on temperate river ecosystems (Pletterbauer et al., 2018). Freshwater fish communities and fish are especially sensitive to the consequences of global change, directly through water and air temperature increase, changes in hydrological regime especially regarding droughts and floods, or indirectly through increased erosion, eutrophication and sea level rise (Daufresne & Boët, 2007; Li et al., 2022; Kelly & Whitton, 1998). These phenomena are likely to intensify in the next decades, and are already causing changes in freshwater communities such as range shifts, contractions or expansions, local extinctions and a lowering of abundances (Comte et al., 2013).

Additionally, anthropization of drainage basins is often pointed as an aggravating factor in already pressurized freshwater ecosystems. Channelization of rivers is known to destroy spawning and feeding habitats and to increase river discharge (Zajicek et al., 2018). Obstacles like dams or weirs are known to modify flow, water temperature, and prevent certain fish species from reaching spawning and feeding grounds, leading to local extirpations (Kominoski et al., 2017; Rincón et al., 2017). Other conspicuous river engineering include the removal of riparian forests during waterway construction has been shown to cause deleterious effects on fish fitness and populations and the proximity of urban and agricultural areas can add to these impacts through habitat loss or alteration and pollution. Likewise, the introduction of non-native species in new habitats disturb food webs and often modify community composition in the long term (Costa et al., 2021; Cucherousset & Olden, 2011).

The dendritic structure of rivers and isolation of drainage basins from each other, as well as the succession of habitats from source to estuary along the river continuum, shelter important fish biodiversity (McDermott, 2021; Van Der Sleen & Albert, 2022) that is associated to a wide array of ecosystem services (Holmlund & Hammer, 1999). At the confluence of anthropogenic influence and climate change, river fish are especially vulnerable. Fortunately, operations aimed at reducing the effects of these pressures and restoring watercourses have been shown in some cases to be linked to more diverse freshwater communities and increased resilience to climate change (Magilligan et al., 2021). The purpose of these restoration initiatives is generally to restore river connectivity. For example, river re-meandering and riparian forest restorations aim at recreating and reconnecting lateral habitats to the river (Studinski et al., 2012), while dam removals are practiced to restore longitudinal connectivity, which shape river fish communities (see Chapter 3 of this thesis). River fish conservation for future generations, aided by purposeful restoration, is thus a crucial challenge both intrinsically and with respect to human livelihoods.

Understanding the mechanisms behind the distribution of fish in anthropized basins is necessary to anticipate their future distribution and the necessary conditions for their conservation. To this end, species distribution models (SDMs) were gradually developed, relying on statistical and machine learning methods to identify patterns in species distribution. SDMs are trained on current conditions of climate and environmental conditions and can be used to predict the potential future distribution of species under new conditions of climate, water and land use, whether in a different time or space (Elith & Leathwick, 2009).

Future environmental conditions are often unknowable, especially in anthropized areas where territorial management is contingent on policy. Accounting for possible futures often implies resorting to a comparison of multiple climate projections, usable at the catchment scale to anticipate future climate change are now widely available (Calvin et al., 2023; Marson et al., 2024), and management scenarios, which must be built according to the needs of the study. Methodology for scenario building varies widely depending on use and means. Scenarios can be defined in this context as coherent stories of the future obtained by a prospective exercise, often told through an "if-then" structure - e.g. if a proactive policy of dam removal is applied, then we can expect higher longitudinal connectivity - where one develops a possible story of the future (March et al., 2012). The scenario is then translated into numeric descriptors - e.g. we may possess an estimator of longitudinal connectivity for current obstacle data, we create a separate set of values for the intended scenario of dam removal. Lacroix et al. (2019) describe in ecology two dimensions according to which scenario can be categorized 1) the intensity of state governance and 2) the quality of the environment, thus differentiating between different scenario types. For example, high governance intensity and low quality of the environment could correspond to a backlash to environmental measures at the state level, this is qualified as “Retreat” in Lacroix et al. (2019). Similarly, high quality and low governance corresponds to a sum of local initiatives for the environment with no clear involvement of state politics - “Local” in Lacroix et al. (2019).

The relative novelty of management scenarios, especially in aquatic ecology, makes their use in the prediction of river fish distribution rare, despite their many advantages. The comparison of several scenarios and the predicted distribution of multiple species under these scenarios may, for example, have the potential to give points of comparison between management decisions, providing precious information to policymakers. Thus, our aims in this study are to (i) develop a set of land management scenarios intended to cover a wide range of possible futures adapted to main issues of river basin management, (ii) compare and assess which of these scenarios are the most impactful on fish species distribution when considering concurrent climate change, and (iii) identify the areas of the Seine basin that are the most at risk in terms of potential loss of fish biodiversity. These results will allow us to evaluate the consequences of management decisions on the future of river fish.

We expect climate change to play a major role in the shaping of river fish distributions, and warmer and drier climate projections being the most unfavorable. We also expect river basin management aligned with high quality of the environment to be the most favorable in comparison to other scenarios, with some variations depending on species. In particular, we expect scenarios with lower connectivity, higher sealing rate of soils, slower rate of river restoration, to be especially damaging for specialist or highly mobile species and to favor generalist species. With this study, we hope to provide insights on the consequences of management decisions and larger policy decisions on river fish species conservation under global change and a re-usable methodological framework to build land use scenarios for river ecosystems.

2.METHODS

2.1.Study Area

This study was conducted in the Seine-Normandie drainage basin located in Northern France. It comprises the basin of the river Seine and adjacent coastal rivers, and spans 95,000 km². It is inhabited by 18 million people. This high population density has led to widespread river engineering, from dam construction - the area counts at least 12,000 intact artificial obstacles, which we obtained via the ROE database (Référentiel des Obstacles à l'Ecoulement, eng: Database of Flow Obstacles, see Fig. 19), made available by the French Office for Biodiversity (OFB, 2024) - to embankment and channelization, including large infrastructures built for flood control and navigation. Largely deforested, the basin is mostly covered by conventional cropland (see Fig. 1 in Felin et al. 2025), including some of the most productive in the country. Large urban areas like Rouen, Reims and the Parisian metropolis are spread throughout the territory, leading to several areas of impervious surface. In order to protect Paris from floods and to sustain low flows, major artificial reservoirs called the "Grands Lacs de Seine" were built on major tributaries of the Seine, for water storage. They regulate flow downstream, leading to heavily modified regimes.

2.2.Environmental and Biological Data

This study acquired a set of covariates and factors intended to both give an overview of the basin's properties and cover the main predictors of fish species distribution (full list in Appendix K; see section 2.5 of this chapter). The single-strand PIREN-Seine river network (Silvestre et al. 2024) was used as a reference network to extract the Strahler index, elevation and catchment area while the SYRAH-CE database (SYstème Relationnel d’Audit de l’Hydromorphologie des Cours d’Eau, eng: Relational System Audit for Watercourse Hydromorphology, see Valette et al., 2012) gave access to river straightness (defined for river reaches as the ratio between actual river length and length of the straight line between the two ends of the reach). Longitudinal connectivity was obtained through the Adjusted Connectivity Index (ACI) as defined in Felin et al., (2025), that accounts for both fish species-specific dispersal abilities and anthropogenic obstacle passability (data from the Référentiel des Obstacles à l’Ecoulement; eng: Database of Flow Obstacles; OFB, 2024) (see Felin et al., 2025, for more details on the calculation of connectivity). Current climate predictors (e.g. air temperature, precipitation averages) were obtained via the French SAFRAN atmospheric reanalysis data (Vidal et al., 2010), and aggregated from 2000 to 2020. Hydrological predictors were calculated from inverse distance weighted geographical interpolation of daily measured streamflow (Dufeu et al., 2022). We obtained pluriannual averages of oxygen, nitrate and ammonium concentration via the pyNuts-Riverstrahler model for 2017-2021 (Renaud et al., 2024). Land use was obtained through the calculation of proportions of land use categories within Seine-Normandie water agency subcatchments, based on THEIA land cover data (Thierion et al., 2021), while the surface of natural vegetation (forests) and lateral bodies of water within the floodplains and riparian areas were calculated using strip-shaped buffers (100-m wide not counting river width, 3-km long, 500 m downstream and 2500 m upstream).

We retrieved fish occurrence data, dated from 2000 to 2020, from the Observatoire des Poissons Seine-Normandie (Seine-Normandie Observatory of Fish, OPSN). Sampling was conducted via electrofishing depletion across 2044 study sites, either by foot or by boat. For the purpose of this study, all samples within the same study site were integrated into a single presence/absence data point (at least one detection over the 2000-2020 period was counted as a presence; see Felin et al. 2025, for more details). The present study focuses on 8 species for which the calibrated species distribution models were considered as sufficiently powerful to be used for future predictions (see selection process in 3.1). These species are the bleak (coded ala), chub (sqc), roach (rur), ruffe (gyc), perch (pef), trout (sat), minnow (php) and dace (lel) - see Appendix B from Chapter 3 for taxonomic information and characteristics. Species like the bleak, chub or roach are either generalists, or at least tolerant to high temperatures and/or disturbances in their habitat, and thus are expected to endure climate change better than fish like the trout or minnow, which dwell in fresh water (Keith et al., 2020).

2.3.Watershed Management Scenarios

Predicting land use in highly anthropized areas is a difficult, politically contingent endeavor, thus using several management scenarios with drastically different premises allows to cover multiple possible futures. We relied on Lacroix et al. (2019)'s schematic typology of management scenarios to qualify political orientation in scenarios, both to facilitate comparison with similar studies and describe political attitudes more finely. Additionally, one can distinguish scenarios according to whether they are rooted in inertia, or following current trends in practices (or limited reform) or in disruption in practices (suggesting wide-ranging reform and paradigm shifts). We built our scenarios through co-construction workshops with the Seine-Normandie Water Agency and the French Office for Biodiversity, with two time periods, 2050 and 2100, in mind. Four distinct scenarios were built, which we describe below (Explanatory section and Figure 1). They can be classified from least to most environmentally-conscious:

FP - "Faucets and Pipes" Disruption Scenario (Lacroix's "Retreat", high governance, low quality): We hypothesize a durable antagonistic backlash against environmental measures with no pretense to try to comply with most national and international guidelines such as those emanating from the European Water Framework Directive (WFD, see directive 2000/60/CE, 2000, JORF) and International Panel on Climate Change (IPCC), suggesting a paradigm shift toward a more authoritarian style of government. It is associated with accelerated urbanization, as well as the progressive stop of operations of restoration. We also hypothesize an increased amount of water used for agriculture, and the digging of large water reservoirs in heavily cultivated regions to cope with increasingly frequent droughts. The use of navigation increases in canals and large rivers, requiring large channelization projects and digging of connecting waterways, such as the currently planned Seine-Nord Europe Canal (eng: Seine-North Europe Canal, see the Ordonnance n° 2016-489, 21 april 2016, JORF - in French), and the channelization of the Seine between Bray-sur-Seine and Nogent-sur-Seine (Décret du 22 juillet 2022, JORF - in French). In addition, the scenario FP implies further projects not yet sanctioned. As for land use, urban land and agricultural land increase while natural land recedes. Water cover increases as well (see Table 1).

PS - "Production and Self-reliance" Scenario (Lacroix's "Growth at any price", high governance, middling quality): This scenario hypothesizes a prioritization of growth-oriented activities when restoration is perceived to go against economic development, tremendously slowing down restoration efforts, never halting it, and encouraging urban sprawl. We do not imply in this case any overt antagonistic action against environmental measures, and thus this scenario is less extreme than FP and allows for democratic exercise. Land use follows current trends with no acceleration: natural land and agriculture recede slightly, despite goals for no net artificialization, to allow for slight urban sprawl (including industrial facilities in a framework of self-reliant industry), agricultural production intensifies further and prioritizes technological solutions and efficiency of environmental concerns (see Table 1). Current projects of channelization (as those mentioned above) are maintained.

RE - "Respectful Executant" Scenario (Lacroix's "Green Growth", high governance, middle to high quality): This scenario hypothesizes a tremendous investment in the scrupulous application of the many recommendations and goals of for instance, the European Water Directive (WFD, see directive 2000/60/CE, 2000, JORF), the Green Deal (Vela Almeida et al., 2023), the national Climate Action Program (Ministère de la Transition Écologique, 2019), and local guidelines, leading to dam removals, riverscape restoration and "zero net artificialization" of soils (LOI n° 2023-630, 2023, JORF). It does not suggest any kind of change in the political system. Under this scenario, urban and natural land increase slightly while agricultural land recedes (see Table 1). River fragmentation and embankment is significantly reduced through accelerated restoration.

EP - "Ecological Planification" Disruption Scenario (Lacroix's "Positive Synergia", medium governance, high quality): It implies profound changes in political organization, demography and multi-scale involvement in ecosystem restoration, from individuals to large entities, the rewilding of urban landscapes and the countryside as well as large-scale restoration of river banks and change in consumption habits. For this scenario, we relied on Barles et al. (2024), who propose a multidisciplinary approach aiming at addressing all planetary boundaries (climate, biodiversity, pollution), although our approach was much more modest in terms of means. We hypothesize that under this scenario, natural land increases through intentional management while agricultural and urban land recedes (see Table 1).

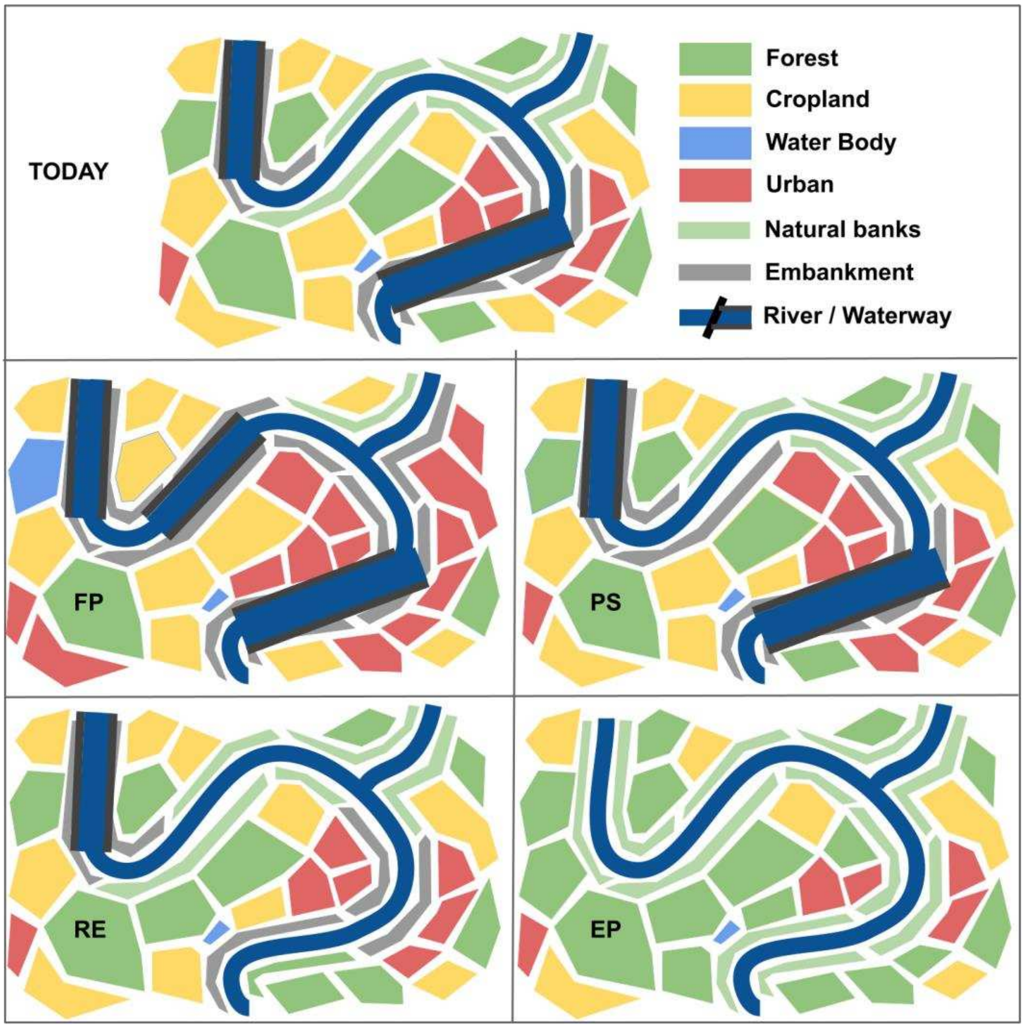

Figure 1: Visual representation of four future scenarios of watershed management on a theoretical mosaic of land uses. FP: Faucets and Pipes; PS: Production and Self-reliance; RE: Respectful Executant; EP: Environmental Planning

We should note that all scenarios described above fall into the broader category of "medium to high governance intensity". We chose not to include the alternatives implying low level of governance because they require either a more restricted focus on local territory with a thorough knowledge of local politics ("Local" and "Fragmentation" scenarios), or a documented understanding of very different systems of governance (or lack thereof in "Chaos") and their likely influence on river management which we could not access in our case.

2.4.Future Climate and Environment

We gathered three categories of predictors of fish species distribution: i) "Fixed predictors" mainly physical geography (STRAHLER order, elevation, drainage area, geological subregion factor) and oxygen, ammonium and nitrate concentrations. ii) "Hydroclimatic predictors" across two time periods, 2020-2050 (thereafter named 2050) and 2070-2100 (2100), extracted from climate or hydrological projections, such as seasonal air temperature or streamflow (see below). iii) "Scenarized predictors" related to river basin uses and susceptible to vary depending on which scenario is chosen and which time period is considered (2050 or 2100). These predictors are land use, river straightness, riparian habitat predictors and connectivity indices.

To generate the climatic predictors, we used a combination of four climate projections relying on the Representative Concentration Pathway (RCP) 8.5 scenario produced within phase 5 of the Coupled Model Intercomparison Project (CMIP5), which corresponds to a steady rise in greenhouse gases concentrations and little to no effort to curb them. We relied on the Explore2 hydro-climate modeling project (Marson et al., 2024), which provides the most up-to-date regionalised data over France. The Explore2 dataset proposes projections based on 3 RCP scenarios and a variety of Global Climate Models (GCMs) and Regional Climate Models (RCMs) spanning the period 1976-2100. Among their complete set of projections, we identified 4 contrasted projections based on the evolution of seasonal precipitation and air temperature among the available RCP 8.5 projections available. All projections describe a significant warming over France (2071-2100 temperatures around 3 to 4 degrees warmer than 1976-2005), and generally wetter winters (temperature and precipitation mapping and complete modeling chain names available in Appendix L) . They differ, relatively to each other, and for the Seine-Normandie area, in the following manner:

-Projection A1: Less warm, wetter than other projections year-round, especially wet summers and autumns, other seasons average.

-Projection B3: Drier year-round, especially dry summers and autumns, winter not as wet.

-Projection C2: Much warmer, especially in summer and autumn, very wet winters.

-Projection F9: Less warm, wetter than other projections year-round, wet summers and very dry springs.

In addition, hydrological projections, i.e. streamflow simulations obtained by forcing hydrological models by the climate model outputs aforementioned, were retrieved. These simulations were obtained using a semi-distributed GR (Génie Rural) rainfall-runoff model, GRSD (De Lavenne et al., 2019), using the airGR (Coron et al., 2017) and airGRiwrm (Dorchies et al., 2024) R packages. While on a large part of the area, the GRSD hydrological projections from the Explore2 project were directly used (Sauquet et al., 2024), on the River Seine course, we used hydrological projections from the IN-WOP project (Dorchies & Ricquier, 2024). Indeed, on the River Seine course, it was necessary to account for the Grands Lacs influence, which was done in the GRSD model version used in the IN-WOP project.

We retrieved a time series of daily air temperature, precipitation and streamflow. Equivalent variables to those used in model training as in Felin et al. (2025) were extracted, including seasonal thermal averages, and precipitation, and streamflow, excluding water temperature, for each projection, and on three averaging periods, 1990-2020; 2020-2050 and 2070-2100, which we will refer to as “2020”, “2050” and “2100” in the rest of the text. 2020 climate variables were extracted to allow for the comparison of current distribution, model estimates and predictions - so that model pertinence could be evaluated, but also as to serve as a reference to which future projections will be compared.

The scenarized predictors, generated for 2050 and 2100, were of three types: i) Adjusted Connectivity Indices were calculated on theoretical networks where a certain portion of dams (see Table 1) were removed; ii) Riparian predictors were assigned a multiplying factor; and iii) For the subcatchment-scale land use predictors, their values (proportions of surface cover) were treated as communicating vessels. When a type of land use is deemed to increase in conditions of land management and climate change, land use value is increased by a certain multiplying factor, and capping at 98 % of land cover, overtaking others equally. Table 1 presents the multiplying factors used for each scenario in both time periods - 2050 and 2100.

Table 1: Multiplying factors employed in the transformation of land use and scenarized predictors for watershed management scenarios (S) and time horizons (2050 and 2100). For land use variables. When a specific land use category decreases, it is in equivalence to value increase in other land use categories. Empty boxes indicate no change.

S	**Year**	**Urban land**	**Agricultural land**	**Water cover**	**Forest**
FP	2050	1.1	1.05	1.5[a]	decrease
FP	2100	1.3	1.15	2[a]	decrease
PS	2050	1.05	decrease		decrease
PS	2100	1.15	decrease		decrease
RE	2050	1.05	decrease		1.05
RE	2100	1.15	decrease		1.15
EP	2050	decrease	decrease		1.1
EP	2100	decrease	decrease		1.3
S	**Year**	**Watercourse straightness**	**Portion of vegetated banks**	**Water bodies in floodplain (m^2)**	**Connectivity index**
FP	2050	0.9	0.8	0.9	0.1
FP	2100	0.8	0.6	0.8	0.1

PS	2050	1[b]	1.1	0.95	0.1
PS	2100	1.05[b]	1.2	0.9	0.2
RE	2050	1.1[b]	1.2	1.05	0.2
RE	2100	1.2[b]	1.5	1.1	0.5
EP	2050	1.4[b]	1.4	1.1	0.5
EP	2100	1.8[b]	1.8	1.2	0.9
a . Water cover increase is calculated after everything else, and appropriates land (generally very small amounts) on everything else b. If Strahler index < 4					

To reduce collinearity among climate predictors and among land use predictors, each group of predictors was put through a Factor Analysis of Mixed Data (FAMD), keeping the two axes with highest explanation of variability. We note that the ACI method for connectivity is species dependent, and so resulting FAMD axes will differ depending on species. The coordinates of the sites along the first two axes of each FAMD were used as training predictors for all SDMs. For scenarized predictors, all numeric predictors led to a Principal Component Analysis (PCA) instead. FAMD and PCA axis coordinates were used to project new values (future hydroclimate, scenarized covariates) into the same two-dimensional space as training predictors. A study of variable importance was conducted on these synthetic variables through a hierarchical partitioning (R package hier.part) to highlight the importance of the unchanged, hydroclimatic and scenarized predictors in fish distribution for each species.

2.5.Ensemble Modeling and Output Analysis

In order to maximize predicting power for future distribution, we conducted an ensemble modeling protocol (Grenouillet et al., 2011) that consisted in using different statistical modeling methods, and averaging their predictions while weighting these predictions depending on the relative performance - through the True Skill Statistic or TSS (Allouche et al.,

2006) - of their respective model. We applied ensemble modeling on all 34 species, using the R version 4.3.1 (R Core Team, 2024), and including three regression models, linear regression (LM, package stats) and generalized linear models (GLM, R package stats), for which all predictors were tested in linear and second-degree polynomial effects, and generalized additive models (GAM, R package mgcv, see Wood, 2017), as well as three machine-learning methods, neural networks (ANN, R package nnet, see Venables et al., 2002), gradient boosting (GBM, R package gbm, see Ridgeway & Developers, 2024) and random forests (RF, R package randomForest, see Liaw & Wiener, 2002). For each combination of projection and scenario, and for each species and time period, we built SDMs for each statistical method, repeating the splitting process 100 times. We randomly split datasets between training and testing data (75 % training) and used the True Skill Statistic - TSS, see Allouche et al., (2006) - as a performance criterion and weighting factor in the model averaging process of statistical methods before averaging all 100 iterations. We also compared actual presence/absence data to ensemble model predictions on both true environmental data and each 2020 projected hydroclimate dataset, using TSS, to guide the species selection process.

For each climate projection, watershed management scenario, study site, time period (2020, 2050 and 2100), and species, a prediction of probability of presence was thus obtained. Presences and absences were then obtained by choosing a threshold of presence through the maximization of TSS (Manel, 2001). Comparing 2020 to 2050 or 2020 to 2100, we were able to evaluate for each species: projected colonization (absent in 2020, present after), persistence (always present), absence (never present) and extirpation (present, then absent) and count the instances of these phenomena for each subcatchment (one value per species, projection and scenario) and for the whole study area.

To reflect the proportion of study sites where said species persists, leading to potential temporal connectivity between time periods, we calculated a Continuity Rate c for each subcatchment (Eq. 4.1):

$$c = \frac{n_{per}}{n_{per} + n_{ext}} \; (Eq. 4.1)$$

where nper is the number of study sites where the species is predicted to be conserved and next the number of study sites where the species is predicted to be extirpated, thus displaying a rate of temporal continuity. To obtain a synthetic information on range contraction and the overall vulnerability of river fish based species on the total number of colonizations and extirpations within a subcatchment across species or geographical units, projections, scenarios, we calculated a Contraction/Expansion Rate t for each subcatchment and for the whole basin (Eq. 4.2):

$$t = \frac{n_{per} + n_{col}}{n_{per} + n_{ext}} \; (Eq. 4.2)$$

where ncol is the number of study sites where the species is predicted to appear, nper the number of study sites where the species remains and next the number of study sites where the species disappears. $t > 1$ corresponds to a range increase, and $t < 1$ corresponds to a range shrinkage, while $t = 1$ corresponds to no change in the species range .

Finally, to reflect the evolution of fish presence, we used the following Dynamic Shift Rate d for each subcatchment and for the whole basin (Eq. 4.3):

$$d = \frac{n_{col} + 1}{n_{ext} + 1} \; (Eq. 4.3)$$

where ncol is the number of study sites where the species is predicted to appear and next the number of study sites where the species disappears. If $d>1$, then the species has gained more range than it has lost. If $d>1$ is true, then $t>1$, however, d is not tied to the original range size. We thus choose d over t for mapping applications while t is used for numeric results.

3. RESULTS

3.1. Model diagnosis, variable and species selection

FAMD and PCA outputs across species led to the creation of six numeric covariates for further processing. The first two were extracted from fixed predictors and were respectively defined primarily by drainage area and hydroecological region (see Appendix K for additional explanations). The two hydrological and climate predictors extracted from FAMD were predominantly defined by summer precipitation and temperature differential (July-January). The two predictors extracted from our PCA of scenarized covariates were predominantly defined by agricultural land use and urban land use. An FAMD output can be found in Appendix M. Outputs did not differ sufficiently between species to lead to differences with respect to predominant predictors.

As mentioned in section 2.2, comparing SDM predictions made on training data and 2020 projected datasets led us to select eight species. Selection criteria were a) an average model TSS above 0.3, b) and average TSS as measured between prediction for 2020 climate projections and model output above 0.3. SDMs highlighted contrasted performances among the six different algorithms used depending on the species - the trout and minnow being associated with the lowest TSS values. Table 2 displays these differences.

Table 2: Average algorithm prediction performance for the eight selected species, measured as TSS (we considered TSS>0.6 very good and TSS>0.4 satisfactory).

Species	**ANN**	**GBM**	**RF**	**LM**	**GLM**	**GAM**
Ala	0.616	0.437	0.482	0.617	0.622	0.621
Sqc	0.534	0.495	0.514	0.484	0.479	0.484
Rur	0.497	0.452	0.445	0.457	0.457	0.457
Gyc	0.215	0.345	0.374	0.605	0.600	0.600
Pef	0.507	0.430	0.452	0.479	0.471	0.478
Sat	0.455	0.453	0.488	0.386	0.422	0.386
Php	0.451	0.380	0.491	0.374	0.386	0.375
Lel	0.563	0.448	0.484	0.530	0.528	0.530

We calculated variable importance for our predictors, classified in three categories. Overall, the group of fixed geographical predictors (i.e. Strahler, altitude, etc.) were generally the most important predictors of species distribution, closely followed by the scenarized predictors (Fig. 3), except for the trout, and minnow for which hydroclimate (i.e. seasonal temperatures, precipitation, discharge, etc.) and scenarized predictors (i.e. land use, longitudinal connectivity, etc.) were the most important, respectively.

