



Evaluating determinants of freshwater fishes geographic range sizes to inform ecology and conservation

Juan Carvajal-Quintero

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THÈSE

En vue de l'obtention du DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par l'Université Toulouse 3 - Paul Sabatier

Cotutelle internationale : Instituto de Ecología A.C.

Présentée et soutenue par
JUAN CARVAJAL-QUINTERO

Le 9 octobre 2020

**Évaluation des déterminants de l'aire de répartition des poissons
d'eau douce pour éclairer leur écologie et conservation**

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To Javier A. Maldonado Ocampo (Nano)

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CHAPTER 1 – General introduction

Geographic range size

Understanding the geographic distribution of species across space and time is one of the long standing challenges in ecology and evolution. Since the first naturalists of the 18th and 19th centuries, we have documented the enormous variation of species geographic distributions (hereafter geographic range) and have long sought to understand the mechanisms underlying such variation (Brown et al. 1996, Gaston 2003). Despite this, we are still a long way from understanding the principal drivers of range size variation and have a satisfactory explanation about why some species occur in larger area than others (Gaston 2009, Coreau et al. 2010, Sheth et al. 2020). The need to answer these questions has become more urgent in the recent decades as this knowledge is crucial to predict changes in biodiversity patterns in response to global changes, such as, climate change and habitat loss or habitat fragmentation (Brown et al. 1996, Jetz and Rahbek 2002, Gaston 2009, Sandel et al. 2011, Grill et al. 2019).

The species' geographic range size has been studied across several taxonomic groups and has been related to multiple ecological and evolutionary factors. However, studies on range size have generally analyzed potential driving factors separately or have limited both the number of species and their spatial extent (Brown et al. 1996, Gaston 2003). Indeed, one of the main reasons for the lack of a comprehensive answer to the question of what determines species' range sizes has been the lack of an holistic view that considers the full extent of species geographic distributions (i.e. extent of occurrence *sensu* Gaston and Fuller 2009) and the complex way in which multiple driving factors may interact with each other and influence the range size differently among regions and taxonomic groups (Brown et al. 1996, Sexton et al. 2009, Morueta-Holme and Svenning 2018, Sheth et al. 2020).

Some macroecological studies have made important contributions to the comprehension of the variation on species' geographic ranges by evaluating quantitatively and statistically, different proprieties of this pattern across the globe (e.g. Li et al. 2016). However, these studies have been only applied to some taxonomic groups, mainly those with more information (e.g. birds and mammals), leaving out many others. Freshwater fishes are one of those groups, still lacking integrative studies describing species distribution patterns. The few studies dealing with the variation of freshwater fishes geographic range size have been species- and location-specific analyses (e.g. Tales et al. 2004, Bertuzzo et al. 2009).

Overcoming these knowledge gaps and applying them to guide conservation strategies for freshwater ecosystems is a critical challenge. Freshwater environments harbor an extraordinary rich and endemic biota, and provide diverse ecosystem goods and services (e.g. providing water quantity and quality as well as food and nutrition for billions of people globally, Costanza et al. 1997, Dudgeon et al. 2006). At the same time, this strong human dependence on freshwater ecosystems' goods and services drives increased pressures, degrading these ecosystems, modifying species range sizes (Comte et al. 2013, Radinger et al. 2017) and ultimately increasing species' extinction risk (Vörösmarty et al. 2010, Albert et al. 2020). These human pressures are projected to substantially increase for freshwater ecosystems in the near future, impacting further species' persistence (Zarfl et al. 2015, Winemiller et al. 2016, Comte and Olden 2017, Albert et al. 2020). Thus, besides understanding the factors and processes explaining species' geographic range sizes and their changes, it is also important from a conservation perspective to quantify the potential impacts that human-induced changes in range sizes could have on species' extinction risks, to guide conservation priorities by pointing where actions are needed.

Historical context: From the biodiversity distribution to the species geographic range

Perhaps, the initial approach to understand the distribution of species was the Noah's Ark, an ancient narrative based on Mesopotamian stories and widely enacted between the 16th and 17th centuries during the biblical doctrine. Back then, the belief was that after the great flood the animals disembarked from Noah's Ark on Mount Ararat and dispersed around the globe (Fig. 1, Mayr 1982). Thinkers at that time would have predicted the same geographic range size for all the living species. However, in the 18th century with the beginning of the age of explorations, a vast number of uneven distributed species were described, and it seemed no longer plausible that they all could be aboard an ark (Mayr 1982, Browne 1983). In the mid 18th century, Carl Linnaeus, the father of systematics, was the first to think about the geography of species distributions alluding a term that later evolved "*the regions in which the plants grow*" (Candolle 1820, Nelson 1978). Linnaeus' interpretation of the distribution of biodiversity (the mountain explanation) did not rely on dispersal from Noah's Ark. Instead, he posited that each species was created in a particular climatic belt of a small mountainous island surrounded by a great flood and, as the floodwaters receded, different species dispersed outward from this island to colonize their preferred environments (Browne 1983). The French

naturalist Georges-Louis Buffon challenged Linnaeus' explanation, recognizing that species were not perfectly suited to an environment; instead, the distribution of species across the globe was the result of the observed shifts in climate (Buffon 1770). Based on this observation, he proposed the Buffon's law, then known as the "*law of the distribution of forms*", stating that similar environments in isolated regions have distinct species assemblages with similar attributes (Browne 1983). This law has represented the basis of the first biotic zoning described during the 19th century (see below).



Figure 1. Representation of the Noah's Ark where animals are descending after the great flood. By Edward Hicks, 1846 Philadelphia Museum of Art. Image obtained from [Wikimedia Commons](#).

In the late 18th century, Carl L. Willdenow and Eberhard A. von Zimmermann, two German geographers who shared a similar view as Buffon, brought a geological perspective to explain the distribution of species. Based on the observation that different regions and continents shared common species, they proposed that the current distributions of species were the results of historical connections and dispersion processes (Mayr 1982). They also recognized early patterns in the spatial variation of species distribution by describing the

restricted range of plants in mountain regions (Morrone 2009). Willdenow transmitted his passion for plants and mountains to his pupil, Alexander von Humboldt (Hiepko 2006), who in the early 19th century, attempted to get a full picture of the phenomenon gathering empirical evidence to directly relate changes in species distribution with different environmental parameters. Through this evidence, Humboldt set up hypotheses on which factors might influence the physiology of plants and in turn their distribution (Morueta-Holme and Svenning 2018). Perhaps, the strongest relation that he inferred was that the physiological requirements of plants to ambient energy restricted their survival and distribution, which could be clearly seen while ascending a mountain (Fig. 2, Humboldt and Bonpland 1805, reviewed in Morueta-Holme and Svenning 2018). Humboldt also noted the effect of temperature seasonality on species ranges. He attributed the observation that many temperate plants spread from lowlands to high elevations to the fact that species in these regions were exposed to the same low temperatures in winter and at high elevations, and thus, that they have adapted to a wider range of temperatures. Conversely, the stable intra-annual temperature in the tropical regions resulted in clearer vegetation bands towards highlands (Humboldt and Bonpland 1805) (The same observation that lead Janzen to later develop the classic hypothesis “*Mountain passes are higher in the Tropics*”; Janzen 1967).

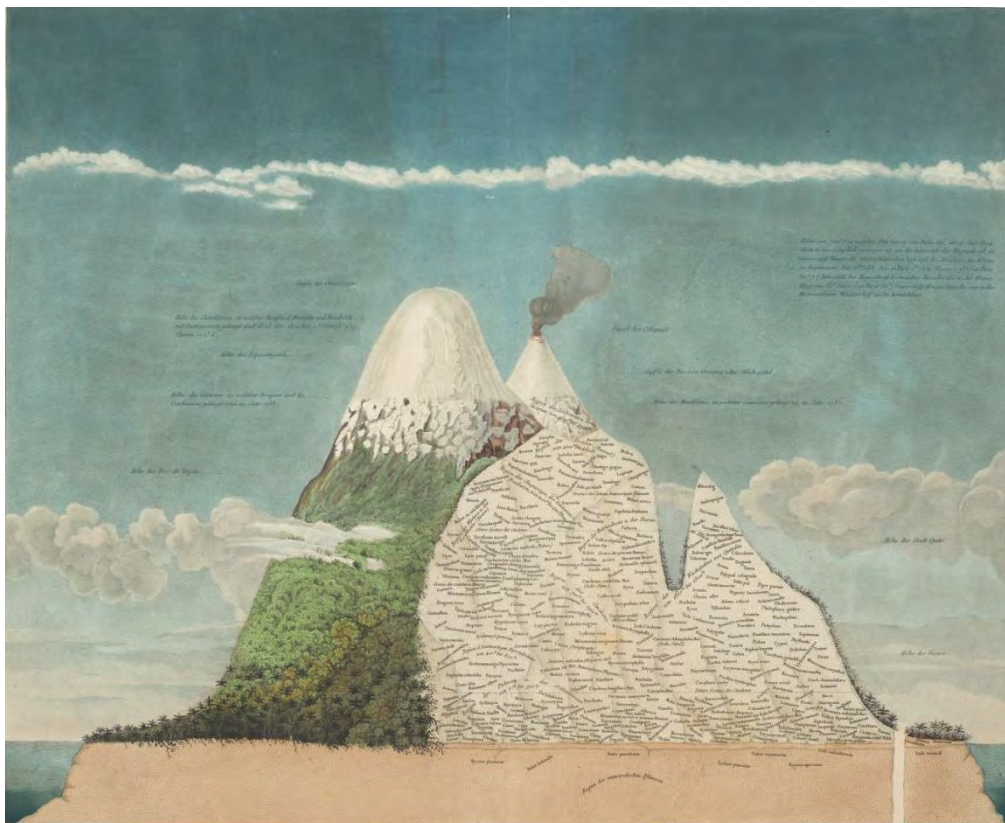


Figure 2. Scientific illustrations by Alexander von Humboldt. His famous illustration of Chimborazo volcano in Ecuador shows plant species living at different elevations (Public domain / [Wikimedia Commons](#)).

The aforementioned biogeographers were very influential in the study of the distribution of species, identifying biotic zones and how environmental factors determined them. But, the first person that conceived the idea of species geographic range was Augustin de Candolle which described “*les habitations*” (dwellings), as “*the country wherein the plant is native*”, and “*les stations*” (the stations) as “*the special nature of the locality in which each species customarily grows*” (Candolle 1820: 383). Another important contribution of de Candolle was the hierarchical notion distinguishing between the factors that determined the distribution of species on a regional scale (temperature, light and the biology of the organisms) and those that influence global-scale patterns (historical factors that restrict the distribution of species into the provinces) (Lieberman 2012).

During the second half of the 19th century, the fields of geology and paleontology added an evolutionary view to the distribution of species. At this time, geologists and paleontologists strongly questioned the view that climate alone could explain the distribution of species across the globe, and were looking for reasons why certain species were found in particular areas. Charles Lyell was the first to establish a relationship between the current distribution of species and their distribution in the fossil record. He proposed a deep-time dynamic where the geographic ranges of animals and plants contracted and expanded according to geologically mediated changes (Browne 1983). Charles Darwin, a profound admirer of Lyell, integrated this deep-time dynamic with the thesis that geological changes left descendants with modifications. This allowed Darwin to explain why species distributed in a certain region were more related among them than species found in other distant regions (“*On this principle of inheritance with modification, we can understand how it is that sections of genera, whole genera, and even families are confined to the same areas, as is so commonly and notoriously the case*”, Darwin 1859: 350-351). Alfred Russel Wallace extended Darwin’s vision proposing a global pattern of species distribution, where higher taxonomic hierarchies such as classes and orders, were generally spread over the whole Earth, whereas more derived ones such as families and genera were confined to more restricted parts of the globe. Overall, the first evolutionary approach of the geographical distribution of species identified that “*the*

natural sequence of the species by affinity is also geographical” (Brooks 1984: 73). In other words, that the relationships between species across the tree of life is spatially structured.

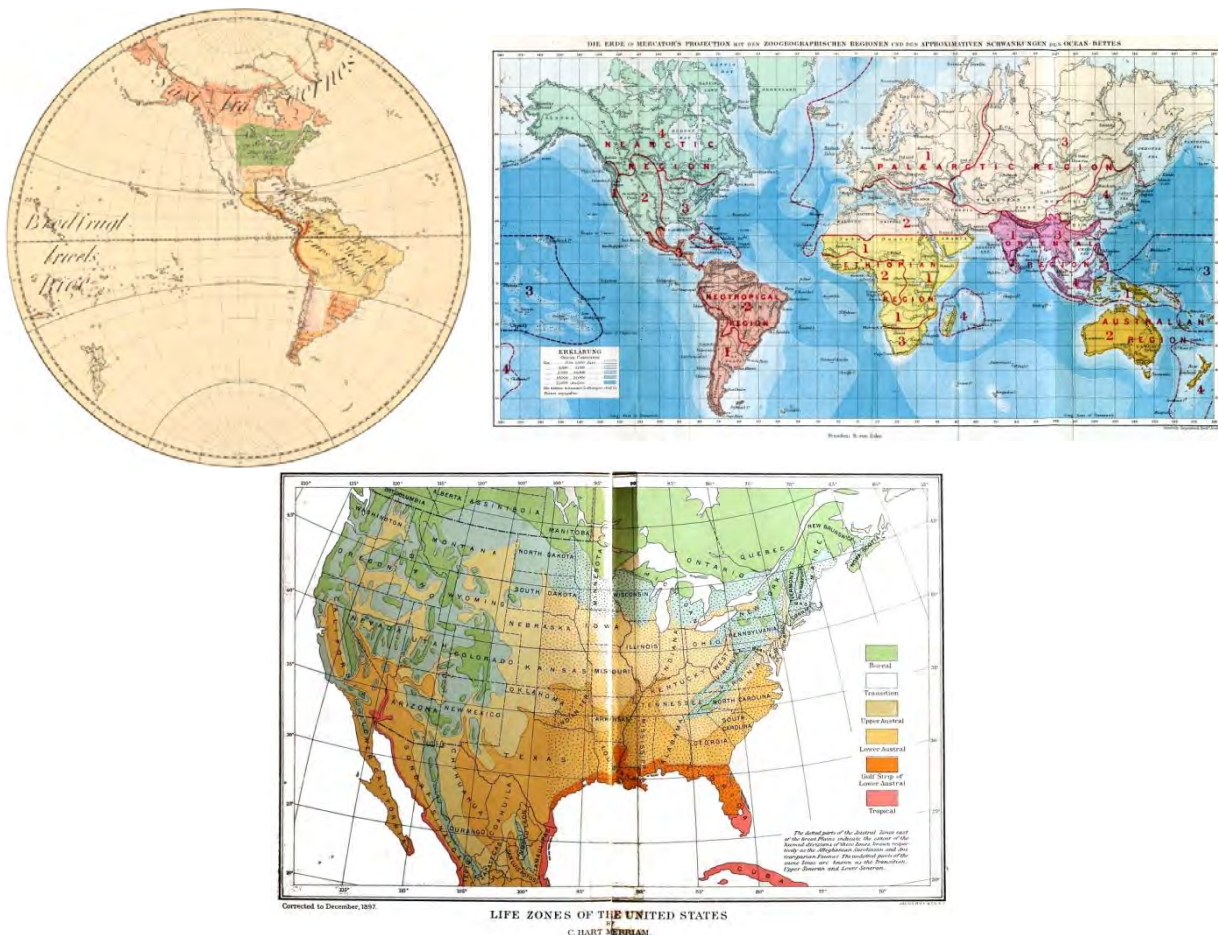


Figure 3. Evolution in the delimitation of geographical-biotic units during the 19th century. Early biotic zones (top) had coarse resolution and strong limits demarcated almost by latitudinal lines whereas Life zones theory (down) integrated climate and topography allowing to reduce resolution and define flexible limits. Top left, first atlas of the geography of plants in the New World, largely based by Humboldt’s collections. By Joakim F. Schouw in 1822 (from Morueta-Holme & Svenning 2018). Top right, biogeographic regions proposed by Alfred R. Wallace in his book *The geographical Distribution of Animals* (Public domain / [Wikimedia Commons](#)). Down, life zones of the United States proposed by Clinton Hart Merriam (Public domain / [Wikimedia Commons](#)).

In the late 19th century, an integrated view in the study of natural and social phenomena began to permeate the biological sciences (Chamberlin 1965) advocating a more comprehensive view of species geographic distributions, where multiple factors interacted as drivers. Following Chamberlin, Clinton Hart Merriam proposed the “life zones” theory where he stated that climate interacted with topography forming circumpolar belts that aggregated

species in climatic zones (Merriam 1894). The interest of this theory was a finer-resolution view of biotic zoning where borders were adjusted to environmental conditions instead of latitudinal lines (Fig 3). The “life zones” theory was widely accepted in its beginnings, however, in the early 20th century, the supporters of the emerging field of ecology considered that *“distribution cannot be explained by the mere mapping of the extent either of hypothetical faunal divisions”* (Ruthven 1920: 248). Ecologists proposed that combining the results of experiments altering the intensities of environmental factors along with the study of habitat preferences across the ranges of species was the correct way to identify the determinants of species distribution (Ruthven 1920, Moore 1920). This resulted in the construction of the first regional maps of species’ ranges based on wide sampling records (Fig. 4) and the nomination of different ecological factors as drivers of the species distribution (e.g. Grinnell 1914, 1917, Talbot 1934, Dennis 1938). Besides the contributions made by the field of ecology during the early 20th regarding the spatial and environmental component of species’ ranges, a temporal dimension was also proposed at that time by John Willis. stated the (Willis 1922). He proposed a positive age-area relationship about the dynamics of species geographic ranges where, in areas with no well-marked barriers, the oldest species would have the broadest geographic ranges.

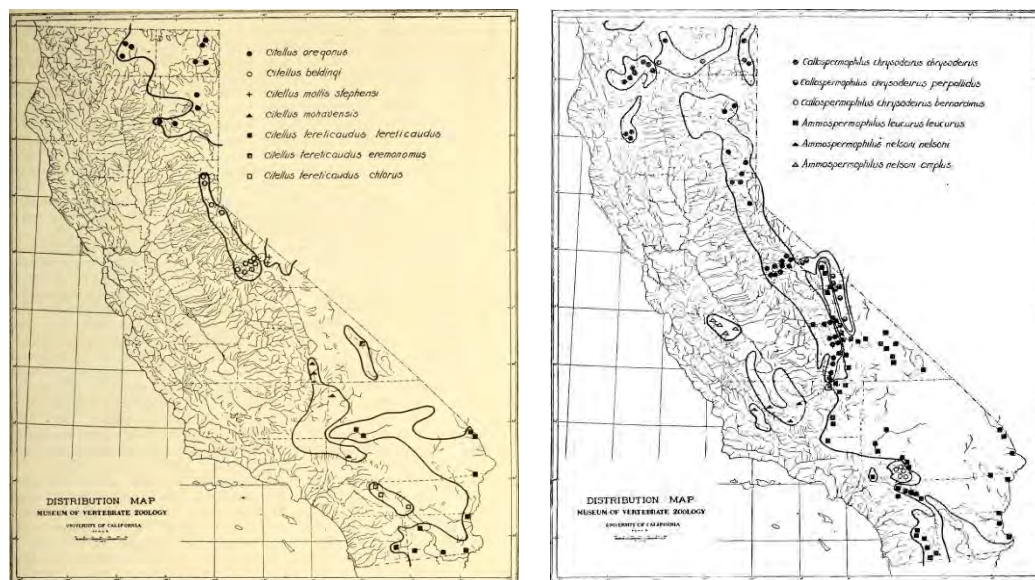


Figure 4. First regional-distribution maps of ground squirrels species elaborated by Joseph Grinnell (1910, Public domain / [Wikimedia Commons](#)).

During the second half of the 20th century, the study of species geographic distributions underwent a pivotal moment and species ranges began to be studied as basic geographic units

(Brown et al. 1996, Jenkins and Ricklefs 2011), transcending the delimitation of biogeographic regions as the only way to explain species distributions and establishing the concept of species range that we currently apply and study (i.e. the area across which a species occurs, Sheth et al. 2020). The first step to consolidate this single-species view of species distribution was the launch of multiple biological surveys (e.g. North American Breeding Bird Survey) and the compilation of maps of geographic ranges for thousands of species that allowed gathering different types of information on the distribution of species (e.g. Hall and Kelson 1959). Then, Eduardo Rapoport used this information to pose the initial guidelines to quantify and analyze different aspects of the species geographic ranges in his seminal book 'Areografía' (Rapoport 1975), clearly differentiating between biogeography ("*the delimitation of faunistic or floristic sets and in the origin of their different elements*", Rapoport 1975: 21), areography ("*the attention on the form and size of the geographical ranges of species and other taxa*", Rapoport 1975: 21), and ecogeography ("*the study of the spatial distribution of taxa, but at a geographic level*", Rapoport 1975: 22). This promoted the description of early spatial patterns of geographic ranges such as the one showing that small-ranged species are much more common than large-ranged ones and that species are not evenly spread through all the potential range (Rapoport 1975, Anderson 1977). Then, these geographic range patterns were rapidly associated with diverse hypotheses: habitat availability (Cody et al. 1975, Anderson and Koopman 1981), density dependent factors (Rosenzweig 1978), abundance (Bock and Ricklefs 1983, Brown 1984), life history (Reaka 1980), and body size (Reaka 1980, Gaston and Lawton 1988).

At the end of the 20th century, the computers-related technology developments facilitated the compilation and digitalization of the first large databases of species ranges, and allowed faster quantification and analysis of distributional patterns. Thus, the study of geographic range size at large spatial scales rapidly received considerable attention (Gaston 1990, 1996, Brown et al. 1996), and the first global patterns were described. One of these patterns is the Rapoport's rule that describe how species latitudinal range decreased toward the Tropics (Stevens 1989). Other relevant contributions were the macroecological relationships between the geographic range and the body size and abundances of species, documented by James Brown and Brian Maurer (1987, 1989). Through these relationships, Brown and Maurer offered insights into the empirical patterns and causal mechanisms that characterize the distribution of food and space across species (Brown and Maurer 1987, 1989). Today, in the 21th century, these patterns set the basis of macroecological theory

(Keith et al. 2012, Brown 2019) where species geographic range size has been related with a long list of driving factors (Morueta-Holme and Svenning 2018, Sheth et al. 2020). Currently, the study of species geographic range sizes keeps growing, being at the interface of different knowledge fields such as ecology, evolution, biogeography and conservation (Li et al. 2016, McGill 2019, Newsome et al. 2020, Sheth et al. 2020).

Determinants of species geographic range size: going from potential drivers to quantification of interacting forces.

Since the time of Linnaeus, we have identified several extrinsic and intrinsic drivers that shape the variation of species' geographic range sizes at both ecological (contemporary) and evolutionary (historical) scales (Sheth et al. 2020). Extrinsic drivers are external environmental conditions such as climate and dispersal barriers that directly affect the physiological requirements and morphological variation of species, ultimately determining the presence and accessibility of suitable habitats across the geographical space. Climate stability has been frequently seen as one of the main extrinsic drivers of species geographic range size (Stevens 1989, Morueta-Holme et al. 2013, Li et al. 2016). At an ecological scale, climate is proposed to select against small range sizes via intra-annual variability (Stevens 1989, Morueta-Holme et al. 2013, Li et al. 2016). Habitat availability is another prevalent driving factor, small range sizes having been associated with discontinuous areas and habitat fragments (Hawkins and Diniz-Filho 2006, Morueta-Holme et al. 2013), or poor habitats representativeness compared to their surroundings (Ohlemüller Ralf et al. 2008). Conversely, widespread habitats can harbor relatively more large-ranged species due to a larger potential for range expansion (Hawkins and Diniz-Filho 2006, Ohlemüller Ralf et al. 2008). For terrestrial organisms, topographic heterogeneity is also an established driver acting negatively on species geographic range (Hawkins 2006, Li et al 2016), e.g. mountain regions acting as dispersal barriers that constrain dispersal movements through steep-climate gradients and rapid changes of habitats (Brown et al. 1996, Hawkins and Diniz-Filho 2006, Morueta-Holme et al. 2013).

Intrinsic drivers of geographic ranges are features of species that condition their response to external drivers (i.e. extrinsic factors) determining their ability to colonize new habitats. Niche breadth (Brown 1984, Slatyer et al. 2013) and dispersal capacity (Glazier and Eckert 2002, Laube et al. 2013) have been proposed as the main intrinsic drivers of species geographic range. Generalist species that can maintain stable or high population densities

across a broad range of environments or resources should become more widespread than specialized species with narrow niches (Brown 1984, Slatyer et al. 2013). Similarly, species with higher locomotion capacities should disperse across longer distances, promoting colonization and achieving larger range sizes (Glazier and Eckert 2002, Laube et al. 2013), whereas, low dispersal ability can lead to population differentiation promoting allopatric speciation into small-ranged species (Gutiérrez and Menéndez 1997). Other species traits related to dispersal capacity have been also associated with geographic range size. For example, when migratory behavior has a low fitness cost, dispersion is expected to be positively related to range size as migratory movements increase the probability of colonizing new areas (Hanski et al. 1993, Polechová 2018). Additionally, the commonly observed macroecological relationship between body size and range size shows an overall positive trend where small-bodied species can have a variety of range sizes, but larger-bodied species are increasingly constrained to larger ranges (Brown and Maurer 1987, 1989; this relationship is explained more in detail below in the section *Range - body size relationship, and its conservation implications* of this chapter).

The above drivers explain the ecological reasons for the geographical variation of species range sizes. However, historical factors associated with species' evolutionary history and/or climatic and geological history of the environment can also influence the size of the area where a species currently occurs. For example, in temperate regions, cyclical variations in the shape of Earth's orbit induced climatic variability occurring at an evolutionary time scale (10^4 – 10^6 year). These variations created long-term climatically unstable conditions that may have selected in favor of large range species by lowering the proportion of small-ranged species (Dynesius and Jansson 2000, Jansson 2003, Sandel et al. 2011). The loss of historical barriers can also drive changes in species geographic range size, the connection of previously isolated areas favouring exchanges of biotas that allows the colonization of newly suitable areas and the subsequent expansion of species ranges (e.g. The Great American Biotic Interchange, Vermeij 1991). Conversely, the emergence of geological barriers fragments species ranges into isolated populations promoting speciation events that result in areas with high endemism and composed of species with small range sizes (e.g. the Andes uplift, Hoorn et al. 2010). Regarding time elapsed throughout species' evolutionary history, the original proposal of the age – area relationship stated that the geographic range of a species continues to expand throughout its life (Willis 1922). However, the fossil record shows a non-linear relation where newly formed species tend to expand their ranges and then undergo a gradual

decline until extinction (Foote et al. 2007, Liow et al. 2010). Average range sizes within clades may also decline with speciation events (Jablonski and Roy 2003, Pigot et al. 2010), as the available space is divided by functionally similar species, leading to a negative relationship between the geographic range size of a species and the diversification rate of the corresponding clade.

Despite the progress already made in identifying several drivers of species' geographic range sizes, the need to go beyond a long list of factors and to develop a more holistic view of species ranges that allows us to predict how biodiversity patterns will change due to global environmental change is still necessary (Morueta-Holme and Svenning 2018, Sheth et al. 2020). The new models of species geographic range size must consider the interactions among driving factors (Sheth et al. 2020) that directly and indirectly influence its variation while considering the factors' effects across scales (Levin 1992, McGill 2010), regions (Morueta-Holme et al. 2013), species traits (e.g. body size, Brown and Maurer 1987), and taxonomic groups (Li et al. 2016) (Fig. 5). This will allow us to have a comprehensive explanation of the distribution of species in specific places and times, but also to dispose of predictive, prescriptive, and scalable models (Hampton et al. 2013).

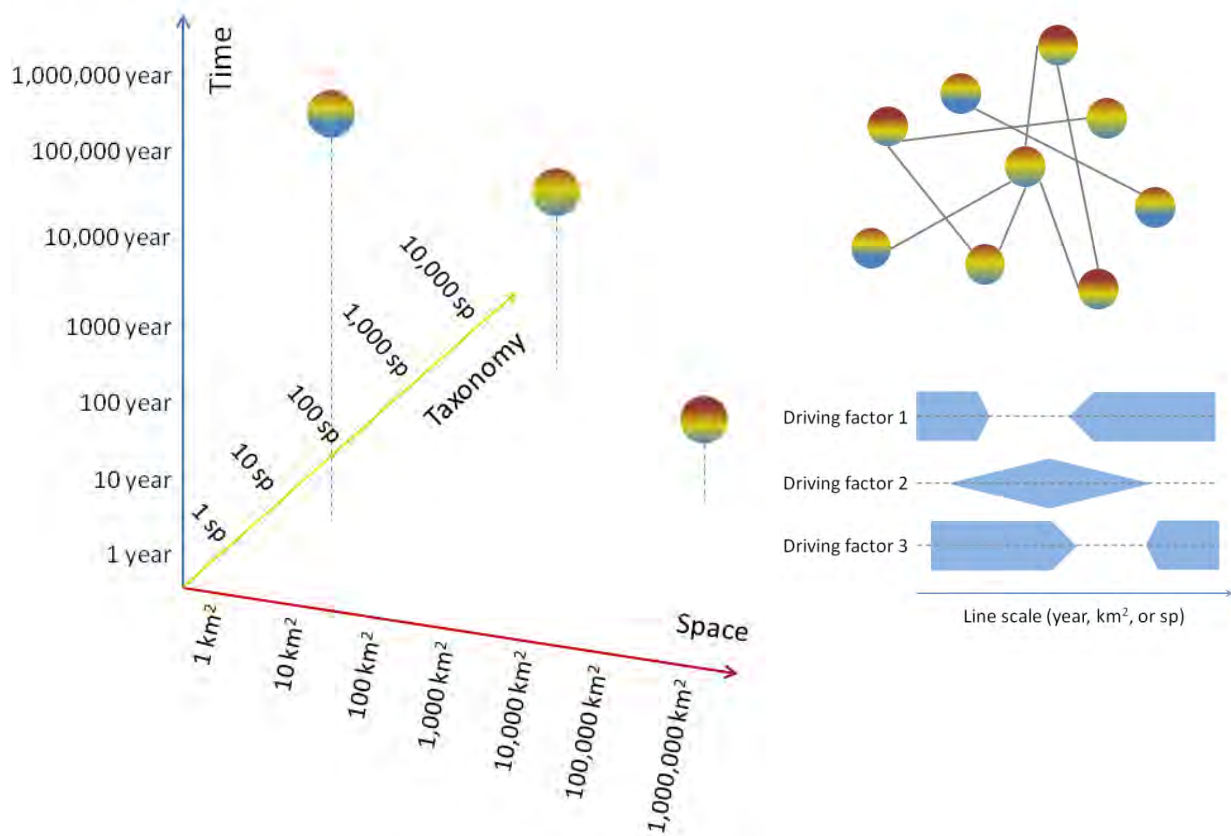


Figure 5. How driving factors operate? Factors that drive species' geographic range size can interact (upper right) and influence geographic ranges at different dimensions scales (left). The relative importance of each driver at each scale (represented with gradient colors with respect to each axis; left) varies among them. At the same time, the importance of each driver can vary across each scale (lower right).

This aspiration for a bigger picture of species geographic ranges builds on recent informatics developments and remote sensing technologies that have brought advances in methods and data availability. Large repositories of ecological and environmental data are becoming increasingly accessible (Hampton et al. 2013, Linke et al. 2019, Wüest et al. 2020), and the expansion of computational capabilities has allowed us to better translate our knowledge into empirical and theoretical models with greater inferential strength and causality (Hampton et al. 2013, Connolly et al. 2017). Today, the so-called biodiversity informatics provides us with the opportunity to test hypotheses at unprecedented spatial and temporal scales and integrate disciplines that typically focus on different levels of biological organization, such as phylogenetics, population dynamics, community ecology and macroecology (McGaughan 2015, La Salle et al. 2016, Benedetti-Cecchi et al. 2018).

Despite being promising, biodiversity informatics is also challenging (Michener and Jones 2012, Hampton et al. 2013, Farley et al. 2018). The enormous amount of information already collected is heterogeneous and spread in different databases or reside on papers or other media from both academic and gray literature, impeding its direct treatment and analysis (Edwards et al. 2000, Farley et al. 2018). Thus, some of the academic and certainly most of the “grey” biodiversity information is often not used for policy or management decisions, nor for scientific research (Edwards et al. 2000). The diversity and scatter of these data lies in the variety of ways in which studies are carried out resulting in large numbers of small and idiosyncratic data sets that accumulate relevant biological, ecological and environmental data collected from thousands of scientists (Michener and Jones 2012). Besides, language barriers and cultural differences across disciplines, institutions and countries hinder the data-sharing (Hampton et al. 2013). Integrating and analyzing massive amounts of heterogeneous data must be carefully planned, and this point is central in contemporary ecological and biogeography sciences (Hampton et al. 2013, La Salle et al. 2016, Wüest et al. 2020).

Thus, through initiatives of developing new databases that make available the massive amount of inconspicuous and disconnected ecological data and the developing of models that

convert these emerging databases into comprehensive and synthetic results, we will be able to have a more holistic vision of species' geographic ranges to better understand the nature and pace of ecological and environmental changes (Michener and Jones 2012).

Geographic range size of freshwater fishes

One of the most important challenges to achieve a unified view of biodiversity distribution is to contrast the proposed hypotheses and explore new ones across all the tree of life (Shade et al. 2018). However, in the case of geographic range size variation and its drivers, most research has focused on terrestrial environments, mainly for large terrestrial vertebrates (Brown et al. 1996, Sheth et al. 2020), skewing our understanding of species distribution toward a reduced group of charismatic species. Studies about this topic on freshwater fishes are scarce and restricted to specific clades and regions, (e.g. Hugueny 1990, Pyron 1999, Rosenfield 2002, Tales et al. 2004, Blanchet et al. 2013). These studies have identified as intrinsic drivers of range size, factors related to locomotion capacity, energetic requirements and the ability of species to occupy different habitats. For example, fish species presenting migratory behavior, high swimming capacity and small eggs have larger home ranges and a higher probability that offspring disperse and recruit successfully to new suitable habitats, resulting in larger range sizes (Blanchet et al. 2013, Giam and Olden 2018). Likewise terrestrial vertebrates, generalist fish species with larger bodies and presenting high local abundances tend to have larger geographic ranges (Pyron 1999, Tales et al. 2004, Giam and Olden 2018).

Among extrinsic factors, river topology has been associated with the variation in the range size of freshwater fishes. Bertuzzo et al. (2009) found that fish species with small ranges can be distributed along all the Mississippi-Missouri river basin, whereas, large-ranged species tend to be restricted to the lowland waters. They attributed this pattern to the network structure of rivers (Fig 6) that increasingly constraint the dispersal movements of freshwater organisms toward the headwaters. Similarly, Carvajal-Quintero et al. (2015) found a negative relationship between the species' regional range size and elevation in Tropical rivers.

River architecture not only restricts dispersion within drainage basins but also among basins, hence freshwater fishes range size may have conserved the signal of historical-geographical patterns (Smith 1981, Hocutt and Wiley 1986). For example, historical connections between rivers (i.e. paleo-connected river drainages) during the last glacial

maximum favored inter-basins colonization (Voris 2000, Dias et al. 2014b) which could have further favored the expansion of geographic ranges of species that inhabited ‘paleo-connected’ basins. Besides, it has been hypothesized that wide river channels and lakes in North America have served as refuges for freshwater fish from adverse environmental changes during glacial periods and allowed them to recolonize northward as glacial sheets retreated (Griffiths 2010, Blanchet et al. 2013), making fish species using large rivers and lacustrine habitats to have larger range sizes than species that do not use these habitats (Giam and Olden 2018).