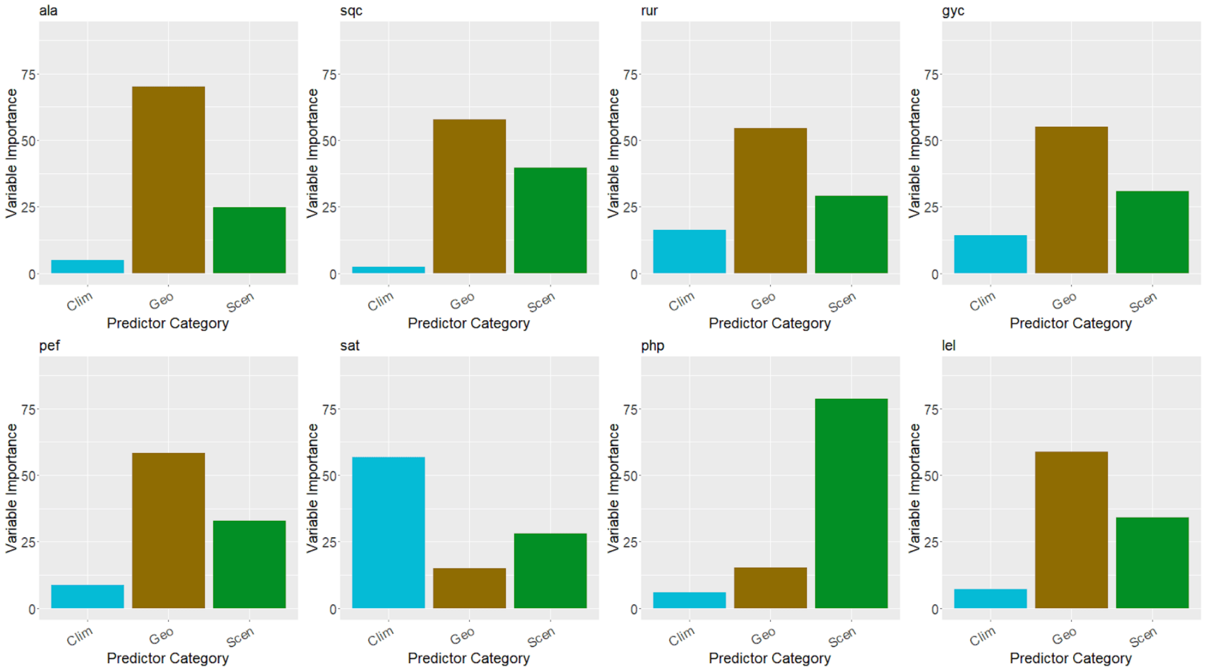

Figure 3: Relative importance (% of variance explained) of groups of predictors in training dataset obtained through hierarchical partitioning, grouped and summed in the three categories mentioned in 2.4. (Clim=hydroclimate, Geo=fixed, Scen=scenarized), for eight selected species.

3.2. Management scenarios and climate projections

Contraction rates were determined for each species, scenario and projection for 2050 and 2100. Contraction values for 2100 averaged across species to 1.08 for projection A1, 0.81 for B3, 0.84 for C2 and 1.04 for F9. Projections A1 and F9 (scenario EP excluded) were broadly linked to lower contraction of species range than projection B3 and C2. In contrast, scenarios FP, PS, RE and EP were respectively associated with average contraction rates of 0.91, 0.94, 0.97 and 0.95. Thus, fish species in general tended to respond more strongly to climate change projections than to watershed management scenarios.

Dynamic shift rates were calculated as well. Among selected species, those with the most spectacular range shifts were the dace (uniquely for projection A1 and F9, with warm summers), the trout (for projection B3 and C2, with dry and hot summers) and the perch and chub (projection F9 and A1). In all cases, these range shifts were positive, meaning that d, the dynamic shift rate, was very high (up to d=184 for the trout).

Extirpations, persistence values, and colonization values were retrieved - an example for projection B3 and calculated values from 2100 predictions, which was the most damaging overall in terms of range contraction foris featured in Table 3 below. Predictions set in the further future (2070-2100) were consistently associated with lower continuity and contraction rates and more numerous extirpations (except for the minnow and trout) than 2020-2050, with some species being predicted to increase in range in 2050 before declining below 2020 range.

Table 3: Count of persistence, colonizations, extirpations, continuity and contraction rates in predicted 2100 distributions for selected species and the B3 climate projection. Results least damaging for each species and metric are highlighted in bold. Continuity, Contraction and Dynamic Shift rates are obtained from persistence, colonization and extirpation counts and represent temporal connectivity, contraction of range and orientation of shift respectively.

Species (code)	Scenario	Persistence	Colonizations	Extirpations	Continuity Rate	Contraction Rate	Dynamic Shift Rate
bleak (ala)	**FP**	545	6	380	0.589	0.596	0.018
	PS	717	11	208	0.775	0.787	0.057
	RE	650	5	275	0.703	0.708	0.022
	EP	**756**	**102**	**169**	**0.817**	**0.928**	**0.606**
chub (sqc)	**FP**	**907**	**146**	**119**	**0.884**	**1.026**	**1.22**
	PS	773	31	253	0.753	0.784	0.126
	RE	602	18	424	0.587	0.604	0.045
	EP	627	64	399	0.611	0.673	0.162
roach (rur)	**FP**	196	0	682	0.223	0.223	0.001
	PS	678	25	200	0.772	0.801	0.129
	RE	**710**	**32**	**168**	**0.809**	**0.845**	**0.195**
	EP	566	24	312	0.645	0.672	0.080
ruffe (gyc)	**FP**	335	0	343	0.494	0.494	0.003
	PS	493	0	185	0.727	0.727	0.005
	RE	472	0	206	0.696	0.696	0.005
	EP	**507**	**0**	**171**	**0.748**	**0.748**	**0.006**
perch (pef)	**FP**	32	0	691	0.044	0.044	0.001
	PS	128	2	595	0.177	0.180	0.005
	RE	121	3	602	0.167	0.172	0.007
	EP	**386**	**35**	**337**	**0.534**	**0.582**	**0.106**
trout (sat)	**FP**	**978**	**736**	**3**	**0.997**	**1.747**	**184**
	PS	970	654	11	0.989	1.655	54.6
	RE	958	573	23	0.977	1.561	23.9
	EP	750	294	231	0.765	1.064	1.27
minnow (php)	FP	1874	**147**	0	1.000	**1.078**	**148**
	PS	1874	111	0	1.000	1.059	112
	RE	1874	104	0	1.000	1.055	105
	EP	1870	123	**4**	0.998	1.064	24.8
dace (lel)	**FP**	334	42	246	0.576	0.648	0.174
	PS	412	31	168	0.710	0.764	0.189
	RE	**468**	110	**112**	**0.807**	**0.997**	0.982
	EP	397	**161**	183	0.684	0.962	0.880

Table 3 also shows that most species were predicted to react differently depending on the scenario. Considering all criteria together, for over half of selected species (5 out of 8), the most unfavourable management scenario was FP (Table 2). We observe that the most favourable scenario varies strongly depending on the species, with 3 species responding most positively to EP, 2 species, to RE (meaning 5 species attached to decent or ambitious restoration) and 2 species (chub and trout), to FP. One species, the minnow, responded similarly to all scenarios and the scenario PS was never preferred for projection B3.

Studying contraction rates across scopes, scenarios and projection (Figure 4), we observe that some species did not follow the general trend (e.g. trout). Across all but one projection, scenario FP (Faucets and Pipes), conceived as the least ambitious in terms of environmental measures, was also retrieved on average as the least favorable for selected species, with exceptions for each projection. Similarly, scenario RE (and more rarely EP), on the other end of the spectrum, were the most favorable to some species among those selected (dace, bleak, perch), although EP was sometimes predicted to be less favorable to some fish species being favored by scenario RC and PS instead (trout, roach).

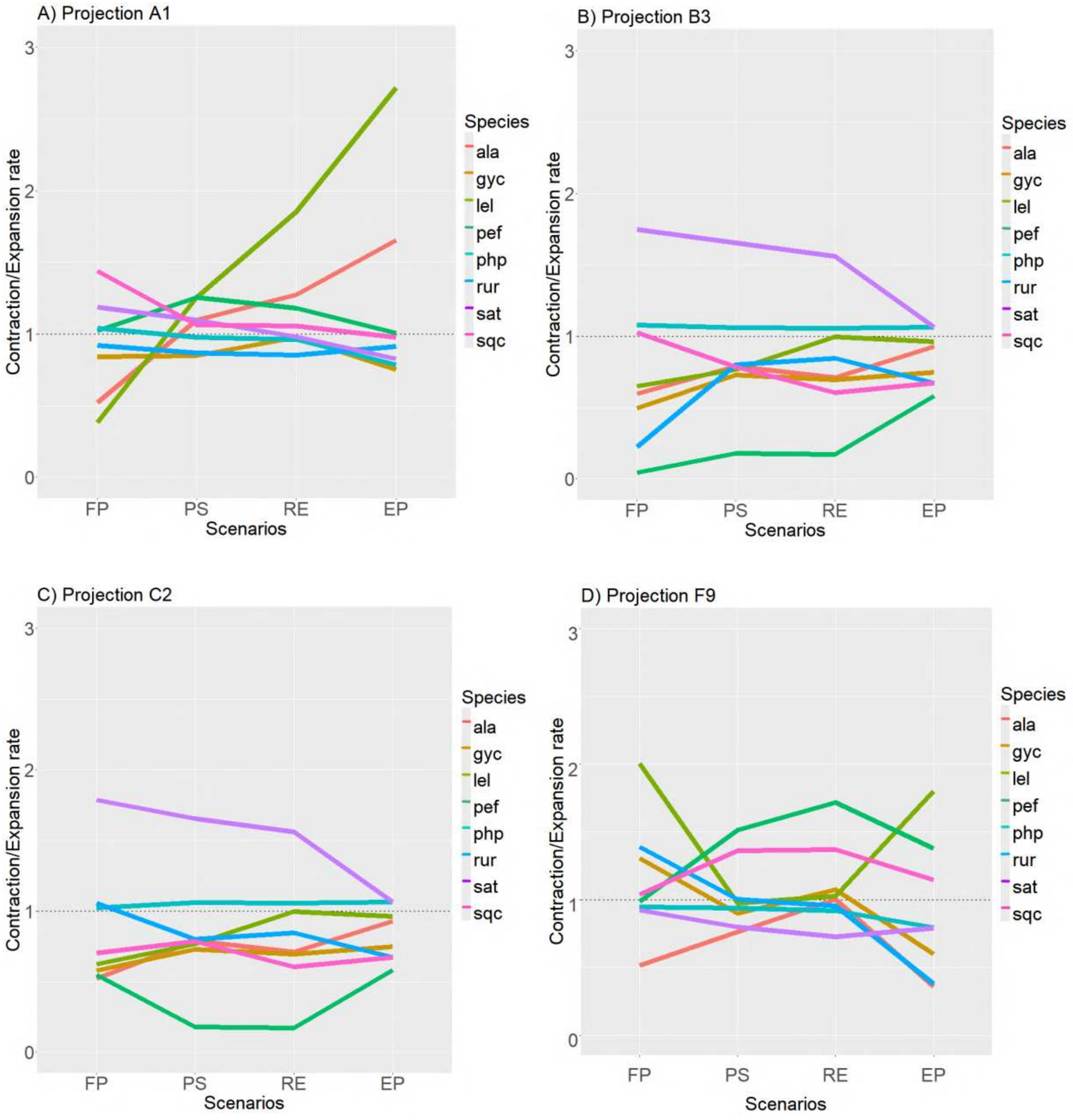

Figure 4: Values of contraction (<1) or expansion (>1) rates across scenarios (2070-2100) for each climate projection, with color-coded single values per species.

3.3. Mapping of future fish species distribution and identification of critical areas

Across multiple species, the conjunction of projections B3 (hot and dry summers) with scenario FP was the single worst for selected species, especially impacting the perch (contraction rate at 0.044), roach and ruffe which are predicted to lose more than half of their previous range, losing range in all parts of the basin. Across scenarios and climate projections, the perch seemed to be more likely extirpated in the northern part of its range, and fare better in the East and South.

In contrast, the trout is predicted to hold up quite well under projection B3 and to experience wide range shifts under projection F9 (warm summer, dry springs), simultaneously appearing in previously unoccupied subcatchments and being extirpated from others. (see examples of maps for trout and perch in Fig. 5-6).

Overall, extirpations and decreasing ranges happened everywhere across the Seine basin, however, some regions, as shown on Figure 5 and 6, seemed to be more closely associated with decline, such as the Champagne, Beauce and Eure localities (the further surrounding of Paris), which are associated with somewhat consistently lower values of expansion. We should note that data availability was not homogeneously spread across the basin, leading to impossible assessment of the estimation of fish survival in certain localities like Western Normandy and parts of the Parisian basin.

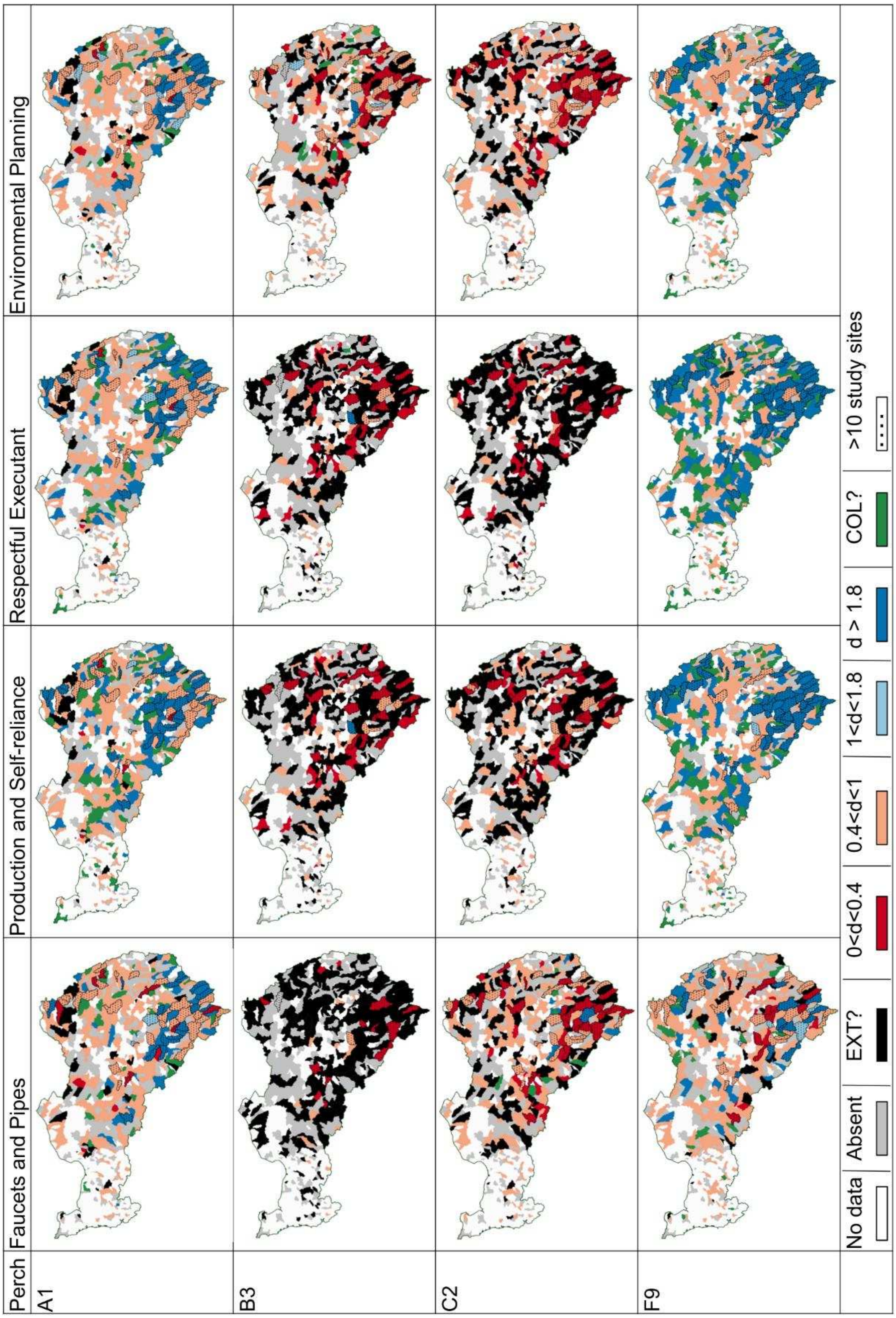

Figure 5: Prediction output of the distribution of the perch (2070-2100) for all watershed management scenarios and climate projections, by subcatchment. Results are expressed in terms of dynamic shifting rate, subcatchments where the species is predicted to be removed from all sites are colored black, those where it could emerge are colored green.

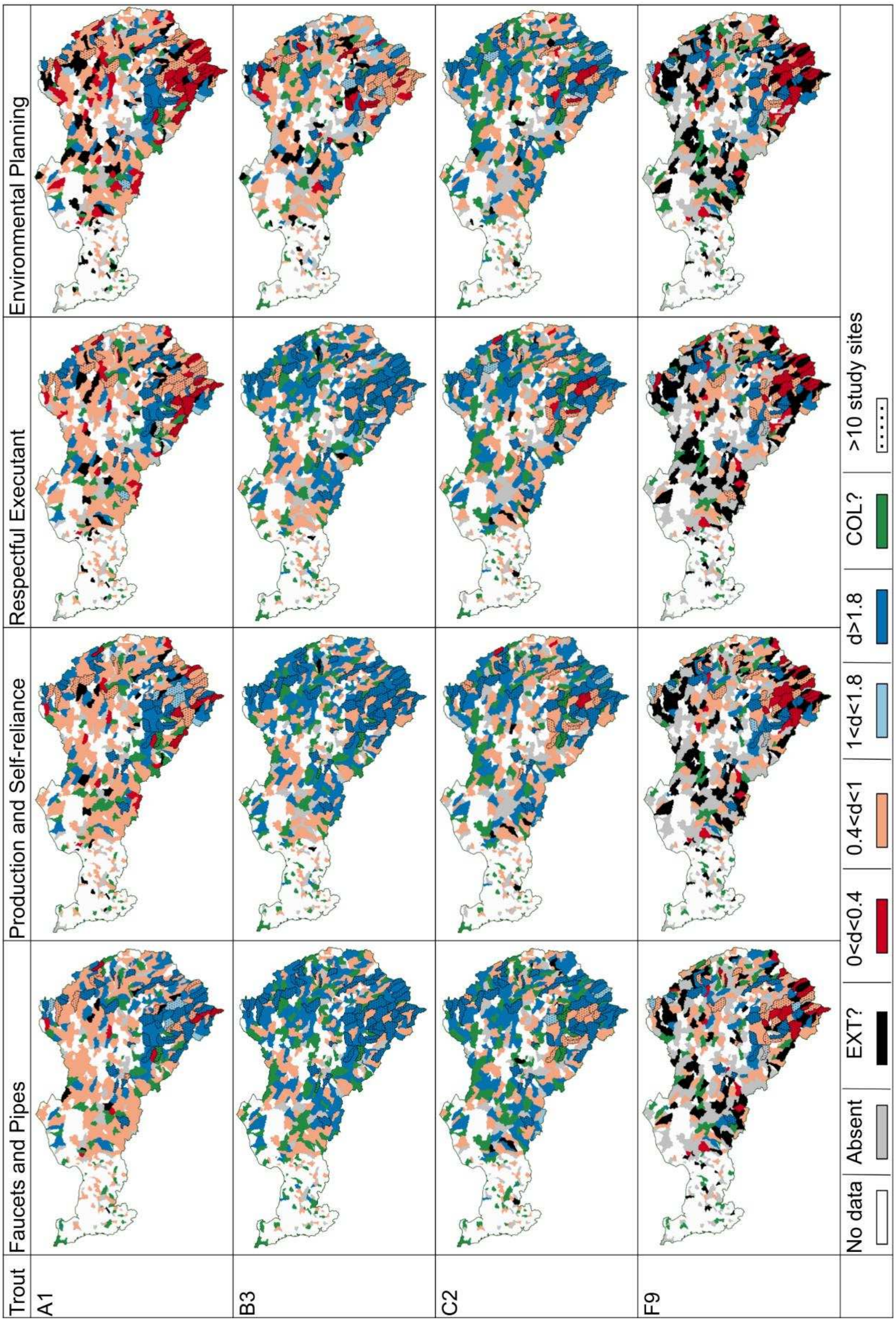

Figure 6: Prediction output of the distribution of the trout (2070-2100) for all watershed management scenarios and climate projections, by subcatchment. Results are expressed in terms of dynamic shifting rate, subcatchments where the species is predicted to be removed from all sites are colored black, those where it could emerge are colored green.

4. DISCUSSION

4.1. River fish in jeopardy

Overall, selected fish species saw a contraction of their range. By 2100, all but 2 combinations or projections and scenarios are associated with a range contraction for four species out of eight or more. Under the conditions set by this study, population decline for fish communities in our study area seems rather ineluctable. This observation seems to transcend projections and scenarios, thus this decline can only be imputable to the common characteristics of all theorized futures: an equally ineluctable change in climate. Under the "Business as usual" paradigm chosen for this study, and according to our projections, full conservation of range for most selected species seems unlikely, whatever management decisions policymakers implement on the basin, which seems to corroborate other studies in different basins (Xenopoulos et al., 2005).

We also show through the variability of average contraction rates from one projection to the next, that the properties of climate change might become the main driver behind predicted distribution change. This result is to be linked to commonly admitted characteristics of climate change, with i) changing flow due to modified precipitation regimes, which lead to changed river morphology, droughts, floods, and jeopardize breeding grounds (Daufresne & Boët, 2007), ii) increased air and water temperature, which may lead to decreased populations in stenotherm species (Keith et al., 2020). Thus, all efforts for conservation of fish species in the Seine-Normandie basin will take place in a context of partly climate-driven distribution.

4.2. Climate projections and fish distribution

Nonetheless, specific characteristics of climate projections produced different outcomes for selected fish species. Climate projections A1 and F9 were associated with a smaller proportion of species experiencing range contraction. Some of the variations in outcomes depending on climate projections can be linked to seasonal characteristics as well, and their match or mismatch with seasonal breeding and feeding practices of fish species might exacerbate their effect. For instance, as shown, projection F9 (which is characterized by relatively dry springs, and cooler summers) was especially unfavorable for the trout regardless of watershed management scenario and over any other species, not leading to great range contraction, but rather to important range shifts. Projection F9 is characterized by uniquely dry springs. Trout reproduce earlier than other species (most of them spawn from November till January), and spring is the period when most young trout fry become active parr (Keith et al., 2020), which may endure higher mortality in drier climates due to lower flow, droughts and resulting increased water temperature. Projections C2 and B3 behaved in broadly similar ways, projection B3 deviating the most from 2020 projections, and for most species, such as the perch, resulted in stronger decline for selected species. These projections happen to be warmer and drier than A1 and F9, and to feature especially dry summers and autumns, which we can tentatively link to species survival in the same way we did for trout and projection F9. The issue of droughts and their consequences on fish fitness and mortality is widely studied (Lennox et al., 2019; Matthews & Marsh-Matthews, 2003; Piniewski et al., 2017) and could constitute a key to more finely understand the impact of climate change on fish populations.

4.3. Watershed management scenarios and fish distribution

Watershed management scenarios as conceived within this article yielded complex results in the prediction of the distribution of eight fish species. Their construction was meant to emulate different levels of state involvement and quality of environmental restoration. We have shown that reaction to watershed management depended on species. Scenarios which favored a good quality of the environment, led to higher survival of the bleak, ruffe, dace, chub and perch in the study area, and in rather unambiguous ways. This majority of species seems to corroborate studies which indicate the many links between river restoration and fish diversity (Birnie-Gauvin et al., 2020; Shen & Liu, 2021). Scenarios most respectful of environmental restoration processes do seem to favor freshwater fish in their conservation, although some nuance is required.

The minnow and the trout, which were associated with the lowest TSS values among species selected, as well as the roach, happened to follow other patterns of response. The minnow was largely unimpacted by watershed management scenarios, and did not seem to lose any significant ground. The minnow being a small, widespread, and relatively eurytherm species, although it is mostly found in well oxygenated streams, this is not necessarily surprising. The roach fared better under scenarios which were linked with poorer environmental management scenarios. The roach being an eurytherm generalist which dwells in lentic watercourses, this is also not unexpected (Keith et al., 2020). More surprising is the response of the trout, which is a stenothermic species, dwelling in cold water, that we have shown to be highly dependent on climate predictors. The trout is often pointed as a sensitive species, due to decline under climate change, and the absence of direct consideration of water temperature in models, instead equated to air temperature as an indicator, may have contributed to this disregard for a more likely end. Modeling performance for trouts was the second lowest of all selected species, which may explain unexpected results. Additionally, the commercial and cultural importance of this species leads to anthropogenic intervention in its conservation through regular supply of fish bred in captivity, which may erase current trends of decline due to rising temperatures, and render modeling outputs less relevant (Caudron et al., 2006; Champagnon et al., 2012). Other explanations which may highlight why scenario FP (the least environmentally-friendly one) was sometimes preferred may be linked to the patterns of distribution of land uses in the basin - most land use subcatchements comprising large troutless urban areas are also associated to semi-natural landscape through suburban forests, leading to negative associations between semi-natural land and fish presence. Thus, we warn the reader that discussing the trout specifically may be done, but only with ample context without which reaching conclusions may be hastily drawn, since despite the aforementioned outliers, a clear pattern of positive influence of restoration on fish remains.

4.4. Areas at risk and range shifts in the Seine basin

We highlighted the complex, species dependent, scenario-dependent, projection-dependent predicted futures of select species. Patterns in the spatial distribution of extirpation and apparition phenomena was difficult to parse due to incomplete data, however no species*projection*scenario combination was recovered as uniformly favorable to selected species, while plenty were entirely unfavorable. Across our study area, we identified potential regions which were associated with lower conservation of fish, namely the Champagne, Beauce and Eure regions, mostly observable in cases with contrasted survival. These observations must be taken with caution, as many subcatchments remain devoid of data, making patterns less clear. However, we can draw a pattern between the three regions mentioned above. The Beauce, Eure and Champagne have lower precipitation than other areas on the basin (see Materials for more details) and are at least in part used for intensive agriculture. We can hypothesize that current and future water stress may be a good predictor of community jeopardy, which ties neatly with our analysis of climate projections. Of course these results are to be taken with precaution, and the inherent uncertainty at every step of our reasoning must be kept in mind (see Chapter 5). If this is confirmed by further studies, mapping outputs such as those displayed in this study may constitute helpful and informative content for decision-makers.

Results showed a broader tendency for fish distributions to shift within the study area due to climate and management. In particular, mobile fish that were found to be well suited by specific scenario and projection conditions (such as the dace in projections F9 and A1), showed spectacular colonization in some cases. Range shifts within watersheds, as in a combination of local extirpations and newly arrived species in previously uncolonized areas, can lead to shifting communities and corresponding shifts in trophic webs and fulfilling of ecosystems functions. At the opposite of mass colonizations by mobile, well-suited fish are instances of drastic decline. This has been shown for the perch in projection B3 and C2, as well as the roach, trout and chub. Extinctions at the scale of a drainage basin cannot be excluded if conditions are fulfilled. For species which cannot dwell in sea water, unaided recolonization becomes near impossible, posing deeper questions on the value of unfit, native species in future ecosystems (we touch on these questions in Chapter 6). The consequences of ample range and community shifts due to colonizations and extirpations are difficult to study, but the phenomenon of trophic cascades (Ripple et al., 2016) linked to shifting communities is well documented and can in some instances lead to profound shifts in landscape and ecology that go beyond fish communities.

Finally, in a majority of species*projection*scenario combinations, 2050 and 2100 yielded broadly similar trends compared to 2020 predictions, declining from 2020 to 2050 and declining more from 2020 to 2100, which we could equate to a broad climate-driven tendency for decline; or the exact opposite. For some species, however, the prediction for 2020-2050 showed an increased range, expanding in more sites than extirpated in others, before a subsequent decrease in 2070-2100; or, again the exact opposite. We could choose to equate all these cases with the principles of niche theory, where a species' Hutchinsonian (Hutchinson, 1957) niche slowly transits through the basin as time and global change goes by. For some combinations, the niche had already been in the process of transiting away, leading to decreased range overtime, in other cases the apex of the niche's transit in the basin is yet to come, but may wane again some time before 2100. If we adhere to this vision of niche transit, then all phenomena cited above (decline, growth etc.) may be seen as the manifestations of the same phenomenon (the waxing and waning of niche hyperspace, and the range shifts that mobile species undertake to follow the niche), and all eventually end in decline.

4.5. Limitations and Commentary

For this study, we built a series of ensemble models to predict the distribution of river fish under climate change and management constraints. We shortlisted eight species for which model performance was satisfactory, meaning that they showed good predictive model performance, as well a certain fidelity between predicted 1990-2020 distribution and our original dataset - species for which we noticed a noticeable disparity between these two metrics could be a testimony of inertia (Moraes et al., 2012) in their range between 1990 and 2020 despite changing environmental conditions. In order to guarantee the best modeling approach possible, we used FAMDs and PCAs for variable aggregation, included connectivity indices in our predictors and ensured performance was assessed. We thus deem that though not perfect our modeling approach guaranteed satisfactory standards for commentary on modeling outputs.

A major limit of this work is the use of aggregative metrics such as our Contraction and Dynamic Shift Rate, which allowed us to enrich our results and discussion, but must be understood within their limitations. Despite our calculations made at the subcatchment scale, input data was purely based on study sites. Our approach does not allow for a complete vision of species distribution, but a snapshot made thanks to our dataset. In this context, we could never predict the extinction or extirpation of a species, even conditionally, but only that all study sites within a sub catchment may lose one species. Thus, in discussing species like the perch under scenario FP and projection B3, our results could never be certain the species would be extinct locally. However, one could assume that such a widespread phenomenon of local extirpation from individual study sites may indeed correspond to a local extinction, and despite this, we are confident indicators of high range contraction and generalized extirpations can be safely interpreted as a negative outcome for the studied species.

5. CONCLUSIONS

This study was able to come to a first observation: global change will be the main shaper of fish distribution in the basin. Selected climate projections and geographic range have suggested that drier seasons especially may be a limiting factor for fish conservation. Despite this climate-driven change for fish distribution, management scenarios were shown to have an influence on fish conservation and range in the near and far future. A general tendency for environmentally-friendly scenarios to favor fish conservation, or diminish range contraction, comforts established knowledge on fish conservation and ecology. However, a few different cases like the trout or minnow brought examples of species which did not fit in this larger tendency. Overall, the diversity of behaviors in modeling outputs incite us to push for further research on two specific points. First, the identification of drier climate, especially in seasons of development for younger fish, if it were to be confirmed, would help consolidate approaches aimed at measuring vulnerability of fish communities. Second, the formulation of scenarios in this context of distribution modeling led to a very rich body of results, which we are convinced ampler means and time would improve in many ways. Extending our tentative conclusions to larger datasets, models, differents areas would allow to test the reproduction of such results, which would tremendously improve our tools to help with the conservation of fish communities.

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APPENDICES FOR CHAPTER 4

Appendix K: List of environmental covariates or factors and of final predictors used in species distribution models in addition to connectivity indices (see section 2.3)

Covariates (summarized into PCA coordinates)	Definition (source)	Handling in predictions (A: Fixed; B: Climate projections and linked hydrological data; C: Scenarios)
Annual Precipitation (mm)	2000-2020 annual average (SAFRAN)	B
Summer Precipitation (mm)	2000-2020 Jun-Jul-Aug average (SAFRAN)	B
Fall Precipitation (mm)	2000-2020 Sep-Oct-Nov average (SAFRAN)	B
Winter Precipitation (mm)	2000-2020 Dec-Jan-Feb average (SAFRAN)	B
Spring Precipitation (mm)	2000-2020 Mar-Apr-May average (SAFRAN)	B
Summer Air Temperature (°C)	2000-2020 Jun-Jul-Aug average(SAFRAN)	B
Fall Air Temperature (°C)	2000-2020 Sep-Oct-Nov average (SAFRAN)	B
Winter Air Temperature (°C)	2000-2020 Dec-Jan-Feb average, (SAFRAN)	B
Spring Air Temperature (°C)	2000-2020 Mar-Apr-May average(SAFRAN)	B

Air Temperature Differential – (July - January) (°C)	2000-2020 average (SAFRAN)	B
Land use: Grassland, Forest, Urban / Agriculture and Water Cover (%)	Proportion of surface area covered by land-uses within whole catchments (THEIA)	C
Buffer strip land use: Bodies of Water and Riparian vegetation (%)	Proportion of surface area covered by land-uses within strip-shaped buffers (THEIA)	C
River Straightness	True Reach Length / Straight Reach Length (SYRAH-CE reaches i.e. hydromorphologically homogeneous sections, see Valette et al. 2012)	C
Elevation (m)	Average of maximum and minimum reach elevation (PIREN-Seine hydrographic network) (Silvestre et al. 2024)	A
QMNA5 ($m^3.s^{-1}$)	Annual minimal monthly discharge with a 5-year return period, obtained from Inverse distance weighting of Hydroportail data (Leleu et al., 2014)	B
Concavity Index (CI)	Expressed as $(Q_1-Q_{10})/(Q_{10}-Q_{99})$, where Q_p is the daily flow exceeded p% of the time (Beaufort et al., 2022), reach CI value obtained from Inverse distance weighting of Hydroportail data points (Leleu et al., 2014)	B
Catchment area (km²)	PIREN-Seine hydrographic network	A
Pluriannual average O_2 concentration ($mg.L^{-1}$)	Simulations produced by the pyNuts-Riverstrahler model on the scale of the Seine-Normandy basin for the time period 2017-2021 (Renaud et al., 2024)	A

Pluriannual average NO_3^- concentration (mg.L^{-1})	Simulations produced by the pyNuts-Riverstrahler model on the scale of the Seine-Normandy basin for the time period 2017-2021 (Renaud et al., 2024)	A
Pluriannual average NH_4^+ concentration (mg.L^{-1})	Simulations produced by the pyNuts-Riverstrahler model on the scale of the Seine-Normandy basin for the time period 2017-2021 (Renaud et al., 2024)	A
ACI (Adjusted Connectivity Index)	Reach-specific metric of longitudinal connectivity taking centrality bias into account (Felin et al., 2025)	C
Factors (included in final model)	Definition (source)	
STRAHLER Order	Strahler (1957)	A
Hydroecological Region	Wasson et al. (2004) - 12 homogenous subregions (from 17: factor levels with <10 data points conflated with neighboring regions) with respect to geophysical factors key in the structure of freshwater ecosystems	A
Hydrological Regime	Mainly pluvial regime groups, labeled 1 through 6 according to classification by Sauquet et al. (2008), obtained from Hydroportail streamflows (Leleu et al., 2014)	B

Appendix L (Fig. L.1 and L.2): Mapping of chosen climate projections and full names over Hexagonal France maps, all calculated for RCP 8.5. Adapted from Marson et al. (2024).

Projection A1 corresponds to modeling chain CNRM-CM5-LR_ALADIN63

Projection B3 corresponds to modeling chain EC-EARTH_HadREM3-GA7-05

Projection C2 corresponds to modeling chain HadGEM-ES_CCLM4-8-17

Projection F9 corresponds to modeling chain Nor-ESM1-M_REMO2015

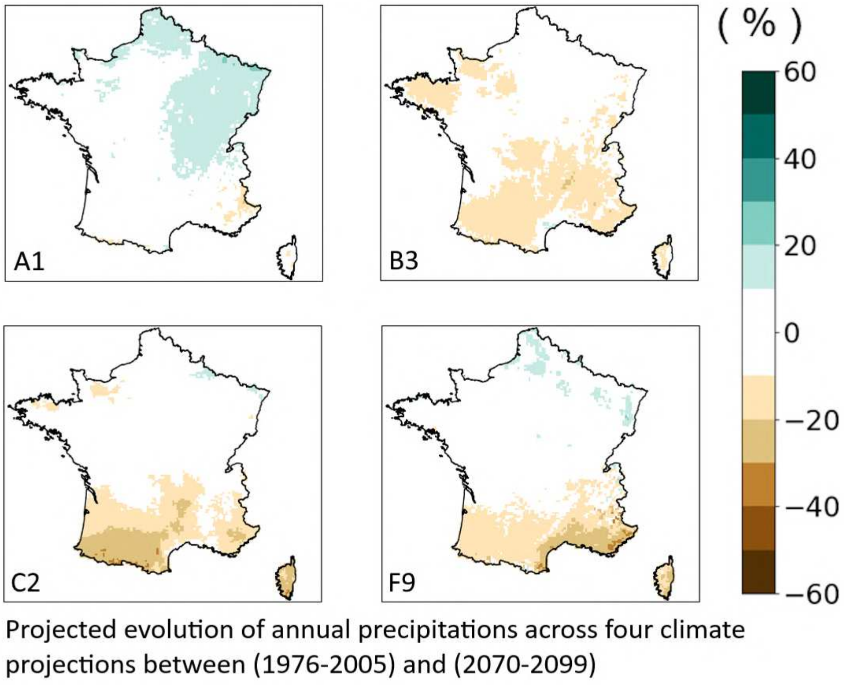
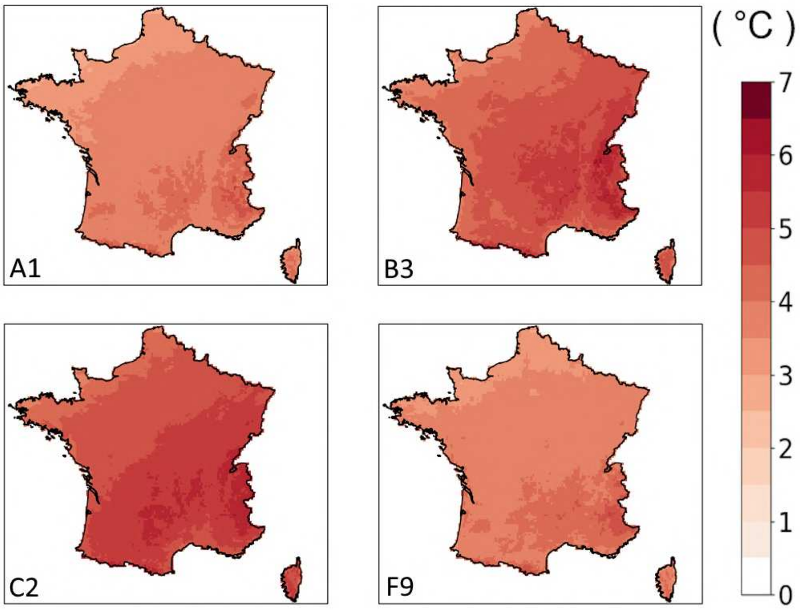


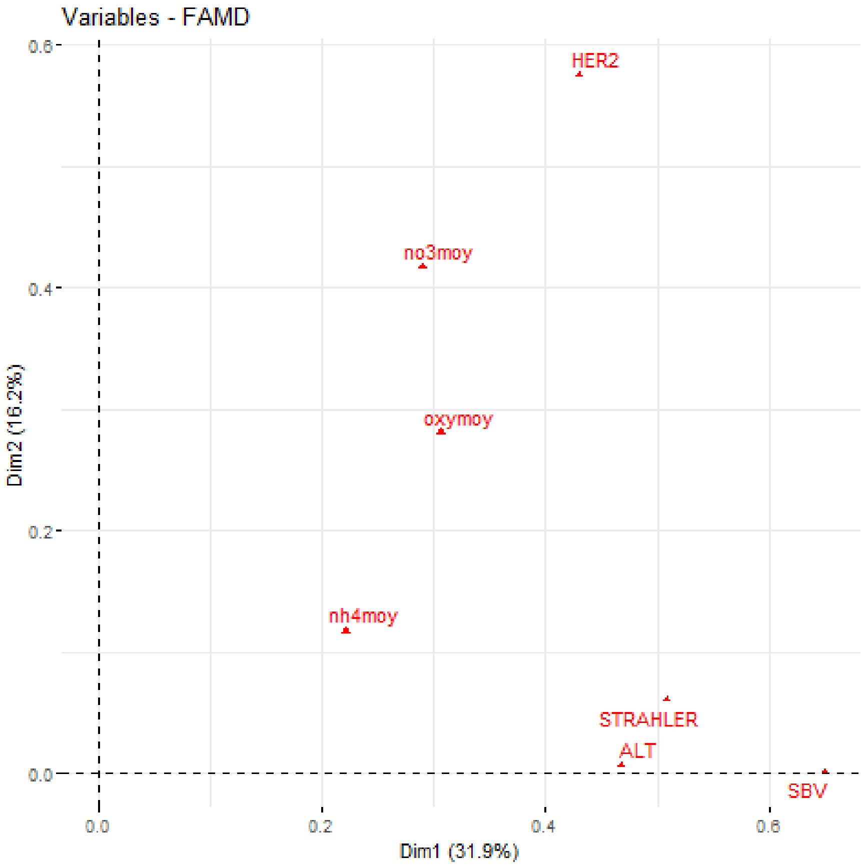
Figure L.1 Projected evolution of precipitations across selected projections (%) between the 2100 time period and reference (1976-2005)

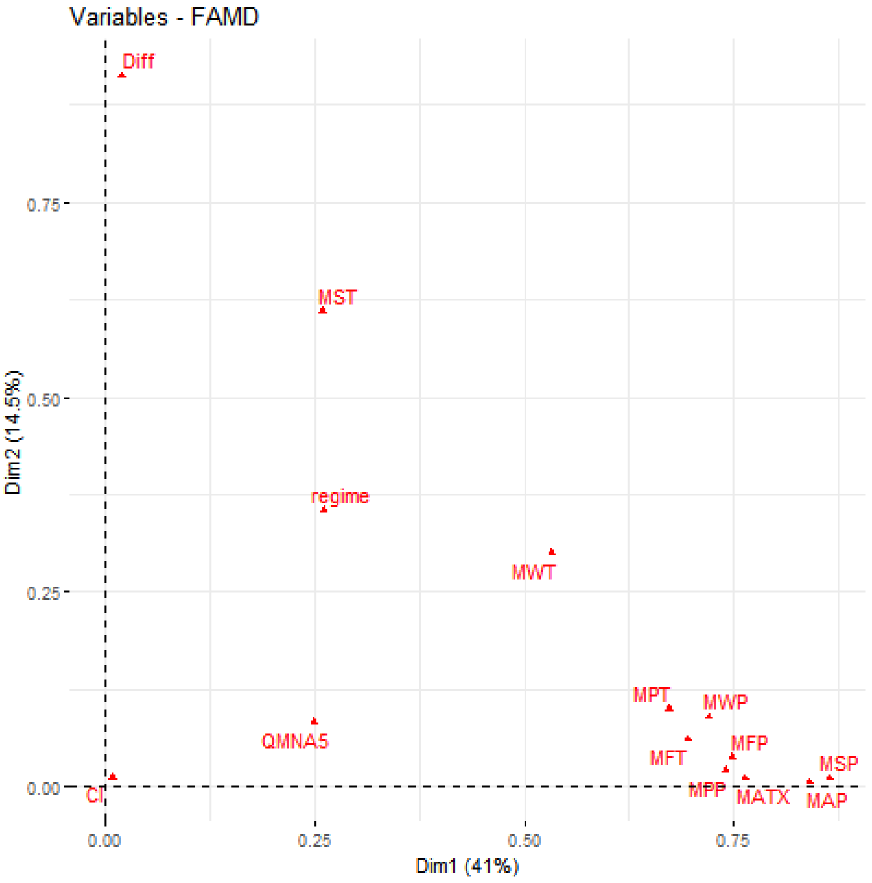
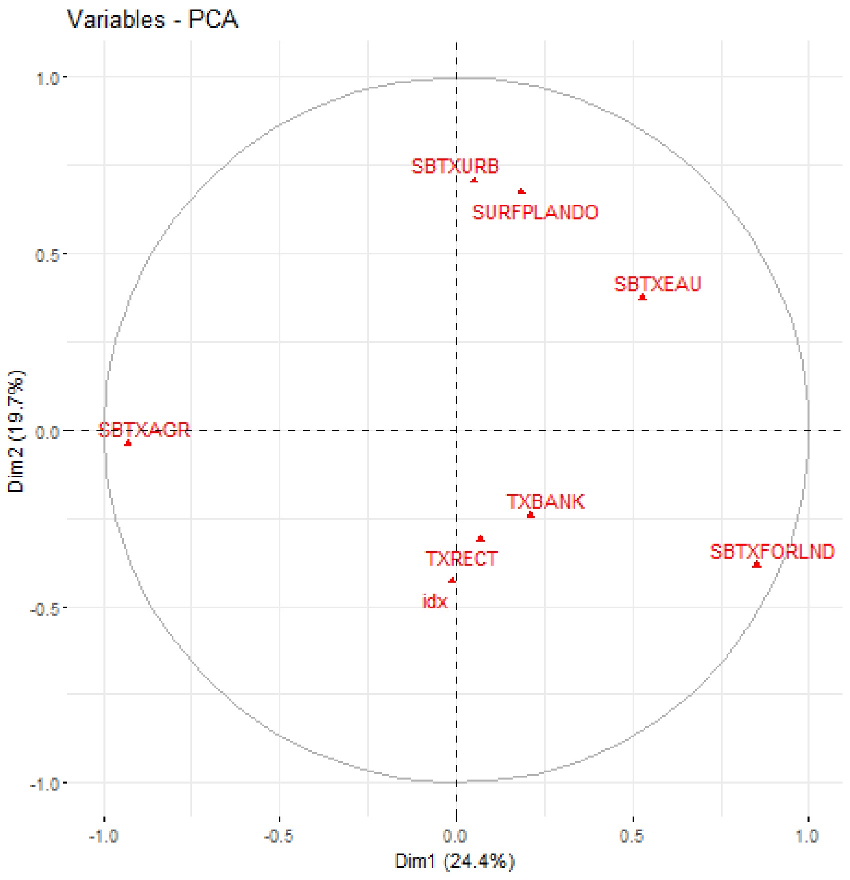


Projected evolution of average annual temperature across four climate projections between (1976-2005) and (2070-2099)

Figure L.2 Projected evolution of temperatures across selected predictions (%) between the 2100 time period and reference (1976-2005)

Appendix M: Table of the results of FAMD/PCA calculations for ensemble modeling. Results for the bleak, all other species have similar outputs (connectivity is the only differing variable), two FAMD and one PCA are practised according to predictors classes, a biplot is displayed for each. (Check Appendix K for details) HER2: Hydroecoregion; NO3moy/NH4moy/O2moy : Nitrate: nitrate, ammonium, oxygen concentration; ALT: Elevation; SBV : Surface area of discharge basin; M(S/F/W/P/A) (T/P): average (summer/ fall ... /yearly)(Temperature/ Precipitation); Diff: July-January temperature differential; QMNA5: low flow indicator (5-year record); regime: monthly profile of discharges; CI: Incision class; idx: Longitudinal connectivity; SBTX: forlnd – semi-natural land use; agr – agriculture; eau: Water cover; urb: urban cover; SURFPLANDO: River bank water cover; TXBANK: Forest cover on river banks; TXRECT: River straightness

Species	Bleak (ala, *Alburnus alburnus*)
Fixed Predictors	 Variables - FAMD

<table>
<tr><td>Hydrology & Climate Predictors</td><td>
</td></tr>
<tr><td>Scenarized predictors</td><td>
</td></tr>
</table>

Chapter 5.

The sources of uncertainty and their importance in river fish species distribution modeling

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Foreword

This third article, a short proof-of-concept on the use of analysis of variance-type methods to assess the contribution of management and climate change to prediction uncertainty, can be seen as a direct sequel to the previous chapter and deals directly with modeling outputs that were produced then, and thus makes reference to its results quite often. The main objective of this chapter is to uncover the relative importance of both components to uncertainty and provide a reflexion on species-specific relationship to uncertainty.

Abstract

A major challenge of prospective approaches in ecology is the consideration of uncertainty originating from the modeling approaches used to either generate predictors or within modeling processes themselves. Following a study of the influence of watershed management, expressed as four management scenarios, on the future distribution of eight freshwater fish species in a context of rapid climate change, expressed as four sets of selected projections, we endeavored to interrogate the portion of uncertainty specifically linked to management and climate change specificallt, through the use of analysis of variance on resulting predictions. We found that the breadth of climate projections selected contributed on average to 65 % of the uncertainty in final predictions, although higly variable, against 15 % for scenarios, which points to the predominance of climate change over the future of fish communities. Nevertheless, specific response to watershed management scenarios was constrasted, with some species (bleak, chub, roach, dace) exhibiting the opposite. We also found a potential link between downstream reaches and lesser response to management, although this could be explained by current management. These contrasted responses to the two sources of uncertainty considered in this proof-of-concept, across species and time, point to a need for further exploration of species-

sensitive modeling uncertainty to ensure accurate management and adaptation to climate change in the conservation of freshwater fish.

I) INTRODUCTION

The value of rivers as a source of water and fish from the human point of view, and as waterways for the transport of people and goods, has led to the disproportionate anthropization of rivers. River fish, which are morphologically and taxonomically diverse (McDermott, 2021), are especially vulnerable to environmental change (Cooke et al., 2012). Due to past management decisions and climate change, they have already suffered from fragmentation, extirpations and range shifts (Baldan et al., 2023; Grenouillet & Comte, 2014; Kominoski et al., 2017). Conversely, a large array of restoration initiatives have been observed to increase social and ecological community resilience in the face of climate change (Foley et al., 2017; Magilligan et al., 2016; Walker et al., 2004), and are broadly associated with more diverse communities.

Understanding freshwater fish distribution prospects under future climate change and management is a key step in prioritizing action for their conservation in the face of future stressors (Felin et al., 2025b). In attempting to produce distribution prospects for river fish using species distribution models (SDMs), one has to provide thinking with respect to future conditions, which are by definition unknowable, especially in the context of anthropized watersheds which entails both the integration of climate change and a reflection on future management.

Prediction of river fish distribution will depend on the future conditions applied to distribution models. Thus, a certain variability of projections is expected, which can be qualified as a portion of the uncertainty linked to these predictions, of which the understanding can provide clues into the mechanisms that shape future river fish distribution. Indeed, if management type was not found to be an influence on future probability of presence, then one may conclude that climate change is the main driving factor for fish distribution, making management efforts less effective. Additionally, understanding the potential spatial heterogeneity of the characteristics of uncertainty and identifying the regions where management is most important in determining fish distribution and which characteristics they share is another tool for prioritizing conservation actions. Thus, the goal of this study is to improve our understanding of the portion of uncertainty linked to scenarios of land management and climate change, upon which watershed management can act, doing so across several freshwater fish species and two time periods, 2050 and 2100. This study relies on species distribution model outputs across several climate projections and management scenarios (Felin et al., 2025b), which constitute the two studied components of uncertainty. It briefly presents a method developed for the determination of the portion of uncertainty from climate change and management and studies spatial prioritization. We calculated uncertainty across study sites, climate projections and management scenarios to obtain spatial information of the portion of uncertainty attributed to both components and hypothesize that the portion of climate change within model uncertainty may be proportionally more important in the far future than the near future. Similarly, we hypothesize that the spatial distribution of studied patterns of uncertainty may be linked to local context, such as river size, and time period, as well as fish species, depending on functional characteristics.

We hope that this study, intended as a proof-of-concept, may lead to further study of species-specific study of the components of uncertainty in SDM contexts, which may in turn provide a range of evidence on the potential impact of management decisions in anthropized basins and highlight differences between different fish species in order to help guide management actions.

2.Materials and Methods

2.1. Obtaining predictions of species distribution

In order to understand the patterns of uncertainty in SDMs with respect to climate change, we relied on the modeling outputs of Felin et al. (2025b), which relied on four climate projections and four management scenarios. Species distribution modeling was conducted on 34 species present in the Seine-Normandie drainage basin through an ensemble modeling approach, and eight of them (the bleak, chub, roach, ruffe, perch, trout, minnow and dace, see Felin et al. (2025a) for full information on species and characteristics) were retained for analysis among those that performed best in terms of prediction performance as measured by TSS (see Felin et al., 2025b). The set of four climate projections was selected to match the current understanding of future climate change under the RCP 8.5 scenario and is described in Felin et al. (2025). Briefly, all projections predict much warmer years, with especially warmer summers. Projections called C2 and B3 are characterized by drier and hotter summers relative to the other projections, while projections A1 and F9 have milder summers, and projection F9 has drier springs. The four management scenarios, described in detail in Felin et al. (2025b), were designed to cover four stories of land and river management ranging from a general halting of environmental measures on restoration, artificialization of riverbanks and urban sprawl - the “Faucets and Pipes” scenario - to an ambitious “Ecological Planning” scenario which implies broad political change, river restoration, increase in natural land use and decrease in anthropized land cover. Other scenarios are the “Production and Self-reliance”, which considers minimal effort for restoration, and “Respectful Executant”, which considers ambitious restoration with little system change. The diversity of futures covered by our two effects - climate and scenarios - were translated into adapted covariates (see Felin et al., 2025b). Ensemble modeling, which involved several statistical and machine learning methods and 100 identical repetitions for each model (see Felin et al., 2025b) which are then averaged, was conducted on 2044 study sites to model the distribution of the eight species. This process resulted into separate probabilities of presence for all eight selected species and all 16 projection*scenario combinations, both for the 2020-2050 time period and 2070-2100 time periods. It is in the variability of probability of presence that we chose to detect the portion of uncertainty of a first component, climate change, through climate projections, and a second component, watershed management, through scenarios.

2.2. Methods for uncertainty

Uncertainty in modeling is necessarily multifactorial. We choose to focus on two components, climate change and management, while other potential sources of uncertainty such as modeling algorithms, climate modeling, procurement of predictors and variability linked to model repetitions were averaged in the ensemble modeling approach. To partition the relative contribution of climate change and management in the uncertainty of fish distribution, we performed for each species, time frame (2050 or 2100) and study site an analysis of variance. Our chosen response was relative change in probability of presence between 2050/2100 and 2020 predictions. Included factors in ANOVA calculations were climate projections and watershed management scenarios. We used the function 'lm.ANOVA' of R package <QUALYPSO> (Evin et al., 2019). The QUALYPSO package functions, originally designed from climate predictions and modeling chains of GCM and RCM, take in available predictions along a multi-model ensemble approach (Jeantet et al., 2023; Evin et al., 2019), in our case climate projection and scenario. For each study site/grid point **s**, each projection **i** and each scenario **j**, lm.ANOVA determines total variance of predictions $P_{i,j}(s)$, which we equate to total uncertainty (Eq. 5.1):

$$\mathrm{Var}[P_{i,j}(s)] = \mathrm{Var}[C_i(s)] + \mathrm{Var}[S_j(s)] + \mathrm{Var}[res_{i,j}(s)] + \quad \text{(Eq. 5.1)}$$

where $Var[P_{i,j}(s)]$ is the total variance of change in predictions of fish presence, $Var[C_i(s)]$ is the portion of variance linked to climate projections, $Var[S_j(s)]$ the portion of variance linked to management scenarios and $Var[res_{i,j}(s)]$ the residual variance which the ANOVA designed was not able to identify. We extract all four, calculating the ratio of uncertainty linked to climate projections, and the ratio linked to watershed management. All data preparation, calculations and analyses were made with R version 4.4.2 (R Core Team, 2024).

3. RESULTS

Uncertainty in the change in probability of presence, attributable to climate change and management, was obtained for eight species, 2044 study sites and two time frames (Fig. 1 and 2). Overall, total variance values in 2100, were higher than 2050 (see Table 1 of averages and maxima). We should note that uncertainty values may seem low due to them being variance values of probabilities of presence but the appearnces here are misleading (i.e. total uncertainty of 0.01 corresponds to a deviation of 0.1 among values ranging from 0 to 1).

Table 1: Averages and maxima across study sites for total uncertainty across the eight selected species, 2050 and 2100. Uncertainty measured on the change in prbability of presence between target time period and 2020.

Species	2050	2100
bleak	avg: 0.002 max: 0.01	avg: 0.003 max: 0.02
chub	avg: 0.0006 max: 0.01	avg: 0.0006 max: 0.01
roach	avg: 0.002 max: 0.03	avg: 0.002 max: 0.05
ruffe	avg: 0.001 max: 0.02	avg: 0.003 max: 0.04
perch	avg: 0.003 max: 0.05	avg: 0.007 max: 0.1
trout	avg: 0.004 max: 0.05	avg: 0.007 max: 0.06
minnow	avg: 0.003 max: 0.03	avg: 0.005 max: 0.05
dace	avg: 0.002 max: 0.01	avg: 0.003 max: 0.02

Climate change was recovered as the main driver of uncertainty, with a percentage of variability in 2100 averaging at 66 % (64 % in 2050) against 15 % (the same in 2050) for scenarios, leaving 19 % (21 %) to unadressed residuals, meaning that overall importance of climate change did not change from 2050 to 2100. However, we observed a higher importance of climate change uncertainty across many species in 2070-2100 compared to 2020-2050, while the opposite occurred for the roach and minnow, while other species exhibited little variation between 2050 and 2100 (the trout, perch, ruffe). Uncertainty for species like the bleak, chub and dace, was recovered as mostly linked to management scenarios in 2020-2050 in a large number of stations (164 for the bleak in 2050, 468 in 2100; for the chub, 624 in 2050 and 127 in 2100). Overall uncertainty linked to climate change was the highest among study sites for the perch and trout.

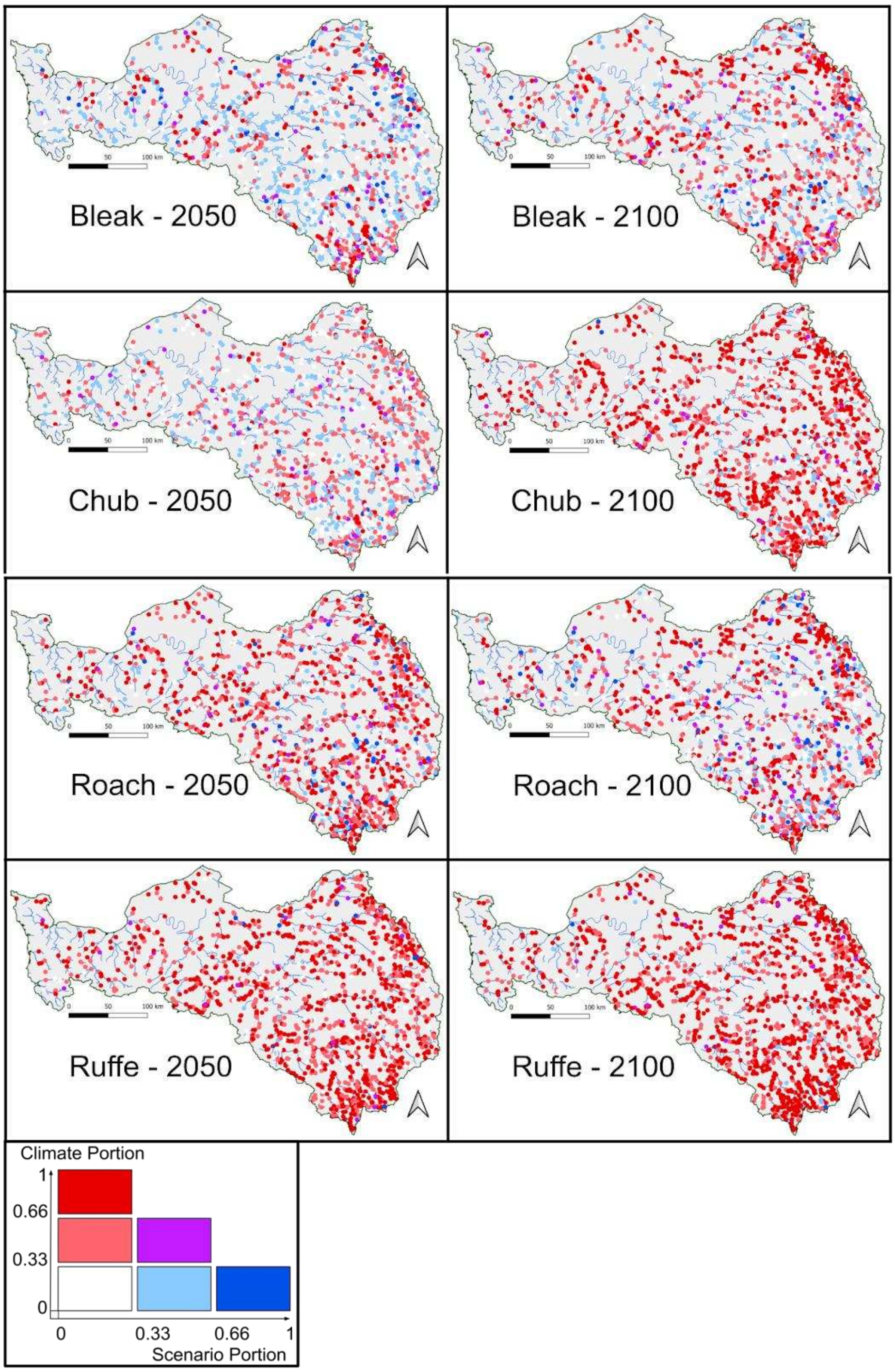

Figure 1. Portion of total uncertainty – measured on the change in probability of presence (2020 to target period), explained by management scenarios and climate projections, omitting residual values, for the bleak, chub, roach and ruffe. Each dot is a study site.