Figure 6. Topologies of contrasting freshwater (left) and terrestrial environments (right). The branching-network and isolated structure makes freshwater environments more fragmented than terrestrial ones. Images obtained from the NASA earth observatory (<https://earthobservatory.nasa.gov/images>).

Overall, because freshwater fishes have current and historical dispersal limitations not found among terrestrial taxa, we may expect fish species to display patterns of geographical ranges that differ from birds and mammals, supporting a growing body of literature that suggests that theories developed in open landscapes, such as terrestrial landscapes, may be

inadequate to predict the properties of complex branching ecosystems, such as river networks (Campbell-Grant et al. 2010, Rinaldo et al. 2014).

Geographic range size in conservation

Beyond its theoretical relevance, studying species geographic ranges is also critical for advancing fundamental knowledge in conservation practice and action (Mace et al. 2008, 2010, Lee and Jetz 2011). By identifying the drivers and processes acting on species' geographic range size we can make projections on the way global change will impact these ranges (e.g. Powers and Jetz 2019), allowing us to develop and prioritize conservation actions for the most affected species. Geographic range size can also be used as a surrogate for identifying species with rapid population decline (Mace et al. 2008), and constantly emerges as a key correlate of extinction risk across animals and plants (Lee and Jetz 2011, Böhm et al. 2016, Chichorro et al. 2019). Additionally, by reflecting the vulnerability of restricted-ranged species, species' geographic range size analyses play a key role in categorizing species according to their likelihood of extinction (including listing on the IUCN Red List of threatened species) and thus contribute importantly to indices of global trends in threat status and to the prioritization of species for conservation (Gaston and Blackburn 1996a, IUCN 2001, Mace et al. 2008). Indeed, almost 50% of overall threatened species are actually listed as threatened on the basis of the geographic range size criterion alone, and in less known groups, such as amphibians, this could go up to 75% (Gaston and Fuller 2009).

However, the variation of geographic range size by itself does not provide a mechanistic explanation for extinction risk. For example, a small range size alone or a range contraction would fail to detect if population processes needed for the species' persistence are fulfilled (Mace et al. 2008). Therefore, it is not enough to know that species with small geographic ranges tend to be at greater risk; rather, we need to know how range size interacts with other ecological traits to make certain species more vulnerable than others (Davidson et al. 2009). Thus, by understanding how different key ecological drivers interact, we may be able to identify the species at greatest risk and to understand what makes them vulnerable (Davidson et al. 2009, Ripple et al. 2017).

Range - body size relationship, and its implications for conservation

One of the most important patterns accounting for the variation in the size of species' geographic ranges is the range – body size relationship (Brown 1995, Gaston and Blackburn 2008). This relationship was proposed as a mechanistic explanation on how physical space and resources are allocated among species (Brown and Maurer 1987, 1989), and currently represents the basis of the seminal macroecological theory (Brown 2019). The range-body size relationship is determined by different ecological and evolutionary constraints that restrict the traits space to a triangular envelope through differential colonization, speciation and extinction processes (Fig. 7, Brown and Maurer 1987, 1989). The upper-horizontal bound of the triangle is settled by the maximum geographic area that species can potentially occupy (geographic constraint), the left-vertical bound corresponds to the minimum body size that a species of a given taxon can reach (physiological constraint), and the lower-diagonal bound represents the minimum viable geographic range size needed for species to achieve long-term persistence given their body sizes (Fig. 7, Brown and Maurer 1987, 1989, Gaston and Blackburn 1996).

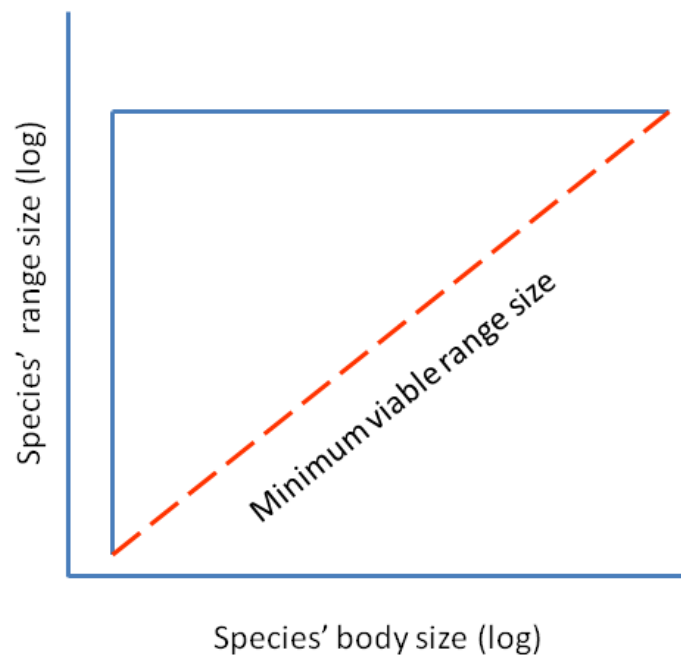


Figure 7. Empirical model describing the geographic range size–body mass relationship proposed by Brown and Maurer (1987, 1989).

Two main hypotheses have arisen to explain the lower-diagonal bound of the range-body size relationship. First, large-bodied species tend to disperse more quickly and efficiently than smaller species filling a bigger portion of their potential distributional range (Gaston 1994a, Gaston and Blackburn 1996a). Second, large species have higher energetic demands than small species, hence large-bodied species occupy larger home ranges to attain enough resources to support viable population size to be able to persist (Brown and Maurer 1987, Swihart et al. 1988). Thus, small species can have a variety of geographic range sizes while species with larger body size are restricted to larger ranges (Gaston and Blackburn 1996a).

From a conservation perspective, the lower-diagonal bound of the range – body size relationship is the most important feature and has been proposed as a probabilistic vulnerability limit whereby any species that is near or beyond this limit is prone to extinction or has a low probability of persistence through time (Brown and Maurer 1987, 1989, Gaston and Blackburn 1996a). Different studies have shown that the distance of species with respect to the lower limit is a reliable and useful predictor of extinction risk (Rosenfield 2002, Diniz-Filho et al. 2005, Le Feuvre et al. 2016, Newsome et al. 2020) and have promoted its use for tracking trajectories of species towards or away from an extinction threshold and to evaluate how different human stressors may affect species vulnerability (Le Feuvre et al. 2016, Newsome et al. 2020).

Despite its applied importance, no test has been done yet to link explicitly this empirical boundary to species' lower probability of persistence. Providing empirical evidence that directly links this lower limit to a lower probability of species' persistence or to the minimum viable geographic range size would be a meaningful advance in our comprehension about geographic ranges and vulnerability of species.

Current conservation status of freshwater fishes

Freshwater ecosystems are essential sources of environmental health, economic wealth and human well-being. Freshwaters maintain hydro-climatic regimes in our planet, have provided us food and water for domestic use and agriculture for millennia, sustained transportation corridors, supported recreation, and more recently, enabled power generation and industrial production (Costanza et al. 1997, Dudgeon et al. 2006, McIntyre et al. 2016). At the same time freshwaters harbor an extraordinary diversity of life. Covering about 2% of Earth's

surface they host approximately one-third of all vertebrate species and 10% of all known species (Strayer and Dudgeon 2010, Reid et al. 2019). Besides, levels of endemism among freshwater species are remarkably high (Dudgeon et al. 2006, Tedesco et al. 2012, Reid et al. 2019). The insular and fragmented nature of freshwater habitats restricts species' distribution resulting in over half of the freshwater fishes confined to a single ecoregion (Abell et al. 2008).

Despite supporting human well-being and an extremely high biodiversity, the management of freshwater ecosystems worldwide most often focuses on macroeconomic profits and human water security rather than on the benefits provided by the ecosystem integrity (Vörösmarty et al. 2018). Consequently, we are living a freshwater ecosystems crisis (Harrison et al. 2018, Albert et al. 2020) where the current rates of wetlands loss are three times as high as forest loss (Gardner and Finlayson 2018), where populations of freshwater species have declined by an average of 83% since 1970 (more than twice the rate of land or ocean vertebrates, Grooten and Almond 2018), and where extinction rates are exceptionally high (e.g. freshwater fish extinction rates have been estimated to be more than 100 times their natural rates in Europe and United States, Dias et al. 2017).

The causes of this biodiversity crisis are widely recognized. Habitat degradation by land use, habitat fragmentation, chemical and organic pollutions, flow modification, overfishing and climate change are the leading causes (Dudgeon et al. 2006, Grooten and Almond 2018, Reid et al. 2019, Albert et al. 2020) (Fig.8). Surface waters receive pollution from commercial activities (e.g. mining, agriculture, oil) and urban settlements, impairing freshwater biodiversity through toxicity or indirect impacts on habitats (Cope 1966). Due to the changes in the use and production of chemicals in the last decades, toxic pollutants are changing and their effects on aquatic populations and communities are largely unknown (Reid et al. 2019). Dams, weirs and levees fragment longitudinal (upstream-downstream) connectivity of rivers and, through flow alterations, also affect lateral (river to floodplain), vertical (surface to groundwater) and temporal (season to season) connectivity, disrupting important processes that support freshwater biodiversity (Albert et al. 2020, Tickner et al. 2020). Today, about 2.8 million of major dams (i.e. dams with reservoir areas $>10^3 \text{ m}^2$) fragment two-thirds of the world's long rivers (Grill et al. 2019) and dams continue to be built across the globe. Three thousand seven hundred major hydropower dams are currently either planned or under construction (Zarfl et al. 2015), and the increased political and economic support for the widespread development of small hydropower plants (SHP) has resulted in approximately

83,000 SHP operating or under construction (Couto and Olden 2018). Despite the impacts of SHPs are largely unknown, 11,000 new projects already appear in national plans, and if all potential generation capacity were developed, the number of SHP would triple (Couto and Olden 2018).

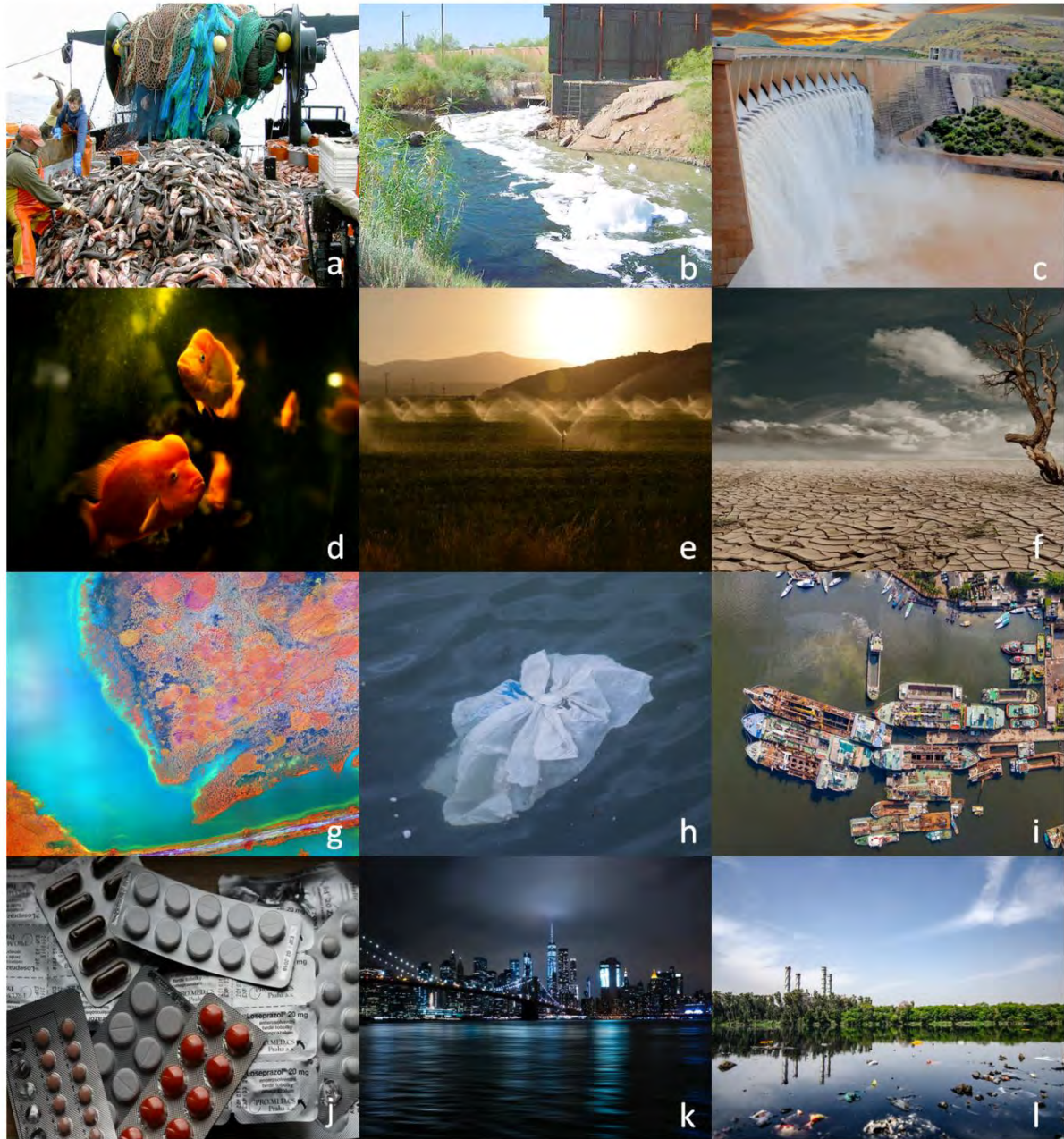


Figure 8. Major and emerging drivers of freshwater biodiversity loss based on Dudgeon et al. (2006), Reid et al. (2019) and Albert et al. (2020). a) overfishing, b) water pollution, c) dams, d) species introduction, e) land change and water withdrawal, f) climate change, g) algal blooms, h) plastic pollution, i) noise pollution, j) emerging contaminants, k) light pollution, l) declining calcium (eutrophication). There are more threats than those mentioned in this figure,

for more information check original sources. Images obtained from [Wikimedia Commons](#), [Unsplash](#), and [Pexels](#).

Climate change alters hydroclimates as well as several ecological processes that underlie freshwater ecosystem functioning at different levels of biological organization (Scheffers et al. 2016). Overfishing, that includes both targeted species harvesting and mortalities through bycatch, has persisted during the last decades driving the decline of biodiversity (Allan et al. 2005). For example, overharvesting remains the key threat for the decrease of freshwater-megafauna populations (i.e. animals that reach a body mass of 30 kilograms), that have declined by 88% on average during the last decades, reaching the highest declines in the Indomalaya and Palearctic realms (–99% and –97%, respectively; He et al. 2019). Also, the introduction of invasive species has caused multiple impacts that range from behavioral shifts of native species to complete restructuring of food webs and extirpation of entire faunas (Gallardo et al. 2016).

There is long-standing recognition that environmental stressors can interact affecting freshwater ecosystems through multiple pathways (Ormerod et al. 2010, Vörösmarty et al. 2010, Craig et al. 2017). Thus, emerging and persistent threats can have potential additive effects that might cause multiple ecological alterations, worsening the prognosis for freshwater biodiversity (Reid et al. 2019).

Although for more than two decades scientists have warned about the global biodiversity crisis in freshwater ecosystems, and the low priority given to these ecosystems for global conservation-oriented actions (Brautigam 1999, Dudgeon et al. 2006, Harrison et al. 2018, Albert et al. 2020), freshwater populations continue to decrease rapidly (Grooten and Almond 2018, He et al. 2019) and the actions to safeguard freshwater biodiversity are still “*grossly inadequate*” (Harrison et al. 2018). This has arisen new emergency recovery plans and recommended actions to promote the restoration of freshwater biodiversity (e.g. Reid et al. 2019, Albert et al. 2020, Tickner et al. 2020).

Thesis

Objective of the thesis

This PhD thesis focuses on identifying the main drivers of geographic range size variation of freshwater fishes at global and biogeographic scales, as well as on understanding the processes that underlie the lower vulnerability limit settled by the range – body size relationship. Results were further applied to the specific case of habitat fragmentation by dams in the Magdalena River Basin (Colombia).

Thesis structure

This thesis is composed of six chapters that address the following topics:

The first chapter consisted in the previous introduction section, where we presented a general context for the species' geographic range and the range – body size relationship doing a special focus on freshwater fishes, and the importance of these two concepts in conservation science.

The second chapter presents an analysis of global patterns of geographic range size variation of freshwater fishes where we identified the main ecological and historical drivers of fish species' range sizes at a global scale and tested their consistency across the biogeographic realms. We found that the variation of geographic range size in freshwater fishes is determined by the complex interaction of multiple variables that influence directly and indirectly the geographic range size, and within this complex system the drainage position network and the historical connections among basins account for most of the variation (about 90%). These highlight the importance of current and historical hydrological connectivity in the variation of the geographic range size of freshwater fishes.

In the third chapter, we show an analysis where we assess the lower limit of the geographic range – body size relationship as boundary of lower probability of species' persistence. For this, we reconstructed the range – body size relationship at a global and biogeographic realm scales and tested if the lower limit matched with the minimum viable range size represented by the spatial scale of synchrony. We found that the two limits matched at both spatial scales, providing empirical evidence that support the lower limit of the range – body size relationship as a species' vulnerability limit.

In the fourth chapter, we use the lower limit of the species range – body size relationship to quantify the effect of fragmentation caused by the hydropower development on geographic range and vulnerability of the freshwater fish fauna of the Magdalena drainage basin (Colombia). We also identified the ecological and human-dependency traits of species related to a higher probability of extinction, both intrinsically and because of hydropower development. We found that both existing and planned dams fragment most fish species ranges, and splits species ranges into more vulnerable populations. Importantly, we found that migratory species, and those that support fisheries, are most affected by fragmentation.

The fifth chapter consists of a global database that contains raw data of time series on fish species identities and abundances in different assemblages. This database gathers 11,441 time-series of riverine fish communities, distributed in 11,125 unique sampling locations distributed, and span 21 countries, 5 biogeographic realms, and 402 hydrographic basins worldwide. These data offer the possibility to identify ecological processes underlying species' geographic range stability as well as to calculate temporal changes in fish diversity at different spatial scales facilitating quantitative analyses of temporal patterns of biodiversity, a critical knowledge needed for the conservation of the freshwater fauna in the Anthropocene.

Finally, in the sixth chapter, we present a general discussion of the results of my PhD thesis and highlight some perspectives to continue advancing our understanding of the geographic ranges of freshwater fishes.

Biodiversity data of freshwater fishes

To carry out the analyses of this thesis, we compiled the following three databases:

A global database of species' geographic range size.

This database includes the geographic range maps of 9,075 species of freshwater fishes representing 31 orders and 177 families which correspond to 70%, 89% and 97% of the known species, orders and families, respectively (Tedesco et al. 2017). Range maps were compiled from two different sources, the IUCN that provided range maps for 6,013 species worldwide (except for a large proportion of South America), and a set of 3,062 species' ranges reconstructed using occurrence records of multiple datasets and following the same methods as the IUCN (for more details see Chapter 1 methods and SI).

A global database of abundance time-series of freshwater fish assemblages (RivFishTIME).

This database gathers 11,463 long-term time series (spanning > 10 years) of freshwater fish assemblages compiled from 47 individual datasets and represents a total of 109,346 surveys and 709,352 individual species abundance records at 11,147 independent locations. Surveys cover 1,417 species ray-finned fish species (Actinopterygii), and span longitudinal and latitudinal gradients, spanning 405 hydrographic basins distributed 25 countries, and 6 biogeographic realms (for more details see Chapter 4).

A database of occurrences and species traits for freshwater fishes of the Magdalena drainage basin (Colombia).

This database contains 11,571 occurrence records for 204 fish species of the Magdalena River. These fish occurrences span from 1940 to 2014 and were compiled from the main fish collections of Colombia, the Colombian Biodiversity Information System (<http://data.sibcolombia.net>) and published literature. Occurrences records were complemented with ecological and human-dependency traits of 179 species. Species traits include: 1) body length, 2) species endemic to the Magdalena River Basin, 3) the species' demographic strategy, 4) the habitat use, 5) species used as fishery resource, and 6) migratory species (for more details see Chapter 3 methods and SI).

CHAPTER 2 – Drainage network position and historical connectivity explain global patterns in freshwater fishes range size



Photo by Jorge García-Melo (Project CaVfish Colombia)

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Abstract

Identifying the drivers and processes that determine globally the geographic range size of species is crucial to understanding the geographic distribution of biodiversity and further predicting the response of species to current global changes. However, these drivers and processes are still poorly understood, and no ecological explanation has emerged yet as preponderant in explaining the extent of species' geographical range. Here, we identify the main drivers of the geographic range size variation in freshwater fishes at global and biogeographic scales and determine how these drivers affect range size both directly and indirectly. We tested the main hypotheses already proposed to explain range size variation, using geographic ranges of 8,147 strictly freshwater fish species (i.e., 63% of all known species). We found that, contrary to terrestrial organisms, for which climate and topography seem preponderant in determining species' range size, the geographic range sizes of freshwater fishes are mostly explained by the species' position within the river network, and by the historical connection among river basins during Quaternary low-sea level periods. Large-ranged fish species inhabit preferentially lowland areas of river basins, where hydrological connectivity is the highest, and also are found in river basins that were historically connected. The disproportionately high explanatory power of these two drivers suggests that connectivity is the key component of riverine fish geographic range sizes, independent of any other potential driver, and indicates that the accelerated rates in river fragmentation might strongly affect fish species distribution and freshwater biodiversity.

Significance

Species' geographic range size is a fundamental aspect of understanding and predicting changes in biodiversity patterns. Investigating the global drivers of geographic range size variation in freshwater fishes, we found clear evidence that current and historical connectivity are, by far, the main determinants of range size. More specifically, we found that, everything else being equal, species displaying basal position in the drainage network (i.e., lowland areas) and found in drainage basins that have had connections during Quaternary low-sea-level periods have larger range sizes than their counterparts. Our findings suggest that connectivity is the key component of riverine fish geographic range sizes. This may have important implications for evaluating the vulnerability of freshwater species to river fragmentation.

Introduction

The factors that determine species' geographic range sizes are complex and interrelated, and disentangling this complexity represents a central concern in macroecology, biogeography, and conservation (Brown et al. 1996, Gaston 2003). At broad geographical scales, the overlapping of species ranges throughout space and time determines the variation in species richness and structure of regional biotas from which local communities are assembled (Gotelli et al. 2009). This overlapping of species ranges ultimately drives the biodiversity patterns that we use as a primary source to define regions of high conservation importance (e.g., Jenkins et al. 2013). Further, species' range size is one of the most important criteria for assigning a species' conservation status [International Union for Conservation of Nature (IUCN) Red List classification (IUCN 2018)], given its negative relationship with extinction risk (Gaston 2003). Quantifying the determinants of range size is also pivotal for evaluating community sensitivity to anthropogenic environmental change (Ohlemüller Ralf et al. 2008) and predicting shifts in response to climate change (Gaston 2003, Sandel et al. 2011, Li et al. 2016). During the last decades, multiple ecological and evolutionary hypotheses have been proposed to explain the variation in species' range sizes (*SI Appendix*, Table S1), including intrinsic biological characteristics of species (e.g., niche breadth, body size, population abundance, dispersal ability), metapopulation dynamics (i.e., colonization and/or extinction dynamics), and current or historical environmental characteristics (e.g., habitat availability and environmental variability) (Brown et al. 1996, Gaston 2003). However, the factors and processes determining the size of species' geographic ranges at broad spatial scales are still poorly understood, as none has emerged as preponderant in explaining the extent of species' geographical distributions (Lester et al. 2007, Calosi et al. 2010). For terrestrial groups (mostly vertebrates and plants), climatic and topographic factors have been recently identified as important determinants of species' range size at continental or global scales, with widespread species having higher thermal tolerance and occurring in areas with higher current and historical climate variability and lower topographic heterogeneity (Whitton et al. 2012a, Morueta-Holme et al. 2013, Li et al. 2016). Although strictly freshwater species (i.e., obligate freshwater dispersal) also inhabit continental landscapes, the global or continental determinants of their range size variation have never been assessed and may greatly differ from those identified for terrestrial ones. Indeed, a growing body of evidence suggests that theories developed in open landscapes, such as terrestrial, may be inadequate to predict the properties of complex branching ecosystems, such as river networks (Campbell-Grant et al. 2007, Rinaldo et al. 2014).

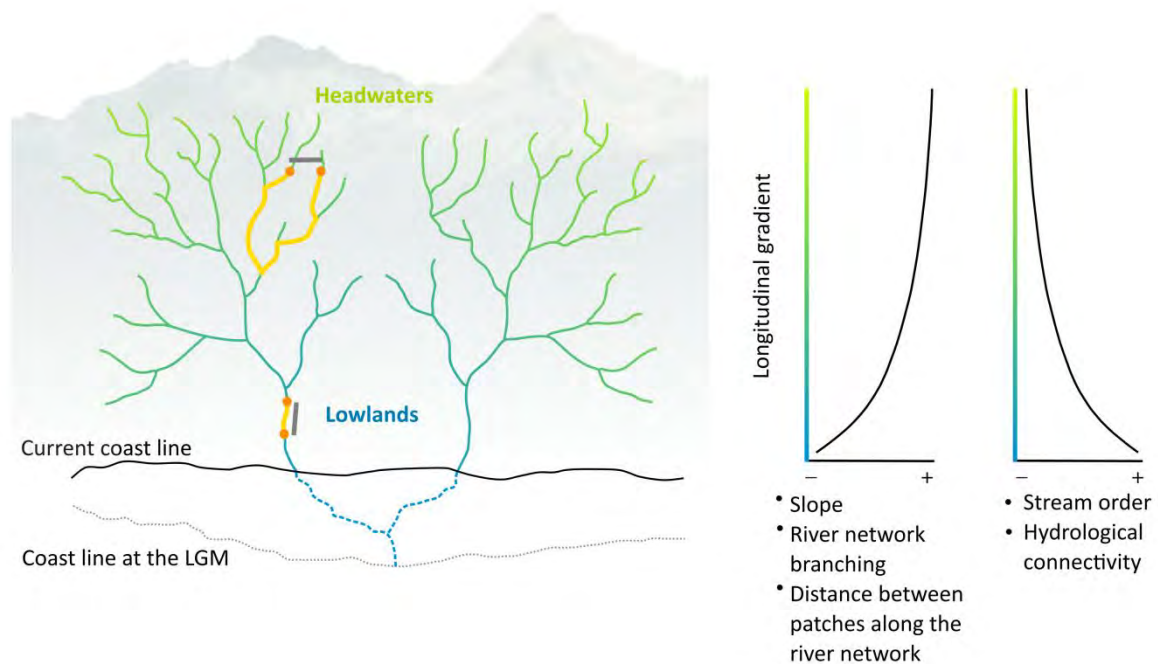


Figure 1. Different features of hydrological connectivity across the longitudinal gradient of schematized river networks. Gradient solid lines represent two river drainages currently disconnected, but that formed a single paleobasin during a lower-sea-level period at the LGM (dashed blue lines). Solid black line shows the current seashore line and the dashed gray line the seashore during the LGM. In a downstream position of the river network, the branching degree is lower and the Euclidian distance between two localities (gray lines) is similar to the distance measured along the river network (yellow lines). As we move to more derivate positions toward headwaters, the dendritic branching increases and the Euclidian distance between two localities can be much shorter than the actual distance through the network (Fagan 2002). This increase in river branching toward headwaters is also accompanied by an increase in river slope that configures changes in habitats along a river drainage basin (Vannote et al. 1980, Benda et al. 2004). This results in a longitudinal gradient of hydrological connectivity that determines the travel distances and dispersal costs for aquatic organisms. On the right side are graphically represented the hydrological connectivity features along the longitudinal gradient.

Strictly freshwater fishes are an ideal model to continue improving our knowledge about the factors and processes that determine species' geographic range sizes. Indeed, unlike vagile terrestrial organisms, movements and dispersal processes of freshwater fishes are constrained by the dendritic and isolated arrangements of riverine ecosystems at different spatial scales (Fagan 2002, Benda et al. 2004). At the largest spatial scales, fish movements are limited by their inability to cross oceans, high mountain ranges, or expansive lands (Parenti 1991). This implies, for instance, that geographic range expansions between drainage basins are restricted

to geological and hydrological events, such as river captures (Albert et al. 2017) or the confluence of river systems during low-sea-level periods resulting from climatic changes (Dias et al. 2014b). At smaller spatial scales (i.e., within drainage basins), fish movements are determined by a combination of biotic and abiotic factors, including species' dispersal capacities and behaviors (Radinger and Wolter 2014), the degree of river network branching (Fagan 2002), the basin slope, and other barriers to dispersal (e.g., rapids and waterfalls) that vary longitudinally along the network (Benda et al. 2004) (Fig. 1). As a consequence, drainage basins are structured by gradients of hydrological connectivity, where the branching and type of habitats encountered by species depend on the species' position within the drainage network, determining the travel distances and dispersal costs for freshwater species (Campbell-Grant et al. 2007, Tonkin et al. 2018) (Fig. 1).

Here we identify the main drivers of geographic range size variation of riverine fishes at global and biogeographic scales. In addition, we explore the complex path system of interactions among these drivers that ultimately determines species' range size variation. To do so, we compiled the most comprehensive dataset available to date for riverine fish species distributions, including 8,147 species (i.e., 63% of all known strictly freshwater species; Tedesco et al. 2017) covering all continents. Using these distributions, we applied multilevel path models (MLPMs) to evaluate at a global scale the effect of several drivers encompassing the main explanations already proposed for the variation of species' geographic range size (*SI Appendix*, Table S1). This allowed us to determine the direct and indirect effects through which multiple drivers influence the geographic range size, while controlling for the effect of random factors (i.e., taxonomic relatedness and spatial dependence). We further examined the strength and consistency of these drivers and pathways among the different biogeographic realms of the world.

Results

The range sizes of freshwater fish species varied over six orders of magnitude, from 13 to 10,996,733 km², with a median of 77,322 km² (*SI Appendix*, Fig. S1). All MLPMs (for global and by biogeographic realms) yielded significant coefficients, indicating that the variation in geographic range size was well represented by our path models, and that no links among variables were missing (*SI Appendix*, Tables S2–S8). The R^2 values of range size for all MLPMs ranged between 0.739–0.909 and 0.758–0.921 for the marginal (R^2_m , fixed factors)

and conditional (R^2_c , fixed plus random factors) variances, respectively (*SI Appendix*, Table S9).

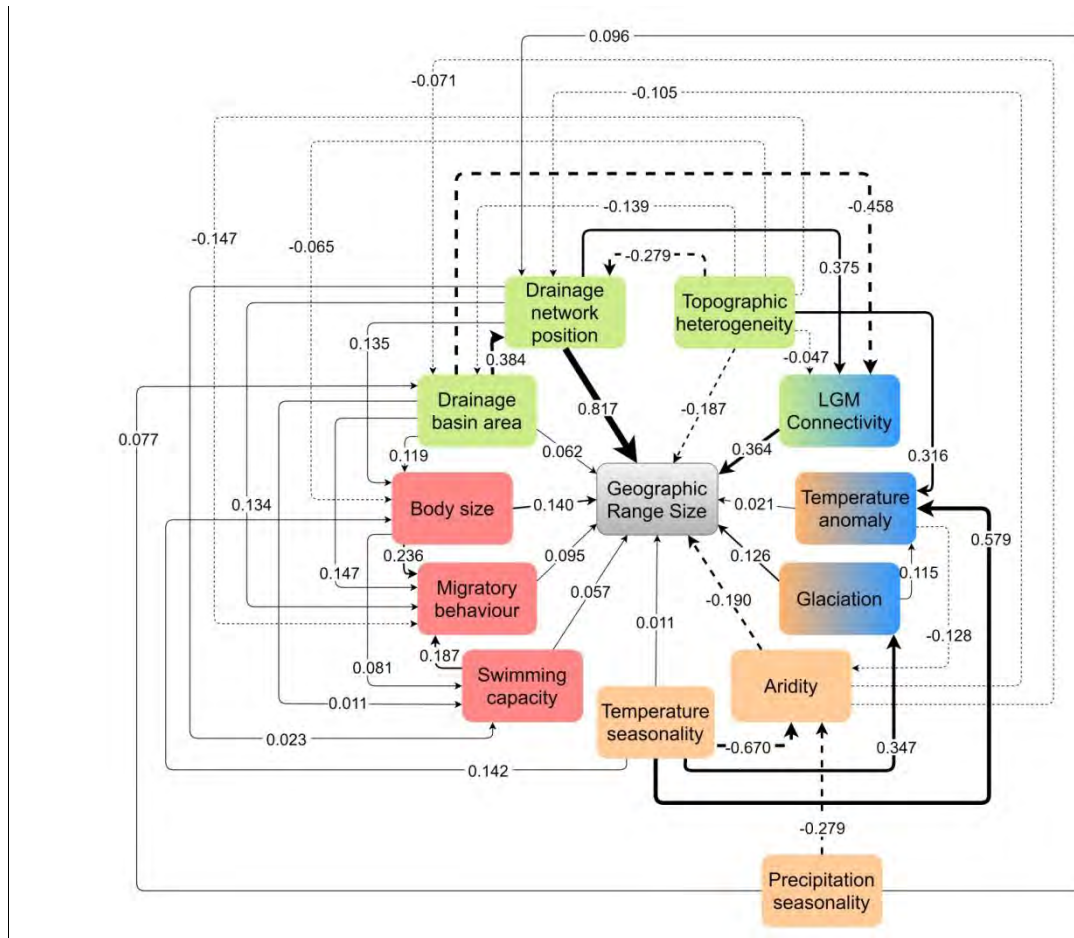


Figure 2. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species at the global scale. Solid lines indicate positive relationships, and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers, and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

Drainage network position (DNP; the average of the stream orders where a species occurs) and historical connectivity (a measure of past connections among drainage basins) were, by far, the most important drivers of range size variation in freshwater fish species at the global scale (Figs. 2 and 3), both with positive standardized path coefficients (SPC) followed by aridity and topographic heterogeneity showing negative coefficients. Glaciation history and body size were, respectively, the most important historical climatic and species

biological trait variables associated with range size, both presenting a positive SPC. Other predictors (i.e., migratory behavior, swimming capacity, drainage basin area, and temperature anomaly and seasonality) showed the lowest coefficients, all of them being positive (Fig. 2). These general results remained stable when using diverse proxies for different predictors (*SI Appendix, Sensitivity Analysis*).

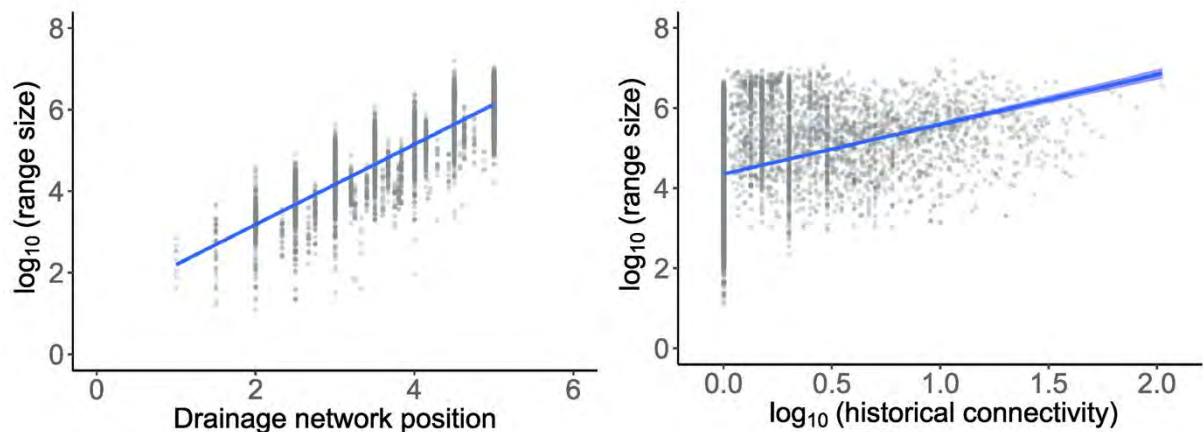


Figure 3. Relationships between species range size and the main predictors at the global scale: drainage network position and historical connectivity.