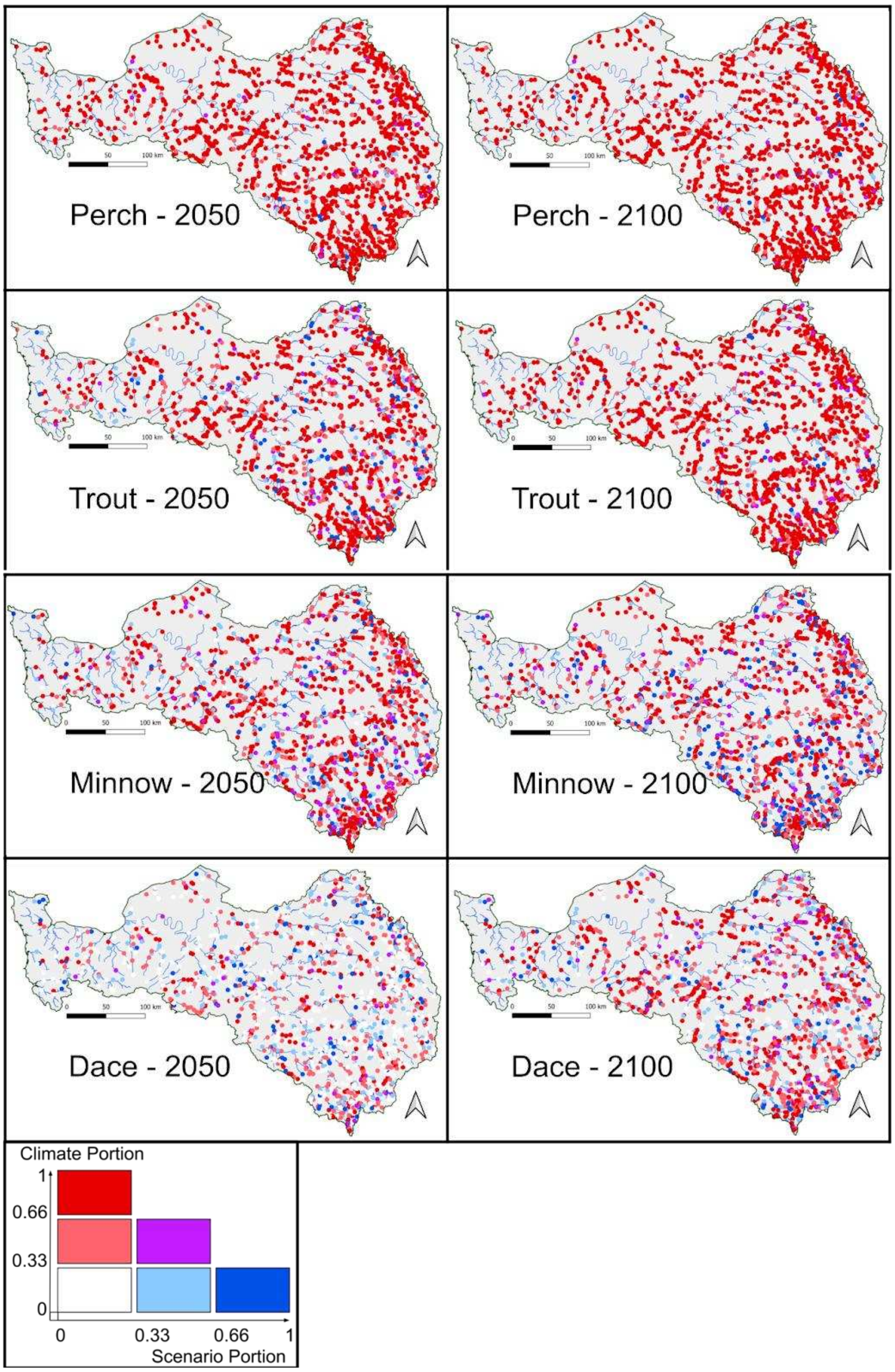

Figure 2: Portion of total uncertainty – measured on the change in probability of presence (2020 to target period), explained by management scenarios and climate projections, omitting residual values, for the perch, trout, minnow and dace. Each dot is a study site.

Studying the spread of uncertainty values along the longitudinal river axis (see examples in Figures 3-4), we observed again the difference in proportion of uncertainty linked to either component in the bleak and perch, two species which exhibited very different profiles in Figures 1 and 2. The portion of uncertainty linked to scenarios was spread across the longitudinal gradient, with some tendency for an absence of high values for higher stream orders, reproduced in seven of eight species.

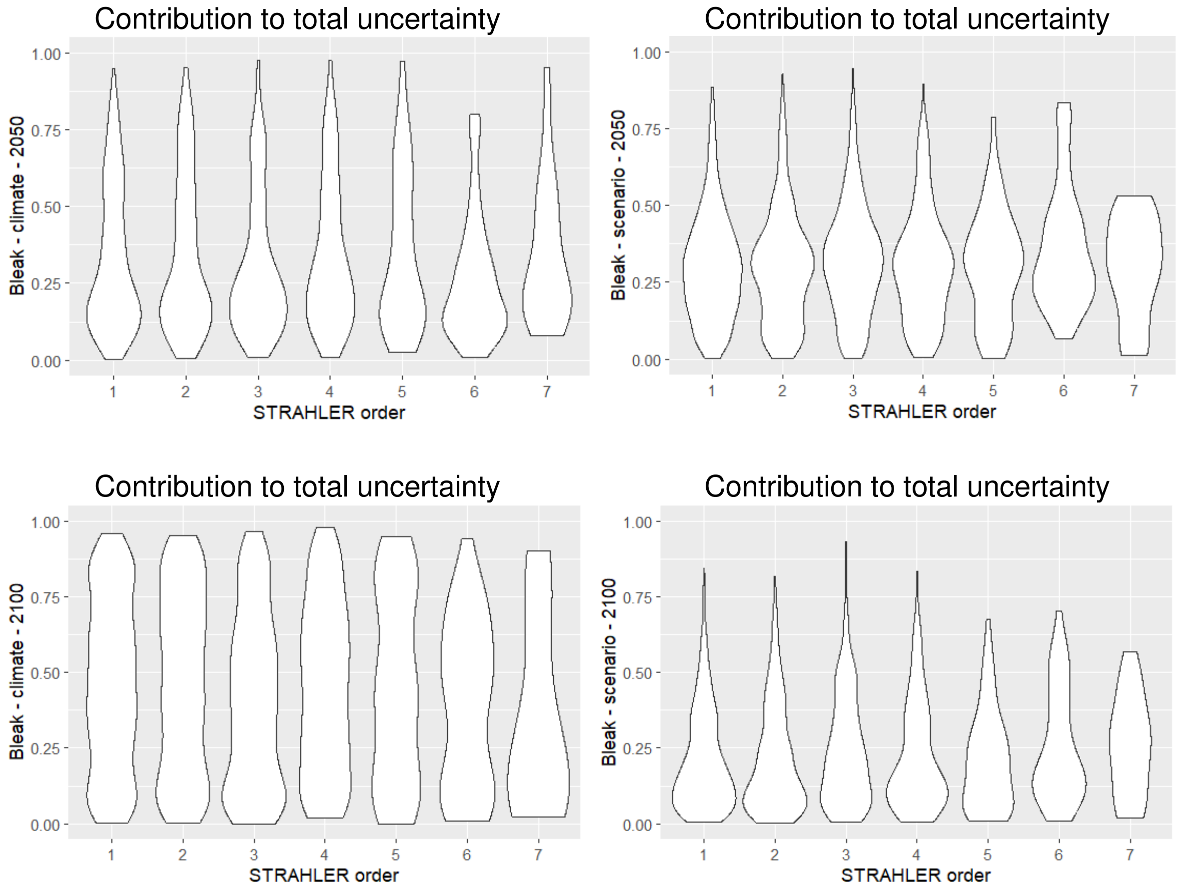

Figure 3: Violin plot of the contribution to total uncertainty on the change in probability of presence, for the bleak, along Strahler stream order values, reflecting upstream (1) to downstream (7) gradient. Climate component on the left, management scenario component on the right. Remaining uncertainty, not shown, corresponds to residual variance.

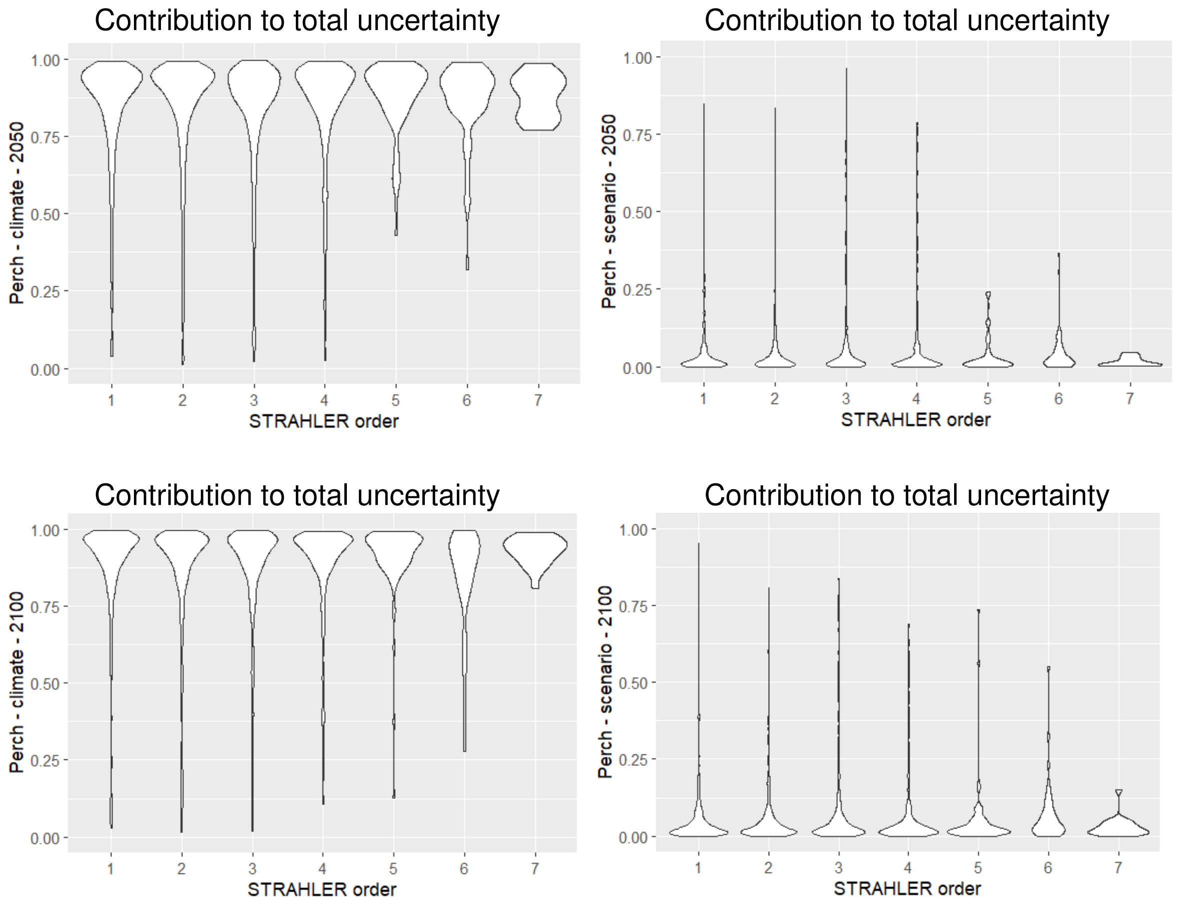

Figure 4: Violin plot of the contribution to total uncertainty on the change in probability of presence, for the perch, along Strahler stream order values, reflecting upstream (1) to downstream (7) gradient. Climate component on the left, management scenario component on the right. Remaining uncertainty, not shown, corresponds to residual variance.

4. DISCUSSION

The study of the uncertainty of fish distribution of fish species was concentrated on the variability of climate change projections and management scenarios computed in our analysis. Recovered values of uncertainty were generally low. However, some study sites did exhibit high relative differences between true value and grand mean, which implies tremendous influence of either climate or management in certain contexts.

The framework used to study uncertainty exposes the consequences of this variability of projections and scenarios. Uncertainty was contingent on the choice of climate projections and design of scenarios, thus, if we had chosen to include outlandish climate projections or land use and river management scenarios (e.g. marked cooling, complete urbanization, etc.) as well as highly diverging scenarios (if for example we had chosen to drastically modify land use instead of adjusting existing values under scenarized tendencies, see Felin et al., 2025), then the measure of uncertainty, presuming an outsized impact of these options, would render this study essentially meaningless, providing high values for uncertainty which would not reflect coherent thinking about future propsects. Instead, by restricting regional climate projections to the breadth of seasonal temperatures and precipitation anticipated within phase 6 of CMIP - and building internally consistent scenarios relying on understood orientation in public policy and management, we ensure the study of relative contribution to the uncertainty of both sources can be commented on.

We found that, with the exception of certain species on the 2020-2050 time frame, selected climate projections selected for this study led to a larger amount of uncertainty in species prediction compared to management scenarios. This result confirms our working hypothesis, matches observations made in Felin et al. (2025) as well as similar works on the contribution of climate change on decision making (Soutif-Bellenger et al., 2023) and is consistent with previous studies that highlight the way climate change overtakes non-climatic anthropogenic impacts in the shaping of river fish communities (Daufresne & Boët, 2007). This predominant role of climate change, which intensified in 2100 for certain species, could be linked to the diversity of GCM and RCM used for our projections (see Felin et al. 2025), resulting in heterogeneous projections. Additionally, this high source of uncertainty of climate change might have been more directly linked to their influence on hydrology in general, and to the occurrence of dry seasons in projections, which have been pointed in Felin et al. (2025) as a potential identifying factor for community and specific vulnerability. Depending on projections, these episodes varied in intensity and season of occurrence (B3 and C2 in summer;

F9 in spring; A1 no dry episodes as intense) and could lead to differing projections of distributions, and thus higher uncertainty. The presence of the trout, proven very sensitive to climate change (Keith et al., 2020), and the perch, which was shown in Felin et al. (2025) to react quite drastically to climate projections as well, were expectedly linked to large shares of uncertainty being linked to climate change in this study. Both species may be directly dependent on the impact of drought on fish (linked to F9 for the trout and B3/C2 for the perch).

Yet, some study sites, and some species distributions, especially in 2050, were sometimes determined by watershed management. Among species concerned with these distinctive responses, the dace and chub are generally widespread and tolerant of different conditions (Keith et al., 2020; Souchon & Tissot, 2012) but less so than the roach and bleak, which can tolerate high temperatures and disturbance (Keith et al., 2020), and for which management scenarios represent a larger share of uncertainty in 2100 than 2050. We posit these species may be found more sensitive to management mostly because they are less sensitive to climate projection variability, although all four species listed here are found in disturbed environments more readily than the perch or trout as well.

Spatial spread of uncertainty, contrarily to our hypotheses, was not a decisive factor. A single tentative pattern was noticed on some species, high Strahler order reaches being linked to lower values of uncertainty linked to scenarios. This could be explained structurally, the downstream study sites being less numerous than upstream ones, or by the current state of these reaches on the basin, which are for the most part heavily navigated, boarded by multiple urban areas, and susceptible to be exposed to pollutants originating from numerous sources. This state of perturbation may be the reason why management has little to no impact on such reaches, and presumably similarly disturbed reaches in upper parts of the basin, as observed by managers concerned with river restoration in urban environments (Jeliazkov et al., 2024).

The vision of uncertainty used in this study deliberately restricted considered sources of uncertainty to two, averaging all others, but of course these results are the consequence of a long modeling chain which implied several independent modeling steps (obstacle heights, connectivity indices, water quality metrics) as well as other uncertainty-generating processes within ensemble modeling (e.g. differing algorithmic methods for prediction). Further exploration of similar problems in different contexts, especially if focused on uncertainty in itself may require include these additional components, which were less thematically linked to the scope of this paper, in order to further explore the remaining 19 % of uncertainty which was detected as residual in this publication.

5. CONCLUSIONS

In this exploratory study, we have shown that within the framework of climate futures and management scenarios we set, climate change was the major source of uncertainty in most, though not all, species and timeframes. Predictions set in the further future (2100) were shown to carry higher uncertainty than those set in the nearer future (2050; up to 2.4 times among species averages), with differing evolution in the proportions of uncertainty linked to climate change and management. However, the breadth of scenarios treated did contribute to uncertainty, and in ways that necessitated attention at the species level, meaning that precise management decisions, informed by climate change, local context, as well as precise research of the effects highlighted in this study may be needed. The prevalence of climate within species prediction uncertainty also points to the necessity of further research in climate change and future local climate to ensure more reliable projections and thus reduce uncertainty linked to climate modeling. We also feel the need to add that despite the overall prevalence of climate in the uncertainty of fish distribution, the few species which were associated with more nuanced responses are reason enough to further investigate specific response of river fish to management decisions at diverse scales to ensure relevant restoration initiatives (Friberg et al. 2017).

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Chapter 6. General Discussion

This thesis has investigated the influence of watershed management on river fish distribution in a context of fragmentation and global change. In particular, Chapter 3 assessed the role of connectivity in fish species distribution thanks to the original development of connectivity-sensitive SDMs. Chapter 4 provided an insight into both the vulnerable fish communities of our study area, and of the complex ways in which future climate and management are causing shifts in species distribution, highlighting some of the management decisions that need to be made in favor of species conservation. Finally, Chapter 5 reflected on the relative contribution to uncertainty of climate change projections and watershed management scenarios, showing inter species variations as well as an increase in importance for climate change in 2070-2100 compared to 2020-2050.

The current section proposes a reflection on the work, limitations and promises of this thesis, first presenting some elements on connectivity constraints, restoration and fish migration, before turning to species extirpations and their consequences. This general discussion is followed by a larger argument about what it entails to think and produce knowledge about the future. Finally, we synthesize a larger thought on the applications of a thesis like this one, the toll of ecological decline on the people who observe it, and a few words of cautious hope.

6.1 The case for a well thought-out restoration of rivers

6.1.1 Our results

We demonstrated the utility of including longitudinal connectivity as a covariate in species distribution models when modeling fish distribution, and have thus shown that longitudinal connectivity significantly shapes fish communities, thereby confirming our first hypothesis. Although we argue that this statement is broadly true, it is of course of varying relevance depending on which fish species is studied, as shown in Chapter 3 of this thesis. Similarly, we have shown that for most, but not all, species in the highly anthropized Seine-Normandie drainage basin, longitudinal connectivity is associated with a higher probability of presence. We designed a Reach Connectivity Index (RCI), following the framework of Baldan et al. (2022), taking into account specific anatomical characteristics in the calculation of obstacle crossing and leptokurtic dispersal kernels (Skalski & Gilliam, 2000). Additionally, noticing a bias favoring downstream reaches in base RCI, we designed additional indices, namely the Adjusted Connectivity Index (ACI), which corrected for network betweenness centrality and the Zonation-sensitive Connectivity Indices (ZCI), which focused on connectivity within specific ranges of centrality. Both the ACI and ZCI outperformed the RCI and the ACI was best overall across a large number of species, showing that longitudinal connectivity in SDMs is better adjusted to river size and local context. In practical terms, the computation times of such indices were directly linked to network complexity and quantity of obstacles processed, causing calculation length to balloon for networks like the one studied. Beyond the exact process of calculation of indices shown in Chapter 3, we deem the messages this chapter vehiculates to be most important: designing indices for longitudinal connectivity in rivers, directed at river fish in particular, if designed in a similar framework, should include functional characteristics of fish in obstacle crossing and dispersal, and check/correct for centrality bias - as shown in ACIs in chapter 3.

Regardless, we consider this set of results as particularly noteworthy due to its originality, as it provides tangible evidence that more complex connectivity indices are a valuable component of species distribution models. Previous works have generally focused on the direct analysis of the consequences of connectivity loss through direct comparison and community study (Cooper et al., 2017), or have employed simpler obstacle-density based metrics (Branco et al., 2012). Evaluating the possibility of generalizing our more detailed results into different contexts may prove useful. Indeed, compensating for the deleterious effect of connectivity loss through various initiatives of riverscape restoration is a relatively common strategy in anthropized watersheds, which requires broad principles of action. There is ample corroborating evidence that barriers like dams and weirs have an impact on fish communities (Dean et al., 2023; Shao et al., 2019). In particular, these obstacles have been shown to impede the migration of potamodromous and diadromous species and their ability to reach feeding and breeding grounds (Birnie-Gauvin et al., 2020), sometimes leading to local extirpations (Kominoski et al., 2017). Additionally, we were able to show that high longitudinal connectivity had a negative impact on a few small or sedentary species. We also showed that fish species which depend on lateral habitats for feeding or breeding reacted in different ways to connectivity indices.

These results are novel and exploratory, and we are interested in seeing if they are corroborated in other watersheds and similar species. Furthermore, from a methodological viewpoint, we deem our results with respect to novel connectivity indices and connectivity-sensitive models to constitute a promising opening for metacommunity ecology. By creating tools for the integration of functional considerations in fish dispersal, we allow for a finer representation of said dispersal, including at larger spatial scales, a necessary improvement on current methods (Comte & Olden, 2018). Connectivity indices like the ACI could potentially help metacommunity ecology parse the complex mechanisms linked to fish dispersal in rivers such as mass effects and effects of colonization (Heino, 2013).

6.1.2 Caution in generalization

Beyond the general results of this thesis, and the ever-present limits of SDM approaches (see section 6.3.1 for a more complete overview), variability in response to connectivity loss across space, species and time is to be expected. Therefore, one must be cautious in generalizing results like the ones we produced, especially in trying to mitigate the effects of connectivity loss. Precisely, we wished to warn against applying “one-size-fits-all” solutions to river restoration when it comes to river fish.

Firstly, each potamodromous and diadromous species is due to respond to barriers and be affected by connectivity loss differently, with respect to the intensity of the effect, as we have shown in Chapter 3. Obstacle density, height, in relationship with the reproductive, behavioral traits of a particular species, are due to impact age classes, morphological traits, local abundance in specific ways which cannot be reproduced on a different species. Notably, we mentioned in Chapter 3 the case of the stone loach, referring to Sun, (2022) and our own results, which favors finer sediments, and prefers low connectivity reaches, and so is locally favored by the presence of dams and weirs. Furthermore, migratory behavior itself seems to be determined in many species by local context, within a single species or even population, leading to the widespread phenomena of partial migration, or heterogeneous migratory behavior (Chapman et al., 2012; Chapman et al., 2020). For some species, these phenomena are well known and studied; for example, the native trout in our study area is found in the Seine in a larger diadromous morph and a small, much more abundant, resident or potamodromous morph. Many individuals have been shown to exhibit lengthy potamodromous migrations (Keith et al., 2020), while simultaneously belonging to populations with leptokurtic dispersal patterns (Skalski & Gilliam, 2000), which imply a larger resident component and a smaller migratory component. The precise migratory behavior of freshwater species is often poorly known, and may vary across time and space, and thus the precise effects of river artificialization on one population is not necessarily the same on another population. Thus every restoration approach would ideally be cognizant of local ichthyofauna, potential migratory behavior of each species and calibrate or prioritize operations accordingly.

Additionally, local importance of one anthropogenic influence on rivers or another are due to vary as well. Among the effects of anthropization in rivers, i) barriers and ii) land use are often mentioned as the main factors structuring fish communities, however, whether one or the other bears more importance varies from one study to the next. Although barriers seem to have wide-ranging effects which also affect less anthropized areas, land use was shown to be more important in species distribution models mostly when dealing with highly-anthropized watersheds (Dean et al., 2023; Van Looy et al., 2014). High general anthropization of territories may lead to muddled effects of precise pedictors like barriers, or navigation (Jeliazkov et al., 2024), and highly-anthropized areas may react differently to certain management decisions targeting barriers, compared to less anthropized areas. In our study area, we find contrasted responses of fish species to dams and land use, which may reflect the heterogeneous nature of anthropization in our study area. We can assume that territorial characteristics, including a rate of anthropization, are bound to influence the outcomes of restoration initiatives, which may lead to strategic prioritization by actors of restoration.

6.1.3 The restoration of connectivity and riverscapes

The loss of longitudinal connectivity due to dams and weirs impacts many freshwater fish species, leading to shifting communities. We deem this statement to be replicable to most anthropized and less anthropized watersheds. Within our study area, we have shown that twenty-three potamodromous and resident species out of thirty-three were negatively impacted by connectivity loss across index types in a significant way, and a majority reacted most significantly to indices built with dams in mind. Similarly, fragmentation was shown to impact fish communities in various contexts (Vega-Retter et al., 2020; Wang et al., 2011).

Thus, our results and corroborating works show enough proof for us to wholeheartedly endorse general initiatives of restoration. As shown above, one cannot ignore the specific local environment and the way fish species are affected by anthropogenic infrastructure. One must take into account local connectivity, the state of fish communities, knowledge of the species of interest, and local practices in diagnosing “the way to go” in restoring connectivity or mitigating the effects of connectivity loss, although lack of knowledge in the study of river fish is a rather pervasive problem (Cooke et al., 2012).

To diminish the effects of river engineering operations, major policy decisions and directives, like the European Water Framework Directive (WFD, see directive 2000/60/CE, 2000, JORF), have led to restoration initiatives like re-meandering operations or bank restoration. Restoration initiatives that target longitudinal connectivity generally focus on barrier removal, something our own work broadly supports, we both showed the negative effect of fragmentation on some fish species, as well as the broader benefit of barrier removal within "greener" watershed management scenarios (see Chapters 4 and 5). Outside of this thesis, these operations have shown in some cases to allow passage for migratory fish, increase in biotic diversity, as well as increased long-term resilience of communities faced with global change (Magilligan et al., 2016). Barrier removals are generally considered beneficial. However, removal operations are sometimes controversial. The release of sediments from the destruction of large barriers is sometimes pointed as a potential public health and ecosystem health hazard, particularly when these sediments are laced with pollutants (Hahn et al., 2018). Furthermore, the destruction of some obstacles may be linked to the facilitation of movement for diadromous and potamodromous species, including some non-native species that are considered invasive or destructive. A commonly cited example is that of Copi or asian carps (a group of species commonly known as such), which are native to East Asia and invasive in large North American rivers, greatly shifting fish communities by feeding on water plants and plankton. Their spread in the Great Lakes and St Lawrence basin via artificial canals remains a speculative prospect, with the hypothesis that it has been temporarily impeded by pre-existing barriers and specially installed fish screens, facilitated by public expenditure in the Northern States of the USA (Li et al., 2021; McCormick et al., 2009). The validity of these concerns is of interest to the management of rivers. However, several solutions to these problems have been cited, such as preliminary curing of sediments upstream of rivers or calibrated fish screens (Parker et al., 2016; Zielinski & Sorensen, 2016), as well as doubt cast on the efficacy of barriers to actually break the progress of invasive species, when climate is a better predictor of invasive species progress in some cases. Additionally, these concerns are often used as motte arguments in a larger bailey of other claims by actors who wish to halt barrier removals. A careful approach with respect to barrier removal is necessary, but the degree to which some concerns may be overblown constitutes an additional layer of complexity to barrier removal operations.

Thus, barrier removal operations can be used to restore longitudinal connectivity, and aid with the restoration of fish biodiversity in anthropized rivers. However, the sole concern with longitudinal connectivity overshadows other dimensions of connectivity which have been proven essential for fish conservation, namely lateral connectivity. Partly addressed in Chapter 3 and employed as background predictors in our models, lateral connectivity constantly relates to the connection between the river and lateral and backwater habitats. We have shown that some species that rely on lateral habitats react differently to certain characteristics of longitudinal connectivity indices compared to others, clustering separately in PCA renderings of index characteristics, indicating a need for closer consideration of lateral connectivity in further studies. Lateral connectivity has been shown to be linked to more diverse fish communities, and has been greatly impacted in recent years by channelization, embankments, draining of floodplains and river straightening (Shao et al., 2019). Although this thesis puts an emphasis in barrier removal, we wish to highlight the need for purposeful, integrated restoration of riverine habitats (Magilligan et al., 2016; Wohl et al., 2015). Barrier removals, ideally, are often instructed to be accompanied, when applicable, by re-meandering efforts, bank restoration and other complementary initiatives, but current restoration, at least in France, operations generally lack such initiatives (Morandi et al., 2014).

Within the European Union, the Water Framework Directive (WFD, 2000) and the series of local initiatives that preceded and followed it preconize barrier removal, as a way to restore hydromorphological and sediment continuity, along with several other kinds of operations, among which lateral connectivity restoration. France adopted its own framework for watershed management and protection of water resources and biodiversity following a 1992 law for water management (Loi n° 92-3 du 3 janvier 1992 sur l'eau), leading to the creation of regional management plans. In particular, and although some projects were implemented on obstacles, as registered by Dam Removal Europe (2025), regardless of their use and state of deterioration, the removal of barriers that were damaged, obsolete or unused became common practice, prioritizing these structures over others because, among many reasons, fewer interests were present to keep them around. Although the benefit of removing these barriers may be real, this bias in choosing obstacles to reweigschmove seems to be suboptimal in choosing these structures for removal. Indeed, although all dam removal situations are different in some way, the targeted removal of unused barriers may lead to a focus on smaller obstacles or streams which may be situated in headwaters and not influence longitudinal connectivity that much anyway.

To choose more accurately which dams to remove, approaches such as barrier prioritization via connectivity index calculations (which can be done through package rivercon, also used in Chapter 3, see Baldan et al., 2022), as in Wegscheider et al. (2024), who add that barrier removal efficiency also requires to study the expected distribution of species of interest. These approaches may highlight which barriers, once gone, would alleviate connectivity loss in the most stricken areas. However, as shown in Chapters 2 and 3, our study area counts an overwhelming majority of small weirs, while larger ones are restricted to precise areas in the basin (Western Normandy, Morvan), which did not lead to localized effects of fragmentation, meaning that small obstacles should not be neglected when it comes to removal. As, corroborated by Baumgartner et al. (2022), depending on placement and density, the largest obstacles are not necessarily the most impactful, and that a watershed-wide initiative for connectivity restoration requires to take into account smaller weirs (i.e. flashy pyrotechnics as used in larger barrier removal operations, most often pictured in the media, are just one piece of the work necessary).

Beyond the influence and removal of physical barriers in riverscapes, another dimension of connectivity largely relegated to this general discussion within the bounds of this thesis nditions, such as anoxia or extreme temperatures, which can represent barriers of their own (Johnson et al., 2024). They may act in similar ways as physical barriers and are to be associated to relevant removal and management – which are beyond the scope of this thesis and are to be included in larger frameworks of management. A necessary complement to restoration work is thus the monitoring of the effects of restoration and management, which can in turn inform future operations. The impact of human activity on watercourses being rather complex, academics and regulators, as well as committees linked to the WFD and regional management plans, have relied on bio-indication as a general methodology to estimate the ”quality” of a given section of river (Siddig et al., 2016). Animal taxa are especially useful in these approaches as indicators of certain environmental characteristics. The Indice Poisson Rivière (IPR, eng: Fish River Index) used in France are examples of indicators that rely on river fish (Belliard et al., 2009). Historically, general considerations about the tolerance of a given species for pollution and other human-caused phenomena were used to estimate ecosystem quality. This differential sensitivity to anthropogenic disturbances was also observed in this thesis, and we can draw parallels to species like the spined loach and perch, which we consistently recovered in high connectivity reaches. However, these proxies have generally been completed today by integrated SDMs in indicators, relying on agreed-upon reference sites deemed largely unimpacted.

River quality assessment and bio-indication, which are useful to decision makers, especially in the context of ecosystem restoration to estimate the impact of restoration initiatives, are frequent uses of SDMs and niche theory in a practical context. With the goal in mind to improve river fish SDMs, we can imagine a practical use of indices designed within Chapter 3 may be to integrate them in some way in said SDMs in future iterations of these indicators.

A broader conclusion to this section would be that despite the relatively unambiguous results of the first paper (Felin et al. 2025) produced by this thesis (our Chapter 3) regarding the important role of connectivity in river fish distribution, tremendous care and planning should ideally be conducted in enacting management decisions based on these results and similar works. Connectivity indices can inform us on strategic barrier removal prioritization, local context and study of impacted communities is essential to guarantee beneficial results, and restoration initiatives should be linked to modeling approaches, conducted to monitor the efficacy of restoration.

6.2 Fish species, global change and community shifts

6.2.1 Past community shifts in Seine-Normandie rivers

Based on Chapter 4, we were able to show that both climate change and river management change had an influence on predicted future fish distribution, thereby confirming the second hypothesis of this thesis. Climate change in particular seemed to be linked to important variations in fish distribution and range, with losses in range exceeding 80 % in some cases (e.g. the perch with projection B3 and the “Faucets and Pipes” scenario). Conversely, some species saw their range expanded (e.g. the dace with projection A1 and scenario “Ecological Planning”). An expected consequence of climate change in our study area is the local extirpation (within the context of shifting range), or complete extirpation, of some fish species in the basin. Although our models cannot directly predict true extirpations (we were tied to study sites), we assumed that wide-ranging extirpations from study sites could be translated as a higher likelihood of true extirpations. In our case, this broadly concerns, among selected species, the perch, roach and ruffe, but which might affect other species in ways our models could not detect.

Local and regional extirpations of fish in the Seine-Normandie basin would not be a new phenomenon. Several large diadromous species like the sturgeon, salmon, shads, saw their range extremely reduced within the basin, driven by overfishing, pollution and the construction of barriers, restricting their access to upper reaches of the basin where they breed, to the point of sometimes being completely extirpated (Beslagic et al., 2013; Merg et al., 2020). Potamodromous species were shown to be depleted in certain rivers of the basin by domestic and industrial pollution (Garnier et al., 2021), leading to species-poor communities in deoxygenated rivers. The nearly unfettered leaching of fertilizers, waste and pesticides in rivers in the second half of the twentieth century also led to the decline of species which were sensitive to organic pollution (e.g. barbel, bullhead) to the profit of more tolerant species (e.g. bream, roach). We show in Chapter 3 that, additionally, fragmentation must have had notable consequences on fish communities, as we notice their effect in a twenty-year dataset.

In recent years (Boucault & Clément, 2020), due to several restoration initiatives and regulations, this trend reversed, leading to newly abundant species which had been in decline the half century prior. The parallel introduction of several opportunistic species (e.g. wels catfish, pumpkinseed), as well as the continuing artificialization of riverbanks, which contributes today to the decline of species relying on lateral habitats and specific substrates (e.g. pike, trout, burbot), constitute other phenomena which are currently shifting fish communities. Concurrently, recent climate change has already been proven to favor warm water species and modify freshwater fish communities in France (Comte et al., 2013; Daufresne & Boët, 2007). These climate and management-induced extirpations and introductions are the cause of widespread range shifts in freshwater fish. These shifting phenomena must be placed within a broader context of already shifting communities at larger scales, in a general context of community diversity decline (Living Planet Report 2022), especially intense in freshwater ecosystems due to an inherent vulnerability to anthropogenic stressors.

6.2.2 Future community shifts and trophic collapse

Thus, “current” communities on which our models are trained are neither “pristine” in any sense of the world, nor at their lowest point in terms of diversity and abundance. Future fish communities, either observed or predicted, should thus not be compared with current fish distribution conceived as a fixed state, but itself as a result of earlier transformations of communities and food webs. A succession of range shifts, extirpations and introductions already left their mark on fish communities.

These phenomena do not stand isolated in riverine ecosystems, instead causing havoc in relevant communities. The past introduction of non-native species and extirpation of some species has been shown to decrease functional diversity (Matsuzaki et al., 2013) and to disrupt trophic food webs (Wainright et al., 2021). In our study area the introduction of the wels catfish (Vejřík et al., 2017) effectively led to the arrival of a generalist apex predator in ecosystems which did not have them previously (the pike being the closest contender), and the pumpkinseed is considered a nuisance and classified as a pest by the French Government (Arrêté du 16 juillet 1953 relatif à la destruction des poissons des espèces reconnues nuisibles, 1953, JORF), in part because it consumes fish eggs and roe.

Climate change is at the center of concerns for the decline and extinction of freshwater fish, through an increase of water temperatures (Li et al., 2022), leading to a reduction of functional diversity (Scherer et al., 2023), and, in rivers with modified discharge, very high proportions of extinctions (Xenopoulos et al., 2005). Our 4th Chapter pointed to climate change as the main contributor to fish distribution, and associated, especially when characterized by dry summers or springs, with substantial extirpations predicted. In some cases, climate change may increase the impact of introductions of exogenous freshwater fish species. Studies have also shown that some species which recently arrived in the Seine basin, and in particular Ponto-Caspian gobies such as the round goby (*Neogobius melanostomus,* Pallas, 1814, e.g. Fig. 23), have wreaked havoc on functional diversity in different basins with more ancient implantations. A warm water species, the round goby is of particular concern for the Seine River, as climate change might favor its progress further (Le Hen et al., 2023).

Additionally, the extirpation of key species in local ecosystems are due to impact trophic webs as well. Certain past extirpations were shown to have impacts that rippled beyond fish communities. For example, Rodriguez-Lozano et al. (2015) show the influence of the extirpation of Mediterranean barbels on macroinvertebrate species assemblages. River fish within our study area are themselves included in wide-spanning trophic webs. Consequently, extirpations and introductions have the potential to produce the same effect on local trophic webs, with trophic shifts as potential consequences , linked in part to the high number of interactions within trophic networks, leading to trophic cascades (Ripple et al., 2016) with drastic consequences on communities (Koel et al.,2017).

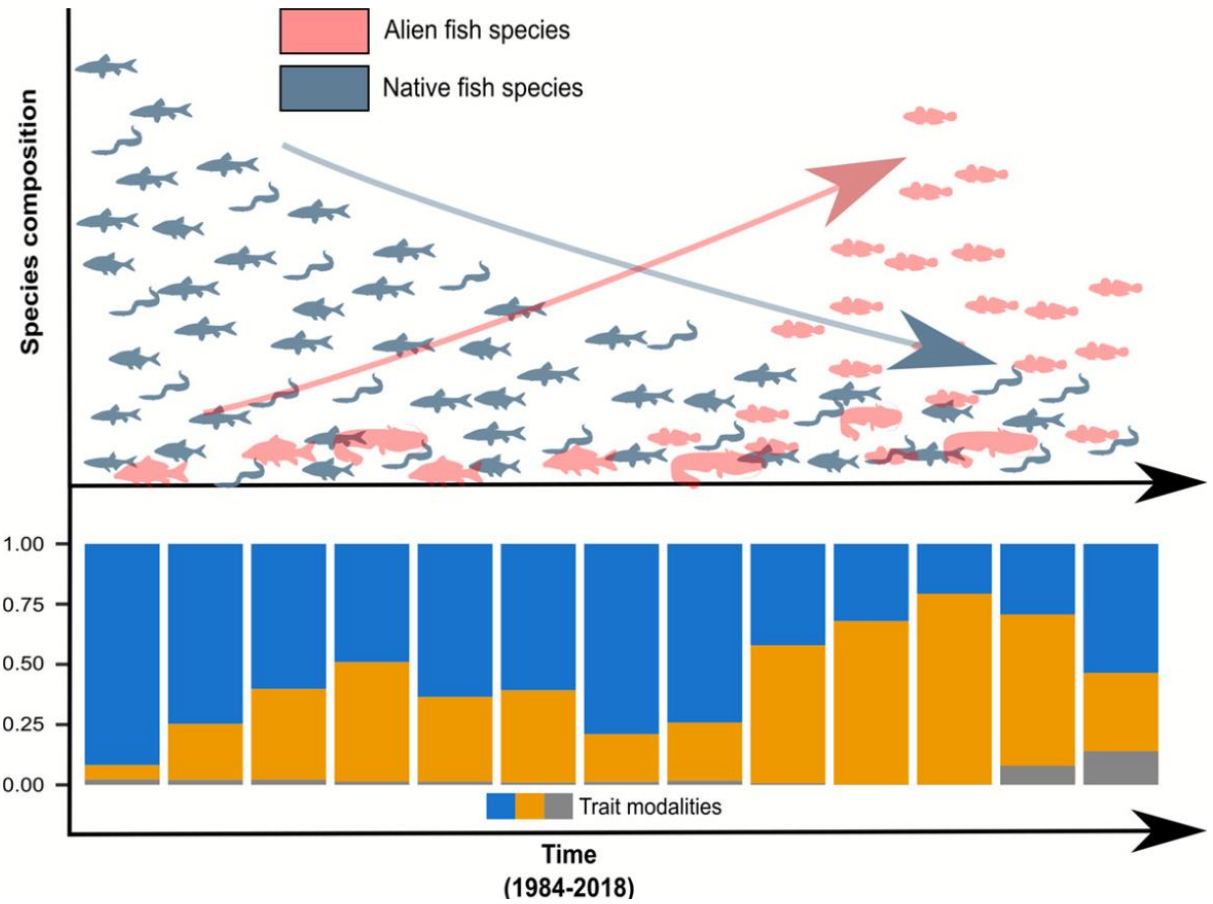


Figure 23: Illustration of cascading effects of an exogenous introduction of the round goby, wels catfish and eurasian carp, in a riverine environment (River Rhine) on the local trophic network. *Emphasis is put on the spread of functional traits as communities shift under exogenous pressure. Adapted from Le Hen et al. (2023),*

The constant flux of introductions and extirpations of river fish in the study area, having already taken place and greatly accelerated by human interference, has caused wide-ranging shifts in communities. One can expect that future equivalent phenomenon may cause similar jeopardising of fish communities. Although this thesis did not use them, some methods exist to either detect interactions between co-occurring species, like Joint Species Distribution Models (JSDM) (Bokhutlo et al., 2023; König et al., 2021), or SDMs taking into account of known trophic interactions in their structure (function trophicSDM in R package <webSDM> for example). These approaches could potentially lead to better prediction of trophic effects beyond individual species conservation, although these would likely require the inclusion of prey species outside of fish.

Furthermore, an often overlooked problem of SDM predictions, joint or otherwise, for practical reasons, is that no conceivable model could predict the future introduction of non-native species not yet present, because they depend on random events (illicit introductions by humans, transportation in ship ballast). As exposed in our Materials (Chapter 2), the Seine-Normandie watershed is especially sensitive to exogenous introductions due to high anthropization, connection to other basins via canals and past initiatives for faunal enrichment. So, the approaches at the disposal of the researcher either ignore the possibility of new coming species or to test a few chosen species selected by dispersal potential, environmental suitability, study of neighboring basins with no clear knowledge of future trends. Whether through a voluntary operation or due to accidental spread of a species newly favored in progressively warmer waters, these newly settled species may perturb already fluctuating trophic networks. Some species have been shown to be currently unable to breed in our study area (e.g. the famous "Asian carps" mentioned above, which breed in warm, fast-moving water, conditions which are currently not found in France), but may meet suitable conditions before 2100, whereas the basin is already suitable for some species (e.g. the Channel catfish *Ictalurus punctatus*, originating from North America, present in Central Europe). These species have been shown to have consequential influence on the basins where they were introduced, reducing native species fitness by competing for resources (Irons et al., 2007; Li et al., 2021) or directly predating on native species (Faria et al., 2019; Haubrock et al., 2023).

In the context of potential trophic collapse, the question of voluntary introductions further leads to several metaphysical questions about the intrinsic value of native and non-native species. The practice of trophic rewilding (Bakker & Svenning, 2018), implies the sustained reintroduction of a species susceptible to fill the trophic niche left vacant by an extirpation, or weakening due to diminishing stocks. The substitute species would be the already native species if possible, but in the case of extirpations due to unsuitable conditions, a substitute species with different tolerance for climate and hydrology may be more suitable. This hypothetical situation leads to a binary choice between risking the shift or collapse of a trophic web with wide-ranging consequences on neighboring communities, or the intentional introduction of an exogenous species. Although not under the name "trophic rewilding", similar operations are regularly conducted as reintroductions, either for conservation or leisure fishing, sometimes leading to population recovery, although often with lower genetic diversity (Cochran-Biederman et al., 2015; Pham et al., 2013). Beyond these, trophic rewilding is mostly mentioned within the context of terrestrial megafauna (Cromsigt et al., 2018; Schweiger et al., 2019) and supposed ecological memory of ecosystems, and little documentation exists on operations of introduction of exogenous freshwater fish for the purposes of trophic support. The potentiality of trophic rewilding with freshwater fish as a restoration approach remains to be academically vetted. In our discussion of Chapter 4, we evoke the waxing and waning of niche hyperspace in the basin we study as climate changes. Concluding that even range growth in the 21st century may be the first phase of a phenomenon which eventually wanes, the question of trophic and niche-conscious rewilding may indeed constitute a singular way to maintain communities of fish in rapidly changing rivers.

Overall, this thesis joins a large body of work predicting general decline of certain species under projected climate change. These declines will likely lead to disrupted trophic networks and problematic questions regarding future community composition and trophic rewilding. The intensity of these phenomena and their exact nature remain to be observed. Our results, and their conclusion, considering our use of scenarios, climate projections, and the possibilities of unforeseen trophic cascades and interspecific interactions, mean that our more precise results should be treated as a model outputs for predicted distribution with necessary flaws and approximations. Our study of uncertainty in Chapter 5 showed that current understanding of climate change in particular led to non-negligible uncertainty in species distribution projection. Although our general results were corroborated by previous studies in different contexts (in geography, scale etc.), we maintain that local context, the local migratory behaviour of fish species in reaction to resource availability and anthropization, must be taken into account in thinking about fish communities and restoration, so that local oddities and differences are properly handled. We develop the practical ways in which our results can be used or replicated in section 4 of this general discussion.

6.3 On the challenges of imagining and predicting the future

6.3.1 Species Distribution Modeling and its limitations

SDMs, because they are based on statistical methods or machine learning, rely on methods that extract patterns from raw data, and as such are subject to biases like overfitting, and often fail to find patterns with high degrees of significance explained, or low portion of explained variability. Standards from SDM use (Araújo et al., 2019), of which it is recommended to respect as many as possible, include checking the accuracy and completeness of sampling data, assessing the quality of predictors used, limiting model complexity and collinearity, and assessing its accuracy and uncertainty. As disclosed in Chapters 3 and 4, the use of PCAs, and the assessment of model accuracy through TSS allowed us to assess model performance and select species for further analysis accordingly, and we amply discussed sampling method and accuracy in Chapter 3. For predicting future distribution, special care must be applied to assess accuracy, and multiply modeling approaches, as we did with ensemble modeling (Chapter 4), and even still, assumptions and methodological issues made in building SDMs become problematic in prediction contexts (Dormann, 2007), such as the assumption of global dispersal, the presumed fixed nature of species niche and tested range - which can be a problem for species currently in expansion, and may explain low performance for non-native species - as well as issues of spatial autocorrelation. Our power to prepare for these problems remained limited, still we included connectivity indices, which take account of dispersal, and aggregated study sites in close proximity.

The limitations of SDM predictions, coupled with the sometimes hard-to-parse distribution of some fish species (generalists, species of commercial interest, non-native species), led to disparate accuracy (in terms of TSS) depending on species (see Chapter 3) which required further species selection in Chapter 4. Evaluating model realism (i.e. comparing model predictions in 1990-2020 to model outputs and presence/absence datasets, lead us to obtain disparate TSS values as well, some quite low despite apparent model performance. This final limitation of predictive SDMs, which could be a problem in river fish, is the now well-documented phenomenon of community inertia (Moraes et al., 2012), or the lagging period between environmental change and community adjustment, which could partly explain the underwhelming prediction quality we obtained in some species, complicates this picture further by blurring the lines between actual niche (in our case a realized niche with some elements of accessibility) and delayed effects.

6.3.2 The state of things

One should note that the doctoral funding associated with this thesis started in October 2021 and ended in March 2025. In that span of time, the societal context has been particularly troubling, diverting us more than ever from the climate emergency and the biodiversity crisis: the COVID pandemic continued to kill (about 2 million deaths in 3.5 years), Russia started its nation-wide invasion of Ukraine, still ongoing as of typing, AI Large Language Models and image generating software were made available to the larger public, the bombing of the Gaza strip occurred in deafening indifference, the Paris 2024 Olympics were a surprising success, launching mediatic discussion on the safety of the waters of the Seine River, Donald J. Trump was elected to lead the American people, among other pieces of news. The last weeks of writing this manuscript felt historically significant in particularly nauseating ways, as the richest person in the world performed a rather significant gesture on stage at the inauguration of the American President, as crowds cheered and borders tightened. The rise of fascistic rhetoric in developed nations, and the ensuing shift of the Overton Window (Beck, 2010), toward the far right, is to be explicitly linked to multiple far-right reactions to the global climate and biodiversity crisis, from denialism and disinformation to the many forms through which environmentalism is co-opted by fascists, from eco-fascism (Ross & Bevensee, 2020) to jingoistic naturalism (Bryant & Farrell, 2024), none of them compatible with incremental restoration of riverscapes. This inherent instability in our political future is noteworthy, beyond its many political implications, to the qualification of our scenarios, through chosen management, which become extremely unlikely under certain political administrations.

This thesis spanned through the respectively 9th (2021), 8th (2022), 2nd (2023) and 1st (2024) years in terms of positive temperature anomaly compared to preindustrial averages, with 2024 beating the ultimate record by a wide margin, exceeding pre industrial averages by 1.6°C and 1991-2020 averages by 0.72 °C (Copernicus, 2024). In Europe specifically, temperatures were 2.92 °C higher than pre-industrial averages and 1.47 °C before 1991-2020 averages. This record threw off even climate scientists, who expected lower temperatures due to a La Niña comeback.

In building predictor datasets for future conditions, we relied on climate projections, as well as watershed management scenarios, to show the ways in which climate change and watershed management may influence river fish distribution in the future. Both climate projections and scenarios fall into the pop-science-friendly discipline of futurology, a subject we would like to expand on. Futurology is an appealing field of study for many reasons, some academic and some not so much, as it intends to create reliable methods to either foretell future events or to think about their likelihood and consequences. It is, however, intuitively difficult to give scientific sense to academic projects concerned with the future, in part due to the inherent unpredictability of future events and multitude of unimaginable paradigm shifts that may occur at any point in the near or further future. The frameworks installed to discuss the future must be kept in mind when commented lest we overextend the reach of associated results.

6.3.3 Climate change, projections and uncertainty

The set of climate projections we obtained from the Explore2 project (Marson et al., 2024) were discussed in Chapters 4 and 5. These projections were treated as plausible descriptions of the future climate conditions under the paradigm of a RCP 8.5 radiative forcing scenario. The models from which climate data were extracted are the result of a large and recent effort of model selection and bias correction over France within the Explore 2 project. These four projections have features in common, namely warmer air temperature than early 21st century averages. However, these projections also differ in significant ways, which our results showed had drastic consequences on potential future fish distribution. Two of them (B3, C2) are characterized by warm and dry summers (an average temperature increase of approximately 6 °C and 35 % lower precipitation by 2070-2100), C2 exhibiting wetter winters, the two others (A1, F9) being milder in these terms (4 °C / 5-10 % lower precipitation), F9 exhibiting drier springs. We found that seasonal variations in climate had a visible impact on fish conservation, for example that drier seasons were linked to lower presence of fish, and that climate contributed predominantly to the explanation of the prediction of fish distribution.

We can use these projections to discuss the likelihood of climate futures and corresponding projections, in the limits of our capacity. In Chapter 5, we have shown that the breadth of projections selected for this thesis, despite their relatively narrow, realistic outlook (they were carefully selected within the bounds of CMIP6 predictions for temperatures and precipitations), were the main component of uncertainty in most selected species. This uncertainty is meant to represent the broadness of projections selected for modeling, and their consequences on fish species. The uncertainty linked to the multiplication of relevant climate projections must be discussed in association with the uncertainty of the climate models themselves. It can be extracted from the combining of a large number of climate models, and has been shown to be particularly problematic to our study area. France is situated in an intermediary geographical area within Europe, namely between a Northern part that is likely to become wetter, and a Mediterranean area that is likely to become drier (Fig. 24 below, from the IPCC, consulted in 2025). Therefore, our study area is still subject to high uncertainty in both rainfall and resulting discharge, as recovered by the IPCC and Explore 2, which we must keep in mind when interpreting precise results, but also may explain the, still, wide breadth of projections used in Chapters 4 and 5..

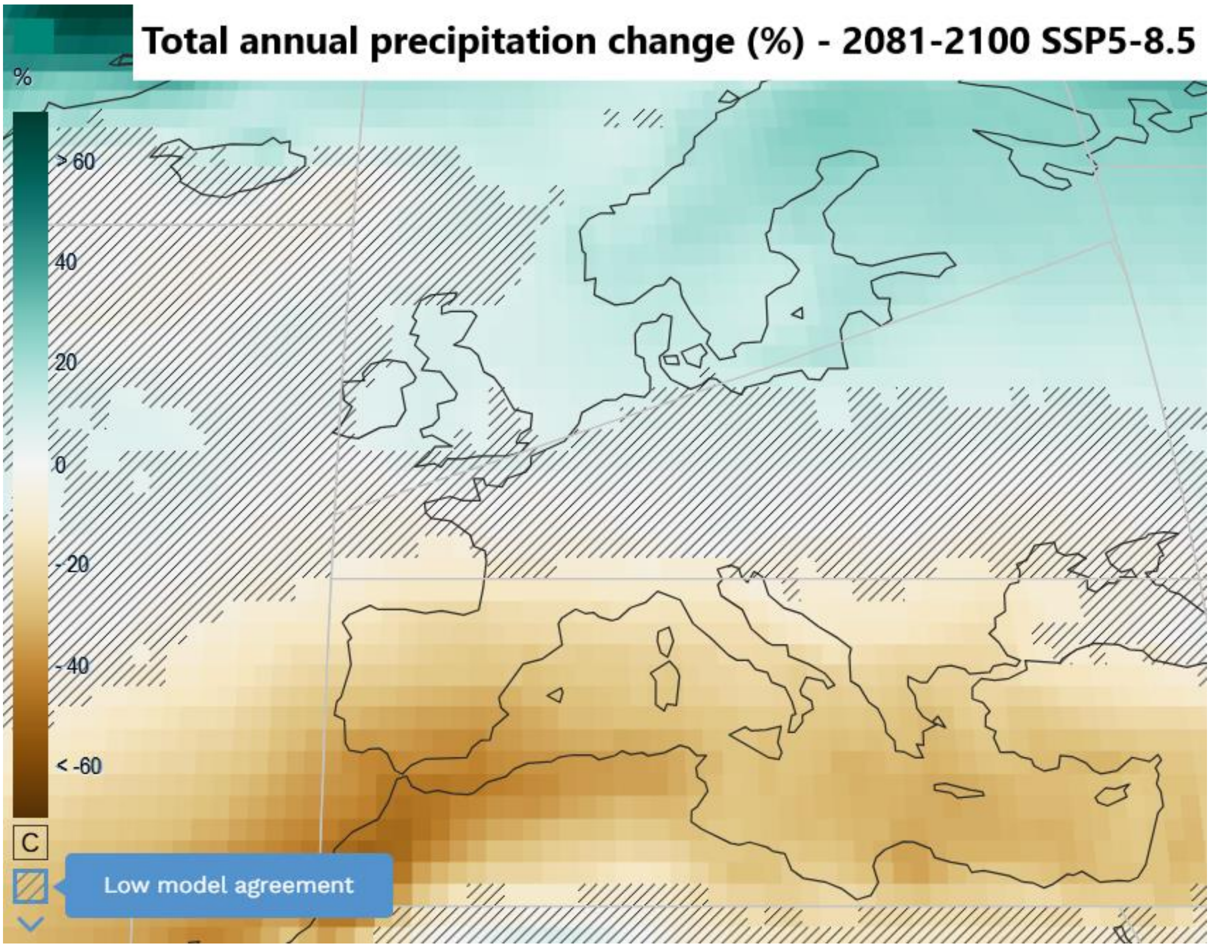


Figure 24: Multimodel average of total annual precipitation change (%) - 2081-2100 - hatched area showcasing low model agreement - CMIP6 projections (IPCC, 2025).

Projections chosen for this project cover different climate futures for our study area, with no lead as to which one is more likely. These projections aim at proposing coherent pictures of plausible futures, which stakeholders can make use of to lead a reflection on the adaptation of their territories. Some overarching caveats to mention as well, in this discussion, are the assumptions that are made by models used, with respect to larger, unplanned or unaccounted for phenomena. For instance, the sea-level rise was not explicitly included as a variable, and for the sake of simplicity, its consequences on coast line, flood likelihood, as well as land use in coastal environments, were not directly computed, because the amount of study sites near coastlines was negligible. Finally, the RCP 8.5 scenario, used in our work, although widespread in research, is not deemed most likely within the RCP approach, merely a pessimistic scenario of climate inaction and business as usual (Harrisson, 2019). We thus wish to emphasize that future climate as it is treated within this thesis is to be considered within these methodological limitations.

6.3.4 Watershed management scenarios

Although software can be used to predict future land cover under IPCC Shared Socioeconomic Pathways or SSP, see Brunner (2024), in large scale studies, or in highly simplified situations (Veldkamp & Verburg, 2004). The complexity of land use mosaics and many intricacies in the political and sociological factors which determine land use change in highly anthropized watersheds precludes the creation of simple modeling approaches predicting land use change in relatively short spatial units and long spans of time.

When modeling approaches, as used for climate, are not available, as in the case of land use and management, thinking about the future needs to come with a lot of precaution - all declarations of certainty concerning the future must be taken as overconfident as a principle. We wished to impart on the reader that the use of watershed management scenarios allows for a framework that circumvents the problems that come with uncertainty, by building plausible stories instead of relying on a sparse knowledge of future events - the uncertainty allows us to assess the consequences of scenario variability and demonstrates clearly the problems with single future approaches, while at the same time providing more space to explore several plausible scenarios. Thus, instead of a corroborative framework of prediction for land use, an anticipatory one if preferred (Maris et al., 2018). Also standing against this framework is a tendency of content both vulgarized and academic to employ prescriptive language, which necessarily brings assumptions to possible future events and narrows the possibilities one can explore. Nevertheless, as for climate projections, we believe that discussing the adequation of our chosen scenarios to realistic trends is essential to make sure uncertainty is considered with reasonable bounds and to generate discussion based on management options.