At the scale of biogeographic realms, four of the drivers found to be important at the global scale were also included in all MLP models: DNP, historical connectivity, topographic heterogeneity, and body size (Fig. 4 and *SI Appendix*, Figs. S2–S7), highlighting consistent results at both global and realm scales. DNP was again the most important range size predictor in all realms. Large-range species were related to higher values of DNP (i.e., located at downstream positions in the drainage network), historical connectivity, body size, and lower values of topographic heterogeneity. Productivity and long-term climatic stability affected range size differently across realms: negatively in Tropical realms (e.g., Neotropics) and positively in Temperate realms (e.g., Nearctic). Our measure of diversification (i.e., the number of species within the species' genus) had a direct and negative effect only in the Tropical realms (Fig. 4 and *SI Appendix*, Figs. S2–S7). When drainage basin area, migratory behavior, swimming capacity, and temperature seasonality were directly related to species range size, effects were always positive. Precipitation seasonality affected geographic range size indirectly mainly through the effect of other climatic and geomorphological variables (*SI Appendix*, Figs. S2–S7).

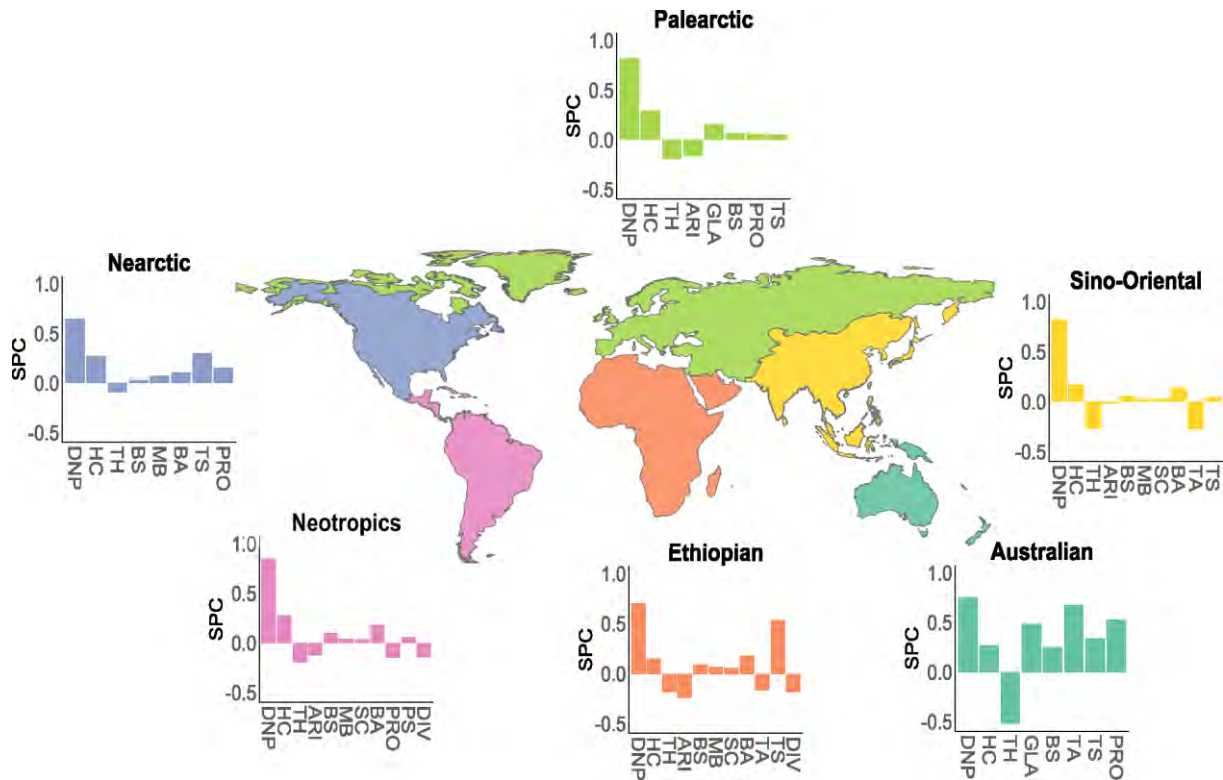


Figure 4. SPC for each direct driver of geographic range size across the biogeographic realms proposed by Leroy et al. (Leroy et al. 2018). Abbreviations for drivers are: drainage network position (DNP), historical connectivity (HC), topographic heterogeneity (TH), aridity (ARI), drainage basin area (BA), temperature anomaly (TA), glaciation history (GLA), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC).

We found that predictors were highly interrelated at the global scale, affecting indirectly the geographic range size of freshwater fishes (Fig. 2 and *SI Appendix*, Table S9). For example, DNP was positively linked to drainage basin area and precipitation seasonality, and negatively with topographic heterogeneity and aridity (Fig. 2). Higher values of historical connectivity were related to high DNP, smaller drainage basin area, and lower topographic heterogeneity. Geomorphological predictors (i.e., DNP, topographic heterogeneity, and drainage basin area) were highly interrelated with all other predictor types (i.e., species' traits, climatic, and historical variables), whereas species traits and climatic predictors mainly linked to predictors belonging to the same type (Fig. 2). At the realm scale, we found slight variations among predictors' relationships, mainly for drainage basin area, DNP, and aridity (Fig. 4 and *SI Appendix*, Figs. S2–S7). The relationships of these predictors with temperature and precipitation seasonality varied in their effect, being positive or negative, depending on the realm (Fig. 4 and *SI Appendix*, Figs. S2–S7). In general, the effect size of the relationships

between predictors was high (*SI Appendix*, Table S9), resulting in complex models with strong relationships, regardless of the spatial scale considered.

Discussion

Our results provide a comprehensive assessment of geographic range size variation in freshwater fishes, quantifying the relative effects of climatic, topographic, historical, and biotic drivers at the global scale and their consistency among the different biogeographic realms (Fig. 2). At both global and realm scales, these drivers explained approximately 90% of the variance in geographic range size, and two of them strikingly accounted for most of this variability: the species' position within the drainage network (DNP; SPC = 0.817 at the global scale, with an amplitude of 0.647–0.851 SPC among realms) and drainage basin historical connectivity (0.364 SPC at the global scale, with an amplitude 0.147–0.378 SPC among realms).

Geographic range size is linearly linked to the species' preferential location within the river network, being larger for fish species occurring in basal positions of the drainage network (i.e., lowlands and lower drainages portions) and lower for species preferentially inhabiting headwaters (Fig. 1). A similar pattern has been reported by Bertuzzo et al. (2009) within the Mississippi drainage basin, showing the absence of species with small geographic ranges in high-order streams. Further, and independent of their position within the river network, species inhabiting drainage basins that were connected during the lower-sea-level periods of the Quaternary exhibit larger range sizes than species inhabiting historically unconnected basins. Within a river drainage, the species' position in the network determines the relative role of geographic and environmental processes in regulating the extent, cost, and rates of dispersal movements across a river drainage basin (Fagan 2002, Campbell-Grant et al. 2007, Tonkin et al. 2018). Indeed, the variation of branching organization across river systems can exert strong regulations on species' metapopulation dynamics (Campbell-Grant et al. 2007, Tonkin et al. 2018), mainly by regulating, throughout the river network, the travel distance between species' suitable habitats (Fagan 2002, Campbell-Grant et al. 2007) (Fig. 1). For example, in low-branching areas such as lowlands and/or lower drainage portions, there may be more “free” movements than in highly branching areas such as headwaters (Fagan 2002, Campbell-Grant et al. 2007, Tonkin et al. 2018) (Fig. 1). Accordingly, headwaters are less open to new arrivals of individuals, and therefore are more isolated than downstream

areas (Carvajal-Quintero et al. 2015, Schmera et al. 2018). In addition, seasonal flooding in lowland areas can connect previously unconnected habitats, leading to movement of organisms between locations that would not occur under base flow conditions (Morán-Ordóñez et al. 2015). Meanwhile, changes in river slope and the direction of flow primarily determine the cost of upstream movements for strictly freshwater organisms along a river basin (Datry et al. 2016). Low river slopes in lowlands promote slow-running waters (i.e., low water velocity) characterized by wide channels and a high proportion of backwaters and pools, whereas in headwaters, streams have most often steeper slopes with torrential waters and higher portions of rapids and waterfalls (Benda et al. 2004, Allan and Castillo 2007). The harsh conditions of headwaters also promote morphological and habitat specialization, resulting in the restriction of fish species distributions toward the headwaters (Carvajal-Quintero et al. 2015). Conversely, the higher-connectivity conditions in lowlands and lower portions of rivers promote demographic connections among populations that are fundamental for species persistence and for their recovery from disturbances (Cowen and Sponaugle 2009). All these factors create a hydrological connectivity gradient along the drainage network, which most probably explains the strong effect of the drainage network position on fish species ranges.

Among drainage basins, it was already found that historical connectivity has promoted fish colonization processes worldwide (Dias et al. 2014b). Our measure of historical connectivity quantifies the extent of connectedness among basins during the last glacial maximum, when sea levels dropped up to 120 m and river mouths progressed through kilometers of exposed marine shelves before reaching the ocean (Voris 2000, Dias et al. 2014b). This resulted in connections among previously isolated drainage basins that left an imprint on global biodiversity, where paleo-connected basins were richer and shared more species (as a result of colonization from other rivers within the same paleo-basin) than paleo-disconnected ones (Dias et al. 2014b). Our findings show that such imprints on the biodiversity of river basins have been driven by the positive effect of historical connectivity in determining freshwater species' range sizes. Overall, our results suggest that lowland freshwater fish were the most efficient to expand their geographic range size, mainly because lowlands have higher levels of current and historical hydrological connectivity (Fig. 1).

Beyond the overall importance of drainage network position and historical connectivity, other factors also played a secondary role in determining freshwater fishes' range sizes. We found that topographic heterogeneity affects negatively species' range sizes. High topographic

relief has long been recognized as imposing constraints on dispersal, resulting in high species turnover and smaller range size for most animals (Brown et al. 1996), including on riverine fishes (Smith 1981, Carvajal-Quintero et al. 2015). Furthermore, high altitudinal gradients imply less frequent drainage connections and fish species crossovers (Smith 1981). Aridity was also a negative driver of species range size. In freshwater ecosystems, aridity fragments rivers' surface, dividing drainage basins in different pieces, which may result in a direct and negative effect on fish ranges by disrupting fish movements (Unmack 2001). Indirect effects of aridity on geographic range size may be mediated by the extrinsic effects of temperature and precipitation seasonality on aridity, which affect the water balance in riverine ecosystems, reducing basin areas and modifying the dendritic structure of river drainages (Seager et al. 2013).

Finally, species' traits related to dispersal ability (i.e., swimming capacity, migratory behavior, and body size) also affected freshwater fish range sizes, but with secondary importance. Better dispersers tend to have larger geographic ranges because they are able to sustain sink populations at large distances from source populations, whereas poor dispersers may lead to a larger proportion of potentially suitable habitats being unoccupied (Lester et al. 2007). This has been corroborated for freshwater fishes, for which greater dispersers and large-bodied species have larger geographic range sizes than poor disperser and small-bodied species (Blanchet et al. 2013). In addition, migratory behavior directly influences fish species range size, as reported for temperate freshwater fishes (Blanchet et al. 2013). Migratory behavior can also indirectly affect range size via dispersal ability and body size, because migrants tend to be better dispersers, which in turn increases range size (Baldwin et al. 2010), and may have larger body size (Zhao et al. 2017).

To summarize, we found that the variation in geographic range sizes of freshwater fishes is jointly determined by the interaction of multiple predictors that create a complex path model, where drainage network position and historical connectivity are the most important predictors at both global and biogeographic realm scales (see *SI Appendix* for a detailed discussion about differences in minor drivers between realms). These results suggest that the geographic range size of freshwater fishes has been mainly shaped by the current and historical hydrological connectivity that determines the effort and distance of fish movements within a drainage basin, as well as the possibility of colonizing new basins during historical connections among basins resulting from sea level changes. Importantly, our results contrast with what has been observed for terrestrial and marine species for which connectivity has not

been identified as a major driver of species' geographic range sizes (Lester et al. 2007, Crooks et al. 2011). It is therefore highly probable that the unique dendritic nature of river drainage basins, in which isolation can occur at much finer spatial scales than in other systems (Hughes et al. 2009), generates unique dispersal processes.

The strong links that we found between range size and hydrological connectivity strengthen the vulnerability of freshwater species to fragmentation caused by damming and human-origin barriers (Fagan 2002, Carvajal-Quintero et al. 2017) and indicates that the accelerated rates in river fragmentation (Zarfl et al. 2015, Grill et al. 2019) might strongly affect fish species distributions, which will likely have profound influences on fish diversity in the future.

Methods

Geographic Range Size. We compiled range maps for 9,075 species of freshwater fishes from two different sources. The IUCN Red List (<https://www.iucnredlist.org/>) provided range maps for 6,013 species worldwide, with the exception of a large portion of South America. We complemented this region covering the Amazon Basin and southern South America, using occurrence records of 3,062 species from different databases of freshwater fishes (see *SI Appendix* for further details on these datasets). To map these complementary ranges, we followed the same methodology as the IUCN, which consists of dissolving the HydroBASINS units or subbasins (Lehner and Grill 2013) where a species was present according to the occurrence records (*SI Appendix*, Fig. S8A). We calculated the species' range sizes as the extent of occurrence (km²) falling within the occupied subbasin areas (*SI Appendix*, Fig. S8B). We assigned each species' range to their native biogeographic realm: Neotropical, Ethiopian, Sino-Oriental, Nearctic, Palearctic, or Australian, following Leroy et al. (Leroy et al. 2018) (Fig. 4), on the basis of the midpoint of its latitudinal and longitudinal range.

Our final dataset of native ranges included 8,147 fish species, excluding island endemics and considering only strictly freshwater Actinopterygii species to ensure that all the analyzed species were restricted to freshwater environments and that their dispersion processes have been continental.

Drivers. On the basis of ecological theory and hypotheses proposed in previous studies, we developed a set of predictions regarding the potential drivers of the geographic range size of freshwater fishes (*SI Appendix*, Table S1).

Current climate. To represent current climate conditions, we measured three variables related to current climatic stability and climatic extremes. As a measure of present climatic stability, we used the average values of temperature and precipitation seasonality within the species' range (Whitton et al. 2012a, Morueta-Holme et al. 2013). For climatic extremes, we calculated the mean value of the Köppen aridity index (Köppen 1931). On a global scale, this aridity index is the best measure to describe water availability and identifies the most humid and arid regions (Quan et al. 2013). The original data on these climate variables were downloaded from WorldClim (Fick and Hijmans 2017).

Long-term climatic changes. We measured long-term climatic changes as the mean temperature anomaly since the Last Glacial Maximum (LGM; 22 ky), encompassed by a species range. Temperature anomaly was calculated as the difference between the current mean annual temperature and mean temperature at the LGM. The current mean annual temperature was obtained from WorldClim (Fick and Hijmans 2017), whereas the mean annual temperature at the LGM was calculated as the average of CCSM4 and MIROC-ESM (Hijmans et al. 2005) Paleoclimate models. Finally, we represented the LGM glaciation history by the proportion of overlapping area between species' range and the glacial extent at 21 ky before present (Peltier 1994).

Productivity. Our measure of within-range productivity was calculated as the mean net primary production. We obtained net primary production values from Zhao et al. (Zhao et al. 2005) proposing a productivity metric that describes the growing season relationship between gross primary production and different respiration metrics.

Drainage network position. We measured the species' DNP as the average of the unique values of stream order (Strahler 1952; *SI Appendix*, Fig. S9) within the species range (e.g., a species occurring in stream orders 2–6 will have a DNP value of 4). The stream orders were obtained from Shen et al. (Shen et al. 2017). Stream order is a numeric measure of the river branching complexity, where increasing values describe a progressive downstream position in the dendritic structure and a lower branching (Fig. 1). As stream order decreases toward the headwaters, the dendritic branching structure becomes more complex (Strahler 1952). The stream order is highly related to other metrics also used to describe the species position in

river networks [e.g., the “direct tributary area” used by Bertuzzo et al. (2009)]. This longitudinal change in stream order also describes a gradient in the basin slope and habitats, with gentle slopes and high proportions of backwaters and pools for high stream order values, and steeper torrential waters mostly composed by rapids and waterfalls for low stream order values (Benda et al. 2004) (Fig. 1). We compared our polygon-based measure of occupied stream orders to the same measure based on occurrence records (*SI Appendix*) to control for any bias related to the potential inclusion of unoccupied streams within the polygons. These two ways of computing DNP resulted in very similar estimates ($R^2 = 0.72$).

Historical connectivity. As a measure of past connections among drainage basins, we focused on how sea-level changes reconfigured the connectivity between river systems during the LGM. Throughout the Quaternary, the Earth’s climate fluctuated periodically, resulting in lower-sea-level periods (Voris 2000) that allowed currently separated drainages to connect at their lower parts, making fish dispersal processes possible within these larger formed paleo-drainages (Dias et al. 2014b) (Fig. 1). According to the paleo-drainages reconstruction proposed by Dias et al. (2014), at the global scale, we derived a metric of historical connectivity as the number of basins in which a species currently occurs divided by the number of paleo-basins covered by that species range. This metric indicates to what extent currently occupied drainage basins were regrouped into larger connected paleo-drainages during lower-sea-level periods.

Geomorphology. We evaluated the effect of two geomorphological drivers of drainage basins on species range size: the area of the drainage basins occupied by each species and the topographic heterogeneity within their distribution range. The drainage basin area can be considered as the maximum surface extent that a freshwater fish species could potentially occupy, analogous to the continental extent applied in a similar analysis for terrestrial vertebrates (Li et al. 2016). We measured this proxy of area availability as the mean drainage area of the basins where a species occurs. To measure topographic heterogeneity, we created a raster layer based on the variance of elevation among each grid-cell and all other grid-cells within a 15-km buffer. High values of this measure represent high topographic heterogeneity between a grid-cell and its neighboring cells. We computed an overall topographic heterogeneity metric for each species as the mean value across all grid-cells that overlapped with the species range.

Diversification. We used the total number of species within each genus as a coarse proxy of the clade's diversification level that each species has experienced (Verdú 2002). Total species numbers by genus were obtained from FishBase (Froese and Pauly 2019).

Species traits. We used four traits related to locomotion ability, migratory behavior, energy demand, and trophic position (*SI Appendix*, Table S1) to evaluate their effect on fish range size. The maximum body length (mm) reported in FishBase (Froese and Pauly 2019) for each species was used as a measure of body size. The presence of migratory behavior (only potamodromous species in our case) for each species was also drawn from FishBase (Froese and Pauly 2019). Prey-capture ability and swimming capacity measures were calculated from morphological measurements available from Toussaint et al. (2016). From this comprehensive morphological database of freshwater fishes, we used six traits (*SI Appendix*, Table S10) commonly used in the assessment of fish functional diversity (Villéger et al. 2010, Pease et al. 2015, Toussaint et al. 2016). This database covered 93% ($\pm 0.03\%$) of the fish species considered here. All six traits were assigned to a species function (i.e., prey-capture ability or swimming capacity; *SI Appendix*, Table S10) and then ordered by a principal components analysis, using a regularized algorithm designed for ordination analysis that handles missing values (Josse and Husson 2016). We retained the first axis of each principal components analysis (which accounted for >50% of the variance; *SI Appendix*, Table S10) to represent each species function.

All the distribution data and spatial variables mentioned were projected into the Behrmann equal-area cylindrical projection, and all rasters were rescaled to a resolution of 2.5 arc-minutes.

Data Analysis. We performed MLPMs (Shipley 2009) to identify the drivers of the geographic range size variation in freshwater fishes and how these drivers are related with each other. MLPMs allow moving beyond the estimation of direct effects and analyze the relative importance of different causal models, including direct and indirect paths of influence among multiple variables (Shipley 2009). To apply MLPMs, we used an integrative modeling approach that sequentially integrates a series of complementary procedures. We first assembled an expected path model to depict the expected relationships and interrelationships between the species range size and the multiple predictors, based on hypotheses previously proposed in the literature (*SI Appendix*, Fig. S10 and Tables S1 and S11). Next, we identified drivers of each endogenous (response) variable, using Multilevel and Generalized Multilevel

Models (MLM and GMLM), in which we included genus, family, and order as random nested factors to account for the taxonomic relatedness among species. Residual spatial autocorrelation in regression models can lead to biased parameter estimates and P values. We found differences in the residuals among biogeographic realms ($P < 0.0001$), suggesting that the inclusion of realms as random effects could improve the parameter estimates of the models. Finally, we ran all the MLM and GMLM, including all possible combinations of the explanatory variables as fixed terms, based on the expected path model (*SI Appendix*, Fig. S10), including taxonomy and biogeographic realms as nested- and multilevel-random factors, respectively. All variables except migratory behavior and DNP were log10-transformed, and weak correlations ($R < 0.5$) among predictor variables were observed (*SI Appendix*, Fig. S11).

We performed multimodel inference based on information theory (Burnham and Anderson 2002) to determine the average parameters from the MLM regressions. As a cutoff criterion to delineate a top model set, we used fitted models with $\Delta AICc \leq 2$ (Burnham and Anderson 2002). Variance explained by each inferred model was estimated with marginal and conditional R^2 (Nakagawa and Schielzeth 2013). Marginal R^2 (R_m^2) is concerned with variance explained by fixed terms, and conditional R^2 (R_c^2) with variance explained by both fixed and random factors.

We then combined the inferred MLMs to set the observed path model and test whether this model was consistent with our data, using the d-separation test (Shipley 2009). The d-separation test specifies the minimum set of independence and examines the validity of conditional independence statements that hold true among all variables in a given causal model. We tested the composite validity of all independence statements combining the P values through Fisher's C statistic and tested missing linkages, using the criterion that unlinked variables are conditionally independent (Shipley 2016). Hence, we obtained the residuals of the inferred models of each endogenous variable to examine relationships among those residuals and unlinked variables. For variables with no predictors (e.g., topographic heterogeneity), we used the raw values instead of the residuals (Grace et al. 2012). Because very large datasets can detect very minor residual associations between variables and lead models with very complex and nonsignificant scientific graphical relations, we only included missing linkages of conditional statements with fixed effects sizes ($R_m^2 > 0.1$ and P values < 0.01) (Grace et al. 2012; *SI Appendix*, Tables S2–S8). To compare the relative strength of each

causal, we calculated SPC of the causal linkages. Finally, we applied the above modeling approach for each biogeographic realm, considering only the species endemic to each realm.

Both data analyses and calculations of variables were performed in R 3.4.3 (R Development Core Team 2017). For details on R packages used, see *SI Appendix*, Table S12.

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Supporting Information

Supporting discussion

Differences in the effect of some drivers among biogeographic realms

The effect of some drivers on the geographic range size variation of freshwater fishes differed among biogeographic realms. These differences can be related to the particularities of each realm. For instance, productivity and long-term climatic changes (glaciated area and temperature anomaly since the Last Glacial Maximum, LGM) negatively affected range size in tropical realms such as the Neotropics and Ethiopian, and positively in temperate realms such as the Nearctic and Palearctic. The productivity hypothesis states that higher productivity supports greater population densities (Storch et al. 2018), which in turn support larger ranges through a reduced risk of local extinction (Brown et al. 1996). However, this hypothesis predicts no simple pattern, given that productivity is generally higher at lower latitudes leading to a reverse Rapoport pattern (Whitton et al. 2012a). The little empirical evidence supporting the effect of productivity on species range sizes suggests that the productivity hypothesis only applies for large-ranged species (Jetz and Rahbek 2002) and in temperate regions (Whitton et al. 2012a), which coincides with our findings. The different effects of long-term climatic changes observed between temperate and tropical realms could be related to the land extensions affected by these climatic changes, being widespread in high-latitude regions (Morueta-Holme et al. 2013, Li et al. 2016), whereas affecting mostly mountain areas in the tropics (Sandel et al. 2011) where steep environmental gradients could limit the available habitat for a species and act as dispersal barriers promoting small-ranged species (Janzen 1967, Hawkins and Diniz-Filho 2006). The effect of our proxy of diversification also varied depending on the realm. We detected a slight negative effect in tropical realms, the Neotropics and Ethiopian, showing that most diverse clades tend to be composed of species with small range sizes. This pattern agrees with what would be expected from intense diversification processes, where the average range size within a clade is divided by functionally similar species, leading to a negative relationship between species range size and diversification rate of the corresponding clade (Jablonski and Roy 2003, Pigot et al. 2010).

Supplementary Methods

Compilation of the global dataset of species occurrences

In order to control for two potential biases in our approach (see below), we built a global dataset of species occurrences obtaining records from different sources (see table below). We removed duplicated records, checked valid species names following (Froese and Pauly 2019), and validated the native geographic location of each occurrence according to an updated version of Tedesco et al. (2017). The final occurrence dataset had 1,114,220 occurrence records for 12,167 freshwater fish species.

Database	Date of access	Web site	Geographic coverage
Bold	02/05/2018	http://www.boldsystems.org/index.php/	World
Fishnet2	02/05/2018	http://www.fishnet2.net/aboutFishNet.html	World
GBIF	02/05/2018	https://www.gbif.org/	World
IdigBio	02/05/2018	https://www.idigbio.org/	World
Obis	03/05/2018	http://iobis.org/	World
FaunAFRI	03/05/2018	http://www.poissons-afrique.ird.fr/faunafri/	Africa
Atlas of Life	02/05/2018	http://spatial.ala.org.au/webportal/	Australia
Biofresh	03/05/2018	http://project.freshwaterbiodiversity.eu/	Europe
SpeciesLink	02/05/2018	http://splink.cria.org.br/index?criaLANG=pt	Brazil
ICMbio	02/05/2018	https://portaldabiodiversidade.icmbio.gov.br/portal/	Brazil
AmazonFISH	09/04/2018	https://www.amazon-fish.com/	Amazon basin
Museo Noel Kempf	05/02/2016	http://museonoelkempff.org/museo/	Bolivia
PUCRS	05/02/2016	http://www.pucrs.br/mct/colecoes/ictiologia/	Brazil
SiBBr	05/02/2016	http://www.sibbr.gov.br/	Brazil
Fundacion OGA	15/06/2010	https://museoscasso.com.ar/fundacion-oga/	Argentina
NeoDatIII	30/06/2010	http://www.mnrj.ufri.br/search.htm	Brazil

Controlling for potential bias

We checked for two potential biases that may affect our data. The first one concerns the data sources used to construct geographic ranges for Neotropical fish species, and the second one concerns 2) the polygon-based approach used to measure the drainage network position for each species.

- 1) The geographic range size of Neotropical fishes. Although we followed the same methodology as the IUCN to map the distribution of fish species distributed in the Amazon Basin and southern South America (i.e. regions where the IUCN does not provide range maps), we still checked for any potential effects related to the use of

a different data source. For this purpose, we compared for the same species the range size directly obtained from the IUCN to the range size obtained from applying the same IUCN methodology but using the distribution information from the independent occurrence dataset described above. These two different data sources provided very similar species range sizes ($R = 0.87$, for 4253 species with both IUCN polygon and occurrence data available), hence eliminating this potential bias from our results.

- 2) The polygon effect in measuring drainage network position. We measured the drainage network position (DNP) of a species using the range polygons. However, DNP can also be measured with a more local and precise approach, i.e. using sampling records. By construction, the polygon-based range may include local habitats and stream orders where a species is not actually occurring. To make sure that our polygon-based approach is not affecting our results, we compared our DNP values with those measured from occurrence records using the global dataset of species occurrences described above. We calculated the occurrence-based DNP for each species as the average of the unique values of stream order among the occupied grid cells (i.e. the same procedure as for the polygon-based approach). This comparison yielded very similar estimates of DNP ($R = 0.72$, for 6,963 species with both polygon and occurrence data available).

Sensitivity analysis

In order to test the sensitivity of our results to changes in predictor metrics, we compiled data for eight metrics or proxies related to two hypotheses: climatic extremes and precipitation (see Table below). For each metric, we calculated the average value within the species ranges. Then, we ran multilevel models considering the same hypotheses and random factors as in our final model (see methods), but replacing the target metric. Additionally, we calculated standardized regression coefficients to compare the relative strength of each predictor among models. All variables were log10-transformed and highly correlated variables ($R > 0.5$) were not included in the models.

Hyphothesis	Metric	Dataset source
Climate extremes	Maximum temperature*	(Fick and Hijmans 2017)
	Minimum temperature	(Fick and Hijmans 2017)
	Maximum precipitation	(Fick and Hijmans 2017)
	Minimum precipitation *	(Fick and Hijmans 2017)
	Potential evapotranspiration	(Abatzoglou et al. 2018)
	Water deficit	(Abatzoglou et al. 2018)
Precipitation	Runoff 1 (Precipitation minus actual evapotranspiration)	(Fick and Hijmans 2017, Abatzoglou et al. 2018)
	Runoff 2 (Precipitation minus potential evapotranspiration)	(Fick and Hijmans 2017, Abatzoglou et al. 2018)

*Highly correlated variables

This sensitivity analysis clearly validated our main findings. Regardless of the metrics used to describe climatic extremes and water availability, drainage network position and historical connectivity remained as the most important drivers of range size variation (Table below), implying that connectivity is the key component of riverine fish geographic range sizes.

Predictors	Standardized Coefficients					
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Drainage network position	0.817	0.819	0.818	0.813	0.808	0.808
Historical connectivity	0.363	0.351	0.351	0.357	0.354	0.354
Topographic heterogeneity	-0.187	-0.194	-0.194	-0.192	-0.191	-0.191
Drainage basin area	0.062	0.092	0.092	0.058	0.061	0.062
Body size	0.139	0.135	0.135	0.128	0.129	0.129
Migratory behavior	0.095	0.088	0.088	0.083	0.083	0.083
Swimming capacity	0.057	0.048	0.048	0.054	0.051	0.052
Glaciation history	0.124	0.133	0.133	0.12	0.124	0.125
Temperature seasonality	0.017	0.092	0.092	0.014	0.017	0.010
Temperature anomaly	0.022	0.101	0.101	0.091	0.088	0.091
Aridity	-0.187	-0.198	-0.197			
Precipitation seasonality	-0.020					
Runoff 1 *		0.101				
Runoff 2 †			0.100			
Maximum precipitation				0.097		
Minimum temperature				-0.065		
Potential evapotranspiration					-0.009	
Water deficit						-0.01

* Precipitation minus actual evapotranspiration

† Precipitation minus potential evapotranspiration

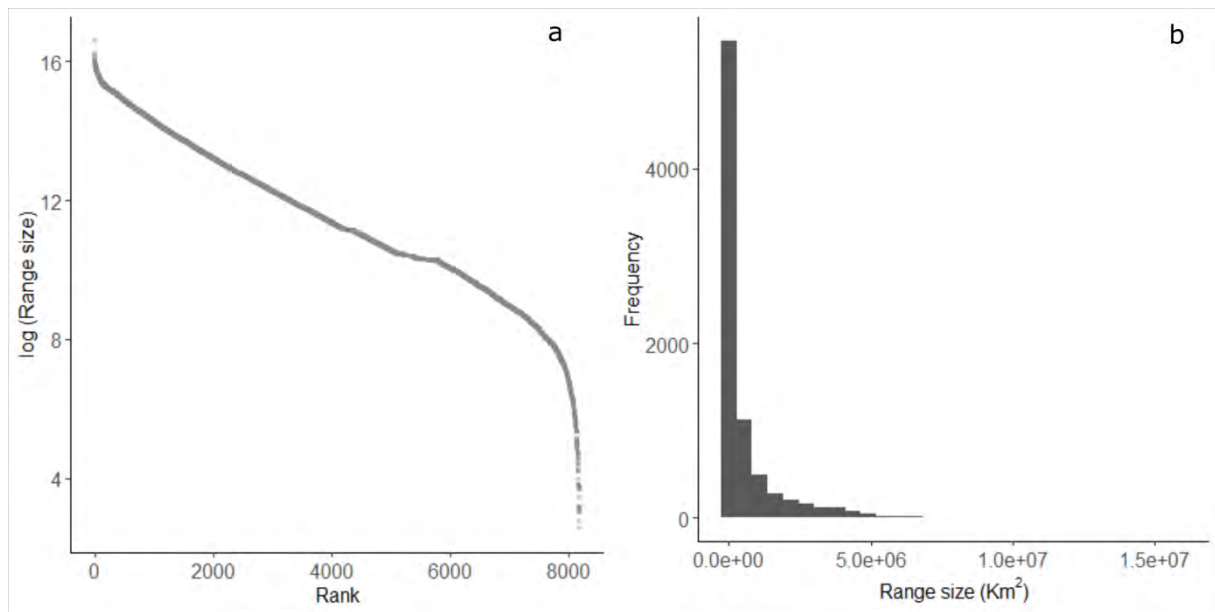


Figure S1. a) Rank-range size curve in a semilogarithmic scale, b) geographic range size frequency distribution (RSFD).