The main phenomena portrayed in our scenarios are land use change, barrier removals and riverbank restoration. A first observation that is made both in Chapter 4 and 5 through different approaches is the overwhelming impact of climate change on watershed management. Still, in many species, our scenarios led to noticeable modifications of species distribution, or were associated with a greater contribution to uncertainty. Watershed management and its many intricate issues should thus be handled properly: they seem to have some effect to combat fish decline, as long as appopriate measures are taken, and in some study sites or geographical subunits, they might remain more decisively important than climate change to safeguard native freshwater species.

Our results showed that scenarios least focused on restoration were overall least favorable to selected species, but also, and quite surprisingly, that the "Environmental Planning" scenario proved unfavorable to some species, although these results may indicate a need for finer detail in scenario building and be linked to overall lower model performance for these specific species, as discussed in Chapter 4. If we now consider the current trends in river engineering to assess the breadth of the change in policy necessary to produce these outcomes, we can note that current texts and recommendations like the WFD and local management plans, which include barrier removals and restoration operations, are taken into account by local actors. Also, based on Dam Removal Europe, we note that yearly count of barrier removals in France currently oscillates between 80 and 170, with a trend upward (France being regularly the primary barrier remover within the EU and a total of 95,000 barriers still remaining in France). So, assuming a continuing trend, a guesstimate of barrier removals, by the year 2100, of circa 15,000 to 30,000 can be considered realistic, although the depletion of easily removed barriers within French basins may put a break on future removals. With this in mind, our most extreme scenarios (Faucets and Pipes, and Ecological Planning) both require the most deviation from current trends and drastic policy change, while our "Production and Self-reliance" scenario edges closer to this window. Beyond local opposition, a notable conflict when it comes to barrier removal is the opportunity of building small hydro-electric power stations on existing structures. This potential brake on barrier removal differs from others in that it is narratively consistent with more environmentally-conscious scenarios despite their negative impact on fish presence. Smaller hydroelectric power stations are generally built through the initiative of a private landowner and it remains impossible to know if their increasing popularity will keep steady in the following decades. A more contentious example concerns the use of fish passes, which have been proven to be effective to allow a fraction of fish to pass otherwise obstacles when well-designed, providing an intermediary solution between kept barriers and full removal, but might necessitate close supervision (Pompeu et al., 2012; Prince, 1914). Indeed their efficacy is highly variable depending on species and discharge (Bunt et al., 2012) and thus their function is contingent on future conditions.

When it comes to land use, current trends tend toward a continuing artificialization of soils within construction projects, despite the goal of net-zero soil artificialization by 2050 entering law in France. While scenarios “Faucets and Pipes” (FP), “Production and Self-reliance” (PS) and “Respectful Executant” (RE) plan for increased soil artificialization, scenario “Ecological Planning” EP plans for a net reduction in impermeable surfaces. Thus, scenario EP requires a significant change either in human demographic trends, occupation rates of available housing or political paradigm to be feasible while the others do not. This same scenario plans for an increased proportion of natural space within the basin, causing a drop in agricultural and urban surfaces, which too is to require planning, change in flow of consumer goods and agricultural resources.

Agricultural land was only considered to be expanding in scenario FP, the one most distant from desirable environmental considerations and predicted to be uniquely damaging to some species. Here we wish to include climate change in our thinking. Indeed, beyond concepts of likelihood of one scenario or another, the question of realism and feasibility comes to mind when integrating climate change in our thinking. Currently, the main agricultural hub in our study area is the Beauce plain, which receives very little rain compared to other parts of the country and is generally shown to receive even less in future summers. An eventual increased likelihood of droughts due to climate change may render these regions unusable for intensive agriculture, or require much larger amounts of irrigation water, an assumption that was made in building scenarios, but which may be impractical in real life. Similarly, lowering discharge is already to this day a major roadblock for barrier removals and is bound to remain in the future, by providing erroneous justifications for the keeping of dams, which create visible reservoirs. Conversely, hypothetical lower flow predicted by some models, including some of the selected projections, is due to make attempts at hydroelectricity increasingly less profitable and efficient. As shown, management scenarios may present some practical incompatibility with certain climate projections and in discussing results. One should keep a critical eye on certain combinations of scenarios and climate projections, but a more interesting perspective for scenario building may be to ask, as we did for the Beauce region, if, while faced with these incompatibilities in the future, the reflex of polities will be to double down (e.g. increasing irrigation in drying steppes climates) or to truly reform land use in relevant territories. More generally, interactions of land use, management and climate change are complex and barely known (Oliver & Morecroft, 2014), yet they must guide and question management decisions. The process of prioritization of dam removal, for example, may gain to be informed by climate change (Beatty et al., 2017). Indeed, as we discussed briefly in Chapter 3, some species may benefit from artificial lentic habitats, and this may be especially true in a context of climate change.

We wish to reiterate that the purpose of this section is not to pass judgment on the futures we studied by deciding which one is to truly happen, but to highlight the complexity and breadth of the necessary policy efforts needed to reach certain desirable futures. We argue that the use value of management scenarios must be separated from their likelihood, as long as they are internally consistent. An interesting approach in that sense is Barles et al. (2024), which provides a reflection on the political reforms and systemic change necessary to bring forth, by 2050, a more environmentally-friendly, ecologically-conscious economic and political organisation on the basin. The use of a transdisciplinary approach is aimed at producing two scenarios heavily based on political organisation, one centred on regional growth and circular economy, the other proposing a multiscale management of basins and drastic political change. They explicitly express their intention not to qualify these scenarios as likely scenarios for future territorial management. The burden of proof regarding past political inertia would cause doubt in the least cynical reader, but these scenarios could be used as a basis for discussion, as radical change is more than useful in this context (see the next section).

6.4 Applications and perspectives

We have spent a few sentences highlighting both the ways in which this thesis has brought novel results to the field of river ecology, proving that connectivity indices had the potential to improve our understanding of fish distribution in highly anthropized rivers through the use of connectivity-sensitive models, and that higher connectivity favored the presence of most studied fish species. We have also shown the advantage of opting for watershed management scenarios as a methodological basis for the prediction of species distribution, and the complex consequences of watershed management decisions on fish survival in a context of rapid climate change.

Discussing the reproduction of our results and observations as we did above leads us to reflect on the opportunity that replicating the same kind of protocol on different geographical areas may bring. This project was conducted during three years by a team of supervisors and one student, and limited by the temporal, technical and academic means at their disposal. For example, works like (Barles et al., 2024) on fleshed out management scenarios, which requires substantial work in political science, sociology, agricultural sciences, economy and biogeochemistry, would allow for a precise crafting of management scenarios with greater geographical complexity. Similarly, the information that in-depth study of social interactions between local and regional actors in the field would bring for their construction, or co-construction with multiple actors in broad workshops, which require time, resources, and a background in political and social sciences, would be invaluable to a scenario-based prediction process for fish species in a neighboring or faraway basin. The process described above, if open to transdisciplinary contribution, would broaden the scope of the work conducted.

This thesis yielded results which we deem of immediate interest to ecologists and ichthyologists alike, but we deem important to dwell on more practical applications as well. The scenarios themselves, and the visual aid provided in Chapter 4, can be used in two ways. First, they can be used as a framework which can be updated and used by different projects working on the future of Seine-Normandie watercourses, where their simplicity and straightforwardness can be an advantage; second, these scenarios can be useful as a material to open discussion efforts between various actors on a selected drainage basin, although the format of scenarios used in that context may be quite different, and rely on more visual approaches, as exemplified by Barles et al. (2024), which provides didactic content to facilitate interactions around proposed scenarios. The results of our model outputs can also bring interesting elements of discussion. We show that climate change is due to cause drastic shifts in fish communities, and that certain management decisions may drastically affect fish communities. In a purely academic setting, we deem the conclusions of this thesis to carry their weight, they can inform that way in which future management should be conducted, or confirm certain management decisions, warning against others. More pointedly, barrier removal as an operation is amply proven as a judicious operation for fish conservation both inside and outside this thesis.

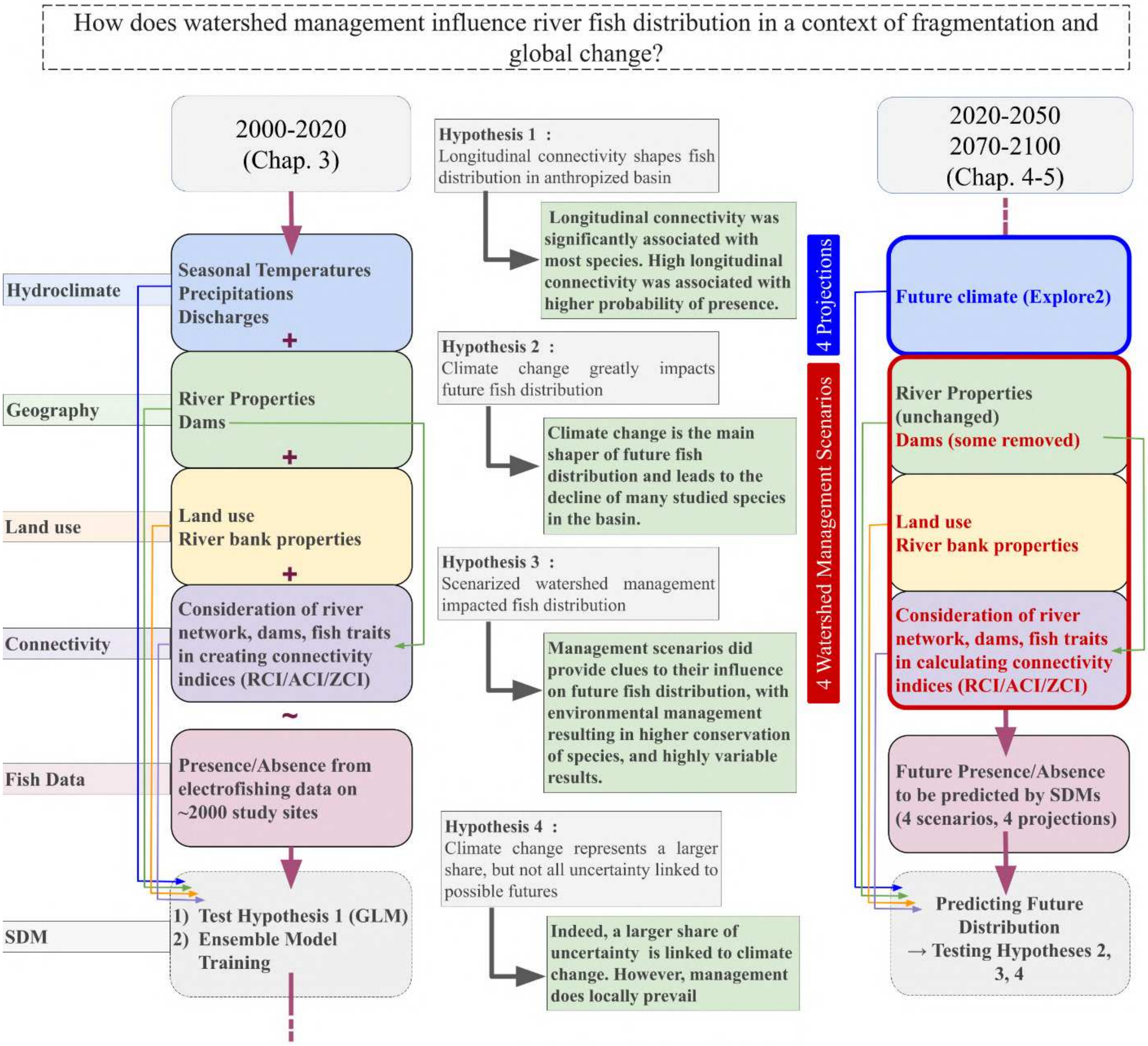
However, we must warn that the sometimes complex results, especially those within Chapter 4 and 5, and the limits within which they can be interpreted, can easily lead to overinterpretation or misinterpretation of data. The fact that our ecological planning scenario has been recovered as unfavourable for some species due to reasons discussed in Chapter 4, for example, could easily be misinterpreted or overinterpreted by an outside actor with special interest as a larger sign that giving up on the most ambitious environmental measures is the way to go - when more general studies on wildlife conservation and human quality of life point to the opposite. Similarly, some results heavily discussed in Chapter 4, related to species like the trout and the minnow, which tend to show higher rates of decline for scenarios designed as environmentally-friendly, should only be considered in the context and discussion that surrounds them, as we point at lower model performance, eventual flaws in scenario design and atypical distributions among other causes which may in part explain these results and diminish the impact of hastily taken conclusions.

Thus, we wish to impart to the reader the need for careful consideration when sharing this thesis's main conclusions and more precise results, in particular with respect to the ways in which they could be used.

Finally, and on this ponderous note, we wished to close this thesis on a brief word regarding the state of things. A reader studying, from up close or afar, the effects of human activity and anthropogenic climate change on our ecosystems and societies, will be familiar with the insidious sense of doom that recent events and current academic consensus may occasionally bring. As of writing, the French Office for Biodiversity (OFB), an essential piece of the public sector for the conservation of wildlife and monitoring of private practices, is the subject of a campaign of vilification, originating from powerful private actors but now also found in a portion of the political spectrum, including the current (as of January 2025) French Prime Minister (Mouterde, 2025). This new development occurs not in a vacuum but in a broader context of slowed economic growth, political instability, growing discontent and backlash against environmental measures. Although there is existing proof (Bolet et al., 2024; Colantone et al., 2024; Stokes, 2016) that the so-called “green backlash” is in fact mostly manufactured by large groups and broadly unpopular within the public, those same sources point to the importance of communication to local actors to ensure the efficacy of environmental measures, although we should mention the potential change in discourse with respect to environmental management that may be associated to a shift of public discourse toward the far right, as mentioned above and amply anticipated in our FP scenario, which may render this state of affairs outmoded. We also wish to point out that despite this current lack of public support for a return on environmental measures, the vested interests of the private sector may lead to equivalent conditions. The successive divestments of the Environmental Protection Agency (EPA, US Government) and public stance of American policymakers can be quoted, as well as the wish of some influential French politicians to completely remove the OFB from the state apparatus. This state of public affairs, joined with the never failing trend of rising temperatures, extreme climate events - take your pick - may lead to the aforementioned feeling of doom, a feeling that is dangerous in many ways, because it may lead to the thought that nothing can be done. “Doomerism”, as in the attitude of considering the end of things inevitable and all effort against it futile, is, in a sense, another form of denialism, because it leads to inaction when climate change mitigation and adaptation are crucial to overcome the coming and current crisis. As this thesis and many other pieces of academic writing have shown, the future of our planet is difficult to predict, and in this breadth of uncertainty lie the options for survival, which can be formulated in scenarios and policies, planned out through modeling, communicated through chosen graphical and textual approaches to a broader public to guarantee their transmission. Researchers in particular must continue to provide the tools for a successful transition - whether this includes activism in any way is another story - and succumbing to doomerism is in no way productive to achieving these goals. As discussed, it is through the sum of incremental operations of restoration, legislative measures, with great care toward local context and extensive preparation and research, that we can ensure the best possible results, with each piece of work a small cog within a larger system, within which we hope this thesis finds its place.

6.5 Conclusion

In endeavoring to understand the influence of watershed management on future fish distribution, identifying its effects in a context of inexorable climate change, we created tools to express longitudinal connectivity, and integrated them in novel connectivity-sensitive species distribution models. This new approach led to this thesis uncovering new evidence of the positive influence of high connectivity on the probability of presence of most fish species, as well as the negative effect brought by the fragmentation by anthropogenic barriers on watercourses. Using these new tools to build connectivity-sensitive ensemble models, we used selected climate projections and co-constructed management scenarios to predict potential fish distribution under diverse futures. We were able to check and often confirm the hypotheses upon which this thesis rested (see Fig. 25) and can now conclude that a) climate change was unambiguously prevalent in the determination of future fish distribution, causing widespread decline of common fish species and a large variability of outcomes, but b) management still bears some importance in the shaping of future fish communities, and although the links between environmentally-conscious management and species conservation has been not been found in all species, and precautions must be taken in generalizing our results, many responded positively to general efforts of restoration and ambitious policy for change. We intend for the results brought by this thesis to join many others in nervously gesturing toward the urgency for entities in charge of management and decision to take action, both in the mitigation of the effects of climate change and the restoration of riverine ecosystems, which may give the ever so vulnerable river communities of anthropized watersheds the edge they need to survive the onslaught of stressors the 21st century promises to bring onto them.



How does watershed management influence river fish distribution in a context of fragmentation and global change?

Hypothesis 1 : Longitudinal connectivity shapes fish distribution in anthropized basin

Longitudinal connectivity was significantly associated with most species. High longitudinal connectivity was associated with higher probability of presence.

Hypothesis 2 : Climate change greatly impacts future fish distribution

Climate change is the main shaper of future fish distribution and leads to the decline of many studied species in the basin.

Hypothesis 3 : Scenarized watershed management impacted fish distribution

Management scenarios did provide clues to their influence on future fish distribution, with environmental management resulting in higher conservation of species, and highly variable results.

Hypothesis 4 : Climate change represents a larger share, but not all uncertainty linked to possible futures

Indeed, a larger share of uncertainty is linked to climate change. However, management does locally prevail

Figure 25: A synthetic recap of the process of this thesis, including key methodological elements, steps and hypotheses in their context.

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(Introduction, Materials, General Discussion)

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Appendix: A global systematic map of knowledge of inland commercial navigation effects on freshwater ecosystems

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Review

A global systematic map of knowledge of inland commercial navigation effects on freshwater ecosystems

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Biodiversity

ABSTRACT

Inland navigation is one of the most sustainable transport alternatives to help decarbonise the world economy. However, the likely impacts of intensifying inland navigation on freshwater ecosystems are difficult to predict. A global map of knowledge that considers both abiotic and biotic responses to increasing shipping traffic and developing infrastructures is lacking. Deriving general evidence-based assessments is challenging, because most studies on inland navigation impacts are merely descriptive and either consist of local case studies, or address single navigation stressors or specific taxa only. We conducted a systematic mapping of the published literature (1908–2021) to provide a global synthesis of the effects of inland navigation on the biotic and abiotic components of freshwater ecosystems. We show that only half of the reported navigation-related impacts were statistically tested. Navigation itself (vessel operation) had mainly negative effects on native taxa (57%), followed by waterway management (40%), and navigation infrastructures (35%). Navigation has direct negative impacts caused by physical disturbances such as vessel-induced waves, and indirect impacts that facilitate the spread of aquatic invasive species, and altering the abiotic habitat conditions. Thirty percent of the tested relationships showed non-significant impacts on the biotic environment, while in 10% of cases impacts were context-dependent. We identified the main gaps of knowledge, namely (i) impacts of waterway management on communities, (ii) underlying processes of navigation impacts on river ecosystems; and (iii) interactions between multiple navigation factors and cascading effects on multi-taxa responses. These future research directions should improve the diagnosis, mitigate the negative impacts of navigation on rivers and provide guidelines for improving navigated river management.

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1. Introduction

Inland freshwater navigation is promoted as one of the most sustainable transport alternatives in the world (Rohács and Simongáti, 2007; Terziev et al., 2023) and a way to achieve carbon neutrality by 2050 (Barros et al., 2022; INE, 2020; Sys et al., 2020). For instance, in Europe, the European Union Green Deal aims to intensify and promote "green shipping" by improving, restoring or creating new Inland Navigation Infrastructures (INIs) such as canals, sluices, dams, locks, and ports (INE, 2019, 2014). Yet, the extent to which intensified inland navigation will impact river integrity and aquatic biodiversity globally is not clear.

Inland navigation can potentially affect all aspects of river integrity as well as the surrounding landscape (Némethy et al., 2022). It has direct and indirect consequences on ecosystem components by triggering secondary mechanisms that affect ecosystems. Indeed, the five major threats for freshwater biodiversity (Dudgeon et al., 2006) can directly or indirectly be driven by inland navigation and the construction and management of inland navigation infrastructures (INIs) - namely, water pollution (Floehr et al., 2013; Maguire, 1991; Weijters et al., 2009), flow modification (Bunn and Arthington, 2002; Tales and Boët, 2005; Wolter et al., 2004; Yang et al., 2023), habitat degradation (Blanton and Marcus, 2013; Wolter, 2001), loss of river connectivity (Belletti et al., 2018; Jones et al., 2020; Poff et al., 2007), and introduction of invasive species (Leprieur et al., 2008; Leuven et al., 2009; Magliozzi et al., 2020). Vessel operation directly disturbs aquatic species, by wake wash (Gabel et al., 2017), draw down (Holland, 1986), return currents (Wolter et al., 2004), propeller wash (Killgore et al., 2011), boat collisions (Miranda and Killgore, 2013), water pollution such as plastics (Climo et al., 2022), hydrocarbons (Gao et al., 2024; González et al., 2024), or salts from ballast water (Duan et al., 2023a), and noise (Duan et al., 2023b; Graham and Cooke, 2008). In addition, infrastructures supporting navigation (e.g., canals, sluices, and boat ramps) as well as waterway management and maintenance (e.g., water level regulation or dredging activities) impact the environment (Cowx and Welcomme, 1998; Lepori et al., 2005; Simons et al., 2001; Staentzel et al., 2020) and facilitate the spread of invasive species (Rodríguez-Rey et al., 2021). For example, while groynes and rip-rap change habitat for aquatic species (Bischoff and Wolter, 2001; Fischer et al., 2018), dams, weirs and sluices will influence their mobility and dispersal (Duarte et al., 2021; Robinson et al., 2019).

On the other hand, INIs can also support selected species and communities, by providing artificial habitats (Harvolk et al., 2015; Horsák et al., 2009), dispersal corridors (Ouédraogo et al., 2020), and preventing the spread of some aquatic exotic species (Favaro and Moore, 2015; Rahel, 2013). Thus, the relative effects of these three main types of navigation-related pressures (namely navigation activity, related-infrastructures and their management), and how they influence both biotic and abiotic components of the river environment are still unclear (but see Wolter et al., 2004) and are difficult to disentangle. Therefore, these effects deserve more attention to better identify and prioritise mitigation actions.

Further intensifying inland navigation will require the creation of new INIs as well as the restoration and upgrading of existing ones (EIWTP, 2021). To minimize impacts on riverine biodiversity a better understanding is needed on how such infrastructures modify water flow, alter habitats, affect river connectivity, and shape species communities by invasions and extirpations. Until now, most studies that addressed navigation impacts focussed on selected INIs, single taxa, or particular components of river integrity (Villemey et al., 2018; Zajicek et al., 2018) which makes it difficult to draw conclusions.

To provide a comprehensive assessment of the global impact of navigation, we carried out a systematic mapping of the scientific literature to provide a global knowledge map of the effects of navigation-related factors on biotic and abiotic components in river ecosystems while considering the robustness of the analysed relationships. The systematic map of knowledge "collates, describes and catalogues available evidence on the topic" and allows addressing open-framed questions (James et al., 2016) such as here, the links between navigation factors and river components. Our specific aims were to: (i) assess and summarise direct and indirect effects of navigation and INIs on river integrity, while explicitly differentiating between evidenced (i.e., statistically tested) vs. asserted (i.e., with no statistical support) results; (ii) comparatively analyse effects of all three navigation-induced pressures – navigation, infrastructures, and waterway management – on abiotic and biotic components of river ecosystems including native and exotic taxa; (iii) identify main gaps in knowledge and propose future research fields to make mitigation actions more effective.

2. Material and methods

2.1. *Literature search and articles selection*

A systematic literature search was done on the September 16, 2021 in ISI Web of Science Core Collection and Scopus, which are considered the main reference sources (Mongeon and Paul-Hus, 2016). The literature search focused on articles published in English between 1900 (first selected paper in 1908 according to Scopus, and in 1983 according to WOS) and 2021. Following methodological recommendations for systematic mapping (e.g. Foo et al., 2021; James et al., 2016), the literature search was conducted using the PECO strategy for systematic search that is considered to be the most powerful and reproducible approach for formulating research questions (Miller and Forrest, 2001; Sordello et al., 2019). The PECO method (Population Exposure Comparator Outcomes) requires the formulation of the research equation including four main aspects: the ***P***opulation object of the study (here inland freshwater ecosystems), the ***E***xposure (here navigation), a ***C***omparator (here any comparator that can reflect a relationship), and the ***O***utcomes or focus of the effects (here biodiversity in the broad sense). The literature search was applied on titles and abstracts using the search equation shown in Fig. 1a (see also **Appendix S1**).

The initial literature search returned 15,058 published articles in Web of Science (5,696) and Scopus (9,362). To analyse and filter this corpus of articles, we then used the PRISMA approach (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Page et al., 2021) (Fig. 1b). After removing duplicates, article titles and abstracts were manually screened and articles were included for further analysis if they met the following eligibility criteria: (1) peer-reviewed (journal articles, reviews and book chapters), (2) dealing with inland navigation, i.e. excluding marine and coastal ecosystems, and (3) having mentioned, discussed and/or analysed a relationship between any navigation factor (i.e. inland navigation, navigation-related infrastructures, or their management and maintenance) and any river biotic response (e.g., biodiversity, vegetation, fish) in the abstract. Articles that focused their analyses on the abiotic response of the river were kept as long as they highlighted the implications of their findings for the biotic response of the river. This first screening retained 506 articles. Then, a second screening was carried out excluding (1) articles that did not directly analyse the impacts of inland navigation rather than evaluate the effects of measures to mitigate or rehabilitate navigation effects were excluded from the analyses (N = 39 papers); and (2) articles dealing with recreational boating, because its impact on the river environment is not comparable to the impact of commercial navigation (Söhngen et al., 2008) and the topic has already been analysed at large scale by Zajicek and Wolter (2019) as well as synthesized by Schafft et al. (2021). All the manual screening was carried out by a team of 18 researchers, experts in freshwater ecology (NAVIDIV consortium). A final cross random screening procedure was carried out by two of the experts to check the inclusion consistency (i.e. each member was assigned two papers initially screened by another member and had to check the inclusion validity – in case of conflict, the member initially in charge of this paper had to verify again their list of papers and revise it following the inclusion rules of the group). The final number of articles included in the systematic review after full-text analysis was 243 (Fig. 1b).

2.2. *Information extraction*

2.2.1. *Geographic and sampling context*

The final 243 articles retained were full-text analysed for information synthesis. We recorded geographic origin and sampling context, including: (1) country and catchment, (2) type of hydrosystems (river, canal, lake, reservoir, floodplain, and pond as the most frequent options) and, its name, (3) spatial extent of the study, and geographic coordinates when available, (4) number of sampling observations, (5) length of river stretch that was sampled and/or analysed by the papers (based on maps and/or protocols provided within the original papers, when applicable), and (6) duration and frequency of sampling.

2.2.2. *Navigation-related factors*

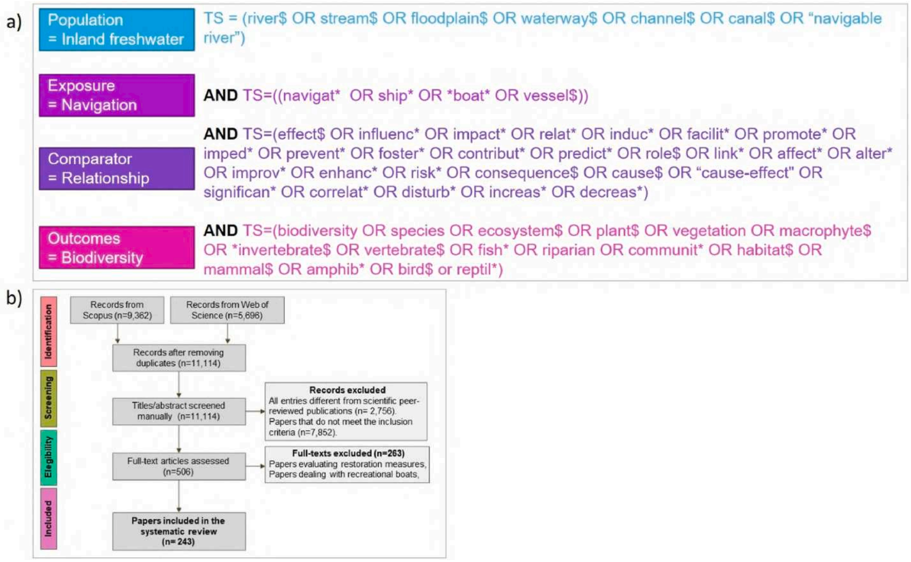
We then identified the navigation-related pressures analysed and found 22 navigation-related factors. These were further classified into three main groups: navigation itself, navigation-related infrastructures and waterway management (Table 1). Navigation itself, hereafter navigation, refers to vessel operation and its direct physical consequences, such as wake wash, draw down, return currents, or noise generation. Navigation-related infrastructures, hereafter inland navigation infrastructures (INIs), refer to those pressures caused by the constructed infrastructures needed to enable or facilitate the navigation, such as locks, canals, channelised rivers, or ports. Finally, waterway management refers to those actions needed to maintain the adequate conditions for navigation such as dredging activities, regular vegetation cutting or water level management. Because some articles analysed combined navigation-related factors, such as the ensemble of shipping activity in canals, or of lock existence plus lock operations, a fourth category was created as the mix of multiple navigation-related factors (Table 1).