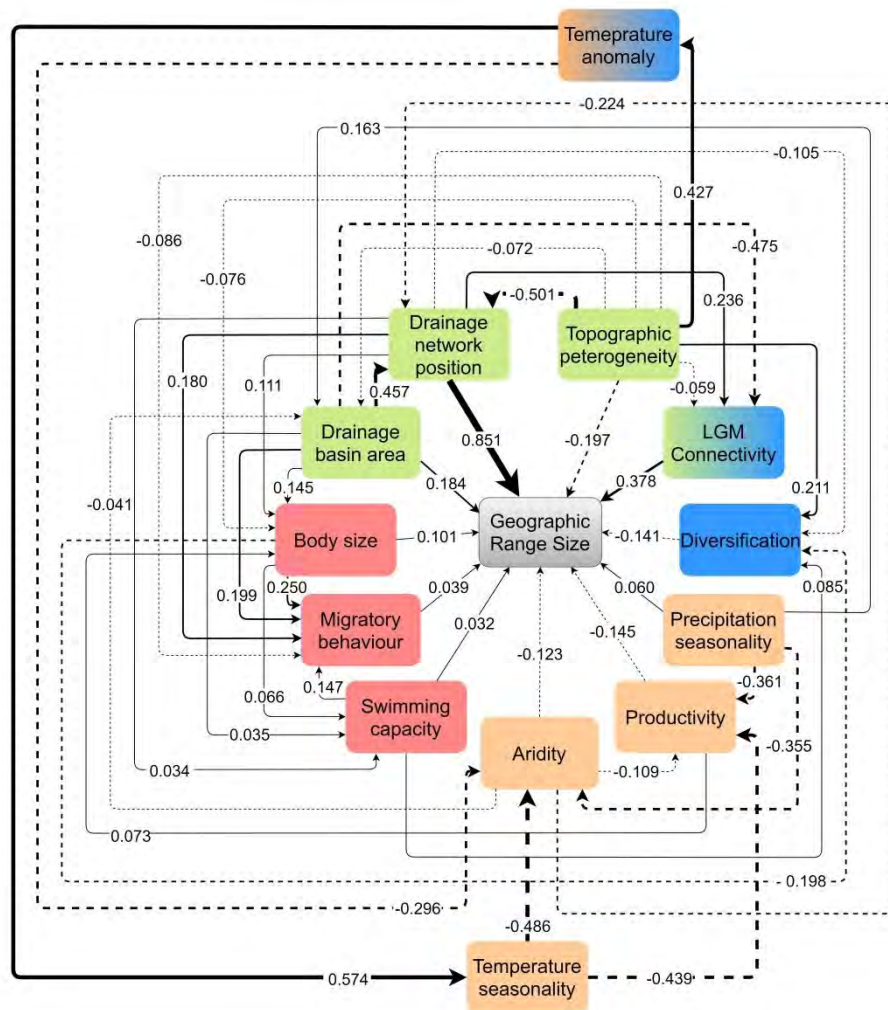


Figure S2. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species in the Neotropics realm. Solid lines indicate positive relationships and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

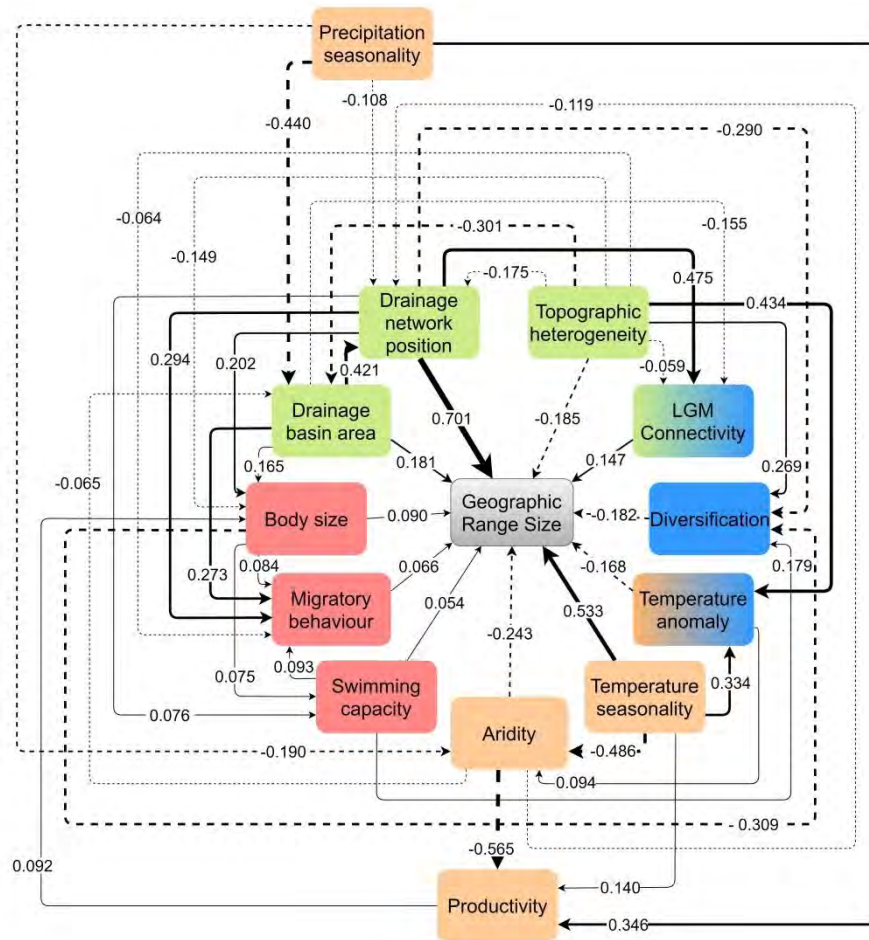


Figure S3. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species in the Ethiopian realm. Solid lines indicate positive relationships and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

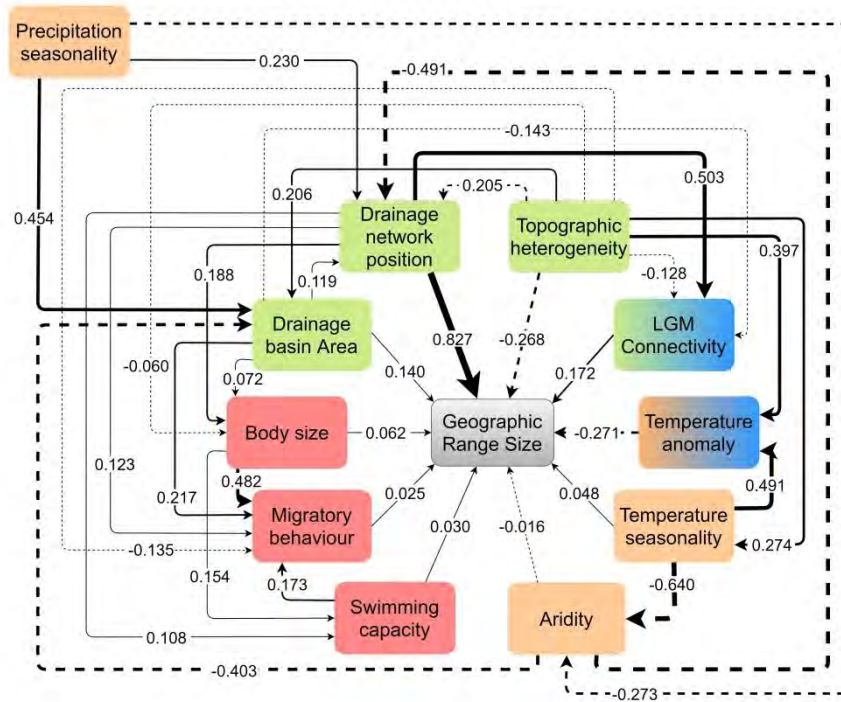


Figure S4. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species in the Sino-Oriental realm. Solid lines indicate positive relationships and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

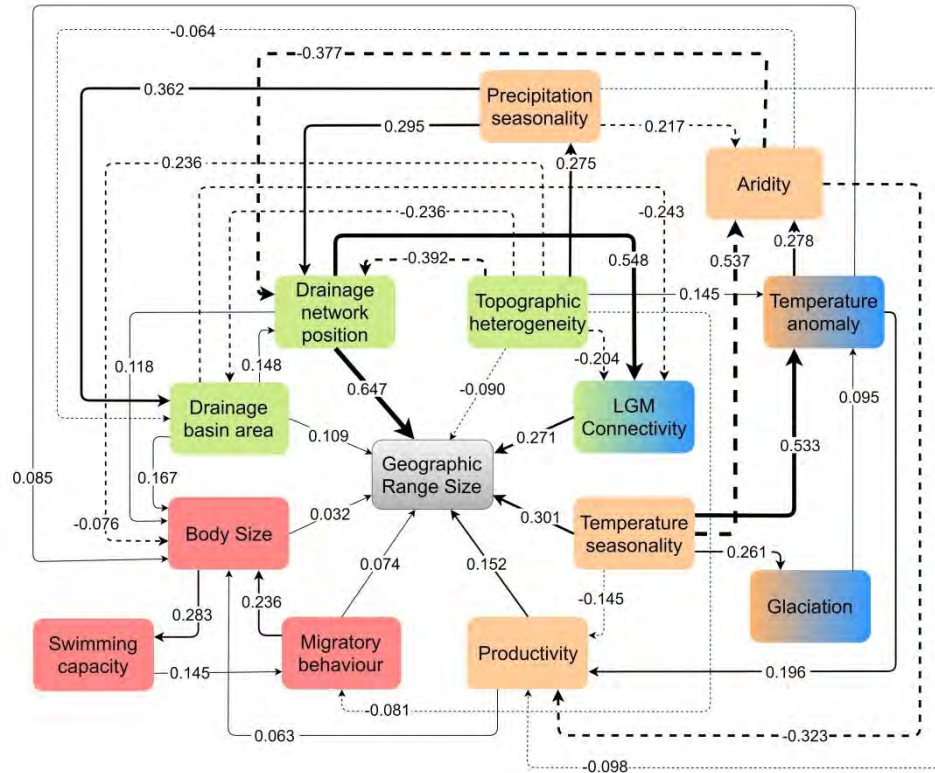


Figure S5. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species in the Nearctic realm. Solid lines indicate positive relationships and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

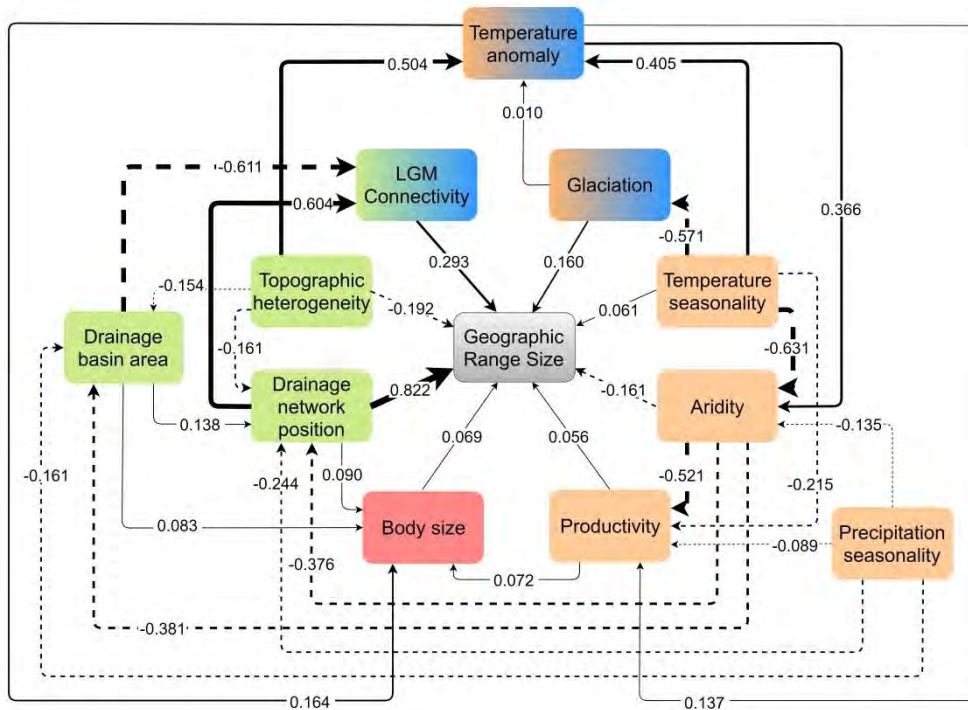


Figure S6. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species in the Palearctic realm. Solid lines indicate positive relationships and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

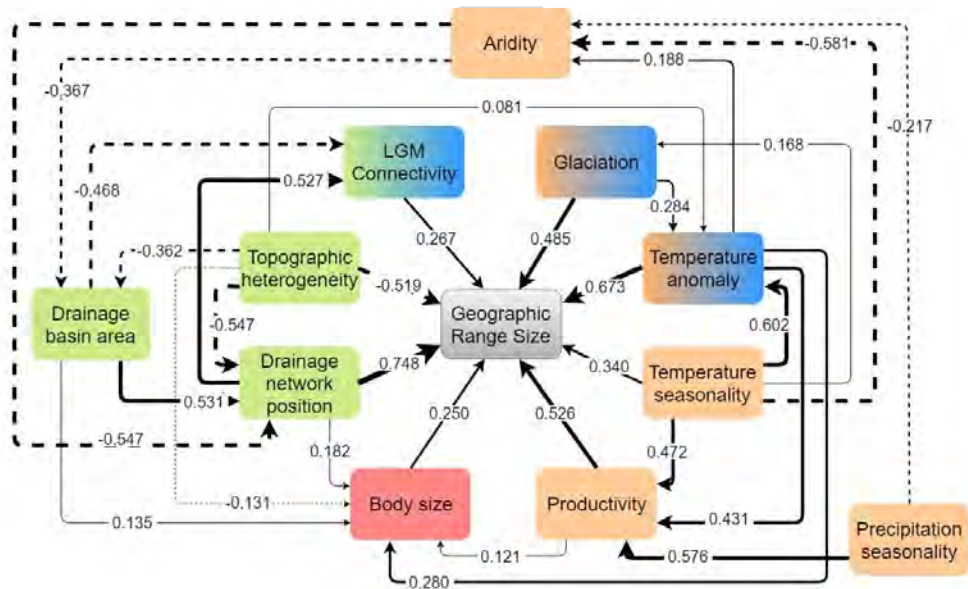


Figure S7. Final path model describing direct and indirect drivers of the geographic range size of freshwater fish species in the Atralian realm. Solid lines indicate positive relationships and dashed lines indicate negative relationships. Arrows indicate the direction of the relationship. Bold lines indicate the strongest relationships, with line widths proportional to importance. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

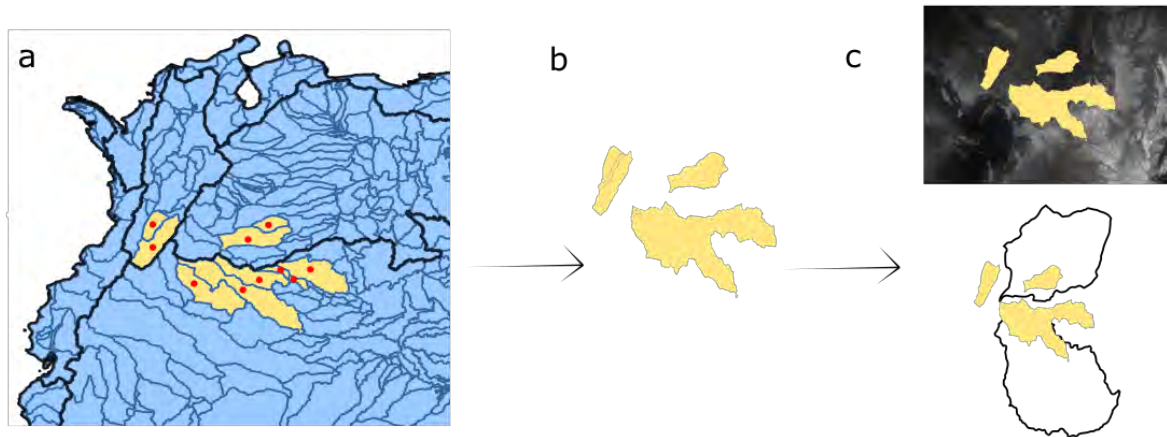


Figure S8. Diagram showing the procedure used to map and calculate a species' geographic range size (i.e. as applied by the IUCN): a) we identified the HydroBASINS units (Lehner and Grill 2013) in all the drainage basins where a species was present according to the occurrence records available; b) we dissolved the sub-basins and calculated the species' range sizes as the extent of occurrence (km^2) falling within the occupied sub-basin areas. c) All predictors were then measured based on these species' ranges extracting data from rasters (top) or through polygons manipulations (down) (see methods in the main text for more details). The basin and HydroBASINS units showed in this figure are only illustrating the methodology and are not based on real data.

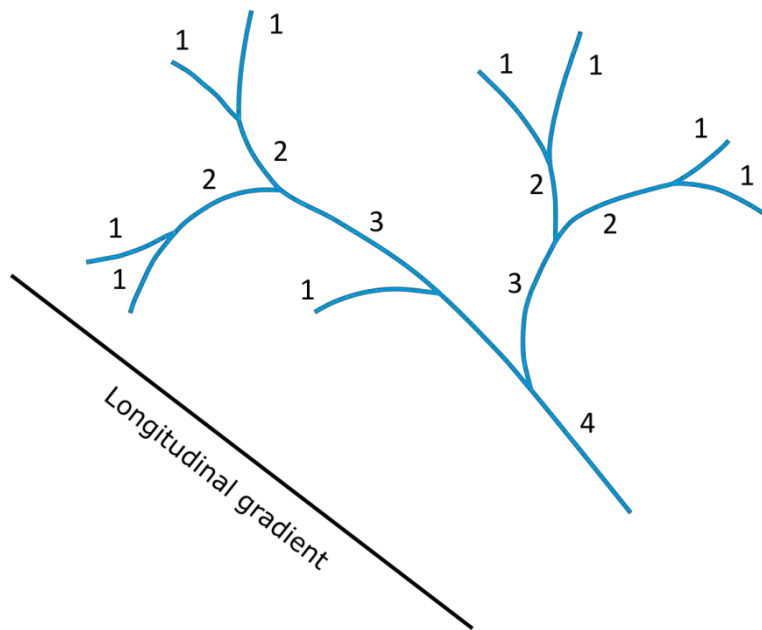


Figure S9. Diagram showing how the Strahler stream order may increase along the longitudinal gradient of a river network.

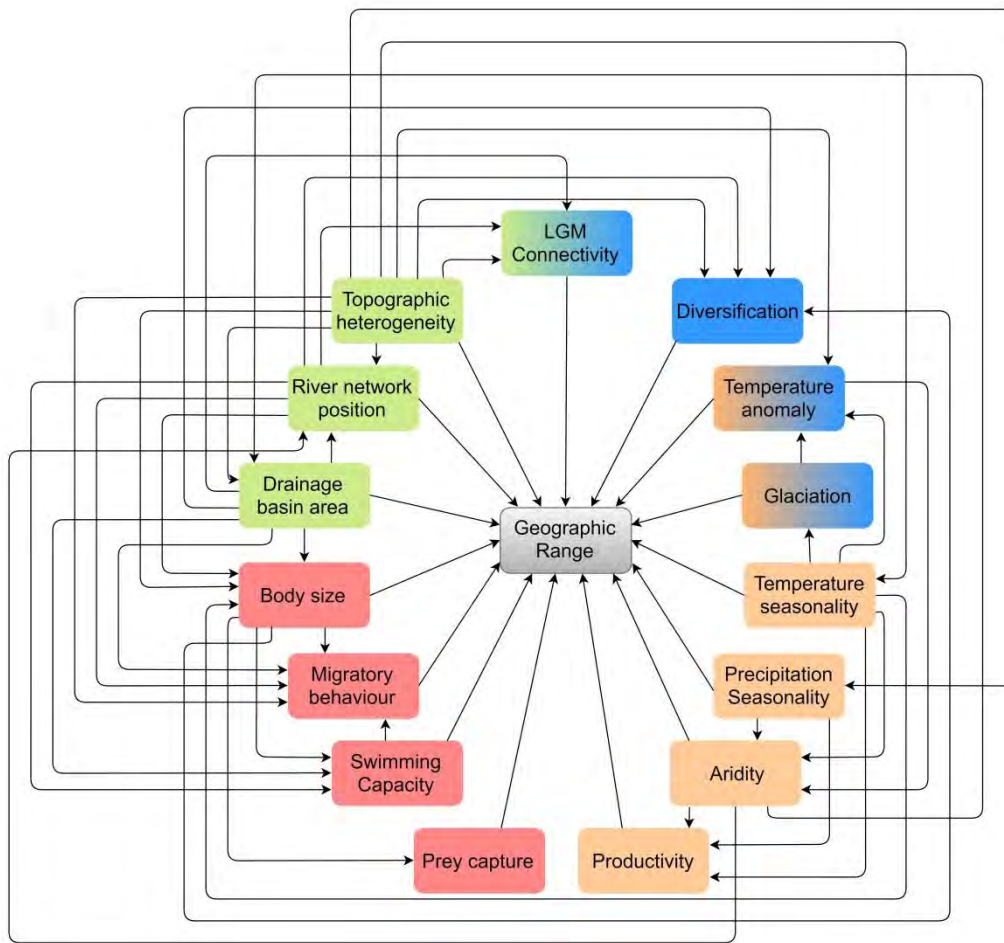


Figure S10. Full expected path model describing potential direct and indirect effects over the geographic range size and the interactions among the multiple predictors. Potential underlying mechanisms are presented in Table S1 and Table S2. Colors in the boxes show the group of hypotheses to which each predictor belongs: orange boxes represent climatic and energy drivers, blue boxes represent historical drivers, green boxes represent geomorphological drivers and red boxes represent species traits. Boxes with two colors are drivers belonging to two different groups of hypotheses.

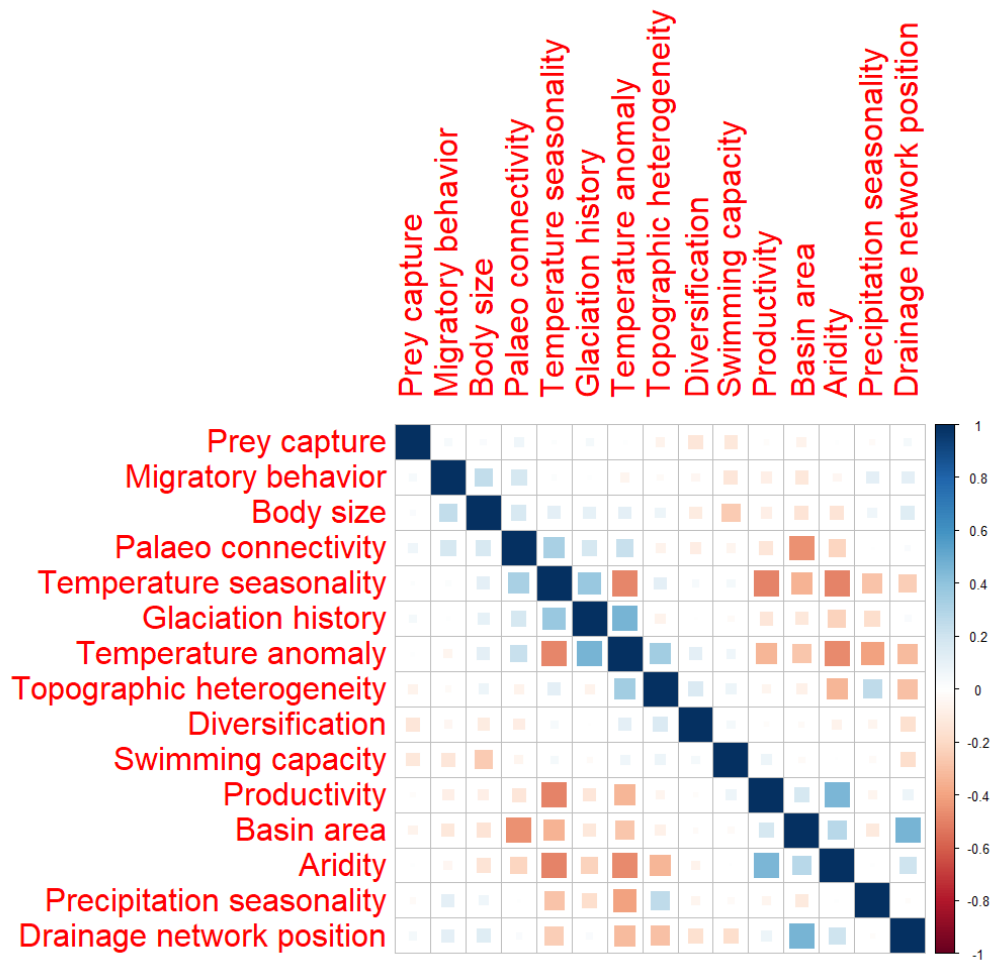


Figure S11. Pearson correlation coefficients among considered predictors of freshwater fishes range size.

1 **Table S1.** Main hypotheses proposed to explain the geographic variation in species range size. Each hypothesis is related to the corresponding
2 predictor tested here for freshwater fishes. These hypotheses were compiled from previous studies or developed from the ecological literature on
3 freshwater fishes and support the expected relationships between range size and the predictors in the full expected path model (Fig. S9).

Predictor/driver	Hypothesis	Group of Hypotheses
Temperature seasonality	The climatic variability hypothesis states that species inhabiting more variable climates have evolved broad physiological tolerances and adaptations. This allow species to tolerate more heterogeneous environments, occupying broader niches and ranges than species in more stable climates (Stevens 1989, Whitton et al. 2012b).	Climatic and energy availability
Precipitation seasonality		
Extreme climates (aridity)		
Productivity	The energy availability hypothesis is based on the premise that higher primary productivity supports greater population densities (Storch et al. 2018), which in turn supports larger ranges through mechanisms such as reduced risk of local extinction (Brown et al. 1996). The energy availability hypothesis has been corroborated in the northern-hemisphere for amphibians, where high primary productivity supports larger species' ranges (Whitton et al. 2012b).	Historic / Climatic and energy availability
Glaciation History	The impact of past glaciations has been proposed as a factor affecting species distributions, differentially selecting against narrow-ranged species in temperate regions (Araújo et al. 2008). Similarly, past climatic conditions have been evoked to explain the Rapoport's rule, due to a greater vulnerability to harsh conditions for small-ranged species in Northern latitudes (Jansson 2003).	
Temperature anomaly	Climate change since the LGM is particularly important for terrestrial organisms because it has strongly affected the distributions of small-range vertebrates (Sandel et al. 2011) and favored larger ranges size (Morueta-Holme et al. 2013, Li et al. 2016).	

Diversification	Average range sizes within clades should decline along each speciation event (Jablonski and Roy 2003, Pigot et al. 2010), as the available space is divided by functionally similar species, leading to a negative relationship between the geographic range size of a species and the diversification rate of the corresponding clade.	Historic
Historical connectivity	The historical connectivity hypothesis predicts that fish species occurring in basins that were connected during lower sea level periods had opportunities to expand their ranges and should have larger distributions. The climatic fluctuations of the Quaternary period resulted in sea level changes that configured the connectivity between river systems (Voris 2000). This historical connectivity between drainage basins has left an imprint on the global diversity patterns of freshwater fishes (Dias et al. 2014a).	Historic / Geomorphology
Drainage network position	River drainage networks are dendritic branching systems (see Fig. 1) where headwater habitats are more isolated and steeper than main-channel habitats (Fagan 2002, Benda et al. 2004). For strictly freshwater organisms, the position in the river network determines the travel distances and dispersal costs to move between two localities (Campbell-Grant et al. 2007, 2010, Terui et al. 2018). As a consequence, the higher connectivity related to downstream positions of the network should be related to larger range size of species.	
Topographic heterogeneity	Topographic heterogeneity is an established driver of geographic range size for terrestrial organisms (Brown et al. 1996, Hawkins and Diniz-Filho 2006, Li et al. 2016). Heterogeneous areas serve as barriers constraining dispersal movements by high elevational gradients with varying climates and habitats (Janzen 1967). In freshwaters, changes in elevation have also been related to restricted species distributions (Carvajal-Quintero et al. 2015).	Geomorphology
Drainage basin area (habitat availability)	The habitat availability hypothesis has been proposed to explain differences in species range size between continents (Letcher and Harvey 1994). In principle, locations surrounded by broad land areas should harbor large-ranged species due to a greater potential for expansion (Hawkins and Diniz-Filho 2006). Small-ranged terrestrial organisms have been associated with small habitat areas and small habitat fragments (Ruggiero et al. 1998, Hawkins and Diniz-Filho 2006, Morueta-Holme et al. 2013).	

Body Size	The commonly observed macroecological relationship between body size and range size shows a triangular shape, where small species can have a variety of range sizes, but larger-bodied species are increasingly constrained to larger ranges (Brown and Maurer 1987, 1989) to achieve their resource needs and long-term persistence (Brown 1984). This triangular constraint has also been reported for freshwater fishes (Le Feuvre et al. 2016, Carvajal-Quintero et al. 2017). An overall positive trend is hence expected between body and range sizes.	Species traits
Migratory behavior	Migratory behavior is expected to be positively related to range size as migratory movements increase the probability of colonizing new areas. However, divergent results have been observed. For instance, migratory birds in the Holarctic region have smaller geographic ranges than non-migrants, potentially because migrations are limited to a longitudinal axis (Böhning-Gaese et al. 1998, Bensch 1999), whereas more general analyses have shown larger geographic ranges for long-distance migrants than for sedentary bird species (Gaston and Blackburn 1996b, Laube et al. 2013). For temperate freshwater fish, migratory behavior is one of the traits that best explain species geographic range sizes (Blanchet et al. 2013).	
Prey capture (trophic position)	The species trophic level has been proposed as a factor influencing range size. Upper and lower trophic levels rely on food resources that greatly differ in their availability and spatial arrangement. For instance in mammals, carnivore species need large home ranges due to their energetic requirements (Carbone et al. 2007), whereas omnivorous and herbivores with lower energy demands tend to have smaller home ranges (Kelt et al. 2001).	
Swimming capacity	The locomotion ability hypothesis is based on the assumption that higher dispersal capacities should promote long-distance dispersal and colonization (Gutiérrez and Menéndez 1997, Glazier and Eckert 2002), avoiding geographic isolation (Laube et al. 2013). In temperate freshwater fish species, higher values in swimming capacity traits have been related to larger range sizes (Blanchet et al. 2013).	

Table S2. Conditional independence claims implicit in the observed path model at the global scale (Fig. 1 in the main text). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for variables are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

GLOBAL		
Conditional independence statements	<i>P</i>	<i>R</i> ² <i>m</i>
(GRS,PS) {TS,ARI,GLA,TA,HC,TH,DNP,BA,BS,MB,SC}	0.1916	0.0044
(SC,TH) {BS,BA,DNP}	0.1532	0.0005
(SC,HC) {BS,BA,DNP,TH}	0.2330	0.0044
(SC,PS) {BS,BA,DNP}	0.4395	5.0813e-07
(SC,TS) {BS,BA,DNP}	0.9074	0.0029
(SC,TA) {BS,BA,DNP,TH,GLA,TS}	0.3709	2.3018e-05
(SC,GLA) {BS,BA,DNP,TS}	0.2820	3.4242e-05
(SC,ARI) {BS,BA,DNP,TA,TS,PS}	0.3401	0.0004
(MB,HC) {SC,BS,BA,DNP,TH}	0.2761	0.0183
(MB,PS) {SC,BS,BA,DNP,TH} *	2.4523e-09	0.0023
(MB,TS) {SC,BS,BA,DNP,TH} *	5.8739e-09	0.0008
(MB,TA) {SC,BS,BA,DNP,TH,GLA,TS} *	1.0086e-20	0.0001
(MB,GLA) {SC,BS,BA,DNP,TH,TS}	0.3996	0.0001
(MB,ARI) {SC,BS,BA,DNP,TH,TA,TS,PS}	0.1794	0.0018
(BS,HC) {SC,BA,DNP,TH}	0.3117	0.0165
(BS,PS) {SC,BA,DNP,TH}	0.2063	0.0003
(BS,TA) {SC,BA,DNP,TH,GLA,TS}	0.2163	0.0025
(BS,GLA) {SC,BA,DNP,TH,TS}	0.7114	0.0023
(BS,ARI) {SC,BA,DNP,TH,TA,TS,PS}	0.3475	0.0023
(BA,TS) {TH,ARI,PS}	0.4094	6.3054e-05
(BA,TA) {TH,ARI,PS,GLA,TS} *	8.9124e-15	4.7554e-05
(BA,GLA) {TH,ARI,PS,TS}	0.1976	0.0189
(DNP,TS) {TH,BA,PS} *	1.4439e-12	0.0013
(DNP,TA) {TH,BA,PS,ARI,GLA,TS} *	5.9153e-18	0.0017
(DNP,GLA) {TH,BA,PS,ARI,TS} *	9.8812e-11	0.0092
(TH,PS) $\emptyset$ *	1.8597e-11	0.0072
(TH,TS) $\emptyset$ *	4.0598e-09	0.0067
(TH,GLA) {TS}	0.2066	0.0006
(TH,ARI) {TA,TS,PS} *	4.0385e-20	0.0526
(HC,PS) {BA,DNP,TH}	0.1755	6.0910e-05
(HC,TS) {BA,DNP,TH} *	1.5870e-14	0.0024
(HC,TA) {BA,DNP,TH,GLA,TS} *	1.0662e-08	3.1493e-05
(HC,GLA) {BA,DNP,TH,TS}	0.1019	0.0053

(HC,ARI) {BA,DNP,TH,TA,TS,PS}	0.2326	0.0064
(GLA,PS) {TS}	0.4443	0.0003
(GLA,ARI) {TS,TA,PS} *	1.3770e-13	0.0026
(TS,PS) {Ø}	0.9248	4.9021e-07
C =		58.5972
Overall p-value (χ^2 df=48)		0.1405

Table S3. Conditional independence claims implicit in the observed path model in Neotropics realm (Fig. S1). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for predictors are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

NEOTROPICS		
Conditional independence claim	<i>P</i>	<i>R</i> ² <i>m</i>
(SC,TH) {BS,BA,DNP}	0.9746	0.0021
(SC,HC) {BS,BA,DNP,TH}	0.7513	0.0116
(SC,PS) {BS,BA,DNP}	0.8902	0.0004
(SC,TS) {BS,BA,DNP}	0.6878	0.0006
(SC,TA) {BS,BA,DNP,TH,TS}	0.5204	6.3066e-05
(SC,ARI) {BS,BA,DNP}	0.8867	0.0002
(SC,PRO) {BS,BA,DNP,TS,PS,ARI}	0.2459	0.0010
(MB,HC) {BS,DNP,BA,SC,TH}	0.0989	0.0237
(MB,PS) {BS,DNP,BA,SC,TH}	0.6736	0.0004
(MB,TS) {BS,DNP,BA,SC,TH}	0.0587	0.0024
(MB,HC) {BS,DNP,BA,SC,TH,TS}	0.4270	0.0008
(MB,DIV) {BS,DNP,BA,SC,TH}	0.9999	2.9068e-30
(MB,ARI) {BS,DNP,BA,SC,TH,TA,TS,PS}	0.9215	0.0014
(MB,PRO) {BS,DNP,BA,SC,TH,ARI,TS,PS}	0.3163	0.0011
(BS,HC) {DNP,BA,TH,PRO}	0.3229	0.0354
(BS,PS) {DNP,BA,TH,PRO}	0.8828	0.0004
(BS,TS) {DNP,BA,TH,PRO}	0.4166	0.0024
(BS,TA) {DNP,BA,TH,PRO,TS}	0.0733	0.0023
(BS,HC) {DNP,BA,TH,PRO,TA,TS,PS}	0.6119	0.0023
(BA,TS) {TH,PS,ARI} *	4.4127e-15	6.3054e-05
(BA,TA) {TH,PS,ARI,TS} *	4.3902e-18	4.7553e-05
(BA,DIV) {TH,PS,ARI,SC,BS,DNP}	0.9999	0.0189
(BA,PRO) {TH,PS,ARI,TS} *	2.1304e-11	0.0021
(DNP,PS) {BA,TH,ARI} *	1.2469e-12	0.0525
(DNP,TS) {BA,TH,ARI} *	2.2109e-13	0.0022
(DNP,PS) {BA,TH,ARI,TS}	0.1065	0.0875
(DNP,PRO) {BA,TH,ARI,TS,PS}	0.1805	0.0067
(TH,PS) { $\emptyset$ } *	4.3777e-12	0.0183
(TH,TS) { $\emptyset$ } *	3.8453e-19	0.0264
(TH,ARI) {TS,PS,TA} *	8.3348e-19	0.0165
(TH,PRO) {TS,PS,ARI} *	1.8649e-17	0.0046
(HC,PS) {BA,DNP,TH}	0.3960	7.5345e-06
(HC,TS) {BA,DNP,TH} *	7.6559e-14	0.0112

(HC,TA) {BA,DNP,TH,TS}	0.2631	0.0257
(HC,DIV) {BA,DNP,TH,SC,BS,TH}	0.4571	0.0001
(HC,ARI) {BA,DNP,TH,TS,PS,TA}	0.0887	0.0553
(HC,PRO) {BA,DNP,TH,TS,PS,ARI}	0.9632	0.0214
(PS,TS) { $\emptyset$ } *	1.0092e-14	0.0269
(PS,TA) {TS,TH} *	5.3803e-11	0.0094
(PS,DIV) {SC,BS,DNP,TH}	0.9999	3.2454e-26
(TS,DIV) {SC,BS,DNP,TH}	0.9999	2.8068e-26
(TA,DIV) {SC,BS,DNP,TH,TS}	0.9999	1.6969e-24
(TA,PRO) {SC,BS,DNP,TH,TS,PS,ARI}	0.9576e-16	0.0057
(DIV,PRO) {TH,SC,BS,DNP,TS,PS,ARI}	0.1743	0.0056
(DIV,ARI) {TH,SC,BS,DNP,TS,PS,TA}	0.6861	0.0197
(GRS,TS) {MB,SC,DIV,PS,PRO,TH,ARI,DNP,BA,HC,BS}	0.9157	0.0019
(GRS,TA) {MB,SC,DIV,PS,PRO,TH,ARI,DNP,BA,HC,BS,TS}	0.6235	0.0020
C =		55.9584
Overall p-value (χ^2 df=68)		0.8514

Table S4. Conditional independence claims implicit in the observed path model in Ethiopian realm (Fig. S2). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for predictors are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

ETHIOPIAN		
Conditional independence claim	<i>P</i>	<i>R</i> ² <i>m</i>
(SC,BA) {BS,DNP,ARI,TH,PS}	0.7326	0.0016
(SC,TH) {BS,DNP}	0.2839	0.0001
(SC,HC) {BS,DNP,BA,TH}	0.4103	0.0027
(SC,PS) {BS,DNP}	0.1278	0.0012
(SC,TS) {BS,DNP}	0.1551	0.0030
(SC,TA) {BS,DNP,TH,TS}	0.6022	2.7183e-08
(SC,ARI) {BS,DNP,TS,PS,TA}	0.2458	0.0011
(SC,PRO) {BS,DNP,TS,PS,ARI}	0.4395	0.0003
(MB,HC) {BS,DNP,BA,SC,TH}	0.0925	0.0249
(MB,PS) {BS,DNP,BA,SC,TH} *	3.1191e-17	0.0185
(MB,TS) {BS,DNP,BA,SC,TH} *	6.0630e-12	0.0008
(MB,TA) {BS,DNP,BA,SC,TH,TS} *	1.9999e-14	0.0076
(MB,DIV) {BS,DNP,BA,SC,TH}	0.9999	0.0014
(MB,ARI) {BS,DNP,BA,SC,TH,TS,PS,TA}	0.1148	0.0178
(MB,PRO) {BS,DNP,BA,SC,TH,TS,PS,ARI}	0.1409	0.0278
(BS,HC) {DNP,BA,TH,PRO}	0.1682	0.0180
(BS,PS) {DNP,BA,TH,PRO}	0.7295	0.0043
(BS,TS) {DNP,BA,TH,PRO}	0.4166	0.0159
(BS,TA) {DNP,BA,TH,PRO,TS}	0.2657	0.0136
(BS,ARI) {DNP,BA,TH,PRO,TS,PS,TA}	0.9088	0.0126
(BA,TS) {TH,PS,ARI} *	7.7065e-34	0.0338
(BA,TA) {TH,PS,ARI,TS} *	5.9721e-58	2.2576e-05
(BA,DIV) {TH,PS,ARI,SC,BS,DNP}	0.9999	4.4184e-21
(BA,TS) {TH,PS,ARI,TS}	0.4890	0.0202
(DNP,TS) {BA,TH,PS,ARI}	0.5872	9.9294e-05
(DNP,TA) {BA,TH,PS,ARI,TS} *	6.0663e-14	0.0214
(DNP,PRO) {BA,TH,PS,ARI,TS}	0.1047	0.0011
(TH,TS) $\emptyset$	0.4278	0.0060
(TH,PS) $\emptyset$ *	1.3105e-10	0.0157
(TH,ARI) {TS,PS,TA} *	4.4062e-20	0.0962
(TH,PRO) {TS,PS,ARI} *	2.6628e-05	0.0245
(HC,PS) {BA,DNP,TH}	0.5177	0.0117
(HC,TS) {BA,DNP,TH}	0.0768	0.0319

(HC,TA) {BA,DNP,TH,TS}	0.2798	0.0041
(HC,DIV) {BA,DNP,TH,SC,BS,TH}	0.9999	1.7977e-28
(HC,ARI) {BA,DNP,TH,TS,PS,TA}	0.4930	0.0071
(HC,PRO) {BA,DNP,TH,TS,PS,ARI} *	2.1109e-12	0.0020
(PS,TS) { $\emptyset$ } *	2.5643e-15	0.0188
(PS,TA) {TS,TH} *	1.3620e-14	0.0009
(PS,DIV) {SC,BS,DNP,TH}	0.9999	6.2217e-27
(TS,DIV) {SC,BS,DNP,TH}	0.9999	6.5580e-28
(TA,DIV) {TS,TH,SC,BS,DNP}	0.9999	6.9072e-25
(TA,PRO) {TS,TH,PS,ARI} *	1.7064e-09	0.0638
(DIV,ARI) {SC,BS,DNP,TH,TS,PS,TA}	0.1505	0.0079
(DIV,PRO) {SC,BS,DNP,TH,TS,PS,ARI}	0.3181	0.0045
(GRS,PS) {MB,SC,DIV,PRO,TH,ARI,DNP,BA,HC,BS,TS}	0.1370	0.0002
(GRS,TA) {MB,SC,DIV,PRO,TH,ARI,DNP,BA,HC,BS,TS}	0.4482	5.0098e-05
C =		70.7947
Overall p-value (χ^2 df=68)		0.3846

Table S5. Conditional independence claims implicit in the observed path model in Sino-oriental realm (Fig. S3). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for predictors are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

SINO-ORIENTAL		
Conditional independence claim	<i>P</i>	<i>R</i> ² <i>m</i>
(SC,BA) {BS,DNP,ARI,TH,PS}	0.1878	0.0085
(SC,TH) {BS,DNP}	0.1446	0.0049
(SC,HC) {BS,DNP,BA,TH}	0.6265	0.0147
(SC,PS) {BS,DNP,PS}	0.5136	0.0005
(SC,TS) {BS,DNP}	0.5772	0.0004
(SC,TA) {BS,DNP,TH,TS}	0.6652	0.0036
(SC,ARI) {BS,DNP,TS,PS}	0.7660	0.0002
(MB,HC) {BS,DNP,BA,SC,TH}	0.9110	0.0073
(MB,PS) {BS,DNP,BA,SC}	0.3554	0.0065
(MB,TS) {BS,DNP,BA,SC,TH}	0.2753	0.0018
(MB,TA) {BS,DNP,BA,SC,TH,TS}	0.1069	0.0098
(MB,ARI) {BS,DNP,BA,SC,TH,TS,PS}	0.9946	0.0007
(BS,HC) {DNP,BA,TH}	0.1573	0.0213
(BS,PS) {DNP,BA,TH}	0.2585	0.0070
(BS,TS) {DNP,BA,TH}	0.5763	0.0040
(BS,TA) {DNP,BA,TH,TS}	0.6439	0.0016
(BS,ARI) {DNP,BA,TH,TS,PS}	0.2187	0.0414
(BA,TS) {TH,PS,ARI}	0.8548	0.0999
(BA,TA) {TH,PS,ARI,TS}	0.8289	0.0100
(DNP,TS) {TH,PS,ARI,BA}	0.4231	6.3054e-05
(DNP,TA) {TH,PS,ARI,BA,TS}	0.1310	0.0004
(TH,PS) $\emptyset$ *	1.2283e-09	0.0145
(TH,ARI) {TS,PS} *	6.0006e-16	0.0316
(HC,PS) {BA,DNP,TH} *	1.9411e-13	0.0149
(HC,TS) {BA,DNP,TH}	0.1862	0.0090
(HC,TA) {BA,DNP,TH,TS} *	6.7965e-15	0.0116
(HC,ARI) {BA,DNP,TH,TS,PS,}	0.2929	0.0243
(PS,TS) {TH} *	9.1106e-21	0.0388
(PS,TA) {TH,TS} *	3.8865e-11	0.0001
(TA,ARI) {TS,TH,PS} *	1.0285e-13	0.0001e-12
(GRS,PS) {MB,SC,TA,TH,ARI,DNP,BA,HC,BS,TS} *	8.4441e-14	0.0554
C =		44.956

48	Overall p-value (χ^2 df=46)	0.5159
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Table S6. Conditional independence claims implicit in the observed path model in Nearctic realm (Fig. S4). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for predictors are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

NEARCTIC		
Conditional independence claim	<i>p</i>	<i>R</i> ² <i>m</i>
(SC,BA) {BS,ARI,TH,PS}	0.3276	0.0178
(SC,DNP) {BS,ARI,TH,PS}	0.3101	0.0121
(SC,TH) {BS}	0.5030	5.2860e-06
(SC,HC) {BS,DNP,BA,TH}	0.9782	0.0232
(SC,PS) {BS,TH}	0.4040	0.0267
(SC,TS) {BS}	0.1326	0.0003
(SC,TA) {BS,TH,TS,GLA}	0.6667	0.0019
(SC,ARI) {BS,TS,PS,TA}	0.2886	8.8653e-05
(SC,GLA) {BS,TS}	0.7859	0.0017
(SC,PRO) {BS,TS,PS,TA,ARI}	0.9328	5.8812e-05
(MB,BA) {BS,SC,TH,PS,ARI}	0.2385	0.0034
(MB,BA) {BS,SC,TH,PS,ARI,BA}	0.2321	0.0130
(MB,HC) {BS,SC,BA,DNP,TH}	0.1573	0.0135
(MB,PS) {BS,SC,TH}	0.2321	0.0017
(MB,TS) {BS,SC}	0.4605	0.0072
(MB,TA) {BS,SC}	0.8374	0.0016
(MB,ARI) {BS,SC,TH,TS,PS,TA}	0.9310	0.0101
(MB,GLA) {BS,SC,TS}	0.9621	0.0001
(MB,PRO) {BS,SC,TS,PS,TA,ARI}	0.5671	0.0101
(BS,HC) {DNP,BA,TH,PRO,TA}	0.3581	0.0650
(BS,PS) {DNP,BA,TH,PRO,TA}	0.4412	0.0202
(BS,TS) {DNP,BA,TH,PRO,TA}	0.2327	0.0145
(BS,ARI) {DNP,BA,TH,PRO,TA,PS,TS}	0.3581	0.0215
(BS,HC) {DNP,BA,TH,PRO,TA,PS,TS,ARI}	0.8487	0.0119
(BA,TS) {TH,PS,ARI} *	5.2149e-19	0.0866
(BA,TA) {TH,PS,ARI,GLA}	0.3027	0.0116
(BA,PRO) {TH,PS,ARI,TS}	0.1446	0.0243
(BA,GLA) {TH,PS,ARI,TS}	0.2196	0.0388
(DNP,TS) {BA,TH,PS,ARI} *	1.0810e-13	0.0210
(DNP,TA) {BA,TH,PS,ARI,TS,GLA}	0.1159	0.0157
(DNP,PRO) {BA,TH,PS,ARI,TS}	0.4558	0.0202
(DNP,GLA) {BA,TH,PS,ARI,TS} *	2.9799e-23	0.0143
(TH,TS) { $\emptyset$ }	0.1446	0.0317

(TH,ARI) {TS,PS,TA} *	4.2843e-19	0.0489
(TH,PRO) {TS,PS,ARI}	0.3461	0.0399
(TH,GLA) {TS}	0.7753	0.0024
(HC,PS) {BA,DNP,TH}	0.3623	0.0778
(HC,TS) {BA,DNP,TH}	0.6414	0.0165
(HC,TA) {BA,DNP,TH,GLA,TS}	0.1778	0.0178
(HC,ARI) {BA,DNP,TH,TS,PS,TA}	0.3825	0.0038
(HC,PRO) {BA,DNP,TH,TS,PS,ARI}	0.5918	0.0117
(HC,GLA) {BA,DNP,TH,TS}	0.1112	0.0165
(PS,TS) {TH}	0.1785	0.0002
(PS,TA) {TH,TS,GLA} *	4.1020e-14	0.0004
(PS,GLA) {TH,TS}	0.4570	0.0145
(TA,PRO) {TS,PS,GLA,ARI}	0.2887	0.0177
(GLA,ARI) {TS,PS,TA}	0.9924	0.0198
(GLA,PRO) {TS,PS,ARI} *	4.7826e-12	0.0030
(GRS,PS) {MB,PRO,TH,DNP,BA,HC,BS,TS}	0.6662	0.0496
(GRS,TA) {MB,PRO,TH,DNP,BA,HC,BS,TS,GLA}	0.0758	0.0182
(GRS,SC) {MB,PRO,TH,DNP,BA,HC,BS,TS}	0.4142	0.0002
(GRS,GLA) {MB,PRO,TH,DNP,BA,HC,BS,TS}	0.1621	0.0196
(GRS,ARI) {MB,PRO,TH,DNP,BA,HC,BS,TS,PS,TA}	0.9295	0.0103
C =		89.6827
Overall p-value (χ^2 df=92)		0.5490

Table S7. Conditional independence claims implicit in the observed path model in Palearctic realm (Fig. S5). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for predictors are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

PALEARCTIC		
Conditional independence claim	<i>P</i>	<i>R</i> ² <i>m</i>
(BS,HC) {DNP,BA,PRO,TA}	0.3424	0.0102
(BS,PS) {DNP,BA,PRO,TA}	0.2742	0.0236
(BS,TS) {DNP,BA,PRO,TA}	0.0562	0.0013
(BS,TA) {DNP,BA,PRO,TA,GLA,TS}	0.7043	0.0427
(BS,ARI) {DNP,BA,PRO,TA,PS,TS,TA}	0.8540	0.0002
(BS,TH) {DNP,BA,PRO,TA}	0.6202	0.0017
(BS,GLA) {DNP,BA,PRO,TA,TS}	0.7047	0.0071
(BA,TS) {TH,PS,ARI} *	6.7926e-11	0.0119
(BA,TA) {TH,PS,ARI,TS,GLA}	0.7988	0.0169
(BA,PRO) {TH,PS,ARI,ARI,TS}	0.3551	0.0049
(BA,GLA) {TH,PS,ARI,TS}	0.3551	0.0652
(DNP,TS) {BA,TH,PS,ARI}	0.8939	0.0921
(DNP,TA) {BA,TH,PS,ARI,TS,GLA}	0.1126	0.0718
(DNP,PRO) {BA,TH,PS,ARI,TS}	0.3930	0.0001
(DNP,GLA) {BA,TH,PS,ARI,TS}	0.6749	0.0001
(TH,ARI) {TS,PS,TA}	0.3792	0.0011
(TH,PRO) {TS,PS,ARI}	0.1401	0.0006
(TH,GLA) {TS}	0.0827	0.0073
(TH,TS) $\emptyset$	0.2491	0.0024
(TH,PS) $\emptyset$	0.2206	0.0021
(HC,PS) {BA,DNP}	0.6000	0.0113
(HC,TS) {BA,DNP} *	2.3392e-11	0.0173
(HC,TA) {BA,DNP,TH,TS,GLA}	0.5024	0.0274
(HC,PS) {BA,DNP,TS,PS,TA}	0.9999	3.7245e-29
(HC,PRO) {BA,DNP,TS,PS,ARI}	0.4257	0.0002
(HC,GLA) {BA,DNP,TS}	0.5024	0.0002
(PS,TS) $\emptyset$	0.7211	0.0003
(PS,TA) {TA,TH,GLA} *	3.2979e-15	0.0278
(PS,GLA) {TS}	0.9247	0.0001
(GLA,PRO) {TS,PS,ARI,TA}	0.5551	0.0001
(GLA,ARI) {TS,PS,TA}	0.1265	0.0055
(GRS,PS) {PRO,TH,ARI,DNP,HC,BS,TS,GLA}	0.4604	0.0090
(GRS,TA) {PRO,TH,ARI,DNP,HC,BS,TS,GLA}	0.2237	0.0107

(GRS,PS) {PRO,TH,ARI,DNP,HC,BS,TS,GLA,PS}	0.8943	0.4897
C =		89.6827
Overall p-value (χ^2 df=62)		0.5489

Table S8. Conditional independence claims implicit in the observed path model in Australian realm (Fig. S6). Fisher's C statistic and p-values are provided at the bottom of the table. Abbreviations for predictors are: geographic range size (GRS), drainage network position (DNP), topographic heterogeneity (TH), drainage basin area (BA), historical connectivity (HC), temperature anomaly (TA), glaciation history (GLA), aridity (ARI), temperature seasonality (TS), precipitation seasonality (PS), productivity (PRO), diversification (DIV), body size (BS), migratory behavior (MB), and swimming capacity (SC). $\emptyset$ represents a null set of control variables (i.e., these are not parental variables required in the conditional statement). * represents conditional statements evaluated but not included to calculate C and p-values (see methods section in the main text for more details).

AUSTRALIAN		
Conditional independence claim	<i>p</i>	<i>R</i> ² <i>m</i>
(BS,HC) {DNP,BA,TH,TA,PROD}	0.3560	0.0309
(BS,PS) {DNP,BA,TH,TA,PROD}	0.0993	0.0135
(BS,TS) {DNP,BA,TH,TA,PROD}	0.7944	0.0592
(BS,HC) {DNP,BA,TH,TA,PROD,PS,TS,TA}	0.7432	0.0794
(BS,GLA) {DNP,BA,TH,TA,PROD,TS}	0.2932	0.0501
(BA,PS) {TH,ARI}	0.3973	0.0373
(BA,TS) {TH,ARI}	0.4963	0.0165
(BA,TA) {TH,ARI,TS,GLA}	0.6113	0.0175
(BA,PRO) {TH,ARI,ARI,TS}	0.2188	0.0321
(BA,GLA) {TH,ARI,TS}	0.9907	0.0083
(DNP,TS) {BA,TH,ARI}	0.3579	7.2099e-05
(DNP,TA) {BA,TH,ARI,PS,TS,GLA}	0.3885	0.0055
(DNP,PRO) {BA,TH,ARI,PS,TS,ARI}	0.2216	0.0359
(DNP,GLA) {BA,TH,ARI,TS}	0.8829	0.0007
(DNP,PS) {BA,TH,ARI}	0.1625	0.0449
(TH,HC) {BA,DNP}	0.9137	0.0924
(TH,GLA) {TS}	0.6848	0.0007
(TH,PS) $\emptyset$	0.8606	0.0004
(TH,TS) $\emptyset$	0.9001	0.0115
(TH,ARI) {TS,PS,TA}	0.1761	4.0691e-05
(TH,PRO) {TS,PS,ARI}	0.6711	0.0113
(HC,PS) {BA,DNP}	0.2155	0.0136
(HC,TS) {BA,DNP}	0.3362	0.0569
(HC,TA) {BA,DNP,TH,TS,GLA}	0.6263	0.0592
(HC,ARI) {BA,DNP,TS,PS,TA}	0.1431	0.0143
(HC,PRO) {BA,DNP,TS,PS,ARI}	0.5923	0.0616
(HC,GLA) {BA,DNP,TS}	0.3209	0.0048
(PS,TS) $\emptyset$	0.5466	0.0055
(PS,TA) {TS,TH,GLA}	0.1679	0.0138
(PS,GLA) {TS}	0.2383	0.0622
(ARI,GLA) {TS,PS}	0.9953	0.0268
(ARI,PRO) {TS,PS,TA}	0.2384	0.0188
(GLA,PRO) {TS,PS,TA}	0.3707	0.0074

(GRS,PS) {PRO,GLA,TH,DNP,TA,HC,BS,TS}	0.7906	0.0064
(GRS,ARI) {PRO,GLA,TH,DNP,TA,HC,BS,TS,PS}	0.6713	0.0251
(GRS,BA) {PRO,GLA,TH,DNP,TA,HC,BS,TS,ARI}	0.3244	0.0104
C =		63.4543
Overall p-value (χ^2 df=72)		0.7537

82 **Table S9.** Effect size (R_m^2 and R_c^2) for all the endogenous-variables in the final path models.

Endogenous variable	Global		Netropical		Ethiopian		Sino- Oriental		Nearctic		Palearctic		Australian	
	R_m^2	R_c^2	R_m^2	R_c^2	R_m^2	R_c^2	R_m^2	R_c^2	R_m^2	R_c^2	R_m^2	R_c^2	R_m^2	R_c^2
Geographic range size	0.792	0.871	0.823	0.836	0.739	0.758	0.801	0.879	0.815	0.889	0.775	0.809	0.909	0.921
Drainage network position	0.262	0.423	0.305	0.440	0.174	0.326	0.332	0.524	0.247	0.416	0.326	0.427	0.416	0.417
Historical connectivity	0.428	0.623	0.326	0.358	0.312	0.431	0.636	0.672	0.591	0.665	0.401	0.450	0.489	0.905
Drainage basin area	0.145	0.729	0.244	0.301	0.182	0.384	0.450	0.525	0.213	0.412	0.179	0.309	0.570	0.764
Aridity	0.748	0.879	0.698	0.707	0.572	0.722	0.573	0.672	0.267	0.831	0.661	0.713	0.619	0.624
Glaciation history	0.505	0.73							0.224	0.398	0.127	0.312	0.258	0.258
Temperature anomaly	0.488	0.574	0.341	0.448	0.554	0.642	0.717	0.741	0.543	0.602	0.272	0.729	0.623	0.662
Migratory behavior	0.229	0.498	0.336	0.570	0.196	0.410	0.292	0.662	0.168	0.404				
Swimming capacity	0.182	0.583	0.138	0.429	0.175	0.486	0.281	0.659	0.146	0.594				
Body size	0.129	0.624	0.210	0.658	0.234	0.508	0.163	0.506	0.157	0.612	0.153	0.744	0.228	0.652
Productivity			0.438	0.473	0.444	0.533			0.363	0.533	0.242	0.358	0.336	0.352
Topographic heterogeneity														
Temperature seasonality							0.275	0.671						
Precipitation seasonality									0.190	0.491				
Diversification			0.259	0.381	0.268	0.399								

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84 **Table S10.** Morphological measures used in the species traits PCA and the variance
 85 accounted for by the first PCA axis (see (Toussaint et al. 2016) for further details on the
 86 morphological measures).

Morphological measure	Link with fish functions	Species trait	Variance accounted by the first PCA axis
Oral gape position	Feeding position in the water column	Prey capture	63%
Relative maxillary length	Size of mouth and strength of jaw		
Body lateral shape	Hydrodynamism and head size	Swimming capacity	52%
Pectoral fin vertical position	Pectoral fin use for swimming		
Pectoral fin size	Pectoral fin use for swimming		
Caudal peduncle throttling	Caudal propulsion efficiency through reduction of drag		

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88 **Table S11.** Main hypotheses for freshwater fishes supporting the interrelationships considered among the multiple predictors of geographic range
89 size. These hypotheses were compiled from previous studies or developed from the ecological literature and support the links in the full expected
90 path model (Fig. S9).

Endogenous variable	Parental variable	Expected link	Reference
Drainage network position (i.e. river drainage branching complexity)	Topographic heterogeneity	Drainage network position should decrease with high topographic heterogeneity because stream order decreases in areas with high topographic heterogeneity.	(Benda et al. 2004)
	Drainage basin area	Drainage branching complexity should increase with the surface area of the drainage basin.	(Horton 1945, Strahler 1952)
	Aridity	Drainage branching complexity should decrease with aridity, because aridity fragments drainage basins reducing their hydrological network complexity.	(Unmack 2001)
Drainage basin area	Topographic heterogeneity	Small drainage basins are mostly found near coastlines (coastal stream) where low topographic heterogeneity is expected	(Benda et al. 2004)
	Aridity	Drainage basin area should decrease with aridity as aridity decreases water availability and fragments basin area dividing river surface.	(Unmack 2001)
Temperature seasonality	Topographic heterogeneity	Temperature seasonality should increase with topographic heterogeneity because high amplitudes in temperature are more frequent in mountain regions.	(Kubokawa et al. 2016)
Precipitation seasonality	Topographic heterogeneity	Precipitation seasonality should increase with topographic heterogeneity because precipitation varies with elevation.	(McGuire et al. 2005)
Aridity	Temperature seasonality	Aridity should decrease with lower temperature seasonality because temperature significantly affects water balance in riverine ecosystems.	(Walton 1969, Seager et al. 2013)
	Precipitation seasonality	Aridity should increase in regions with low annual precipitation because evapotranspiration exceeds water availability.	(Walton 1969, Seager et al. 2013)

	Temperature anomaly	Aridity should be greater in regions with greater long-term increases in temperature.	(Sherwood and Fu 2014, Huang et al. 2016)
Productivity	Aridity	Productivity should decrease with higher values of aridity because productivity and CO ₂ exchange are determined in large part by soil moisture conditions.	(Suyker et al. 2003, Polley et al. 2010)
	Temperature seasonality	Productivity should decrease with low-temperature seasonality because productivity is regulated by both temperature and the amount and timing of precipitation.	(Parton et al. 2012, Peng et al. 2013)
	Precipitation seasonality	Productivity should decrease with low-precipitation seasonality because productivity is regulated by both temperature and the amount and timing of precipitation.	(Parton et al. 2012, Peng et al. 2013)
Glaciation history	Temperature seasonality	Ice cover extent during glacial periods should increase with high-temperature seasonality because glaciations have occurred in regions with low temperatures and a high seasonal range of temperatures.	(Savin 1977, Annan and Hargreaves 2013)
Temperature Anomaly	Glaciation history	Temperature anomaly should be greater in regions covered by ice during glacial periods because these regions have experienced greater changes in temperature since the LGM.	(Annan and Hargreaves 2013)
	Temperature seasonality	Temperature anomaly should be greater in regions with greater temperature seasonality because the LGM was harsher in regions with greater seasonal ranges of temperatures.	(Savin 1977, Annan and Hargreaves 2013)
	Topographic heterogeneity	Temperature anomaly should be higher in regions with a greater topographic heterogeneity because climate change velocity since the LGM has been greater in temperate and mountain regions.	(Sandel et al. 2011)
Diversification	Drainage basin area	Diversification should be greater in regions where species have higher habitat availability.	(Preston 1960, Pagel et al. 1991)

	Drainage network position	Diversification should be greater on intermediate river orders because network branching promotes genetic diversity and differentiation between local populations, but headwater streams (the most branched region in the river networks) have high extinction and low colonization rates due to their high rates of disturbances and greater isolation.	(Resh et al. 1988, Thomaz et al. 2016)
	Topographic heterogeneity	Diversification should be greater in regions with greater topographic heterogeneity because diversification is higher in mountain regions and with high habitat heterogeneity.	(66–68)
	Body size	Diversification should be greater in clades with smaller body size because diversification is constrained by the ability of individuals to turn resources into offspring. The same relationship is expected based on the lower dispersal capacities of smaller bodied species.	(68–70)
Palaeo-connectivity	Topographic heterogeneity	Drainage basins with high topographic heterogeneity should have lower chances for palaeo-connectivity because palaeo-connections between drainage basins occurred mainly in flat regions with large continental shelf.	(Vorisi 2000)
	Drainage network position	High order streams should have greater palaeo-connectivity because the historical connection between drainage basins has occurred among lowland river portions.	(Vorisi 2000)
	Drainage basin area	Larger drainage basins should have lower chances for palaeo-connectivity because palaeo-connections were most frequent between small basins located in coastal regions.	(Dias et al. 2014a)
Body size	Topographic heterogeneity	Smaller-bodied species should occur in regions with high topographic heterogeneity because species body size tends to decrease with elevation.	(Fu et al. 2004, Hu et al. 2011)
	Drainage network position	Fish species in low stream orders should have a smaller body size because headwater streams are located in the most elevated portions of the drainage basins, and fish body size tends to decrease with elevation.	(Fu et al. 2004)
	Drainage basin area	Fish species body size should be greater in larger drainage basins because large-bodied species require greater areas to meet their energy requirements.	(Brown and Maurer 1987, 1989)

	Temperature seasonality	Species that inhabit regions with high-temperature seasonality should have greater body sizes. According to Bergmann's rule, species inhabiting high latitudes (i.e. regions with low temperature and great temperature seasonality) tend to be larger in size.	(Bergmann 1848, Ashton et al. 2000, Belk and Houston 2002)
Migratory behavior	Body size	Species presenting migratory behavior should have greater body sizes because larger-bodied species tend to present more efficient migratory strategies.	(Zhao et al. 2017)
	Drainage basin area	Migratory behavior should be more frequent in species that inhabit large drainage basins because freshwater migrations tend to occur over long distances.	(Aidley 1981, Dingle 2014)
	Drainage network position	Fish species with migratory behavior should inhabit high-order streams because riverine fish migrations are commonly associated with species that inhabit lowlands and perform upstream migrations.	(Lucas and Baras 2001)
	Topographic heterogeneity	Fish species with migratory behavior should be distributed in areas with lower topographic heterogeneity because migratory freshwater fishes mainly inhabit the basal portions of the river network (i.e. river lowlands).	(Lucas and Baras 2001)
	Swimming Capacity	Fish migratory species should have higher swimming capacities.	(Lucas and Baras 2001, Tudorache et al. 2008)
Prey capture	Body size	Findings on the relationship between the trophic position and body size are not straightforward, but some studies report a positive relationship.	(Arim et al. 2010, Ou Chouly et al. 2017)
Swimming capacity	Drainage network position	Swimming capacity should be greater in high order rivers because dispersal strategies are different in low order rivers with turbulent waters.	(Ward et al. 2003, Tudorache et al. 2008)
	Drainage basin area	Fish species inhabiting large drainage basins should have greater swimming capacities to cover large areas.	(Taylor et al. 1982)
	Body size	Large-bodied species should have greater swimming capacities because they must forage larger areas to satisfy their energetic requirements.	(Taylor et al. 1982)

Table S12. R packages used in this study.

Methods section	R packages	Reference
Species geographic range	sf (version 0.7-2)	(Pebesma et al. 2018)
Current climate	sf (version 0.7-2) , raster (version 2.8-4)	(Hijmans et al. 2018, Pebesma et al. 2018)
Long-term climate stability	sf (version 0.7-2) , raster (version 2.8-4)	(Hijmans et al. 2018, Pebesma et al. 2018)
Productivity	sf (version 0.7-2) , raster (version 2.8-4)	(Hijmans et al. 2018, Pebesma et al. 2018)
Drainage network position	sf (version 0.7-2) , raster (version 2.8-4)	(Hijmans et al. 2018, Pebesma et al. 2018)
Historical connectivity	sf (version 0.7-2)	(Pebesma et al. 2018)
Geomorphology	sf (version 0.7-2) , raster (version 2.8-4)	(Hijmans et al. 2018, Pebesma et al. 2018)
Diversification	rfishbase (version 2.1.2)	(Boettiger et al. 2012)
Morphological species traits	rfishbase (version 2.1.2), missMDA (version 1.13)	(Boettiger et al. 2012, Josse and Husson 2016)
Data analysis	lme4 (version 1.1-18-1), mgcv (version 1.8-24), MuMIn (version 1.40.4)	(Bates et al. 2015, Bartoń 2018, Wood 2018)

CHAPTER 3: Does the lower limit of the range-body size relationship represents the minimum viable range of the species?



Photo by Jorge García-Melo (Project CaVfish Colombia)

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Abstract

Current rates of environmental degradation and species extinctions have prompted development of various approaches to assess species extinction proneness. However, these efforts are often limited by the lack of detailed population data required for a formal evaluation of extinction risk, pressing scientists to look beyond the population level and to build on predictive frameworks. The lower limit of the macroecological relationship between the species range size and body size is usually interpreted as a link between the minimum viable range size (MVR) needed for the species persistence and organismal traits that restrict the use of space and resources across species. Nonetheless, this link has never been explicitly tested. Here, we compare the MVR predicted by this macroecological limit with an independent MVR estimated through the temporal fluctuations of population abundances across space. Our results support the lower limit of the range – body size relationship as a reliable method to assess the species MVR and an effective conservation prioritization tool to assess vulnerable species, especially in poorly studied areas and taxonomic groups.

Introduction

Extinction risk or species vulnerability estimates are essential for prioritizing conservation actions (Joseph et al. 2009). Geographic range size consistently emerges as a key correlate of extinction risk in vertebrates (Gaston 1994b, Sodhi et al. 2008, Cardillo et al. 2008, Lee and Jetz 2011), where species occupying smaller geographic ranges are assumed to have a higher risk of extinction. However, species are not all equally vulnerable when facing a small geographic range. The minimum viable range size (MVR) needed for long-term persistence likely depends on the species traits that determine the local and regional abundance of their populations. Body size scales with many of the species attributes that influence geographic ranges (e.g. population density, individual home range size and dispersal capability) (e.g. Schmidt-Nielsen 1984). In particular, the energetic constraints shaping the relationship between body size and metabolic requirements (Swihart et al. 1988) cause larger species to have larger geographic ranges to compensate their lower population densities (Damuth 1981, Brown and Maurer 1987) as populations of large species with small ranges are more likely to be extirpated, both because of low effective population sizes and high vulnerability to catastrophic events (Gaston 1994b). Conversely, small-bodied species can maintain higher population abundances in smaller areas. Large-bodied species also tend to have higher dispersal capacities than smaller species filling a bigger portion of their potential distributional range (Gaston and Blackburn 1996a).

These assumptions have been advanced to explain the triangular relationship between species geographic range and body size, one of the earliest patterns documented in macroecology (Brown and Maurer 1987, 1989) that has been already observed for several taxonomic groups and at various geographic scales (e.g. Taylor and Gotelli 1994, Gaston and Blackburn 1996, Diniz-Filho and Tôrres 2002, Diniz-Filho et al. 2005, Agosta and Bernardo 2013, Le Feuvre et al. 2016, Carvajal-Quintero et al. 2017, Inostroza-Michael et al. 2018, Newsome et al. 2020). This range-body size relationship shows a triangular shape in a bivariate trait space and is defined by three boundaries (Fig 1), two considered hard and one flexible. The two hard limits are boundaries set by extrinsic and intrinsic properties of the species, with the first one setting the upper limit (i.e. maximum range size) determined by the spatial extent of the study area, whereas the second boundary sets the left limit (i.e. minimum body size) settled by physiological constraints (Brown & Maurer 1987, 1989). Finally, the third and flexible boundary results from the direct positive relationship between the species'

body size and its minimum range size needed for attaining viable populations (Brown and Maurer 1987, 1989).

This lower and flexible boundary has been associated with a high probability of extinction (Brown and Maurer 1987, 1989) and used to define the MVR for species given their body size (Gaston and Blackburn 1996a). Hence, from a conservation perspective, this boundary is of utmost importance as potentially constituting a vulnerability limit, a species being near or beyond the boundary having a low probability of persistence through time (Brown and Maurer 1987, 1989, Gaston and Blackburn 1996a). Several studies have contributed empirical evidence showing that distance of species to the lower boundary of the range-body size relationship is a suitable predictor of species' threatened status (e.g. Rosenfield 2002, Le Feuvre et al. 2016, Newsome et al. 2020). This has prompted assessments of the range-body size lower boundary to evaluate the conservation status of poorly studied species as well as tracking and forecasting changes in species extinction risk due to anthropogenic perturbations (Le Feuvre et al. 2016, Carvajal-Quintero et al. 2017).

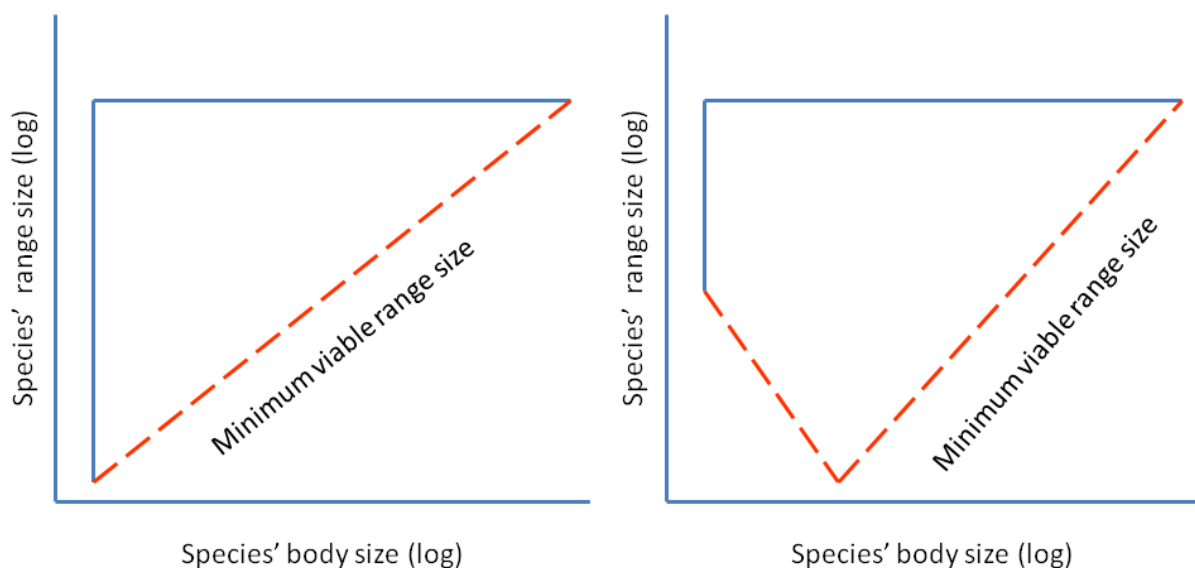


Figure 1. Left, the theoretical model describing the geographic range size–body mass relationship proposed by Brown and Maurer (Brown and Maurer 1987, 1989). Right, the relationship uncovered by Agosta and Bernardo (2013), who found a breakpoint in the lower boundary for mammals.