Table 1
Classification of the 22 navigation-related factors into four main groups: navigation itself and its direct physical consequences (NAVI), navigation infrastructures (INI), waterway management and maintenance (MANAG), and the mix of multiple navigation-related factors (MULTI).

Group/navigation-related factor	Definition
Inland Navigation (NAVI)	
SHIP	Shipping activity as a general factor, presence of ships
TRAF	Traffic as a quantitative measure of navigation activity, number of ships per time unit
WAVE	Waves, propeller wash and drawdown due to boat passage (WAVE + PROP + DRAW)
STRIK	Strikes by boats or boat propellers
POLL	Chemical pollution
AC.POLL	Acoustic pollution
BALL	Ballast water and solid ballast (BALL + SOLID.BALL)
MULTI_NAVI	Mix of multiple navigation-related factors
Inland Navigation Infrastructures (INI)	
CAN	Canals - as new river connections
CHA	Channelised river - as modified river stretch to allow for navigation
MODIF	Large-scale river bed modification to allow for navigation, including both channelisation, floodplain modifications and infrastructure development
LOC	Locks and sluices (LOC + SLU)
DAM	Navigation dams, weirs and bridges (DAM + WEI + BRI)
EMB	Embankment
IMP	Impoundment
PORT	Ports
YARD	Shipyards
MULTI_INI	Mix of multiple INIs
Waterway Management and Maintenance (MANAG)	
DRE	Dredging for building or maintaining waterway navigability
LEV	Water level regulation
FLOW	Flow regulation
BWTS	Ballast water treatment
VEGCUT	Vegetation cutting
LOCOP	Lock operations for ship passage
MULTI_MANAG	Mix of multiple waterway management or maintenance factors
Multiple Navigation-related Factors (MULTI)	
MULTI	Mix of multiple navigation-related factors across NAVI, INI and MANAG (e.g. SHIP + CAN, LOC + LOCOP, etc.)

2.2.3. *Biotic and abiotic responses*

Biotic and abiotic responses analysed in the articles were identified. For biotic responses, we extracted information such as the taxonomic group (e.g., fish, macrophyte, or invertebrates); the level of organisation at which the analysis was carried out (e.g., individuals, populations, or communities); and the response metric analysed in the navigation-response relationship (e.g., mortality, abundance, or species richness;



TS = (river$ OR stream$ OR floodplain$ OR waterway$ OR channel$ OR canal$ OR "navigable river")

AND TS=((navigat* OR ship* OR *boat* OR vessel$))

AND TS=(effect$ OR influenc* OR impact* OR relat* OR induc* OR facilit* OR promote* OR imped* OR prevent* OR foster* OR contribut* OR predict* OR role$ OR link* OR affect* OR alter* OR improv* OR enhanc* OR risk* OR consequence$ OR cause$ OR "cause-effect" OR significan* OR correlat* OR disturb* OR increas* OR decreas*)

AND TS=(biodiversity OR species OR ecosystem$ OR plant$ OR vegetation OR macrophyte$ OR *invertebrate$ OR vertebrate$ OR fish* OR riparian OR communit* OR habitat$ OR mammal$ OR amphib* OR bird$ or reptil*)

Fig. 1. Literature search and analysis. *a) Literature search equation used for Web Of Science following the PECO search strategy. Note that $ should be replaced by * when search is performed in SCOPUS database (see* ***Appendix S1****). b) PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow diagram* (Page et al., 2021) *showing the procedure of article selection applied after the literature search.*

full table available here: https://doi.org/10.57745/N6Y6QR; Jeliazkov, 2024).

In particular, we carefully considered the status of the taxa analysed, namely either (1) natives, (2) exotics (including invasives), (3) both (for communities mixing both natives and exotics), and (4) unknown.

For abiotic responses, we noted the variables of interest (e.g., salinity, water temperature, conductivity) and their units. Given the high diversity of variables studied, we grouped them for synthesis into eight broad categories: 1) acoustic environment or noise, 2) flow conditions, 3) geomorphological conditions, 4) habitat characteristics, 5) soil characteristics, 6) water conditions, 7) bank characteristics, and 8) mixed (a mix of several responses) (Table 2).

2.2.4. *Characteristics and testedness of the relationships analysed*

Each individual relationship between a navigation-related factor and a river component analysed was listed along with the particular response metric analysed (fish species richness, vegetation composition, dissolved oxygen, etc.). In addition, evidence of impact was assessed based on statistical testing procedures reported in the paper. An effect was considered evidenced if it was statistically tested; otherwise, the purported effect was considered asserted (i.e., without statistical support). All statistically tested relationships were coded as “negative” (NEG), “positive” (POS), “non-significant” (NS), “change” (CHANGE) when the relationship significance or sign varied depending on a third factor, e.g. location, river, level of alteration, species considered, nonlinear behaviour, etc., or “unclear” (UNK) when the sign of the relationship was ambiguous, not reported or inappropriately interpreted (e.g., a discussion affirming an effect that is not supported by the raw figures). All asserted relationships were similarly coded as “negative” (NEG), “positive” (POS), “no effect” (NS) when authors explicitly discuss neutral effect/absence of effect, “change” (CHANGE) when authors explicitly mention that the relationship depends on other factors, or “unclear” (UNK) when the authors remain elusive about the effect discussed.

Each individual relationship was the statistical unit of observation in the present study, and the main focus of the following analyses. Although some papers analysed and presented multiple relationships, 75% of the papers analysed less than five relationships (Fig. S1). All information was extracted and compiled into a single data table (see original data available in Jeliazkov, 2024).

Table 2
The eight categories of abiotic responses considered in the synthesis and examples of response variables included in these categories.

Category of abiotic response (label)	Examples of responses studied
Acoustic environment/noise (Acoustic)	Sound duration; sound frequency; mean number of sounds per day; spectral density
Flow conditions (Flow)	Wave energy; wave height; flow velocity; water level fluctuation; Indicators of Hydrologic Alteration; bed shear stress
Geomorphological conditions (Geomorpho)	Water depth; river width; geomorphological dynamics; river bed erosion; morphology; fluvial forms
Soil characteristics (Soil)	Organic matter content; sediment size; silt-clay fraction; contaminant concentrations; sedimentation rate
Water conditions (Water)	Water turbidity; water quality indices; pH; dissolved oxygen; temperature; conductivity; ionic concentrations
Bank characteristics (Bank)	Bank erosion rate, retreat, stability; riverine habitats; sand bar size (excluding in-water habitats and mainly taxon-unspecific environmental characteristics)
Habitat characteristics (Habitat)	Habitat availability; habitat structure; habitat suitability; environmental change; floodplain area; spawning area (including both riverine and in-water habitats and mainly taxon-specific environmental characteristics)
Mix of several responses (Mix)	Habitat and substrate; water and river bed conditions; soil, topographical, flooding dynamics, biotic and abiotic parameters (Note: Usually, these fuzzy responses are not tested but mainly discussed.)

2.3. *Data analysis and synthesis*

The final corpus of 243 articles included 89% empirical research articles (including 10% experimental articles), 8% review/synthesis/opinion articles, and 3% simulation/analytical modelling articles. These articles reported in total 1103 navigation-river ecosystem relationships, which constituted our dataset for assessing and synthesising the current knowledge on the effect of navigation-related factors on river ecosystems.

First, to assess the knowns and the unknowns about navigation effects on river ecosystem, i.e. the potential imbalance in actual evidences, we counted and graphically compared the proportions of relationships evidenced vs. asserted across the different types of navigation-related factors, response types (biotic vs. abiotic), biotic compartment (non-natives, natives, or both), and taxa (fish, invertebrates, etc.).

Second, to quantitatively synthesize the evidence of navigation-**biotic** relationships, we focused only on the statistically tested relationships ($N = 564$ relationships) for each biotic compartment (natives, exotics, and both) and calculated the proportion of relationships reported as negative, positive, non-significant, unknown, and changing across the four categories of navigation-related factors INI, NAVI, MANAG, and MULTI. All data analyses were performed in R (R4.3.0, R Core Team, 2023). To assess whether there is significant imbalance of effect signs across navigation factors, we statistically compared these proportions using Pearson’s goodness-of-fit Chi-squared tests for count data (function ‘chisq.test’ in package {stats}) with a threshold p-value of 0.05. We further tested the relative dominance of the effect signs (negative [NEG] vs. positive [POS] vs. changing [CHANGE] vs. non-significant [NS]) with separate Chi-squared tests on each combination of navigation factor by biotic response when the sample characteristics allowed it (i.e., expected counts for each factor combination$\geq$5, which excluded all UNK effects). Given the limited sample size for the evidenced **abiotic** responses (77 evidenced relationships for 8 categories), we only explored the number and signs of the relationships graphically for each combination of navigation factors and abiotic responses.

Finally, to draw the map of knowledge, that is, the schematic representation of the hypothesised causal relationships between navigation factors and biotic components, we used the proportions of relationships calculated above and kept the two most supported ones for each factor-response couple to facilitate figure reading. For instance, 40%, 21%, 19%, 15%, and 5% of NAVI-Exotics relationships were reported as POS, NS, NEG, CHANGE, and UNK, respectively. Then we included the two most frequently observed links on the map, i.e. POS and NS.

It is worthy of note that first, we are creating a systematic map of knowledge and not a meta-analysis. To synthesize data that are mainly textual and/or categorical, and to more deeply review the broad topic of navigation effects on rivers, the principle of systematic mapping was the best compromise between a fully narrative, qualitative literature review, and a quantitative analysis fulfilling the strict constraints of a meta-analysis (Haddaway et al., 2016; Miake-Lye et al., 2016). Especially as we already know there are too few papers fulfilling these constraints on our topic (Ouédraogo et al., 2020; Villemey et al., 2018). The systematic map allows us to use our evidence collection to address an open-framed question (Haddaway et al., 2016; James et al., 2016) - namely the impacts of navigation on river ecosystems - and does not target effect sizes analysis. Therefore, our analyses are contingent on the categories (or ‘knowledge clusters’ (James et al., 2016)) that emerged from our evidence collection, such as the three main types of navigation factors, or the eight types of abiotic responses of the river environment. Second, we used a ‘vote counting’ approach (Koricheva and Gurevitch, 2013;

Siddaway et al., 2019), where we synthesized the counts of positive, negative, and non-significant navigation-environment relationships. This can be problematic when one does not account for potential differences across studies in statistical power nor reliability of the methods used to test these relationships (Haddaway et al., 2020). In our case, the differentiation we made between evidenced vs. asserted relationships allowed us at least to distinguish two levels of reliability among the examined studies. In addition, we did not detect many papers with noticeably low statistical power; the rare ones that aroused severe doubts were classified as "unknown/unclear" (UNK). Thus, the positive and negative counts – focus of the map – should not be severely biased by the 'vote counting' approach. The count of non-significant effects is interpreted with caution (see *Discussion*), that is not necessarily as an evidence of absence of effect, but rather as insights on the knowledge gaps and study limitations. Questioning further the validity of the studies would equate discrediting the peer-review process that these studies underwent, which seemed rather counter-productive given our objective of first attempt of comprehensive, qualitative knowledge mapping. Furthermore, the extensive metadata information provided in the synthesis table, such as sample size, methods of analysis and comments we made (see original data in Jeliazkov, 2024) will allow the readers to easily check the studies and make their own critical appraisal about those. Finally, another limit classically criticised in any literature syntheses (including meta-analyses) is the reporting bias, where non-significant results would be under-reported, resulting in biased conclusions about the importance of the effect studied (e.g., Kotiaho and Tomkins, 2002). Our approach of dissecting each study and extracting each individual relationship evidenced vs. asserted precisely allowed us to detect the many instances of non-significant results, and even the unexpected ones, which are reported in the figures but not necessarily put in the front by the authors. Therefore, we can be confident that our literature synthesis has managed to detect a substantial and representative part of the complexity and depth of the topic. Due to this relatively good representativeness, our focus on the academic evidences, and the difficulty to access and process non-academic evidences without any country/language bias, we did not add grey literature to our systematic map (Livoreil et al., 2017).

Data accessibility statement:

The data and code supporting the results have been archived on the public repository recherche.data.gouv and are available at: https://doi.org/10.57745/N6Y6QR.

3. Results

3.1. General overview of navigation-environment studies

Studies of navigation-environment interactions were published across the globe with highest numbers from North America, Europe, and China (Fig. 2). Still, we noted four inter-continental studies that covered mainly Europe and North America (Audzijonyte et al., 2008; Czerniejewski et al., 2012; Marescaux et al., 2016; Nagrodski et al., 2012).

The total river length studied varied from several metres to 100,000 km (Fig. 3a). The temporal extent in terms of monitoring years varies from "snapshots" (single observation in time) to more than 100 years with historical data (Fig. 3c). Most relationships involved a biotic response (85%), while 14% evaluated an abiotic response, and 1% a mixed response (Fig. 3d). The majority of navigation-biotic relationships concerned fish and invertebrates (Fig. 3e), mainly native species (Fig. 3f). A wide range of responses were used to assess the biotic responses to navigation, across all levels of biological organisation (from individuals to populations to communities to ecosystems), including DNA damage, organism's metabolism, behaviour, movement, abundance, area or percentage of cover, mortality, distribution, presence/absence, taxonomic and functional diversity and composition (alpha and beta diversities). The majority of the navigation-abiotic relationships were about water quality (32% of the relationships) and hydrological/flow conditions (21%) (Fig. S2).

The studied navigation-environment relationships, including both biotic and abiotic responses, investigated effects of navigation itself (47%), navigation infrastructures (35%), waterway management (10%), or a mixture of two (9%) (Fig. 3b). Three quarters of the navigation was represented by shipping activity, traffic, and waves; slightly more than half of the infrastructures were represented by canals, locks and dams; and more than half of the waterway management was represented by dredging, and flow regulation (Fig. S3).

3.2. Navigation effects on river ecosystems

Half (52%) of the 1103 navigation-environment relationships were statistically tested, the other 48% were asserted or only narratively discussed without any statistical test. We observed the highest proportions of tested relationships from studies that analyse the effects of navigation (Fig. S4a), and the responses of mixed communities pooling both exotics and natives (Fig. S4c). We observed the smallest proportions of tested relationships from studies that analyse the effects of

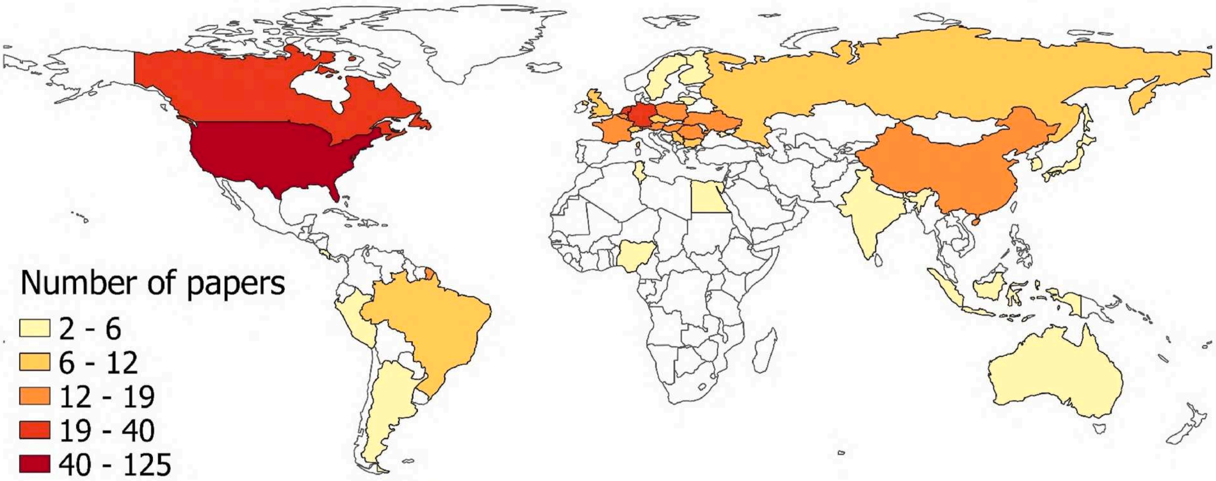


Fig. 2. Global distribution of navigation effects studies. Geographical map of the number of papers per country that study navigation effects on the river environment (country of the study area, not of the author's affiliation). Uncoloured countries are countries with no paper on navigation according to our literature search. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

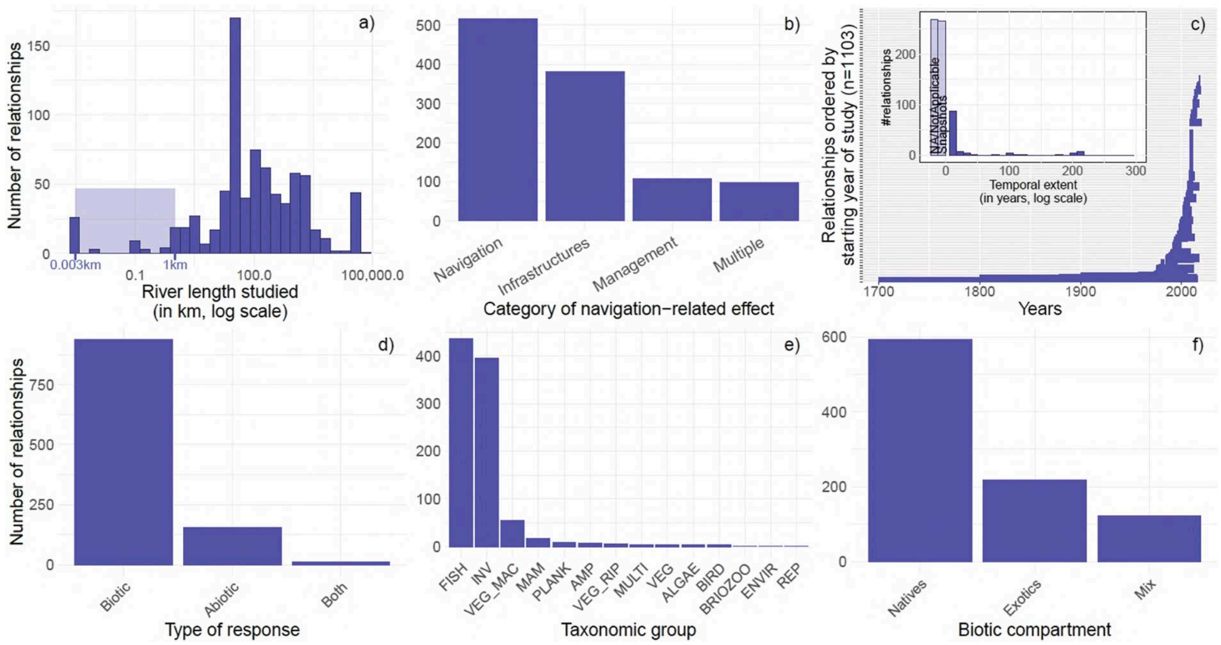


Fig. 3. Metadata of the navigation-river environment relationships studied. Distribution of the number of studied navigation-river environment relationships across: a) the river length studied (the blue transparent box represent the number of relationships that are local studies, i.e. single site studies of less than 1 km length); b) the four categories of navigation-related factors (navigation, infrastructures, waterway management, and multiple factors); c) the time span of the studies in years with starting and ending years of study (on Y-axis, relationships are represented by ticks, only every 10 are shown to facilitate visualization); the insert represents the distribution of the study durations; d) the type of river response (biotic, abiotic, and both); e) the taxonomic group (FISH = fish, INV = invertebrates, VEG_MAC = macrophytes, MAM = mammals, PLANK = plankton, AMP = amphibians, VEG_RIP = riparian vegetation, MULTI = multiple taxa, VEG = multiple vegetation strata, ALGAE = algae, BIRD = birds, BRIOZOO = bryozoans, ENVIR = general biotic environment, REP = reptiles), and f) the biotic compartment (natives, exotics or mix of both). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

infrastructures (Fig. S4a), the responses of exotic taxa (Fig. S4c), and the responses of macrophyte and riparian vegetation (Fig. S4d). We also noticed that integrative influences such as multiple navigation effects (Fig. S4a) and integrative responses such as multiple taxa (Fig. S4d) or whole ecosystems (represented by the mix of biotic and abiotic responses in Fig. S4b) are less statistically investigated than their individual components. Finally, most of the statistically tested navigation effects were evidenced negative or non-significant, while most of the asserted effects were considered negative or positive (Fig. S6).

3.2.1. *Navigation effects on the biotic components of the river*

Focussing on the tested effects of navigation on the biotic components, separate analyses were carried out for native, exotic and mixed compartments. In case of native taxa, most effects were negative, with highest proportions of negative relationships found for navigation itself (55%) and the combination of multiple pressures (52%) (Fig. 4a). In addition, positive relationships between native taxa and navigation-related factors were also found, in particular with infrastructures and waterway management.

For exotic taxa most navigation-related effects were positive, with

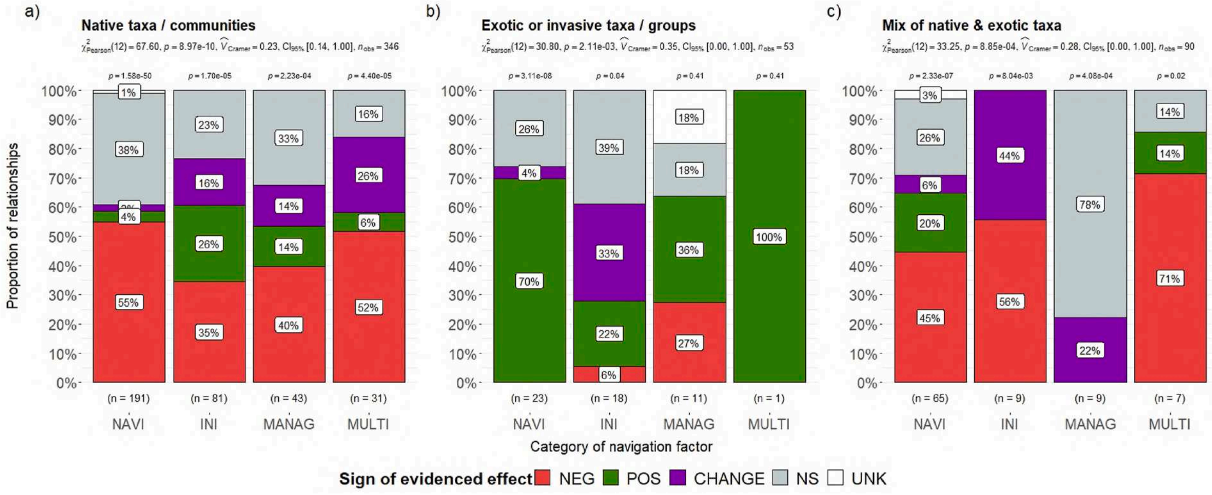


Fig. 4. Tested effects of navigation on biota. Chi-square analyses of the tested effects of navigation-related factors on the different biotic compartments of the river, namely a) native taxa/communities, b) exotic or invasive taxa/groups, and c) mix of both native and exotic taxa. For the association degree and significance between relationship sign and navigation factor, see Fig. S7.

the highest interpretable proportion of positive relationships from navigation itself (70%) (Fig. 4b). Effects from infrastructures and waterway management were harder to discern. Infrastructures effects were mostly non-significant or contingent on other factors. Waterway management effects were statistically balanced between negative, positive, non-significant and unknown (Fig. 4b).

Finally, regarding the navigation-related effects on the mix of both native and exotic taxa, most of the effects were negative, except from waterway management where relationships were either non-significant or contingent on other factors (Fig. 4c).

Overall, we observed the highest amount of unknown effects between the waterway management and the exotic taxa (Fig. 4b); the highest amount of non-significant effects between the waterway management and the mix of native and exotic taxa (Fig. 4c); and the highest amount of contingent/changing effects between the infrastructures and the mix of native and exotic taxa (Fig. 4c).

3.2.2. *Navigation effects on the abiotic components of the river*

Given the small amount of statistically tested relationships between navigation factors and abiotic components (only 77 out of the 160 when including combined responses such as “habitat”, “environment”, “nature”, etc.) and the diversity of abiotic responses studied (8 categories; Table 2), we only could explore the results graphically. In general, more categories of abiotic responses were asserted rather than actually tested, with acoustic environment, water quality and hydrological conditions being most often statistically tested (Fig. 5). Negative effects of navigation were reported on almost all responses, and contrasting effects (both positive and negative) for the response of water quality and hydrological conditions to infrastructures (Fig. 5).

3.2.3. *Map of knowledge*

Based on the synthesis of statistically tested relationships and selecting only the significant associations obtained from individual Chi-squared tests of navigation-biota relationships (Table S8), we created a map of knowledge that draws and compares causal links supported by the scientific literature. These causal links relate the four types of navigation pressure Navigation, Infrastructures, Management and Multiple with the native, exotic and abiotic ecosystem components (Fig. 6). Navigation has the strongest positive relationship with the exotic taxa that are mainly represented by invertebrates. Both navigation, management and combination of multiple navigation pressures have the strongest negative relationship with the native taxa that are mainly represented by invertebrates and fish. The prevalent signs of the other relationships are less distinct according to our analyses (Fig. 6; Table S8).

4. Discussion

Inland navigation has a long and rich history, from the Lingqu Canal (China), one of the oldest canals of the world (2300 years ago, Qian, 2023), to nowadays. Here, our synthesis had to start at the 18th century, following two centuries of major development of canal construction to connect interior countries to sea, or sea to sea (e.g. in Europe, Ketelaars, 2004; Rijkswaterstaat, 2011). Water transport has prospered through the 18th-19th centuries, as being the cheapest mode of transport for people, materials and goods. It then temporarily declined due to the advent of the railway freight and was finally revived in the 20th century (Crompton, 2004). The replacement of steam ships with first motorised vessels and push barges, the invention of radars, the popularization of containers and bow thrusters, all contributed to the improvement and expansion of inland navigation over the last decades (Crompton, 2004; Rijkswaterstaat, 2011). This has led to the change of vessel fleets towards larger (lowest cost per freight) and more powerful ships (better manoeuvrability and safety of operation). As a result, and in parallel of navigation development, the regulation and legislation of inland navigation on rivers had to evolve from localized, rudimentary controls to sophisticated, internationally coordinated frameworks. Several commissions have born with the role of setting the rules for inland navigation regulation and ensuring its durability in a context of international cooperation, e.g. the CCNR (Central Commission for the Navigation of the Rhine, created in 1815), the European waterway network, and the International Joint Commission (between Canada and the USA). This evolution reflects broader societal changes, technological advancements, and a growing recognition of the need for sustainable and environmentally responsible navigation practices (Wiegmans and Konings, 2016). Indeed, navigation development came with adverse effects from the ecological point of view, including physical impacts of vessel operation, and the need to enlarge, deepen and reinforce bank protections of the fairways (Söhngen et al., 2008). To guide further activities and development of inland navigation, our synthesis provides a knowledge-based assessment of the impacts that inland navigation has exerted on river ecosystems globally over the last decades and proposes

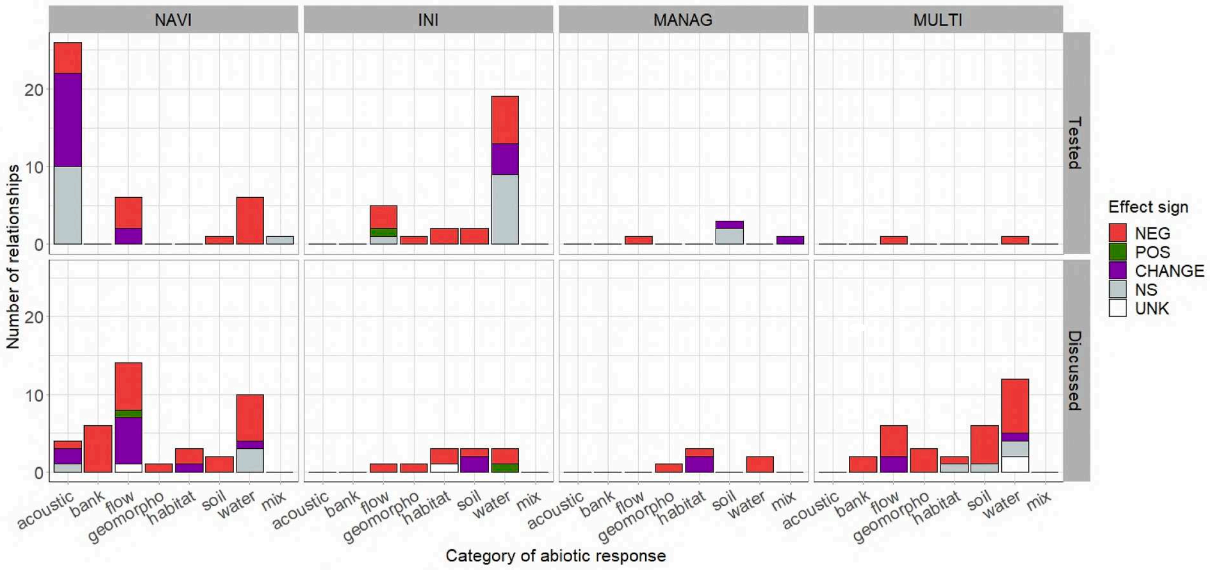


Fig. 5. Abiotic effects of navigation. Distribution of tested (evidenced) vs. narratively discussed (asserted) effects of navigation factors on the abiotic responses of river environment.