However, despite three decades of applying the lower boundary of the range-body size relationship to define the MVR of species, no test has been done yet to link explicitly this

empirical boundary to species' lower probability of persistence. Here we intend to fill this important theoretical and applied knowledge gap by relating the MVR estimated from the lower boundary of the range-body size relationship (here after called 'macroecological MVR') with an independent MVR estimated from spatio-temporal dynamics of population abundances (here after called 'spatio-temporal MVR'). To estimate the spatio-temporal MVR of a given species we used the concept of spatial synchrony; i.e. the synchronous temporal dynamics in the abundance of spatially separated populations. Spatial synchrony has indeed well-recognized implications for the long-term persistence and extinction probability of species (Allen et al. 1993, Liebhold et al. 2004). Notwithstanding the fact that different populations of a same species are connected or not, synchronous population dynamics can increase species vulnerability to common stochastic events leading to higher species extinction risk, while population asynchrony dynamics may lead to longer term stability and persistence (Allen et al. 1993, Heino et al. 1997, Gonzalez and Loreau 2009). Spatial populations synchrony usually decreases with increasing geographic distance between populations (Ranta et al. 1995, Bjørnstad et al. 1999, Liebhold et al. 2004), allowing to define a "limit of synchrony", i.e. the maximum distance or geographic range where synchrony can still be observed between populations (Bjørnstad et al. 1999). Above the area defined by this limit, divergent population dynamics allow for compensatory mechanisms, preventing local declines and extinctions (Heino et al. 1997, Liebhold et al. 2004). We can hypothesized that this unit may represent the minimum viable population range size for a given species hence defining a spatio-temporal MVR that should mirror the macroecological MVR set by the species range-body size spatial pattern.

Focusing on riverine fishes, we first estimated the macroecological MVR using a global dataset of species distribution and body size for 9.075 species to estimate the macroecological MVR. In a second step we used population abundance time-series available for 62 species distributed worldwide to evaluate the limit of population synchrony and further estimate the spatio-temporal MVR. Our findings clearly support the use of the macroecological MVR as a vulnerability limit to identify species with higher extinction risks in conservation targets, both at global and biogeographic realm scales (based on Leroy et al. 2019).

Methods

Geographic range and body size data

To build the range-body size relationships at global and biogeographic realm scales we used the geographic range size of freshwater fishes estimated by Carvajal-Quintero et al. (2019) for 9075 species (~70% of all described freshwater fish species) distributed worldwide, and the maximum body length provided by FishBase (Froese and Pauly 2020) as a measure of body size.

Time series data

The time series of population abundances needed to define the spatio-temporal MVR were obtained from RivFishTIME, the largest database of long-term (≥ 10 years) time series of freshwater fish assemblages collected to date (Comte et al. 2020). This database provides time series for 1,603 species across 13,131 sampling locations resulting in 136,545 time series of local populations (i.e. the abundances of a given species in a given sampling location over 10 years or more). To ensure the direct comparison of local populations across geographic space and time, we divided the global database into comparable datasets where all records were sampled during the same climatic season, using the same protocol and registered with the same type of abundances (e.g. individuals /m²) throughout the time period (see Comte et al. 2020 metadata for more details). Non-native species occurrences were filtered out according to the global freshwater fish distribution database provided by Tedesco et al.(2017). When an occurrence did not intersect with any of the drainage basins reported in Tedesco et al. (2017), we assigned the species status (native or exotic) of the closest basin belonging to the same country. In other cases, we used the species distribution status reported in FishBase (Froese and Pauly 2020). Species usually not occurring in continental waters (i.e. fresh and brackish waters) were excluded based on FishBase information (Froese and Pauly 2020). We applied a sample size criterion (i.e. number of time series per species) to ensure reliable estimates of the spatio-temporal MVR, retaining only species with 10 or more comparable years (i.e. same sampling years) from at least 10 locations. The application of the above data selection criteria resulted in species occurring in temperate and sub-temperate regions exclusively (see below and Fig S1). Consequently, we only kept time series based on samplings performed between April and September (i.e. the warm season) to integrate major fish reproductive and movement events (Wootton 1990, Bromage et al. 2001, Bradshaw and Holzapfel 2007) that primarily occur during that season in temperate regions due to increasing temperatures and photoperiod (Sommer et al. 1986, Winder and Schindler 2004). Because this selection of time

series may result in different combinations according to the number of sampled years and sites, we always kept the group of time series that covered the highest number of sampled sites to include the largest portion of the species geographic range in the spatio-temporal MVR estimates. All time series using non-continuous abundance values were excluded, and all abundance values $> 99.9\%$ quantile were considered as potential data errors and further excluded. All these data selection criteria resulted in 62 species and 3918 time series that were sampled in three different biogeographic Realms (Nearctic, Palearctic and Australian, following Leroy et al. 2019, Fig S1) which were used to estimate the spatio-temporal MVR.

Macroecological MVR

We estimated the macroecological MVR at the global and biogeographic realm scales using range-body size relationships based on log10-transformed variables and quantile regressions to determine the lower (0.10 quantile) and upper boundaries (0.90 quantile) of the relationship (Scharf et al. 1998). To consider the possibility of a breakpoint in the lower limit as proposed by Agosta and Bernardo (2013), we fitted quantile segmented regressions with respect to body size. For each segmented regression, we estimated the location of the breakpoint through an iterative search procedure (Crawley 2013). We obtained the coefficient and a goodness of fit measure (analogous to the conventional R^2 , (Koenker and Machado 1999) on either side of the breakpoint and reported the results only for the significant model ($p < 0.05$) with the best fit and showing a negative slope at the left side of the breakpoint as reported by Agosta and Bernardo (2013). Our estimates of the macroecological MVR were based on 9,075 species at the global scale and 733, 584 and 76 species for the Nearctic, Palearctic and Australian realms, respectively. These species represent 70% of the global freshwater fish fauna and 88%, 53% and 21% for Nearctic, Palearctic and Australian realms respectively.

Spatio-temporal MVR

As mentioned before, we used the concept of spatial population synchrony and, more specifically, the limit of population synchrony as an estimate of the spatio-temporal MVR for each selected species. We measured this limit as the x-intercept distance in a spline correlogram (Bjørnstad and Falck 2001) based on the time series of each species and their spatial distribution. Spline correlogram differs from commonly used spatial correlograms (and Mantel correlograms) as it estimates dependence as a continuous function of distance, rather than by grouping into distance classes. This brings to spline correlograms a greater precision and the capacity to adapt well to the different underlying covariance structures (Bjørnstad et al. 1999, Bjørnstad and Falck 2001). The x-intercept in a spline correlogram is the distance at

which the spatial autocorrelation of a variable reaches zero or turns negative (Sokal and Wartenberg 1983, Bjørnstad et al. 1999), and can be used as an estimate of the spatial scale of a regional autocorrelation pattern (Sokal and Wartenberg 1983, Epperson and Li 1997). In our case, the distance determined by the x-intercept is the minimum distance needed to obtain uncorrelated abundances between populations, i.e. the limit of population synchrony for a given species. We then converted this distance into a geographic range area using this distance as the diameter of a circle. We chose a circular shape as the best way to represent the minimal area ensuring that we are covering the limit of population synchrony in any direction across the geographical space. For species with more than one value for the limit of population synchrony (i.e. species with time series available for more than one comparable dataset), we calculated the average. To obtain an estimate of the spatio-temporal MVR, we finally relate each species-level MVR value to the corresponding species body size applying a log10-linear regression. Importantly, we controlled for the potential bias that could affect our estimates of spatio-temporal MVR values if larger ranges formed by the time series sampling sites would provide systematically larger MVR values (i.e. no correlation was observed between the convex-hull area formed by the time series sampling points of each species and the corresponding spatio-temporal MVR values, $R^2 = 0.0004$, $p = 0.866$, Fig S2).

Comparing MVR estimates

We build the spatio-temporal MVR to provide a mechanistic basis and validation of the macroecological MVR based on their graphical comparison. We further compared these two vulnerability limits of species range size through a linear regression using 100 values predicted by each limit model (i.e. quantile and linear regression for the macroecological and spatio-temporal limits respectively). These values were sampled equidistantly along the minimum and maximum values of body sizes reported in the spatio-temporal MVR. Finally, we contrasted the distance of species in respect to the macroecological and spatio-temporal MVR using a Gaussian linear model.

We applied the all above approach at the global and biogeographic realm scales. Because large sampling size can detect very minor residual associations between variables and lead models with not significant-scientific relations, we only considered models with effect sizes (Goodness of fit or R^2) > 0.1 and $p < 0.05$ (Anderson 2008). Data analyses were performed in R 3.4.3 (R Development Core Team 2017). For details on R packages used, see supplementary methods, Table S1.

Results

The shape of the range-body size relationship was reconstructed at a global scale and for the three biogeographic realms (Fig 2, table S2). At the global scale, a linear relationship better described the lower boundary of the macroecological relationship, whereas for the considered realms we found evidence for both, linear (Australia) and segmented relationships (Nearctic and Palearctic) (Fig 2, Table S2).

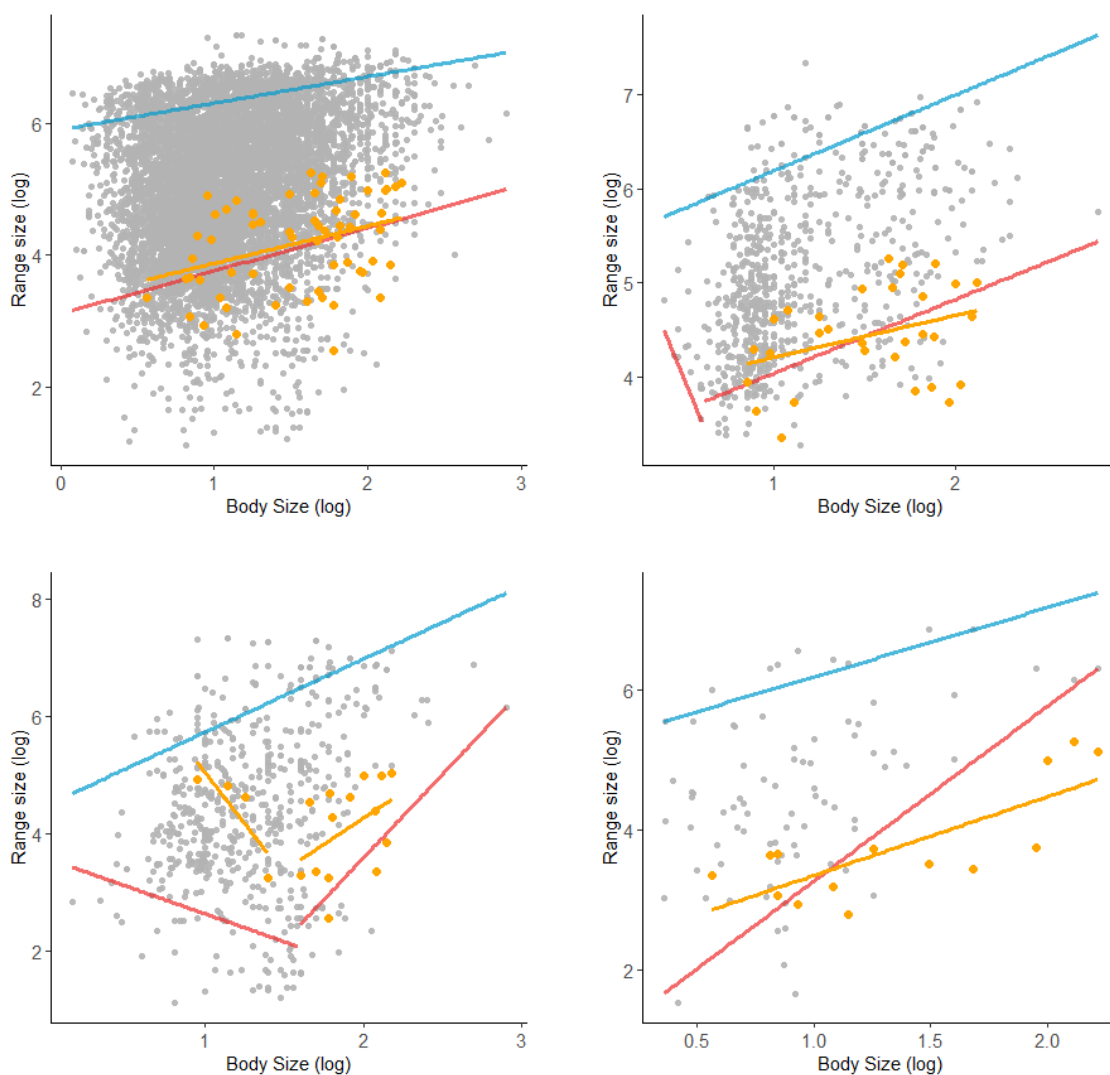


Figure 2. Representation of the range-body size relationship at different spatial scales. The red line represents the regression of the 10% quantile and the expected MVR settled by the macroecological relationship. The blue line represents the regression of the 90% quantile. Orange line and dots represent the observed MVR described by the relationship regional scale

of synchrony and body size. Up left global scale, up right Nearctic, down left Palearctic, and downright Australian.

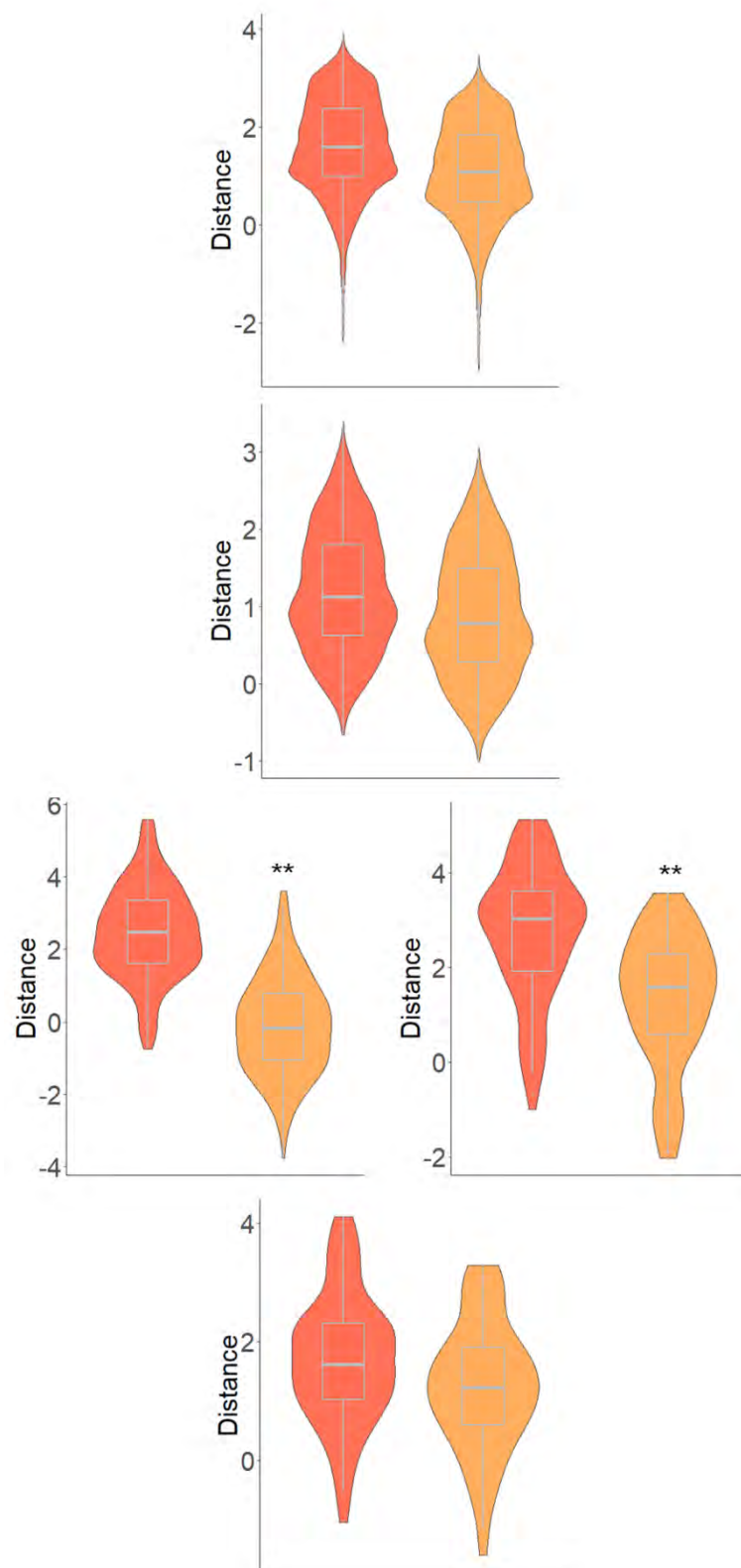


Figure 3. Distance of species respect to macroecological MVR (red, quantile 0.10) and spatio-temporal MVR (orange). The boxes represent the median, the first quartile and the third quartile of the distances, and violin plots represent sideways density plots. From top to bottom: Global scale, Nearctic, Palearctic and Australian. The two box plots for the Palearctic region represent the two portions of the quantile-segmented regression

We calculated the spatio-temporal MVR for 62 species at a global scale, distributed across the biogeographic realms as follow: 31 Nearctic, 18 Palearctic and 14 Australian. The range of body sizes of these species covered between 62 and 89% of the body size intervals reported in this study (Fig 2) allowing us to build the spatio-temporal MRV at both global and realms spatial scales. Only for the Nearctic realm, because of no available small-sized species, it was not possible to represent the first segment of the lower bound (Fig 2). In all four cases we broadly observe coherent shapes of the macroecological and spatio-temporal MVR. We further found a highly significant relationship when comparing the sequence of values predicted by both MVR estimates ($R^2 = 0.96-0.99$, Table S3), showing that the spatio-temporal MVR limit recreated well the shape and tendency of the macroecological MVR limit. At the global scale, the spatio-temporal and macroecological MVR limits matched perfectly showing a similar distance of species respect to both limits, and at the realm scale, distance of species to the spatio-temporal and macroecological MVR limits varied slightly but with no significant difference for the Nearctic and Australian region (Fig 2 and 3, Table S4). These results remained stable when using 0.05 quantile regressions, instead of 0.1, for the macroecological MVR (Fig S2 and S4, Table S4).

Discussion

By linking the lower bound of the range – body size relationship to the synchrony limit estimated from spatio-temporal dynamics of population abundances, we contribute for the first time empirical evidence supporting that this macroecological bound represents a vulnerability limit established by the minimum viable range size required for long-term persistence of species. The macroecological and spatio-temporal limits matched across all the spatial scenarios that we evaluated, showing a linear and positive relationship respect to species body size at a global scale, and both linear and segmented relationships across biogeographic realms.

Our study extends our comprehension about the processes that shape the lower bound of the range - body size relationship giving us a framework to understand how different population and species level factors interact, determining the long-term persistence of species

according to their geographic range and body size. Here we showed at a global scale that the species' MVR increases linearly with body size establishing a vulnerability limit that restrict large-bodied species to large geographic areas to ensure their long-term persistence (Fig. 2). Large-bodied species present high dispersal capacities that allow them to forage widely to face temporal and spatial variation in resources and thus fulfill their high energetic demands (Kleiber 1975, Brown and Maurer 1987, 1989), besides, higher dispersal can also protect small local populations from extinction by allowing the influx of immigrants (Abbott 2011). However, dispersal is a 'double-edged sword' and can result in high the risk of global extinction by spatially synchronizing local populations (Liebhold et al. 2004, Abbott 2011) over greater distances (Marquez et al. 2019). Thus, occupying only wide geographic range large-bodied species can ensure enough resources to sustain viable populations and avoid synchronizing dynamics caused by their high dispersal. At the same time, large geographic ranges sizes are commonly associated with habitat-generalist strategies and wider environmental niches (Slatyer et al. 2013, Cardillo et al. 2019) being less sensitive to climate-synchronizing drivers and occupying habitats with different environmental conditions (Loreau and de Mazancourt 2008, Pandit et al. 2016) where populations can fluctuate independently.

Meanwhile, small species have lower energetic constraints being viable in both small and large geographic ranges. However, be smaller brings alternative challenges, especially to those species with a small range that are more sensitive to catastrophic events (Gaston 1994b, Sodhi et al. 2008, Cardillo et al. 2008, Lee and Jetz 2011) and tend to have ecological traits related to high population synchrony (i.e. specialist-habitat strategies and restricted environmental niche; (Liebhold et al. 2004, Slatyer et al. 2013, Cardillo et al. 2019). To counter these adverse conditions, small-bodied species with smaller ranges are more abundant to reduce the probability of local extinctions (Gaston 1994b, Gaston and Blackburn 1996a), and through lower dispersal capacities and short life histories diminish the rates and scale of spatial synchrony (Liebhold et al. 2004, Marquez et al. 2019). Small-bodied species with large geographic range are the most viable species (i.e. the furthest from the vulnerability limit) as they tend to present lower energetic constraints (Kleiber 1975, Brown and Maurer 1987, 1989) and reduced spatial synchrony due to their wide niche and large ranges (Liebhold et al. 2004, Slatyer et al. 2013, Cardillo et al. 2019).

Finally, because species' geographic range and body size are continuous instead of binary variables (small/large), the distribution of a gradient of combinations of range and body with a greater or lower degree of viability are distributed across the bivariate space

outlining a triangular envelope and settling the minimal geographic range needed to fulfill in the long term their energy demands and meet the demographic requirements (i.e the MVR limit, Fig 1).

The different patterns (i.e. linear and segmented) that we found across biogeographic realms suggest that the evolutionary history of areas have favored certain combinations of species' range and body sizes. Climate instability of temperate regions has been commonly proposed to select against small geographic ranges and body size via intraannual variability and extreme colds, as invoked in Rapoport's (Stevens 1989) and Bergmann's rules (Bergmann 1848) respectively. Besides, long-term climatically unstable areas have been found to harbor lower proportions of small-range species because their increased extinction under climate changes due to narrow climate niches and poor dispersal capability (Dynesius and Jansson 2000, Sandel et al. 2011). Along with climate-driven extinctions, the earliest human activities have also affected fundamental macroecological patterns. In mammals, for example, the shape of the range–body size relationship has changed over time as a result of human-driven extinctions promoting the body size downgrading during the late Quaternary (Smith et al. 2019). These human transformations have mainly affected species with the smallest and largest body size (Smith et al. 2019). Thus, the current and historical climate instability together with human activities over the late Quaternary may be related to the low proportion of fish species with small range and body size that generate the segmented pattern in temperate realms (i.e. Palearctic and Nearctic), while at in the Australian realm (and at a global scale), the linear patterns seem to be related the presence of species that inhabit tropical ecosystems that can maintain a large number or small ranged species in a reduced space (Hawkins and Diniz-Filho 2006).

Beyond the theoretical importance of our results, the validation of the lower limit of the range – body size relationship also has important applied implications, as this limit can be used to address the main challenges faced today by IUCN in the red listing of species (see (Bachman et al. 2019) for more details in red listing challenges). Through the initiative Barometer of life (Stuart et al. 2010), the IUCN is increasing the number of assessed species to understand the conservation status of global biodiversity and provide a solid basis for informing conservation decisions. The goal by the end of 2020 is to assess at least 160,000 species and even this colossal effort will only represent 8 % of all known species (CoL 2019). As IUCN continues expanding the species coverage of extinction risk assessments, it is possible to use the lower limit of the range – body size relationship as a “low-data approach”

to rapidly identify vulnerable species (i.e. species below the MVR limit) across un-assessed and data-deficient taxa, creating a first global assessment of the conservation status of species. Additionally, the lower vulnerability limit of the range – body size relationship can be used to update and monitor changes in the vulnerability of their species. As vulnerability assessments of species become outdated after 10 years under IUCN rules, it is important to keep the species conservation status updated to better address national and global environmental legislation, identification species and sites for conservation investment (Rondinini et al. 2014), and actions to mitigate species threats (Butchart et al. 2010). The monitoring of species conservation status allows measuring our progress in tackling the biodiversity crisis (Pereira and Cooper 2006, Butchart et al. 2010) and better understand the changes in the vulnerability of species under human stressors (e.g. Carvajal-Quintero et al. 2017).

Our validation of the lower bound of the range - body size relationship is based on freshwater fish data. However, the triangular shape of this macroecological relationship and the presence of the linear and segmented lower bounds have been widely documented across multiple vertebrate taxa (e.g. Agosta and Bernardo 2013, Inostroza-Michael et al. 2018, Newsome et al. 2020), therefore, we believe that our findings can be extrapolated to other taxonomic groups (at least vertebrates). This could be corroborated using the using BioTIME (Dornelas et al. 2018) an extensive database of biodiversity time series covering different taxonomic groups.

In conclusion, our results validate the lower limit of range –body size relationship as an approach to evaluate the MVR needed for long-term species persistence. This MVR limit is determined by different physiological and ecological factors that constrain the use of the geographic space and the spatial dynamic of populations according to the combination of range and body size of species. The shape of the lower limit can vary according to the evolutionary history of the study areas that have selected certain combinations of species range and body sizes. The lower limit of the species range –body size relationship can be used for different conservation purposes, such as to identify vulnerable species (i.e. species close or beyond the lower limit), and track changes in the vulnerability of species due to the impacts of the current environmental change.

Supporting information



Figure S1. Map with the occurrences of time series that we used.

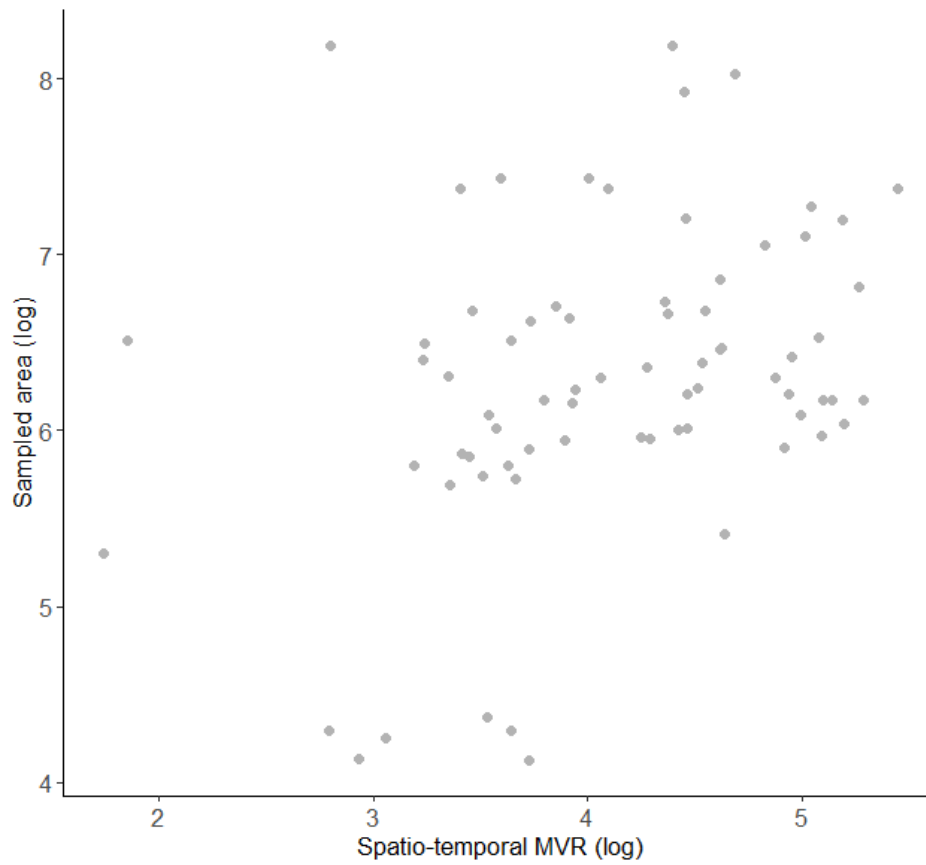


Figure S2. Scatterplot showing no relation between the spatio-temporal MVR and the sampling area across the studied species.

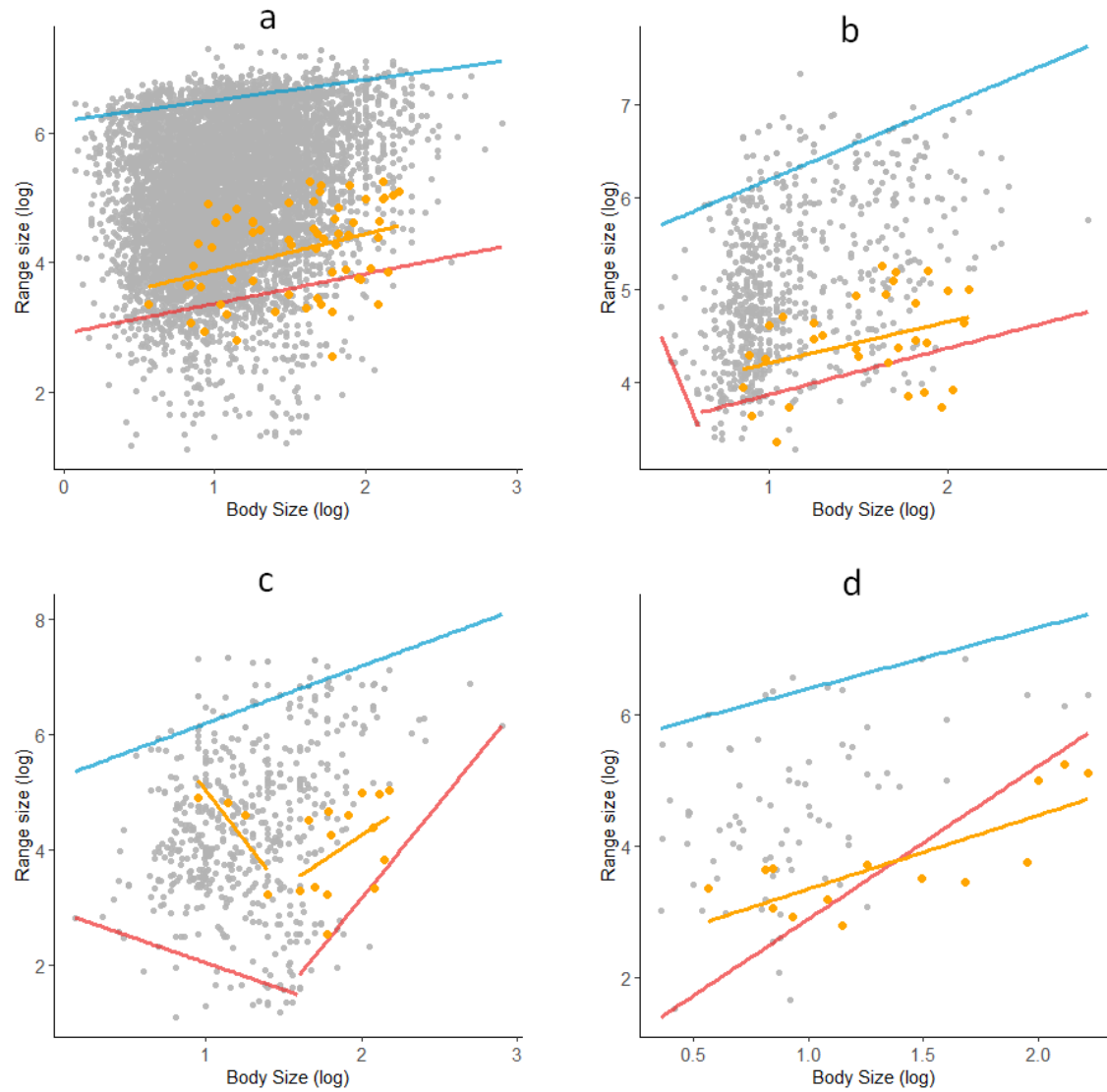


Figure S3. Representation of the empirical range-body size relationship at different spatial scales. The red line represents the regression of the 5% quantile and the empirical MVRS settled by the macroecological relationship. The blue line represents the regression of the 95% quantile. Orange line and dots represent the Theoretical MVRS described by the relationship regional scale of synchrony and body size. (a) Global scale, (b) Nearctic, (c) Palearctic, and (d) Australian.

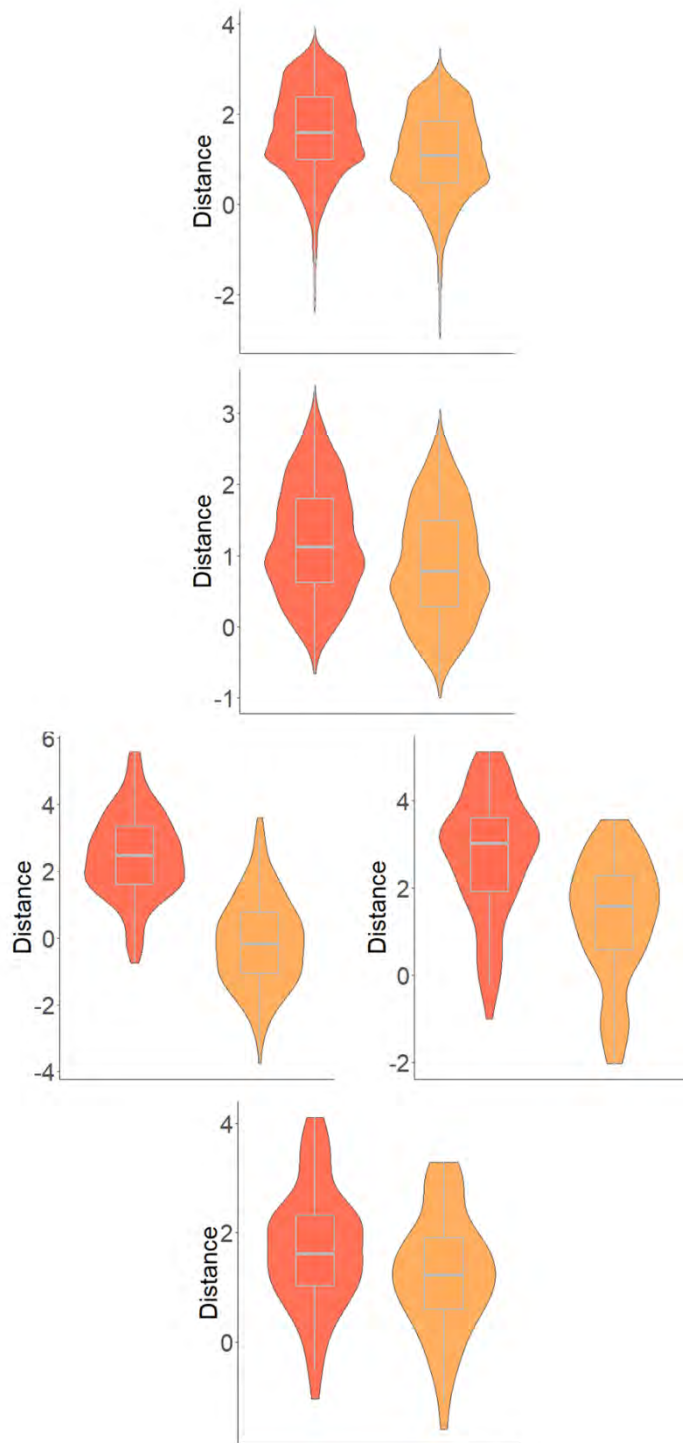


Figure S4. Distance of species respect to macroecological MVR (red, quantile 0.05) and spatio-temporal MVR (orange). The boxes represent the median, the first quartile and the third quartile of the distances, and violin plots represent sideways density plots. From top to bottom: Global scale, Nearctic, Palearctic and Australian. The two box plots for the Palearctic region represent the two portions of the quantile-segmented regression

Table S1. R packages used in this study.

Methods section	R packages	Reference
Species' body size	rfishbase (version 2.1.2)	Boettiger et al. 2019
Freshwater-species Filter	rfishbase (version 2.1.2)	Boettiger et al. 2019
Spline correlograms	ncf (version 1.2-9)	Bjornstad 2019
Quantile regressions	quantreg	Koenker et al. 2019

Table S2. Result of the quantile and quantiles segmented regressions fitted to represent the macroecological limits.

	Quantile	Value	t value	p	Goodness of fit	
Global	0.10	0.40259	15.58693	< 0.000001	0.37069851	
	0.05	0.46257	4.88686	< 0.000001	0.31114404	

	Quantile	Value	t value	p	Goodness of fit	Segment
Nearctic	0.10	-4.67749	-3.40676	0.00468	0.3296705	1
	0.05	-4.67749	-3.22824	0.00660	0.4778336	
	0.10	0.78786	4.91744	< 0.000001	0.6132081	2
	0.05	0.50543	4.31184	0.00002	0.4959111	

	Quantile	Value	t value	p	Goodness of fit	Segment
Palearctic	0.10	-0.95154	-2.37616	0.01795	0.15668515	1
	0.05	-0.93593	-3.71531	0.00023	0.14686891	
	0.10	2.86538	2.53001	0.01265	0.11221277	2
	0.05	3.32765	2.16596	0.01221	0.13595863	

	Quantile	Value	t value	p	Goodness of fit	
Australian	0.10	2.48890	2.83201	0.00590	0.15892946	
	0.05	2.32392	2.24824	0.02742	0.2041558	

Table S3. Results of the linear models relating the 100 values predicted by the macroecological and spatio-temporal limits.

	Quantile	Estimate	t value	p	R ²
Global	0.10	2.32028	56.43	<2e-16	0.969
Neartic segment 2	0.10	5.7249	84.57	<2e-16	0.986
Paleartic segment 1	0.10	0.2673	89.64	<2e-16	0.992
Paleartic segment 2	0.10	1.850	91.57	<2e-16	0.993
Australian	0.10	6.3394	56.42	<2e-16	0.968

Table S4. Results of the linear models contrasting the species distance respect to the macroecological and spatio-temporal limits. Models with $p < 0.05$ but a low effect size ($R^2 < 0.1$) were not considered significative.

	Quantile	Estimate	t value	p	R^2
Global	0.10	-0.10774	-6.8	1.089e-11	0.002972
	0.05	-0.33121	-7.007	4.222e-12	0.04164
Nearctic segment 2	0.10	-0.09694	-2.068	0.06891	0.00295
	0.05	-0.33121	-7.007	4.222e-12	0.04251
Palearctic segment 1	0.10	-2.00879	-16.86	$< 2.2e-16$	0.3699
	0.05	-2.58049	-21.65	$< 2.2e-16$	0.492
Palearctic segment 2	0.10	-0.9233	-5.129	6.00e-07	0.09878
	0.05	-1.4456	-8.027	4.465e-14	0.2083
Australian	0.10	-0.08967	-0.470	0.639	0.001697
	0.05	-0.4644	-2.449	0.01566	0.0441

Table S5. Results of the regression fitted to represent the spatio-temporal limits.

	Estimate	t value	p	R ²
Global	0.5697	2.932	0.004759	0.1707
Neartic segment 2	0.4476	1.985	0.005663	0.1697
Paleartic segment 1	-3.501	-2.151	0.0644	0.6982
Paleartic segment 2	1.7988	1.695	0.0116	0.1931
Australian	1.1219	4.225	0.00118	0.598

CHAPTER 4 – Damming Fragments Species' Ranges and Heightens Extinction Risk



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Abstract

Tropical rivers are experiencing an unprecedented boom in dam construction. Despite rapid dam expansion, knowledge about the ecology of tropical rivers and the implications of existing and planned dams on freshwater dependent species remains limited. Here, we evaluate fragmentation of fish species' ranges, considering current and planned dams of the Magdalena River basin, Colombia. We quantify the relationship between species' range and body sizes and use a vulnerability limit set by this relationship to explore the influence that fragmentation of species' ranges has on extinction risk. We find that both existing and planned dams fragment most fish species' ranges, splitting them into more vulnerable populations. Importantly, we find that migratory species, and those that support fisheries, are most affected by fragmentation. Our results highlight the dramatic impact that dams can have on freshwater fishes and offer insights into species' extinction risk for data-limited regions.

Introduction

Nearly two-thirds of the world's largest rivers were fragmented by dams at the start of this century (Nilsson et al. 2005), and the remaining proportion of free-flowing rivers are rapidly declining (Finer and Jenkins 2012, Zarfl et al. 2015, Winemiller et al. 2016). Despite diverse impacts from dams on freshwater ecosystems, tropical and subtropical regions of South America, Africa, and Asia are experiencing booms in dam construction due to growing human population, economic development, and demand for low-carbon energy sources (Kareiva 2012, Finer and Jenkins 2012, Zarfl et al. 2015). At the same time, our understanding about the consequences of dams on species' extinction risk remains limited. Numerous studies have focused on impacts to species' diversity post dam construction (Poff et al. 2007), but approaches are needed that quantify potential consequences of new dams prior to their implementation. Such approaches could be particularly useful in regions where dam expansion is imminent (Kareiva 2012, Zarfl et al. 2015, Winemiller et al. 2016), and where biological information for species remains limited (Meyer et al. 2015).

Expanding fundamental macroecological relationships between species' range and body sizes (primarily documented in terrestrial vertebrates to date) could help us to better understand the potential impacts that dams can have on the vulnerability of freshwater-dependent species. The range-body size relationship commonly forms an approximate triangular shape (Gaston and Blackburn 1996a); the spatial extent of the study area sets the upper limit of the triangle, and forms the upper limit of species' range size (Figure 1). The slope of the lower bound of this relationship forms because smaller species have a variety of range sizes, but larger-bodied species only have relatively large range sizes. Across assemblages, the minimum range size required for a given species, based on body size, generates a "probabilistic" vulnerability limit in bivariate space (Figure 1), whereby any species that is near or beyond this limit is prone to extinction or has a low probability of persistence through time (Gaston and Blackburn 1996a). In this way, the triangular constraint space formed between range and body size could change as species' range size changes. Such changes could occur because of natural processes or because of dams or other human-induced factors that influence habitat loss or fragmentation. Indeed, changes

in range size have quite consistently been shown to be a strong predictor of extinction risk (Di Marco et al. 2015).

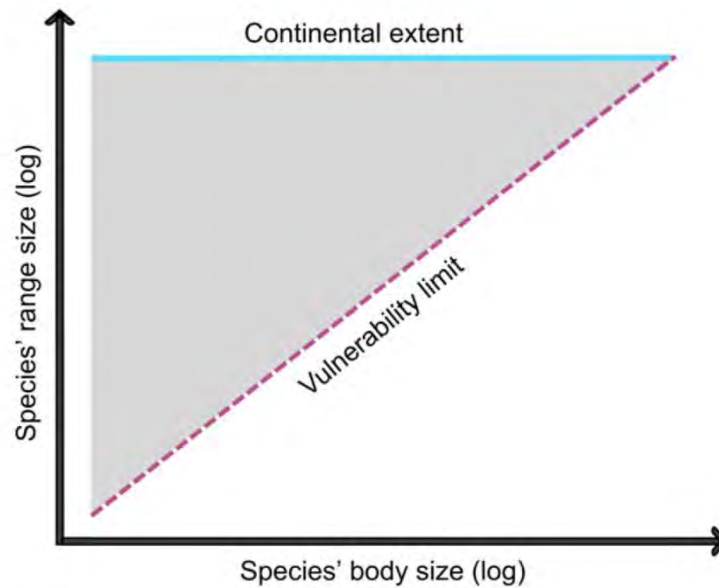


Figure 1. Representation of the theoretical constraint envelope described by the interspecific functional relationship between species' body size and geographical range size (modified from (Brown and Maurer 1987)). Note that small-bodied species show both small and large range size (high variance), whereas large-bodied species show only large range size (low variance). The solid line indicates the absolute space constraint, whereas the dashed line (referred to here as a vulnerability limit) is commonly associated with a minimum viable population size that is necessary for species' persistence. Based on the vulnerability limit, larger-bodied species are highly sensitive to fragmentation, because they require large range sizes for their persistence (i.e., to maintain sustainable population sizes), and so too are smaller-bodied species with restricted range sizes.

From a conservation perspective, the lower boundary of the range-body size relationship is an important feature because it has been shown to represent a lower limit of range size (from here “vulnerability limit”) below which species have heightened extinction risk (Figure 1; (Brown and Maurer 1989, Gaston and Blackburn 1996a)). Furthermore, to our knowledge, the range-body size relationship has not yet been used to quantify potential effects of anthropogenic fragmentation on species' extinction risk. With this in mind, we draw on the range-body size relationship to evaluate fragmentation caused by current (fully

constructed and under construction) and current + planned dams (under consideration or proposed) on the range sizes of 179 freshwater fish species in the Magdalena River basin. We further evaluate whether range-size fragmentation, and subsequent reduction in range size results in species shifting closer to the vulnerability limit, and subsequent extinction risk. For both current and current + planned damming, we summarize species' extinction risk at two scales: (1) within fragments of species' natural ranges, which we consider the "population" level and (2) across all fragments created within a species' natural range, which we considered the species level. Finally, we evaluate whether fragmentation from both current and current + planned damming differentially affects certain ecological traits or human-dependency factors.

Methods

Study area, species' ranges, and dam occurrences

We compiled a comprehensive data set of fish species' occurrence records for the Magdalena River basin, Colombia. The Magdalena River is the main fluvial ecosystem of northwest South America (1,540 km long; 7,100 m³/s discharge), and is a major source of hydropower (Jiménez-Segura et al. 2016) and economic development in Colombia (Galvis and Mojica 2007, Barletta et al. 2015).

Our data set included occurrence records from 1940 to 2014, with 11,571 occurrence records for 204 fish species (Supporting Information: Dataset). We represented range size for each fish species as the extent of occurrence *sensu* International Union for Conservation of Nature (IUCN 2016). Range size was represented as the area (kilometer²) falling within the convex hull formed around each species' occurrence records in the Magdalena River basin (Supporting Information: Methods and Figure S1). Species with less than three occurrence records were excluded from our analyses (25 species, see Supporting Information: Dataset), and all subsequent analyses were undertaken for 179 fish species. We further checked the distribution of each species based on an updated freshwater fish checklist that is in progress for Colombia (Maldonado-Ocampo et al. 2005) and the Colombian fisheries catalog (Lasso et al. 2011). This additional step allowed us to corroborate the narrow distribution of species with a small number of records (<10),

certifying that these were rare and locally endemic species. Importantly, given the intensification of human induced changes to the land- and waterscapes of the Magdalena River basin over the last several decades, it is possible that our range size estimates are conservative.

The geographic location and construction status of large impassable dams (>20 MW hydropower capacity) either those known to occur, or planned for, the Magdalena River basin were obtained from Lehner et al. (Lehner et al. 2011), Opperman et al. (Opperman et al. 2015), and The Nature Conservancy (TNC, unpublished data). We focused our assessment on these large dams because they have been shown to prohibit fish species' dispersal (e.g., (Pelicice and Agostinho 2008, Winemiller et al. 2016). Our assessment included a total of 29 current (fully constructed and under construction) and 29 planned (under consideration or proposed) dams, respectively.

Ecological traits and human-dependency attributes

We collected information on maximum body length (millimeters) for each of the 179 fish species from FishBase (Froese and Pauly 2016) and published literature (Supporting Information). When different sources provided different values, we used the largest body size, and used maximum body length as a measure of body size. We collected additional information about each fish species ecological characteristics and human dependences, including: (1) species' endemism to the Magdalena River basin, (2) species' demographic strategy, (3) species' functional group and (4) whether a species is used as resource, commercially or for subsistence, including migratory species (Table S1).

Data analyses

We used quantile regression (with “quantreg” package; Koenker 2015) in R statistical software (R Core Team 2013) to determine the relationship between species' natural range and body sizes, and to define the lower (0.05 quantile) and upper boundaries (0.95 quantile) of the relationship (Scharf et al. 1998). Two statistical analyses were implemented to verify that the relationship between species' natural range and body sizes is actually triangular, testing for a significant slope parameter of the lower boundary. First, we fitted linear quantile mixed models (LQMMs; using “lm4” package; (Bates et al. 2015)) considering quantiles 0.05 and 0.95 with genus, family and order as random factors to account for the

taxonomic relatedness of species. Second, we quantified the significance of the lower boundary (0.05 quantile) with a randomization test procedure where body size values were permuted 4,999 times resulting in a null distribution of slope values.

After determining the relationship between range and body size, and respective thresholds, we determined those species that either did or did not fall below the upper limit of the 95% confidence interval of the lower boundary (as defined by the 0.05 quantile). Scharf et al. (Scharf et al. 1998) demonstrated that quantile regression produces robust estimates, and that the 0.05 quantile produces a similar, but more conservative, estimate than the 0.10 quantile, which is also frequently used. For all subsequent analyses, we considered this limit to be the vulnerability limit, as suggested by Le Feuvre et al. (Le Feuvre et al. 2016).

To determine fragmentation of species' ranges by current and current + planned dams, we overlaid each species' geographic range (i.e., the range we considered to be their natural range) with the fragments resulting from the subdivision of the whole drainage basin by both current and planned dams (Figures S1 and S2). Fragmentation from planned dams was accounted for by including all current and all planned dams. The intersection of species' natural geographic ranges with the fragmented drainage basin resulted in multiple occupied fragments, and subsequently, these fragmented ranges were assumed to be independent populations because of dam size and the impossibility of dispersal between dams. These fragmented ranges combined with the vulnerability limit, as defined by species' natural ranges, resulted in a binary output of populations that we considered to either have heightened extinction risk (i.e., with ranges occurring below the vulnerability limit defined by species' natural range-body size relationship) or not. This "lower boundary rule", applied to each of the 179 species, produced (1) a mean value of the fragmented geographic range and (2) a proportion of endangered "populations" for each species, respectively.

To determine the relative importance and effect of the ecological and human-dependency attributes, we fitted generalized linear mixed models (GLMMs) with "binomial" distribution errors to the two extinction risk measures using "lm4" package (Bates et al. 2015). We ran models for all possible combinations of the explanatory

variables and then performed model averaging based on the “Akaike Information Criterion” (AIC). As a cut-off criterion to delineate a “top model set” providing average parameter estimates, we used models with $\Delta AICc < 2$ (Grueber et al. 2011). As with the LQMMs, we included genus, family and order as random factors in the GLMMs to account for the taxonomic relatedness of species and to avoid pseudoreplication.

Results

At the species level, the triangular relationship, based on species natural range and body sizes was stronger than could be predicted by chance ($P = 0.0042$; Figure 2A). The LQMM accounting for the taxonomic relatedness of species also revealed a significant positive slope for the lower bound of the relationship between range and body sizes ($P = 0.01$). Based on natural range and body sizes, 11% (~20) of species in the Magdalena River basin have intrinsically heightened extinction risk (Figure 2A).

Current dams subdivide the Magdalena River basin into 30 fragments (~8,700 km²/fragment on average; Figure S2). Consequently, fish species’ natural ranges are split into multiple smaller disconnected fragments. We found that, on average, species’ natural ranges in the Magdalena River basin are currently split into nine (± 8) fragments by large dams. On average, each species currently has 60% ($\pm 21\%$) of their fragmented populations falling below the vulnerability limit based on the range-body size relationship. Put another way, based on current damming, at least 74% (132) of fish species in the Magdalena River basin have at least half of their fragmented populations falling below the vulnerability limit (Figure 2B).

Looking to the future, the potential doubling of current dams through planned dams (for a total of 58 large dams) would again double the number of fragments (i.e., 59 fragments) dividing the Magdalena River basin, and decrease average fragment size (~4,400 km²/fragment on average; Figure S2). Subsequently, planned dams would greatly increase the average number of fragmented populations (29 ± 18.7) per fish species, and result in 79% (141) of fish species having at least half of their fragmented populations falling below the vulnerability limit (Figure 2C, Supporting Information: Dataset). On

average, across the 179 fish species, 64% ($\pm 20\%$) of the fragmented populations are projected to fall below the vulnerability limit if all planned dams are implemented along the Magdalena River.

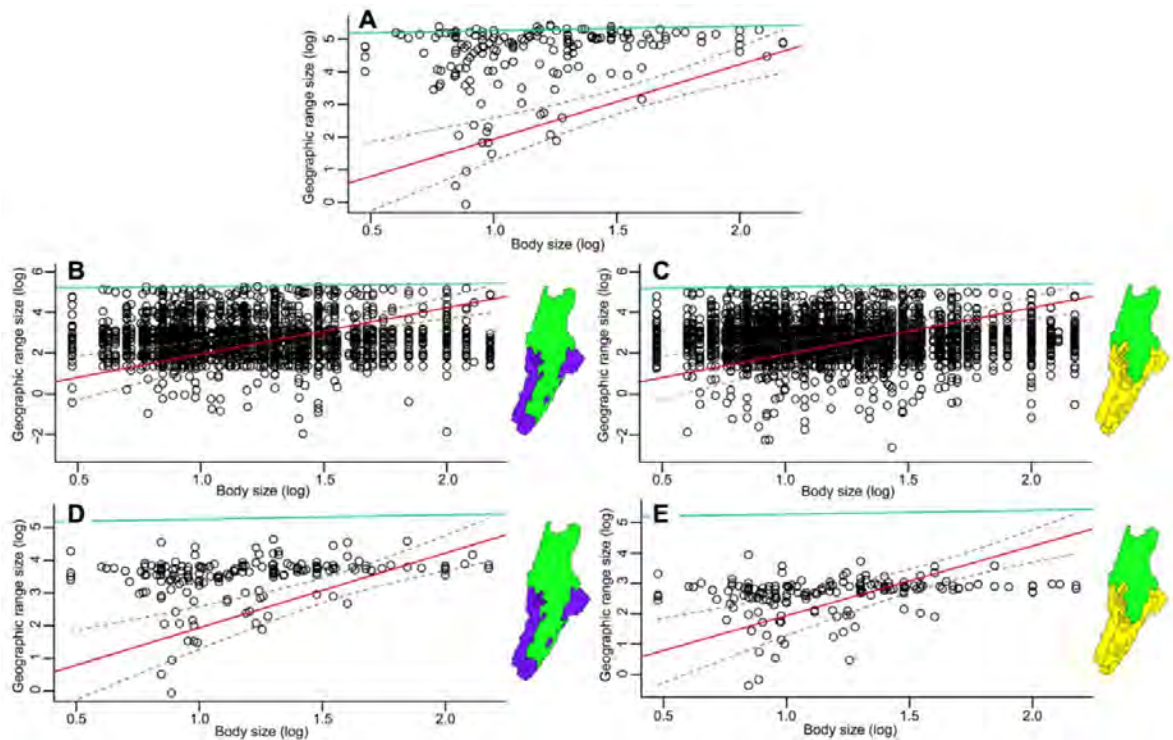


Figure 2. Range and body size relationship for 179 freshwater fish species of the Magdalena River basin. The blue solid line represents the regression of the 95th quantile. The red solid line represents the regression of the 5th quantile, and the dashed lines the 95% confidence intervals. The upper confidence interval (the red line) represents the species' vulnerability limit, built from the natural scenario (without fragmentation; A). For each of the 179 species, range size is shown for each fragmented population caused by damming (current [B] and current + planned [C]), and the species-level range size, which is the mean range size of all species' fragmented populations (current [D] and current + planned [E]). On the right side of each plot is a map to illustrate the scenario of fragmentation evaluated.

We also found that both current and planned damming heightens extinction risk at the species level (where each new species-level fragmented range size is the average size of their “populations”). Current damming reduces the range size for the majority of species (92%) and increases the percentage of species that fall below the vulnerability limit by 11% (Figure 2D). Similarly, we found that construction of planned dams in addition to current

dams would further heighten extinction risk at the species level; all 179 fish species would have reduced range size and 41% of fish species would shift below the vulnerability limit (Figure 2E). Regardless of the damming scenario considered, we found that the proportion of species falling below the vulnerability limit increased as fragment size decreased (Figure 3).

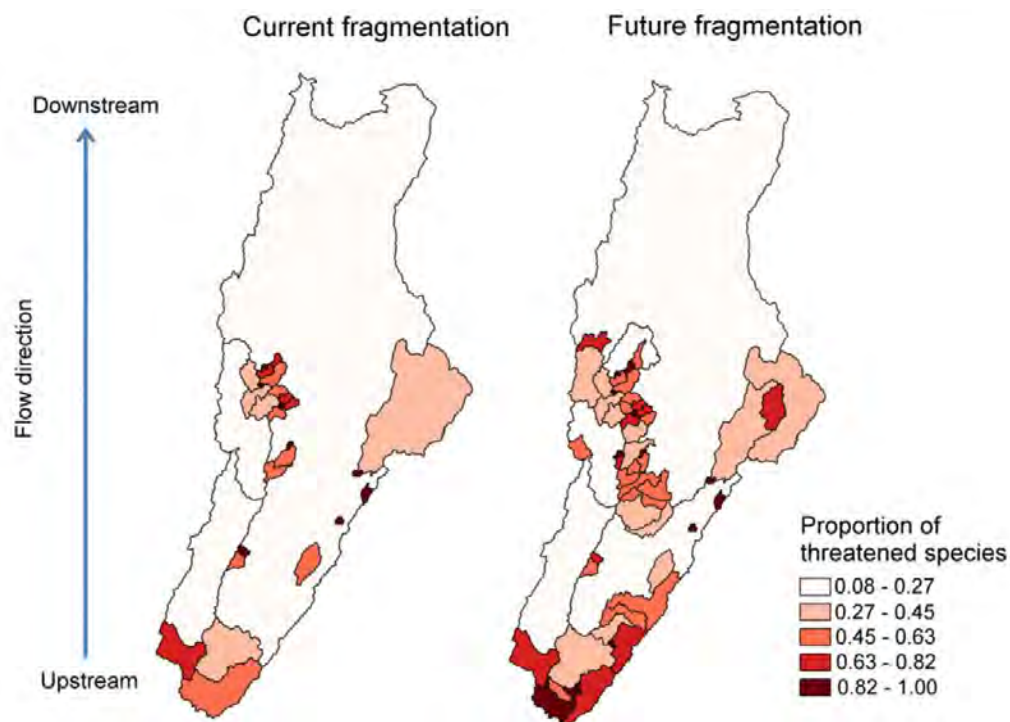


Figure 3. The Magdalena River basin with fragments based on current (left) and planned (right) dams. The shade of each fragment reflects the proportion of threatened species based on their body size, fragment size, and the vulnerability limit as defined by the relationship between species’ ranges and body sizes.

We found that under natural conditions, endemic and “opportunistic” species have heightened extinction risk (Figure 4), and endemic species are significantly closer to the vulnerability limit than others (Table S2). At the population level, we found no particular species trait or human-dependency factor to be more affected by current and planned dams than another (Table S3). However, we found that regardless of ecological traits or human dependency factors, fragmentation of species’ ranges caused by both current and planned dams increases the percentages of species falling below the vulnerability limit (Figure 4).

We also found a notable and significant increase in extinction risk for both migratory species and known fisheries species (Figure 4; Table S2) when considering both current and current and planned dams, respectively.

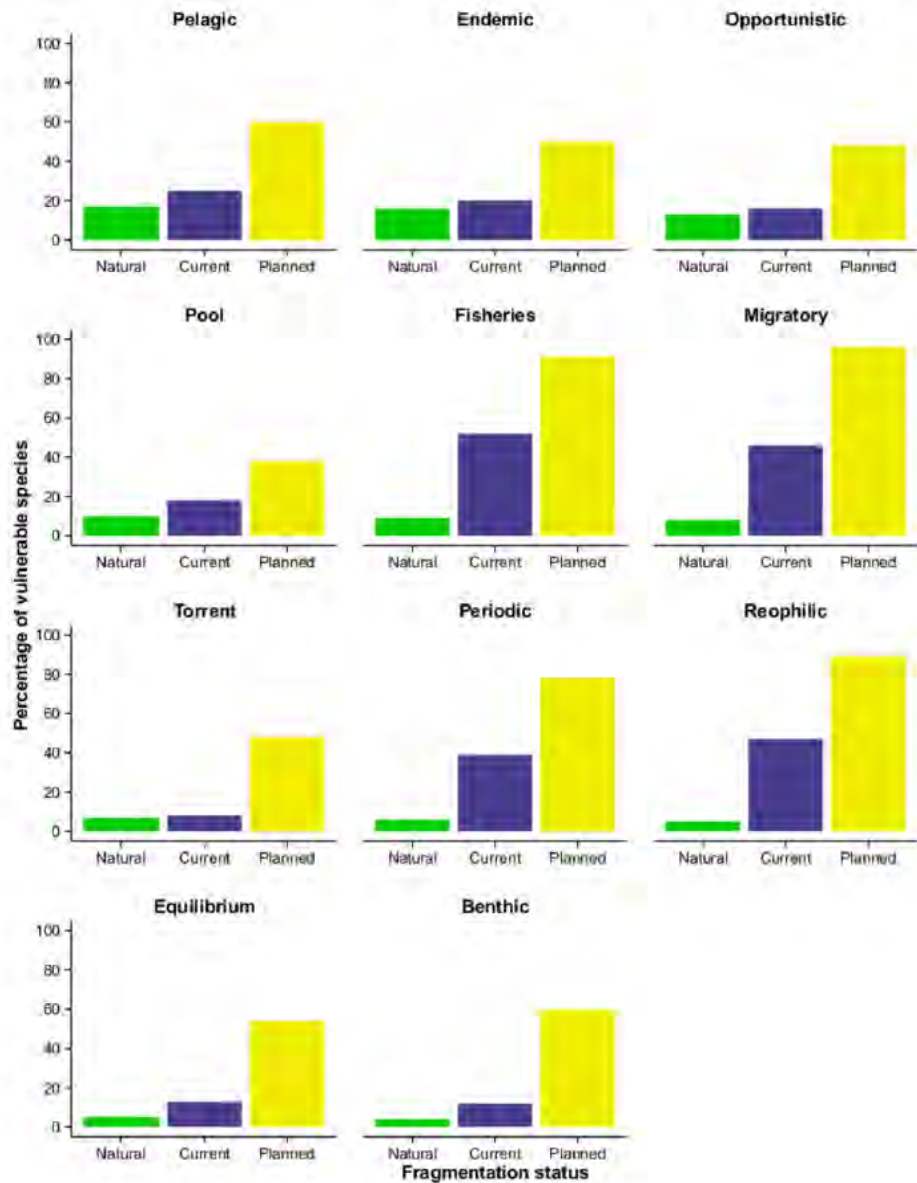


Figure 4. Percentage of vulnerable species for each trait and each scenario of fragmentation evaluated.

Discussion

Drawing on the macroecological relationship between fish species' range and body sizes, we determined the extent to which current and planned dams fragment fish species' ranges, and the effect that this fragmentation has on species' extinction risk. Our findings solidify the sensitivity of freshwater-dependent species to fragmentation caused by damming (Fagan 2002).

We found that fish species endemic to the Magdalena River basin are inherently under heightened extinction risk compared to non-endemic species. We also found that current and planned damming increases the percentage of vulnerable species regardless of the ecological traits considered. Our findings suggest widespread impacts from current damming are likely to have already occurred in the Magdalena River basin. Indeed, under current damming, there is an 11% increase in fish species with heightened extinction risk compared to natural conditions.

The range-body size relationship used in our analyses is particularly relevant for overcoming data limitations that are often faced when making decisions about species' extinction risk (Lasso et al. 2011, Bland et al. 2012). Around the world, diverse criteria are used to evaluate species' extinction risk, and many assessments, such as those undertaken by the IUCN, are based on changes in range size. By quantifying the impact of current and potential human disturbances on species' range sizes, our approach offers a quantitative approach that complements ongoing efforts to evaluate freshwater species' extinction risk (Carrizo et al. 2013), and our analyses could be applied to other regions to improve our understanding about species' extinction risk now and in future. In addition, systematic data on current and future land use, roads or low-head dams were unfortunately not available for our analyses, but such data could be explicitly integrated into future studies. Using these additional data, our approach could also be used to quantify how different human disturbances influence species' extinction risk based on reductions in range size over time. An additional refinement to our approach could include the explicit consideration of species' habitat preferences to reduce any overestimation of fragmentation impacts on species.

Ultimately, species extinction depends on remaining fragment size (Morita and Yamamoto 2002), the minimum viable population of each species supported (Fagan 2002), and potentially, other interacting human disturbances that we were unable to account for here. Depending on the generation time of a species, documenting losses caused by range fragmentation can take years to decades (Tilman et al. 1994). However, loss of individual populations, and localized extinctions, could be more frequent than the extinction of an entire species depending on fragment size, the potential for dispersal between fragments, and suitability of remaining habitat (Fagan 2002). Our analyses could be used proactively to identify populations and species with heightened extinction risk because of fragmentation and losses in range size, and to identify those populations in greatest need of conservation action to avoid imminent losses. Several studies have explored species traits and found that smaller body sizes, migratory behavior, limited ranges, and specialized habitats often explain freshwater fish extinction risk (e.g., (Angermeier 1995, Reynolds et al. 2005). We found that both migratory fish species and species of fisheries importance are particularly affected by fragmentation from current dams, and will be more greatly affected if planned dams are implemented along the Magdalena River. In tropical river fisheries, like those of the Magdalena River, migratory species are highly valued by local fishers (Orr et al. 2012, Winemiller et al. 2016). Indeed, the Magdalena River fishery is the most productive in Colombia, and has been increasingly depleted over the last three decades (Galvis and Mojica 2007, Barletta et al. 2015). There remains limited understanding, and general lack of quantitative data, to pinpoint the primary causes of fishery decline in the Magdalena River basin (Barletta et al. 2015), but our analyses suggest that damming could be a major contributing factor by disconnecting fish populations. Furthermore, our findings highlight that if all dams that are currently planned for the Magdalena River are implemented, fragmentation of species' ranges will increase, further fragmenting fishery species' ranges, and heightening extinction risk.

Our findings support recent calls for more informed and systematic approaches to assessing dam expansion feasibility at basin scales (Winemiller et al. 2016, Lees et al. 2016), and our analyses begin to address this need, offering a repeatable method to quantify the impacts of current and expanding dams on biodiversity. While our results offer important insights about freshwater dependent fish species' extinction risk, outputs from

our assessment could also be integrated into more formal optimization analyses like those presented by Ziv et al. (Ziv et al. 2012). Outputs from our own, or other similar analyses, could be used to generate scenarios that explore both the allocation and potential removal of individual or groups of dams to minimize fish species' extinction risk while ensuring benefits returned from hydropower. Indeed, integrating our methods and findings within a decision theory framework could reduce regional scale impacts from fragmentation caused by damming to ensure retention of large enough range sizes to support species persistence.

Acknowledgments

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Supporting Information

Methods

We compiled a comprehensive dataset of fish species' occurrence records maintained by the seven main fish collections of Colombia (Universities: Javeriana, Antioquia, Tolima, Católica de Oriente; and the Institutes: Alexander von Humboldt, Instituto de Ciencias Naturales, and Instituto para el Patrimonio Natural y Cultural del Valle del Cauca). This dataset was complemented with occurrences from the Colombian Biodiversity Information System (<http://data.sibcolombia.net>) and published literature (see reference list below). We followed species taxonomy presented in Fishbase (Froese & Pauly 2015).

Tributary drainage areas used to determine species range area were obtained from a modeled hydrologic network based on the EarthEnv-DEM90 digital elevation model (Robinson et al. 2014). We verified the accuracy of the modeled hydrologic network with existing hydrologic maps of Colombia (IGAC, the Colombian Geographic Institute). All analyses were carried out in ArcGIS 10.3.

List of references used to complement the species occurrence dataset:

(Ardila-Rodriguez 2009)

(Castellanos-Morales 2008)

(Castellanos-Morales 2010)

(Román-Valencia 2000)

(García-Alzate and Román-Valencia 2008)

(Ortíz-Muñoz and Alvarez-León 2008)

(Román-Valencia and Arcilla-Mesa 2009)

(Román-Valencia and Arcila-Mesa 2010)

(Román-Valencia et al. 2008)

(Taphorn et al. 2013)

(Torres-Mejia et al. 2012)

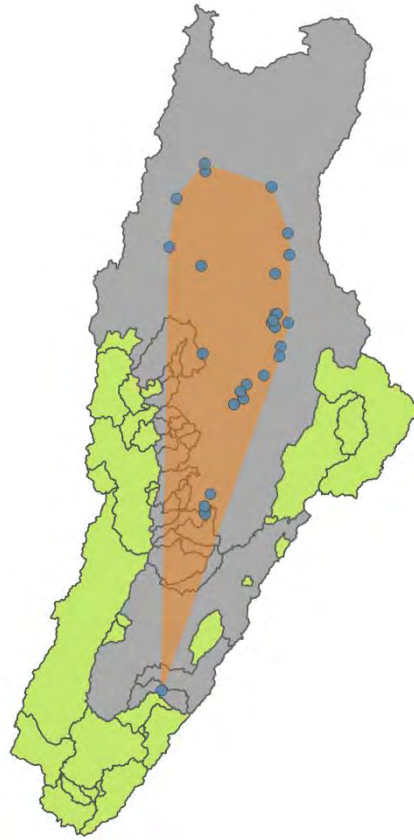


Figure S1 The Magdalena River basin showing an example of species' distribution records (blue dots), the fragments created by current and planned dams (gray and green polygons) and the convex hull formed by the most external species records (orange polygon). Gray polygons are those fragments where the species is considered to be present. The orange polygon represent the area that we measured (in km²) to obtain the natural geographic range size of a given species. The intersection between orange polygon and each gray polygon represent the areas measured to obtain the fragmented geographic range size of a given species (*Pseudoplatystoma magadaleniatum* [Buitrago-Suárez & Burr 2007] in this example).