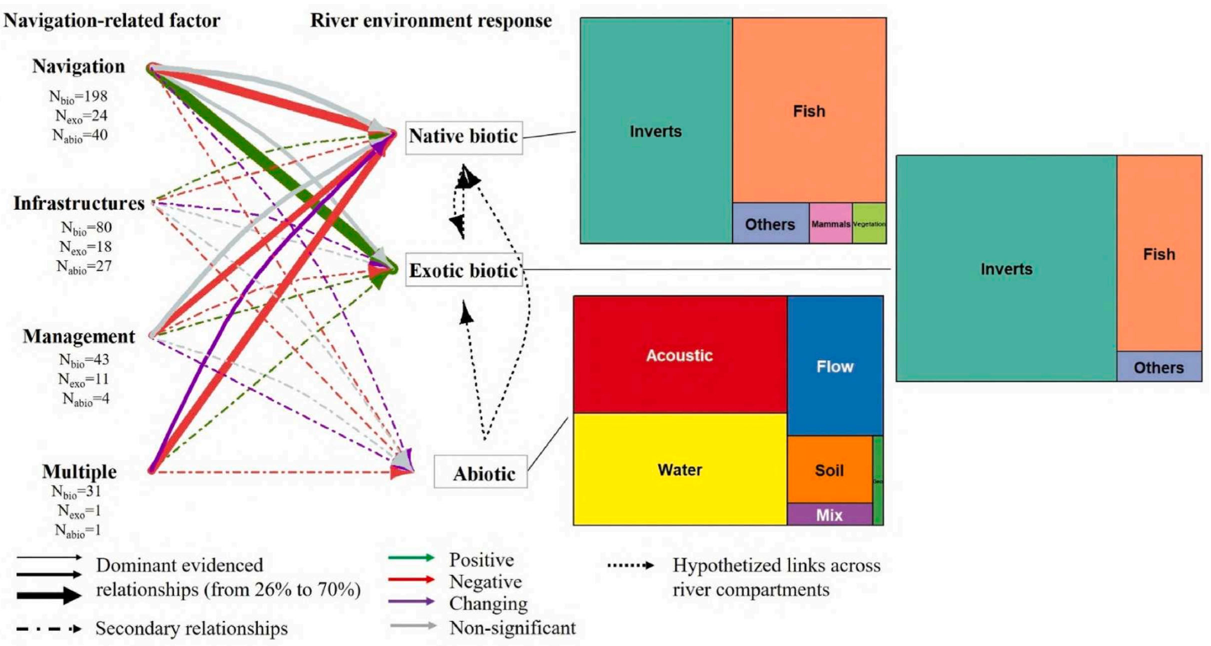


Fig. 6. Map of knowledge of navigation effects on river ecosystem. Evidence-based causal map of knowledge of navigation-related factors effects on river environment. Left panel: The dominant relationships (i.e. the ones showing significant imbalance from proportion analyses) are represented with plain arrows. The secondary relationships (i.e. the ones showing no significant imbalance from proportions analyses for the biotic component, and not testable for the abiotic component) are represented with dot-dashed arrows. Thickness of the arrows is proportional to the percentages revealed by the proportion analysis and colour of the arrows indicate the sign of the relationship. Right panel: treemaps showing the relative representativeness of the main taxa and the types of abiotic responses into the map of knowledge. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

future research directions for sustainable inland navigation.

4.1. Effects of navigation-related factors on the river environment

Our literature synthesis shows that, on average, half of the evidenced relationships between commercial inland navigation-related factors and riverine biota were negative for native taxa and positive for exotic taxa and highlights the generalisation of these impacts at the global scale. This assessment confirms impacts of navigation stressors on native biota reported by many empirical, local-scale studies from all over the globe (e.g., Dey et al., 2019; Huckstorf et al., 2011; Killgore et al., 2011; Leclere et al., 2012; Luttenton et al., 1986; Luttenton and Rada, 1986; Moog et al., 2018; Peng et al., 2020; Rivero et al., 2013) or by continental-scale studies mainly from Europe (e.g., Leitner et al., 2021; Zajicek and Wolter, 2019). The general assessment of positive effects of navigation-related stressors on exotic biota results from the synthesis of previous studies reporting significant effects of shipping intensity, ballast water and inland navigation infrastructures on the spread or diversity of exotic and regularly becoming invasive species, such as Ponto-Caspian gobies in Germany (Tavares et al., 2020), zebra and quagga mussels (Allen and Ramcharan, 2001; Rodríguez-Rey et al., 2021), Silver carp (Fritts et al., 2021) and fishhook waterflea (Maxson et al., 2023) in the USA, and several exotic invertebrate species all over Europe (Bij de Vaate et al., 2002; Leitner et al., 2021; Leuven et al., 2009).

In particular, our study supports that navigation impacts native river biodiversity directly and indirectly. Direct impacts include shipping disturbance (e.g., otter, Gomez et al., 2014), propeller wash/wake wash/waves produced by boat passage leading to fish drift and stranding (Gabel et al., 2011; Kucera-Hirzinger et al., 2009; Schludermann et al., 2014), invertebrate dislodgment from preferred habitats (Gabel et al., 2008, 2012), injuries resulting from boat collisions including dolphins (Bechdel et al., 2009), sturgeons (Hondorp et al., 2017), and other fish species (Killgore et al., 2001). Navigation activities further impact native biodiversity indirectly. It does so first through facilitating the spread of invasive species via the transport of macrophytes, fish and invertebrates propagules by boats themselves (Jacobs and Keller, 2017) or by their ballast water (Adebayo et al., 2014 for invertebrates; Tavares et al., 2020 for fish) that might in turn affect native species (Gallardo et al., 2016; Gaye-Siessegger et al., 2022). Second, navigation activities lead to the changes in the abiotic conditions of the river, such as the alteration of acoustic environment (Putland et al., 2021; Rountree et al., 2020) potentially affecting mammals (Dey et al., 2019; Duan et al., 2023b) and fish (Graham and Cooke, 2008; Wysocki et al., 2006), the decrease of water quality (Henry Ogbuagu et al., 2013; Wehr et al., 1997) potentially affecting benthic invertebrates (Arbačiauskas et al., 2008; Xu et al., 2014), and disturbance of hydrological conditions potentially affecting all groups (Habersack et al., 2016). However, only 37 out of the 243 studies actually analysed both the abiotic and biotic responses of the river ecosystem to navigation stressors. Among those, even fewer explicitly analysed the links between the two components in a context of navigation pressures, although they are expected to influence many groups (Niimi, 1982). In particular, vessel traffic and waves influence water turbidity, hydrological conditions, and habitat suitability that in turn affect fish diversity (Gutreuter et al., 2006; Hanafiah et al., 2013; Kano et al., 2013; Koel and Stevenson, 2002), and invertebrates' attachment to their substrate (Fleit et al., 2016). Similarly, vessel traffic results in short-term flow velocity changes and draw down, bed shear stress, bank erosion, sediment alteration and water quality alteration that in turn affect both macrophyte and riparian vegetation (Ali et al., 1999; Karle et al., 2005; Racine et al., 1998; Thunnissen et al., 2019). However, the rarity of comprehensive studies plus limitations of study designs (e.g., difficulty to cross multiple effects *in situ*) challenge drawing general causal conclusions on underlying processes of direct and indirect effects of navigation on biodiversity (see next section *Gaps of knowledge & future research avenues*).

Although navigation itself was the main factor influencing both native and exotic taxa, we showed that inland navigation infrastructures certainly indirectly add to this impact. In particular, navigation dams negatively influence fish, invertebrates and phytoplankton communities and populations via habitat modification and connectivity loss (Arai et al., 2019; Argent et al., 2016; Brewer et al., 1995; Wehr and Thorp, 1997; Yi et al., 2010), and channelization and embankment negatively influence riparian vegetation and fish diversity mainly due to habitat loss (Harvolk et al., 2015; Kano et al., 2013; Valová et al., 2014). Most of the effects of inland navigation infrastructures on river biota are potentially mediated by their primary effects on different abiotic aspects of the river environment, such as water quality (Wehr et al., 1997), flow conditions (Mirza, 1997; Rivero et al., 2013), and geomorphological and sediment characteristics (Brewer et al., 1995). However, considering both direct and indirect effects, infrastructures and waterway management may not be more impactful than navigation alone. This is also supported by studies reporting successful mitigation of navigation-induced impacts, such as by regulating boat traffic (Bradbury et al., 1995; Grant; Lewis, 2010; Rüdel et al., 2007) and ballast water (Ricciardi and MacIsaac, 2022), or by restoring more natural flow conditions (Collas et al., 2018; Schorg and Romano, 2018; Theiling et al., 1996). However, it must be noted that most INIs were constructed, and impacted riverine communities decades before the first studies of navigation-induced environmental impacts. One example being the documented historical extinction of diadromous fish as a result of earlier dam construction (e.g., Le Pichon et al., 2020; Merg et al., 2020). The rarity of evidence-based studies at this time scale probably resulted in an underestimation of the impacts of INIs on aquatic biota in the present synthesis.

More surprisingly, INIs and waterway management sometimes showed positive effects on native taxa (26% and 14% of the tested relationships, respectively). This could be observed for instance when studies analysed the abundance of generalist or highly-tolerant native species, or the diversity of communities that shifted from small, highly-specialised communities to bigger, more generalist communities, reflecting an overall homogenisation of the river ecosystem (Angradi et al., 2009). In addition, INIs such as groynes or dams could tend to favour some invertebrate and phytoplankton taxa through the creation of impounded habitats (Buczyński et al., 2017; Wehr and Thorp, 1997) and waterway management such as specific lock operations could favour fish passage (Fritts et al., 2021; Turney et al., 2022).

Notwithstanding, 30% of the statistically tested relationships between navigation stressors and river ecosystems were not statistically significant. This may be due to lack of power of some of the studies on the topic (e.g., difficulty in obtaining high enough sample sizes, or in defining proper baselines (Moog et al., 2018; Xiong et al., 2021). However, in fact, it is more likely that this number comes from rather well-designed studies that test multiple relationships among which only some turned out significant (see large-scale studies with numerous spatio-temporal replicates such as (Leitner et al., 2021; Rountree et al., 2020; Zajicek et al., 2018); for more information, see the synthesis table in Jeliazkov, 2024). Detecting effects of navigation-related pressures also seems more difficult in naturally highly variable environments (e.g., in a delta, Liashenko et al., 2022) or under the influences of complex hydrological connectivity (e.g., river-lake connectivity, Xiong et al., 2023). This leaves open the question of navigation impacts, especially for the quantitative effects of shipping intensity (Leitner et al., 2021; Xiong et al., 2021, 2023) but see (Sexton et al., 2024), shear stress (Gabel et al., 2012), lock operations (Fritts et al., 2021), and embankments (Brabender et al., 2016) on a number of fish and invertebrates species or communities.

Finally, around 10% of the relationships depended on one or more covariates, i.e., where the sign of the effect depended on the effect of a third variable. This figure is likely underestimated given that in the present synthesis, we consider each relationship separately while the articles analysing several relationships are likely to find different responses for each depending on a third factor, such as the type of response analysed, the study design used, etc. We here highlight the context-dependent nature of some navigation effects on biodiversity, particularly in relation to river (Harnish et al., 2012), mesohabitat of the river (Rountree et al., 2020; Scharf and Brunke, 2013), taxa or functional groups (Munawar et al., 1991; Zajicek and Wolter, 2019), season (Zadnik et al., 2009), or river uses and climate change (Templeton et al., 2024). We further noticed that this context-dependency might play a stronger role in the study of INIs effects on exotic taxa (33%), and of the combination of multiple stressors on native taxa (26%). Therefore, we advocate that context-dependency likely shapes the impacts of inland navigation on river integrity and deserves further attention (Sexton et al., 2024).

Our literature synthesis approach provides a comprehensive literature review on the topic of navigation effects on river ecosystems (243 papers), a certain accuracy in the information extracted, a substantial amount of data collected (1103 navigation-environment relationships), a relatively fine degree of interpretation and generalisation (see the Results), a good degree of repeatability (data and R codes available at https://doi.org/10.57745/N6Y6QR) and has been successfully used in other synthesis works in freshwater ecology (Jackson et al., 2016; Lange et al., 2018). While it does not have the strength of a strict meta-analysis (neither its weaknesses, Kotiaho and Tomkins, 2002) and is limited by the 'vote counting' perspective (Koricheva and Gurevitch, 2013; Siddaway et al., 2019), our approach was appropriate and more performant than a traditional narrative review to achieve our objectives, that were to summarise and reinterpret the knowledge on the topic, and to identify potential gaps in this knowledge.

4.2. *Gaps of knowledge and future research avenues*

When considering the total number of relationships studied between navigation-related factors and river components, we showed that waterway management - e.g., ballast water treatment and vegetation cutting - is the least studied effect of navigation (but see Ricciardi and MacIsaac, 2022). The lack of evidence on waterway management effects is a result of the fine classification we proposed between different drivers of navigation impacts. This driver is less investigated than the others, maybe because this requires an elaborative monitoring design such as before-after intervention (e.g., dredging, cutting, McCabe et al., 1998; Moog et al., 2018), developing holistic frameworks to account for other stressors (Suedel et al., 2024), and interviewing navigators or operators on their practices (e.g., ballast water treatment, Locke et al., 1993), which can be more complicated, long and costly than measuring navigation intensity or infrastructure density, for instance.

Thanks to the separation of asserted vs. evidenced effects of navigation, and to the report of unknown effects from tested relationships, we have been able to further characterise the gaps of knowledge in the topic of navigation-environment relationships. For instance, we have three times less evidence (in both absolute and relative terms) on exotic taxa responses to navigation factors than on native taxa, despite the widely advertised influence of the former on the latter (Byers, 2002; Havel et al., 2015; Leppäkoski et al., 2013). To better understand the effect of navigation on native communities and isolate the indirect effect precisely due to the navigation-induced spread of invasive taxa, it would be worthwhile to systematically analyse both parts of the communities' responses and check the links between those responses instead of pooling those. This could be done for example by analysing species association matrices from joint species distribution modelling (Ovaskainen et al., 2019; Pollock et al., 2014; Zurell et al., 2020). In addition, although infrastructure effects are relatively well studied, they are almost twice less strictly tested. This may be due to the high number of studies that describe local biotic responses (e.g., number of fish passage) around one particular infrastructure (e.g., one weir or one lock system), which allows addressing the question descriptively but not statistically. Many studies lack control and historical baseline information, especially in multiple-pressure contexts (e.g., Christie et al., 2019). Such underpowered assessments result in a certain difficulty to clarify the role of navigation infrastructures in river ecosystems, which is reflected in our synthesis where positive and negative effects come out as balanced.

Although our search equation was mainly centred on the response of the biotic component of the river environment to navigation factors, we detected a certain amount of evidence about the effects on the abiotic component, as long as these were addressed in relation with any biotic response. However, this amount remained quite low (15%). This suggests that among studies addressing the effects of navigation on biodiversity, relatively few of them actually investigate the potential processes underlying these effects, including the modification of the abiotic conditions that allow species to persist (but see Fischer and Claflin, 1995; Flinn et al., 2008; Kano et al., 2013; Peng et al., 2020; Wolter et al., 2004). Although many studies analyse the links between biotic and abiotic conditions in the context of navigated rivers (47 papers), the main driver as traffic intensity, dam or channelisation is often assumed and not systematically measured neither actually linked with the abiotic response (e.g., Ali et al., 1999; Best et al., 2001; Freund and Hartman, 2005). A couple of recent works make the exception that strive to apprehend this causality chain from navigation pressure to abiotic response to biotic response. They deduce these chains empirically, such as the effect of waterway construction and ship traffic on water quality that in turn affects benthic invertebrates (Dou et al., 2022), the effect of ballast water on water salinity that in turn affects freshwater phytoplankton (Duan et al., 2023a), or the effects of boat traffic on acoustic pollution that in turn affects porpoise survival (Duan et al., 2023b). The low amount of investigation of the abiotic component in relation with the biotic response to navigation may also be due to a historical legacy effect where the abiotic components drastically changed immediately after river regulation (Mossa and Chen, 2022) and thus, already formed baseline conditions for later navigation impact studies ("shifting baselines"; Humphries and Winemiller, 2009; Soga and Gaston, 2018). We thus need further investigation and evidence-based assessment to understand direct and indirect effects of navigation on the river environment, including the role of historical river modifications. Here, we explore hypothetical causal relationships, which opens new questions of research and methodological challenges such as: how to assess directness of the navigation effect; how to disentangle biotic and abiotic processes involved in river environment response to navigation pressures; and how to design sampling schemes to address these questions.

We generally lack knowledge about the influence of combined navigation pressures as well as the mix of responses (abiotic and biotic, exotics with native, and mixed taxa) and more than 75% of the current knowledge relies only on fish and invertebrates. This suggests a need for more integrative studies where interaction effects of multiple navigation factors could be analysed on biotic responses that may be representative of the whole river ecosystem, e.g., metacommunities with several trophic levels (e.g., Borthagaray et al., 2015). The potential feedback loops between, for instance, the navigation and riparian vegetation that in turn may affect aquatic communities through habitat changes or trophic interactions modifications are not studied (Hohensinner et al., 2018). We need to scale up to metacommunities and metaecosystems (Cid et al., 2021; Gounand et al., 2018; Heino, 2013; Schiesari et al., 2019) in order to better account for the spatialized and functional effects of navigation on river biodiversity and ecosystems. Such studies allow important progress, such as showing, for instance, that more natural waterway management practices can enhance trophic functioning of freshwater communities (Brauns et al., 2022). We need these more integrative studies, also because the river functions as a continuum with lateral and longitudinal connectivities (Boulton et al., 2017; Manfrin et al., 2020; Ward, 1989). Very few studies address the effects of navigation on river connectivities, except local specific ones tagging fishes and monitoring their movement and behaviour around and through a given sluice-lock system (Fritts et al., 2021; Garrone Neto et al., 2014; Vergeynst et al., 2019). We do not know for instance the cumulative effects of navigation locks and dams on biodiversity at the watershed scale, although this scale is considered as relevant for river restoration (Fausch et al., 2002; Friberg et al., 2017). In the context of future inland navigation development, we need approaches to better anticipate collateral damages and avoid adverse effects of waterway construction on freshwater ecosystems (Dou et al., 2022), such as prospective work (Wantzen et al., 2024) and simulation modelling (Yin et al., 2022).

New technologies play a crucial role in enhancing the tracking and monitoring of river navigation (Bandini et al., 2023). The implementation of advanced Global Positioning Systems (GPS), remote sensors, and real-time data management platforms has revolutionized the way river routes are supervised. These tools enable continuous and precise surveillance of maritime traffic, improving the safety and efficiency of transportation. The integration of these technologies also supports environmental protection by enabling more stringent control over activities that could negatively impact river ecosystems. The combination of high spatiotemporal resolution satellite imagery and deep learning methods offers great opportunities for the monitoring of human footprint in inland waterways, which can improve local and regional assessment of environmental impacts of anthropogenic activities on riverine ecosystems (Guan et al., 2023; Smigaj et al., 2023).

We have also noticed a strong geographical bias in the knowledge available in the English-speaking, white scientific literature, with an overrepresentation of China, Europe, and North America. Complementing this work with a synthesis of the grey literature in national languages would help fill this gap. It remains nonetheless that increasing navigation is a global phenomenon. While for some rivers there are international conventions and committees dealing with conservation aspects (e.g., International Commission for the Protection of the Rhine), for others, there are transboundary treaties that mostly focus on navigation and water use for damming and irrigation (e.g., Niger), while many rivers are increasingly used for navigation but lack any consideration for the potential impact of both INIs and shipping on the riverine ecosystem services (e.g., the Paraguay River in Brazil, Wantzen, 2023; see also Jähnig et al., 2022). If we are to plan future inland navigation management in coherence with other environmental policies (Convention on Biodiversity, Aïchi targets, European Framework Directives), we have to develop a more sustainable navigation (Plotnikova et al., 2022) and to adapt the management strategies to functional scales for a better resilience of the ecosystems in the face of global change.

5. Conclusions

Our literature synthesis organises, summarizes and reinterprets the great but scattered amount of knowledge on the topic of navigation effects on river ecosystems by proposing an original classification of navigation-related pressures – namely navigation itself, infrastructures and waterway management – and by analysing the literature through this novel prism.

Our synthesis shows the generalised negative impacts of inland navigation on native biodiversity and its positive effects on exotic taxa. The strongest impacts are due to navigation itself (such as shipping intensity and wave drawing) and to the combination of multiple navigation factors (i.e. navigation, infrastructures, and waterway management or maintenance). This suggests that inland navigation policies will need to reinforce regulation on boat traffic to limit erosion and nuisances, e.g., by limiting boat speed and/or access (Bradbury et al., 1995; Kuhajda and Rider, 2016), on lock operations to improve connectivity, e.g., by increasing the frequency of opening (Arai et al., 2019; Simcox et al., 2015), and on ballast water to avoid contamination, e.g., by water treatment (Elskus et al., 2015) (and see more recommendations in PIANC, 2003). Waterway management will need to minimize or conceive environment-friendly dredging activities (Mossa et al., 2020; Pledger et al., 2021; Suedel et al., 2022) and to apply creative suites of restoration actions to mitigate the impacts of navigation (Flores et al., 2022; Schmitt et al., 2018; Söhngen et al., 2018; Weber et al., 2012). Waterway policies will have to account for the importance of interactions between multiple navigation impacts by adopting a more integrative view of the river ecosystems (Cid et al., 2021; Friberg et al., 2017). The future inland navigation regulation will further need to adapt to the context of global change where some rivers are and will be increasingly exposed to flow modifications (Olsen et al., 2012), and species invasions (Rahel and Olden, 2008).

Our synthesis nevertheless reveals that in half of the cases, some impacts of navigation-related pressures remain unclear, either due to lack of evidence/proper testing or contradicting responses. This reflects the current absence of consensus and hence, the remaining gaps of knowledge in the topic that need to be addressed in order to better guide river management planning. The main research priorities we identified are to investigate (i) the effects of waterway management on communities, (ii) the indirect effects of navigation pressures on biodiversity through the analysis of abiotic responses that condition the biotic responses to gain deeper understanding of the underlying processes of navigation impacts on river ecosystems; and (iii) the interaction between multiple navigation factors and their effects on multi-taxa responses.

This and future research provide policy makers and waterway managers with more evidence-based and large-scale guidance that will help build and coordinate inland navigation management policies and fulfil the objectives of transboundary consistency of inland navigation.

CRediT authorship contribution statement

Alienor Jeliazkov: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Vanesa Martínez-Fernández:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Vassil Y. Altanov:** Writing – review & editing, Visualization, Validation, Methodology, Data curation. **Jean-Nicolas Beisel:** Writing – review & editing, Validation, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Anthonie Dirk Buijse:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Sofia Consuegra:** Writing – review & editing, Data curation. **Swann Felin:** Data curation. **Carlos Garcia de Leaniz:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Wolfram Graf:** Data curation. **Fengzhi He:** Writing – review & editing, Data curation. **Sonja C. Jähnig:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Patrick Leitner:** Data curation. **Astrid Schmidt-Kloiber:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Aaron N. Sexton:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Cybill Staentzel:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Evelyne Tales:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Karl M. Wantzen:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Christian Wolter:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data and R codes are publicly available at: https://doi.org/10.57745/N6Y6QR.

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Appendix A. Supplementary data

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Titre : Prospectives de distribution des poissons dans le bassin Seine-Normandie face aux contraintes de connectivité et de changement global

Mots clés : Changement global, Bassin Hydrographique, Biodiversité ichthyologique, Modélisation de distribution d'espèces, Connectivité écologique, Scénarios

Résumé : Les écosystèmes dulcicoles sont parmi les plus riches en espèces au monde. Le changement climatique, l'anthropisation et la fragmentation des rivières, mettent en péril les communautés de poissons et leur conservation future. Malgré un besoin urgent de connaissances sur la conservation des écosystèmes d'eau douce et des poissons, l'influence des stresseurs anthropiques sur la répartition et la conservation des poissons est encore mal comprise. Cette thèse visait à combler ce manque de connaissances en étudiant le rôle de la gestion des bassins versants et de la fragmentation sur la répartition des espèces de poissons au 21e siècle dans un contexte de changement climatique, afin de fournir des informations et outils à l'appui à la gestion des rivières. Pour ce faire, nous avons étudié la connectivité longitudinale et son influence sur les communautés de poissons fluviaux, et construit des scénarios de gestion des bassins versants que nous avons intégrés dans des modèles de distribution des espèces pour étudier l'influence du changement climatique et de la gestion des bassins versants sur les futures communautés de poissons, avant d'étudier la répartition de l'incertitude entre ces deux composantes.

Le bassin Seine-Normandie a été choisi comme point focal de cette étude. Un ensemble de données comprenant plus de 2 000 sites d'étude a été compilé pour l'analyse de la connectivité longitudinale. Des indices de connectivité informés par les caractéristiques fonctionnelles des poissons ont été développés, certains intégrant des aspects locaux. Nous avons pu évaluer l'importance relative de la connectivité dans la distribution des poissons, les indices qui incluaient le contexte local étant les plus performants, et constaté que les barrages jouent un rôle central dans la détermination de la distribution des poissons.

Afin d'explorer les scénarios futurs possibles, quatre projections climatiques ont été sélectionnées sur deux horizons temporels, 2050 et 2100. Nous avons construit quatre scénarios de gestion pour décrire différentes orientations politiques futures en matière de restauration et de gestion des rivières. Les multiples perspectives de distribution des espèces ainsi obtenues grâce aux modèles d'ensemble ont montré un déclin des communautés de poissons lié au changement climatique. Les scénarios de restauration limitée étaient liés à des taux élevés d'extirpation tandis que les scénarios avec des perspectives plus ambitieuses entraînaient un taux de survie accru de nombreuses espèces. Une grande variabilité selon les espèces a néanmoins empêché l'identification d'un scénario idéal.

Enfin, nous avons constaté que dans la plupart des cas, le changement climatique contribuait à une plus grande part d'incertitude. La part portée par la gestion territoriale était néanmoins importante, variant entre 6 % et 30 % en moyenne selon les espèces. Certaines espèces (l'ablette, le gardon) plus tolérantes aux facteurs de stress environnementaux associés au changement climatique étaient plus impactées par la gestion territoriale dans des sites spécifiques.

Grâce à cette thèse, nous avons apporté des éclairages sur le rôle de la connectivité sur la composition des communautés de poissons de rivière ainsi que sur l'influence de la gestion et du changement climatique sur les futurs écosystèmes fluviaux. Nous avons également pu fournir des pistes pratiques pour la gestion future et de nouvelles méthodologies pour évaluer la connectivité dans les réseaux fluviaux et l'intégrer dans les approches de modélisation. Nous avons produit des futurs plausibles pour la distribution des poissons de rivière, nous permettant d'évaluer l'importance du changement climatique et de la gestion territoriale sur la conservation des espèces de poissons. Nous pensons que bon nombre de ces approches peuvent contribuer à la création des connaissances nécessaires à la mise en œuvre des mesures requises pour préserver les écosystèmes fluviaux dans les décennies à venir.

Title: Fish distribution prospects under climate change and connectivity constraints in the Seine-Normandie drainage basin

Key words: Global change, Watershed, Fish Biodiversity, Species Distribution Modeling, Ecological connectivity, Scenarios

Abstract: River ecosystems are among the most species-diverse in the world. Global change, coupled with anthropization of watersheds and fragmentation of riverscapes jeopardize river fish communities and put their future conservation in peril. There is an urgent need for knowledge to inform the design of the operations necessary to the conservation of freshwater ecosystems and fish species. However, the influence of watershed management, river fragmentation and land use on fish distribution and conservation is still poorly understood. This thesis aimed to address this knowledge gap by investigating the role of watershed management and fragmentation on fish species distribution in a warming 21st century, in order to provide information in support of river management and produce tools to better approach this issue. We first studied longitudinal connectivity and its influence on river fish communities, built watershed management scenarios which we integrated into species distribution models to study the influence of climate change and watershed management on potential future fish communities, before studying the spread of uncertainty between these two components.

The Seine-Normandie basin, a highly anthropized watershed in Northern France, was selected as the focal point of this study. A dataset comprising over 2,000 study sites was compiled for analysis of longitudinal connectivity. Connectivity indices informed by functional characteristics of fish were developed, with some incorporating local context (eg. river size and centrality). We were able to assess the relative importance of connectivity in fish distribution via species distribution modelling, indices which included local context performing especially well. We found that dams play a pivotal role in shaping fish distribution.

In order to explore possible future scenarios, four climate projections were selected across two time horizons, 2050 and 2100. We constructed four territorial management scenarios to describe different future political orientations with respect to environmental restoration and river management. We were able to produce several prospects of species distribution through ensemble modeling. Most species were found to exhibit a decline in range over time due to climate change, management scenarios producing more complex outcomes. Scenarios linked with limited environmental restoration were linked with high rates of extirpation while scenarios with more ambitious prospects resulted in enhanced survival rate of many species. However, these responses exhibited wide variation across species, hindering the identification of a universally applicable scenario.

Finally, we highlighted the relative importance of uncertainty linked to climate change and territorial management across eight species. We found that, in most cases, climate change carried more uncertainty, especially in 2100. However the portion of uncertainty carried by territorial management was still important, ranging between 6 % and 30 % on average depending on species. Some species (the bleak, the roach) that are tolerant for warm water or environmental stressors associated with climate change were more impacted by territorial management in specific sites.

Through this PhD we provided insights into the role of connectivity on the composition of river fish communities as well as the influence of management and climate change on future river ecosystems. We were able to provide new practical clues for future management and new methodologies for assessing connectivity in river networks and integrating it into modeling approaches, producing plausible futures for river fish distribution, allowing us to assess the importance of climate change and territorial management on fish species conservation. We believe many of these approaches can be applied in similar contexts and contribute to the creation of knowledge necessary to implement the urgent measures required to safeguard river ecosystems in future decades.