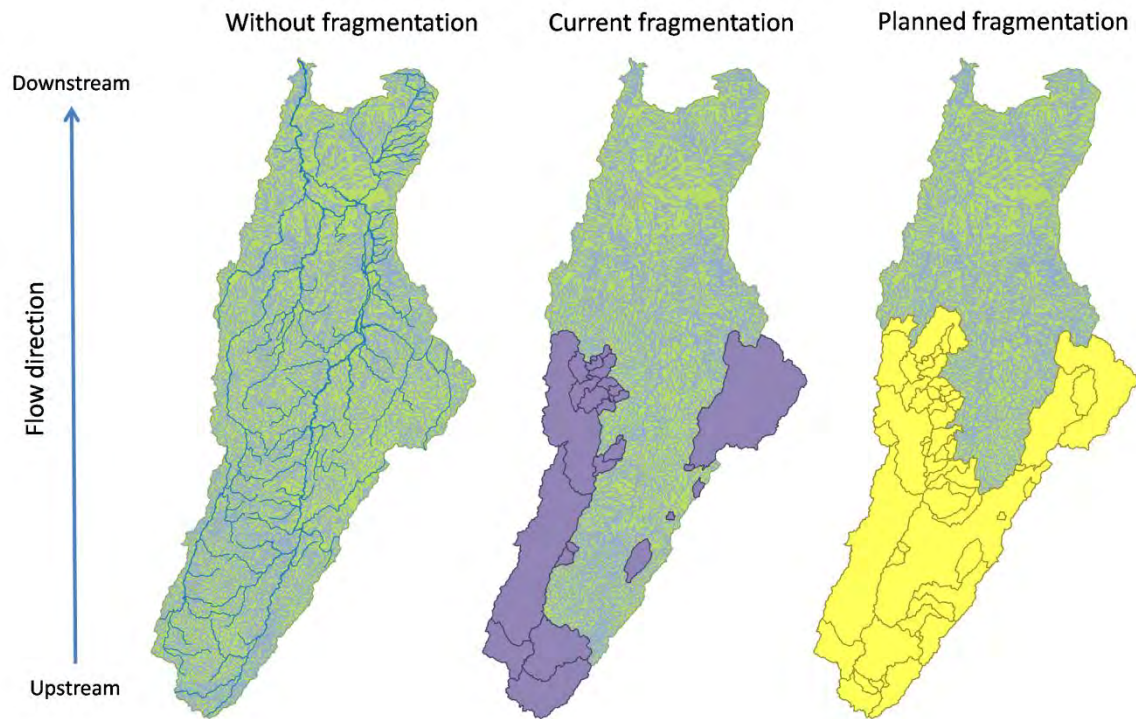


Figure S2 Maps of three different fragmentation scenarios evaluated for the Magdalena River basin: a natural scenario without human-induced fragmentation (left), a current fragmentation scenario based on current dams (center), and a future fragmentation scenario based on both current and planned dams (right). The main channel of the watershed is represented with the dark blue line (in the left scenario) and tributaries are depicted with clear blue lines.

Table S1 Summary of the methodology and the bibliography used to determine different ecological traits and human-dependency attributes.

Biological trait or human-related attribute	Meaning	Data source
Endemic species	Endemic species of the Magdalena Basin.	(Maldonado-Ocampo et al. 2005)
Migratory species	Species that present migrations.	(Lucas and Baras 2001, Carolsfeld et al. 2003)
Functional group	Classification is based on body shape, habitat use, morphological and/or behavioral adaptations, and it separates species into five groups: torrent, pool, pelagic, rheophilic, and non-torrent benthic.	(Carvajal-Quintero et al. 2015) [†]
Life history strategy	Life strategies based in the trade-offs among different demographic traits (reproduction, growth and survival): Equilibrium, Periodic, Opportunistic (Winemiller and Rose 1992).	(Carvajal-Quintero and Maldonado-Ocampo 2014) ^{*†}
Fisheries resources	Species that represent commercial and subsistence fisheries resources within the Magdalena basin.	(Lasso et al. 2011)

* Information based on expert knowledge.

† For species with no available information, we used information from species within the same genus.

Table S2 Final most parsimonious generalized linear mixed models (GLMMs) with binomial distribution errors at the species level for natural, current fragmentation caused by damming, and current + planned fragmentation caused by damming. Model parsimony was determined using the AIC value.

Natural scenario			
Variable	Estimate	z value	p value
Endemic species	1.4109	0.5916	0.0171
Current fragmentation			
Variable	Estimate	z value	p value
Migratory species and fishery resources	1.7030	3.296	0.0009
Endemic species	0.5836	0.4540	0.2025
Current + planned fragmentation			
Variable	Estimate	z value	p value
Migratory species and fishery resources	2.6681	3.073	0.0021
Functional group - Pelagic	-0.0391	0.048	0.9614
Functional group - Pool	-0.9146	1.144	0.2527
Functional group -Reophilic	21.4711	0.029	0.9765
Functional group - Torrent	-0.4643	0.620	0.5352
Endemic species	0.2390	0.635	0.5254

Table S3 Final most parsimonious generalized linear mixed models (GLMMs) with binomial distribution errors at the population level for current and current + planned fragmentation. Model parsimony was determined using the AIC value.

Current fragmentation			
Variable	Estimate	z value	p value
Endemic species	0.5830	1.782	0.0747
Migratory species and fishery resources	0.3968	0.898	0.3694
Current + planned fragmentation			
Variable	Estimate	z value	p value
Endemic species	0.3736	1.108	0.2680
Migratory species and fishery resources	-0.2723	0.694	0.4877
Life history - Opportunistic	-0.1681	0.416	0.6773
Life history - Periodic	-0.7191	1.456	0.1455

CHAPTER 5 – RivFishTIME: A global database of fish time-series to study global change ecology in riverine systems



Photo by Jorge García-Melo (Project CaVfish Colombia)

Manuscript submitted to Global Ecology and Biogeography

Abstract

Motivation: We compiled a global database of long-term riverine fish surveys from 46 regional and national monitoring programs as well as individual academic research efforts upon which numerous basic and applied questions in ecology and global change research can be explored. Such spatially- and temporally-extensive datasets have been lacking for freshwater systems compared to terrestrial ones.

Main types of variables contained: The database includes 11,441 time-series of riverine fish community catch data, including 649,703 species-specific abundance records together with metadata related to geographic location and sampling methodology of each time-series.

Spatial location and grain: The database contains 11,125 unique sampling locations (stream reach), spanning 21 countries, 5 biogeographic realms, and 402 hydrographic basins worldwide.

Time period and grain: The database encompasses the period 1951–2019. Each time-series is composed of a minimum of two yearly surveys (mean = 8 years) and represents a minimum time span of 10 years (mean = 19 years).

Major taxa and level of measurement: The database includes 949 species of ray-finned fishes (Class Actinopterygii).

Software format: .csv

Main conclusion: Our collective effort provides the most comprehensive long-term community database of riverine fishes to date. This unique database should interest ecologists who seek to understand the impacts of human activities on riverine fish biodiversity, and model and predict how fish communities will respond to future environmental change. Together, we hope it will promote advances in macroecological research in the freshwater realm.

Introduction

Increasing awareness of the ongoing biodiversity crisis has motivated global initiatives to compile large-scale datasets of population and community abundance records that have been consistently sampled through recent times (Pereira and Cooper 2006). Included among these are the Global Population Dynamics Database (Inchausti and Halley 2001), the Living Planet Index database (Loh et al. 2005), and more recently, the BioTIME database (Dornelas et al. 2018). These databases have proven extremely useful and allowed major advancements in ecological research (e.g. Kendall et al. 1998, Sibly et al. 2005, Butchart et al. 2010, Dornelas et al. 2014); however, they remain highly biased towards terrestrial and marine assemblages (e.g. only 0.50% of the records concern riverine fishes in BioTIME, the most recent of these initiatives). This is unfortunate as effective strategic plans for conserving water resources that support human well-being and ecosystem integrity rely on access to comprehensive, pertinent, quantitative information regarding the status and trends of riverine biodiversity over regional to continental scales (Tickner et al. 2020).

Long-term studies of riverine species are limited because they require highly specialized and time-consuming sampling methods. Furthermore, rivers in remote areas are often difficult to access (Olden et al. 2010, Radinger et al. 2019). Nevertheless, over the past decades, large-scale policies have been enacted in response to the rapid degradation of freshwater resources, such as the Water Framework Directive in the EU (adopted in 2000, Hering et al. 2004) and the Clean Water Act in the USA (passed by US congress in 1972, Paulsen et al. 2008), which require countries to monitor and evaluate the biological integrity of surface waters through time to adopt quality standards that restore and maintain ecological integrity (Kuehne et al. 2017). Beyond these official national and regional monitoring programs, the temporal dynamics of riverine systems and their fish communities have also been assessed through various independent, though often local in extent, academic research programs (e.g. Gido 2017, Matthews and Marsh-Matthews 2017b). All of these institutional and academic monitoring efforts have produced considerable freshwater fish temporal data that remain largely inaccessible to the broader scientific community due to the inherent difficulty in gathering and harmonizing field data from disparate institutions and sampling protocols (Buss et al. 2014).

To fill this important gap, we here present RivFishTIME, a compiled and curated database of long-term (≥ 10 years) surveys of riverine fish communities at a fine spatial (stream reach) and taxonomic (species) resolution, using data mining approaches to

harmonize existing but currently fragmented biomonitoring data sets. Riverine fish are extremely diverse in spite of the small surface they inhabit on Earth: they represent about 40% of all known fish species while occupying <1% of available aquatic habitat (“the freshwater fish paradox” *sensu* (Lévêque et al. 2008, Tedesco et al. 2017)). However, they are also among the most threatened taxonomic groups on Earth because of the convergence between the high concentration of biodiversity and the many pressures resulting from human uses of freshwater resources and habitat change (Reid et al. 2019, Tickner et al. 2020). The RivFishTIME database provides a unique opportunity to understand the rate, magnitude, and geography of biodiversity trends, and to identify opportunities to mitigate human impacts on riverine systems (Pereira and Cooper 2006, Anderson 2018). Due to the paucity of spatially- and temporally-extensive datasets in freshwater compared to terrestrial systems (Heino 2011), RivFishTIME should also help ecologists close the gap between these two systems and to address a wider range of taxa in unraveling large-scale spatio- temporal biodiversity patterns.

Methods

Data acquisition

We gathered time-series of fish community abundance data for riverine (lotic) ecosystems, broadly defined as freshwater bodies that are continually or intermittently flowing. We tried to the extent possible to exclude wetlands and brackish habitats (salinity > 0.5 ‰). Note, however, that due to the complex nature of the datasets, we do not guarantee that sites are located on free-flowing river segments (i.e. natural condition without impoundment, diversion, or other modification of the waterway). We used the following criteria for data inclusion: (1) the location of the sampling sites is known and consistent through time, (2) the sampling protocol is known and consistent through time, (3) the sampling survey sought to quantify all species in the fish community according to well-established protocols, (4) species-specific abundances are available for each survey, (5) surveys at a given site were conducted over a period of at least 10 years, and (6) at least two yearly surveys with non-null abundance are available. We considered abundance measures derived from direct fish counts, catch-effort indexes such as relative abundances (%) and catch per unit effort (CPUE), abundance classes, as well as statistically estimated abundances (e.g. Leslie method; (Ricker 1975)).

To identify potential datasets, we used Google Search, Google Scholar and Dataset Search with different combinations of the keywords “time series”, “fish”, “abundance”, “stream”, “river”, “freshwater”, “community”, “temporal”, and “monitoring” or “monitoring program”. We screened the scientific as well as the grey literature to identify studies involving temporal datasets of fish communities and conducted similar searches in data repositories such as Dryad (<https://datadryad.org/stash>) and FigShare (<https://figshare.com/>). We also conducted targeted searches for national and regional monitoring programs by adding country names to the previous keywords. For the European Union, we further used the EuMon database as a reference to identify fish monitoring databases (available at http://eumon.ckff.si/about_daeumon.php).

We contacted all the authors and monitoring program coordinators to request and obtain permission to publish the data and/or ensure that the license under which the data were publicly released allowed their inclusion in our global effort (e.g. Open Government License, CC0 1.0 Universal). We excluded the datasets for which we did not receive permission, unless the reusability of data was clearly stated on the online repositories where the data were released.

Quality control

Taxonomy. We validated species scientific names using the online database Fishbase (Froese and Pauly 2019). We used the R package rfishbase (as of December 2019; (Boettiger et al. 2012) and confirmed names with no match manually using the Catalog of Fishes (Fricke et al. 2018). We then selected only records involving ray-finned fishes (Class Actinopterygii), excluding rays and lampreys, and unidentified species.

Coordinates. We harmonized the coordinate system by projecting (if necessary) the coordinates of the individual datasets using the World Geodetic System (WGS84) as reference geographic coordinate system. We visually inspected the spatial distribution of the sites with respect to their respective country, region, or state borders as given in the original data sources and discarded sites with dubious coordinates (e.g. sites located in the ocean). We also removed sites whose coordinates were located outside of any hydrographic basin using the global major river basin GIS layer in HydroSHEDS (Lehner et al. 2008).

Consistent sampling methods. We excluded surveys lacking information on sampling methods and selected only time-series collected using a consistent sampling protocol through time. The latter evaluation was dataset-specific as dictated by the complexity of the monitoring scheme

and the available metadata. For instance, surveys were deemed consistent if they did not experience any major deviation in sampling protocol, and disregarded minor variations (e.g. number of anodes or traps, area sampled) due to survey-specific constraints (e.g. water depth, habitat complexity). By contrast, several monitoring programs implemented alternate sampling protocols to compare the efficiency of different gears (e.g. seining versus electrofishing) or sampling methods (e.g. continuous versus point electrofishing); these time-series conducted at the same sites but using different sampling protocols were kept separate in the database.

Duplicates. We removed duplicates within individual datasets based on the coordinates of the sites, date of the survey, and species collected (e.g. due to different name attribution for the same site). We also identified potential duplicates among datasets (e.g. overlap between state-level and national databases) based on the coordinates of the sites rounded to three digits to account for different post-processing of the individual datasets.

Database formatting

Each entry (species abundance record) was assigned a unique (1) site, (2) survey, and (3) time-series identifier. The site ID corresponds to a given pair of coordinates, the survey ID to a sampling campaign, and the time-series ID to a combination of site $\times$ sampling protocol. Additionally, each site ID was assigned to a biogeographic realm (Olson et al., 2001) and hydrographic basin (HydroSheds; Lehner et al., 2008) based on its coordinates. For each sampling ID, we aggregated abundance records if they were given separately for individuals, size classes or sub-species for each validated species name or if different sampling passes, hauls, or sub-sampling areas were considered. We also converted time-series species abundances to densities or CPUE whenever possible. The different surveys were kept independent when conducted on different occasions within the same calendar year. We provided the year together with the quarter of the survey (1: January-March; 2: April-June; 3: July-September, 4: October-December). We also provided the associated unit (abundance class, count, CPUE, individuals/100m², Leslie index, relative abundance) for each species abundance record. Finally, we extracted basic information regarding the sampling protocol, including details on electrofishing (backpack, shore-based or boat mounted electrofishers), netting (dip nets, gill nets, beach or pelagic seines), trapping (minnow traps, fyke nets or hoop nets), snorkeling, and trawling techniques. Many survey protocols involve a combination of sampling approaches; therefore, we encourage the data user to refer to each data source for more information on the sampling methods.

The database is organized in three tables (.csv format): the time-series table, the survey table, and the information source table. The tables can be linked using the unique dataset source ID and time-series ID. The time-series table contains: (1) source ID, (2) site ID, (3) time-series ID, (4) primary sampling method, (5) secondary sampling method, (6) latitude (WGS 84), (7) longitude (WGS 84), (8) hydrographic basin, and (9) biogeographic realm. The survey table contains: (1) time-series ID, (2) survey ID, (3) sampling year, (4) sampling quarter, (5) species scientific name, (6) abundance, and (7) abundance unit. The information source table contains the full citation(s), online link to the raw data when publicly available, as well as the name(s) and contact of the data responsible(s) for each individual dataset. A list of the data sources is found in Appendix 1; for further information consult the metadata. Data curation was performed in the R (3.6.0) programming environment (R Core Team 2019).

Results

Our database includes 11,441 time-series of riverine fish compiled from 46 individual source datasets, representing a total of 107,464 surveys and 649,703 individual species abundance records at 11,125 unique sites. Survey-specific species richness across all time-series ranges from 1 to 50 species, and covers 949 ray-finned fish species. The surveyed sites display a wide distribution along longitudinal and latitudinal gradients, spanning 21 countries, 402 hydrographic basins, and 5 biogeographic realms (Fig. 1a). Despite broad geographical coverage, we note a clear spatial bias towards the Palearctic (European Union) and, to a lesser extent, Nearctic (North America) and Australasia realms. The abundance time-series are largely represented by individual counts, followed by densities (individuals/100m²) and CPUE (Fig. 1b). Abundance classes, Leslie index and relative abundance represent < 1% of the time-series. Electrofishing is by far the main sampling technique used to record the time-series, although variations are noticeable among biogeographic realms (Fig. 1c). For instance, snorkeling and dipnetting sampling techniques are only represented in the Neotropics, whereas gillnetting is the most common gear in the Afrotropics.

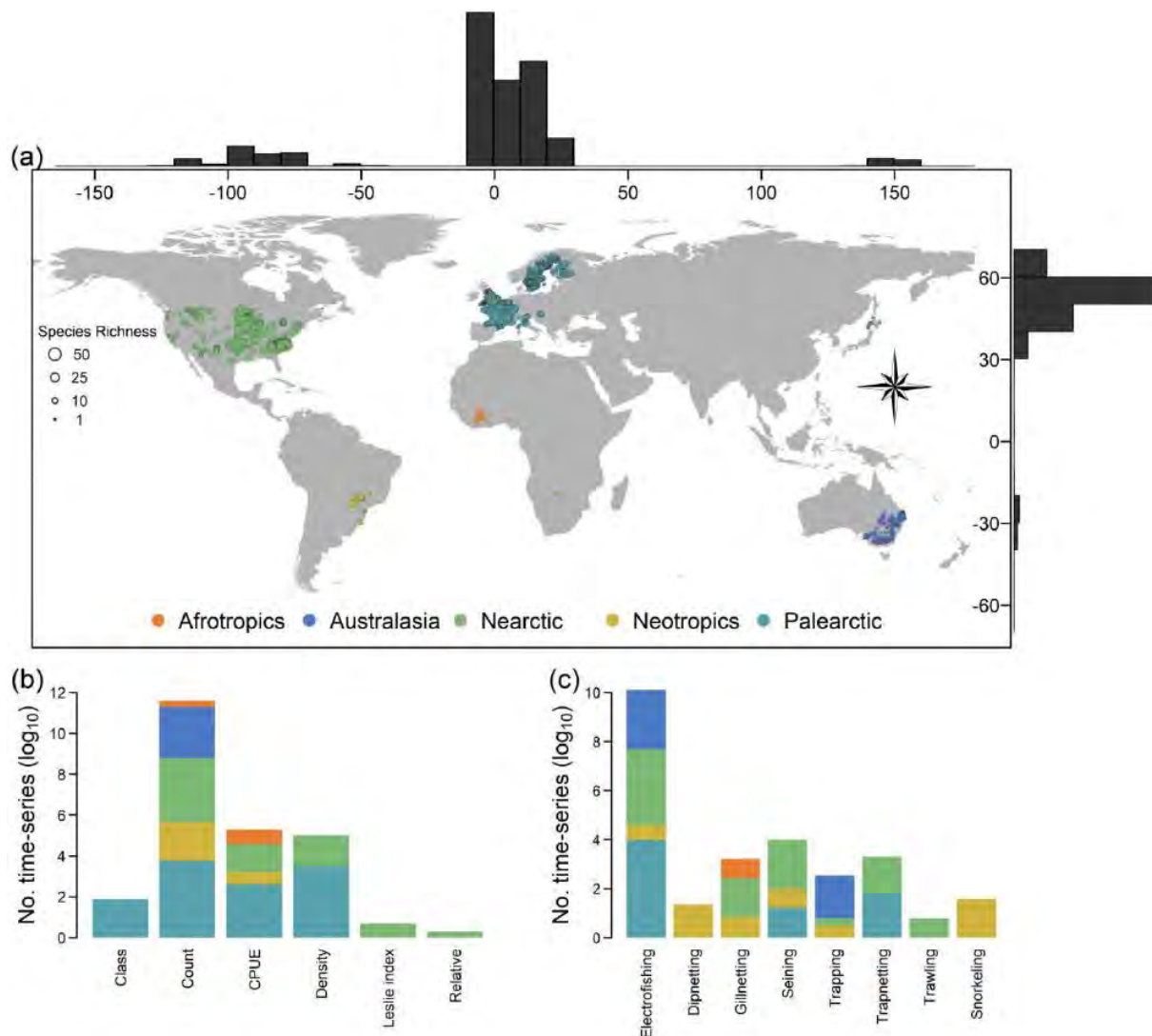


Figure 1. (a) Map showing the distribution of the time-series where each time-series is represented by a dot with colors indicating the biogeographic realm and size representing fish species richness (averaged across surveys). Inset histograms display the distribution of the time-series according to latitude and longitude. Barplots show the distribution of the time-series with respect to the (b) type of abundance, and (c) primary sampling method. Note the $\log_{10}(x+1)$ y-axes in (b)-(c).

The time-series cover a time period from 1951 to 2019 and are mainly concentrated over the last two decades (average first year = 1996; Fig. 2a). Surveys have been conducted primarily in the 3rd (July-September) and 4th (October-December) quarters of the year, especially in the Palearctic and Nearctic realms (corresponding to periods of low flows), but all quarters are represented in the different biogeographic realms (Fig. 2b). The mean time span of the time-series is of 19 years and ranges from 10 to 68 years, with the longest time-series located in the Palearctic (Fig. 2c). The sites were sampled from (non-necessarily

consecutive) 2 to 52 years, with an average number of yearly surveys of 8 years (Fig 2d). Again, the highest number of yearly surveys was found in the Palearctic. The completeness of the time-series (i.e. ratio of number of yearly surveys to the overall time span) ranges from 4 to 100%, with a mean value of 45% (Figure 2e). Importantly, the degree of completeness is largely uncorrelated to the time span of the time-series ($r = 0.05$).

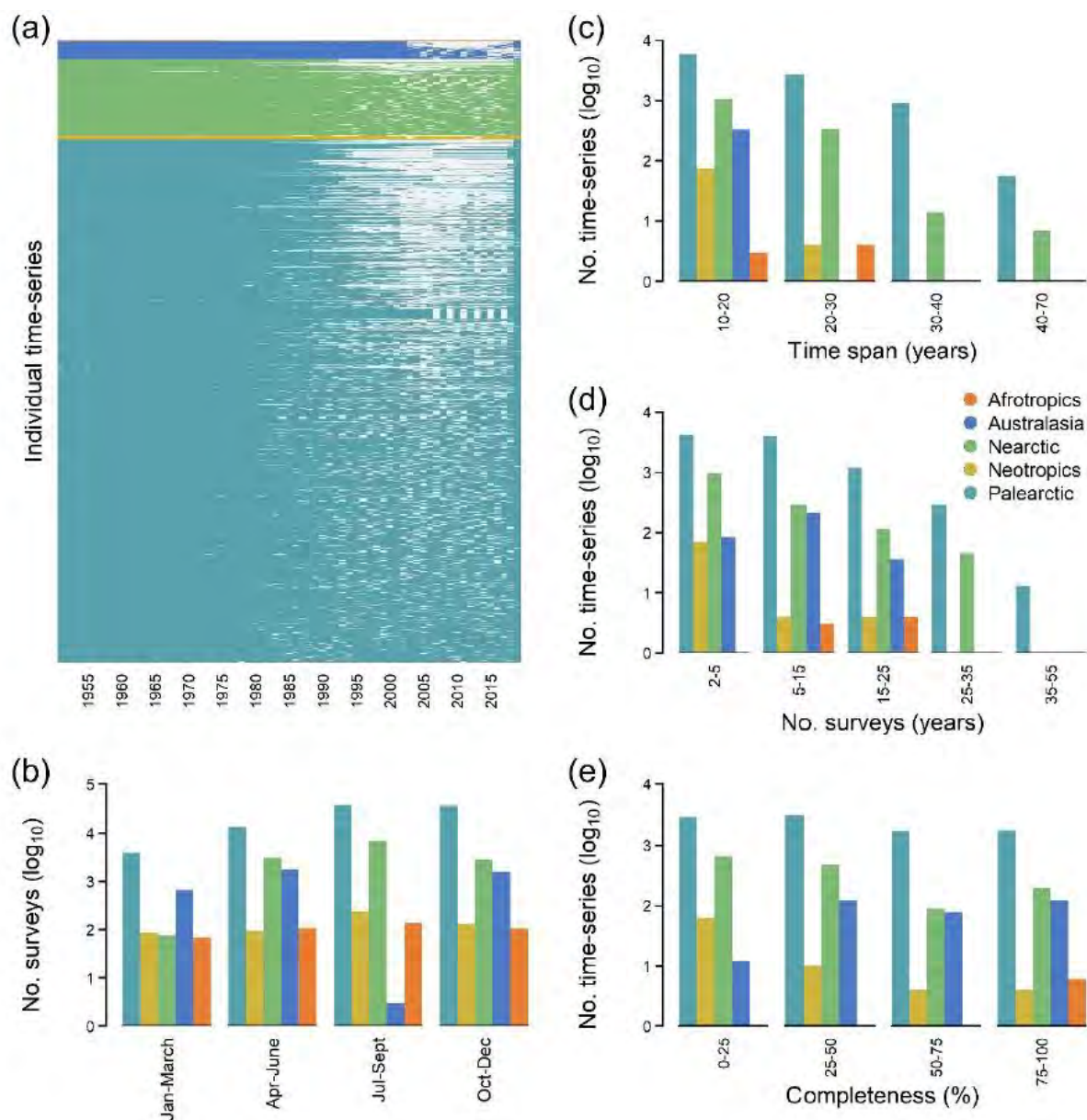


Figure 2. (a) Temporal distribution of the yearly surveys relative to the period covered by the database (1951-2019). Each time-series appears in rows where the background colors correspond to the biogeographical realms and white indicates sampled years. (b) Temporal distribution of the surveys with respect to the quarter of the year. Temporal characteristics of the time-series with respect to the (c) overall time span, (d) number of yearly surveys, and (e) completeness defined as the ratio between the number of yearly surveys and the overall time span (expressed in %). Note the $\log_{10}(x+1)$ y-axes in (b)-(e).

Conclusions

Our collective effort provides the most comprehensive long-term community database of riverine fishes to date, spanning large biogeographic, climatic and hydrographic gradients. Almost all biogeographic realms are represented but it is important to note that our database is not exempt from spatial bias. For instance, less than 1% of the time-series belong to the Afrotropic or Neotropic realms, whereas 84% belong to the Palearctic realm. These spatial gaps often present in biodiversity-rich regions (tropical areas, southeast Asia) are likely to mirror the current networks of freshwater monitoring programs (Buss et al. 2014, Radinger et al. 2019) as well as biodiversity research efforts (Martin et al. 2012), and hence will be prioritized in future updates of RivFishTIME. We also warn data users that species abundance may not be directly comparable across sites without a full understanding of the specifics of sampling approach and effort, with respect to their selectivity and efficiency (Goffaux et al. 2005, Portt et al. 2006, Benejam et al. 2012, Oliveira et al. 2014), and refer to the original data sources for more information about the sampling protocols. Despite these unavoidable limitations associated with secondary datasets collected for multiple purposes, we are convinced that this unique database will stimulate new research in the fields of global change ecology and macroecology in the freshwater realm. We provide a static version of the database with this article (1951-2019), but we aim to continue interacting with data contributors to update and add new time-series datasets to be released through the iDiv portal (<https://idata.idiv.de/idiv/Content/Databases>) and the more specialized Freshwater Biodiversity Data Portal (<https://data.freshwaterbiodiversity.eu/>). This unique database provides the needed baseline information for conservation and restoration efforts.

Supporting information

Appendix 1 - Data sources

SourceID	Citations	URLaccess
1	((Agència Catalana de l'Aigua 2003, 2010, 2018))	http://aca-web.gencat.cat/
2	((Casatti et al. 2009, Zeni et al. 2017))	—
3	(Universidad de Antioquia-Empresas Publicas de Medellin 2019)	—
4	(Erős et al. 2014)	—
5	(Gammon 2003)	—
6	(Ecosystem Health Monitoring Program Queensland 2019)	https://hlw.org.au/report-card/
7	(Finnish electrofishing register Hertta 2019)	https://www.wp2.ymparisto.fi/koekalastus_sahko/yhteinen/Login.aspx?ReturnUrl=%2fkoekalastus_sahko
8	(Sigouin 2017)	https://open.canada.ca/data/en/dataset/fe2441a6-8ae4-4884-b181-cd7ec53bd842
9	(Whitney et al. 2016)	—
10	(Gido et al. 2013, 2019)	—
11	(Kesner and Marsh 2010)	https://www.rosemonteis.us/documents/kesner-marsh-2010
12	(Griffith 2017, Griffith et al. 2018)	https://doi.org/10.23719/1376690
13	(Occhi, V. T. & Vitule, J. R. S. Unpublished data)	—
14	(Terui et al. 2018)	—
15	(Iowa DNR [Department of Natural Resources] 2013)	https://data.iowa.gov/Environment/BioNet/e7yf-f5fs
16	(Milardi et al. 2020)	—
17	(Lévêque et al. 2003)	—

18	(Pyron et al. 1998)	—
19	(Gido 2017)	https://doi.org/10.6073/pasta/150e218b069074a8ecede85a7406d43f
20	(McLarney et al. 2013)	http://coweeta.uga.edu/dbpublic/personnel_bios.asp?id=wmclarney
21	(Long Term Resource Monitoring Program 2016)	https://www.umesc.usgs.gov/data_library/fisheries/fish1_query.shtml
22	(Matthews and Marsh-Matthews 2017a)	https://doi.org/10.5061/dryad.2435k
23	(Murray-Darling Basin Authority 2018)	https://data.gov.au/data/dataset/murray-darling-basin-fish-and-macroinvertebrate-survey
24	(Minnesota Pollution Control Agency 2018)	https://cf.pca.state.mn.us/water/watershedweb/wdip/search_more.cfm?datatype=assessments
25	(Montana, Fish, Wildlife & Parks 2019)	http://gis-mtftp.opendata.arcgis.com/items/8192e75218c6460ba97ba3dd0a2fb3a5
26	(U.S. Geological Survey 2019)	https://aquatic.biodata.usgs.gov/clearCriteria.action
27	(U.K. Environmental Agency 2019)	https://data.gov.uk/dataset/d129b21c-9e59-4913-91d2-82faef1862dd/nfpd-freshwater-fish-survey-relational-datasets
28	(North Carolina Department of Environmental Quality 2018)	https://deq.nc.gov/about/divisions/water-resources/water-resources-data/water-sciences-home-page/ecosystems-branch/fish-stream-assessment-program
29	(Fagundes et al. 2015)	—
30	(Winston et al. 1991, Taylor 2010)	https://onlinelibrary.wiley.com/doi/full/10.1111/fw.13211
31	(Ineelo Mosie and Kaelo Makati 2018)	https://www.gbif.org/dataset/77929c0a-7506-4b2d-a49d-10fc3312d50d
32	(Office français de la biodiversité 2019)	http://www.naiades.eaufrance.fr/acc-es-donnees#/hydrobiologie
33	(Oklahoma Water Resources Board 2019)	http://home-

		owrb.opendata.arcgis.com/search?tags=fish
34	(Agencia Vasca del Agua 2019)	http://www.uragentzia.euskadi.eus/informazioa/ubegi/u81-0003341/eu/
35	(Ortega et al. 2015)	—
36	(Davenport, S.R. Unpublished data)	—
37	(Dala-Corte et al. 2016)	—
38	(The Resh Lab 2019)	https://nature.berkeley.edu/reshlab/
39	(Toronto and Region Conservation Authority (TRCA) 2018)	https://data.trca.ca/dataset/2018-watershed-fish-community
40	(U.S. Fish and Wildlife Service 2017)	—
41	(Stefferd, J. A. Unpublished data)	—
42	(Sers 2013)	https://www.slu.se/en/departments/aquatic-resources1/databases1/database-for-testfishing-in-streams/
43	(Benejam et al. 2010, Merciai et al. 2017)	—
44	(Miyazono and Taylor 2015)	https://bioone.org/journals/The-Southwestern-Naturalist/volume-60/issue-1/MP-02.1/Long-term-changes-in-seasonal-fish-assemblage-dynamics-in-an/10.1894/MP-02.1.short
45	(Rinne and Miller 2006)	—
46	(Van Thuyne et al. 2013, Brosens et al. 2015)	https://ipt.inbo.be/resource?r=vis-inland-occurrences

CHAPTER 6 – General discussion and perspectives

The results of this thesis revealed that the most important drivers of the variation of geographic range size of freshwater fishes at global and biogeographical scales are the mean drainage network position of species and the historical connectivity between basins, highlighting the importance of current and historical hydrological connectivity in shaping fish distribution across fresh waters (Carvajal-Quintero et al. 2019, see chapter 2). These findings contrast with the ones reported for terrestrial ecosystems, where the main drivers of species range sizes are more related to climate and topography (Whitton et al. 2012a, Morueta-Holme et al. 2013, Li et al. 2016). Such contrasts raise the question of whether drivers of species range size variation varies among lineages of the tree of life. It is widely recognized that current macroecological patterns are not independent of the evolutionary history of lineages (e.g. Hernández et al. 2013). Indeed, lineage-specific drivers of macroecological patterns may arise because of unique ecological features developed throughout the evolutionary history of lineages. In addition to the specific drivers of range size that we found for freshwater fish, Sheth et al. (2020) recently proposed that mechanisms explaining the variation in range size among plant species may also be unique given their sessile nature, diversity of mating systems and ploidy levels, and prevalence of hybridization and sympatric speciation. This shows the importance of continuing to explore and contrast macroecological patterns across the tree of life and adds to recent calls asking to include less charismatic groups in macroecological studies to reach a more unifying theory (Shade et al. 2018, Phillips et al. 2019).

The challenge of understanding the whole picture of species geographic distributions goes beyond contrasting different hypotheses across the tree of life. Today, ecological and evolutionary research has recognized the need of shifting toward a re-emphasis on the complexity and interconnection of processes (Morueta-Holme and Svenning 2018, McGill 2019), integrating previously separated disciplines and accounting for multiple driving factors that interact and influence each other along and among scales (McGill 2010, Chase et al. 2018, Morueta-Holme and Svenning 2018, McGill et al. 2019, see chapter 1). This step towards evaluating more complex models is supported by our entry into the Big Data age that allows us to test hypotheses at unprecedented spatial, temporal, and phylogenetic scales (La Salle et al. 2016, Benedetti-Cecchi et al. 2018). As the assembly, storage, sharing and access to data continue growing, it is also important that we develop new models that merge data from

different environmental realms (freshwater, marine and terrestrial) and test new driving factors of species' geographic range size. For example, despite a long-standing theory [originating with Darwin (1859)] suggesting that biotic interactions set species range limits, this hypothesis has not been clearly tested (Louthan et al. 2015). Because interactions constrain the patterns of species occurrence (Tingley et al. 2014, Louthan et al. 2015), the spatial variation in the intensity of interactions may influence the size of species' geographic range. Species plasticity is another important driving factor to explore. Despite some previous studies failed to find strong support for a positive relationship between the phenotypic plasticity of species and their geographic range size (e.g. Sheth and Angert 2014, Hirst et al. 2017) future studies should evaluate the different facets of plasticity (genotypes, populations, species and clades) and consider only traits that contribute to environmental adaptability (Sheth et al. 2020).

As future avenues to continue advancing our understanding of species' geographic ranges size, specifically for freshwater fishes, we propose that it is first important to test, besides connectivity *per se*, the effects of other environmental factors associated to species' drainage network position (DNP). Along with the variation in the species DNP, there are indeed multiple correlated factors (e.g. temperature, dissolved oxygen, slope; see chapter 1 for more details). Partitioning and quantifying the effect of these factors would be valuable to achieve a more deterministic understanding of the geographic range size of freshwater fishes. It is also important to continue testing other hypotheses that have been widely recognized in terrestrial environments but poorly explored in fresh waters. For example, the abundance, niche breadth and/or niche position/ range size hypotheses have received strong support for terrestrial organisms (e.g. Slatyer et al. 2013, Sheth et al. 2020, Vela Diaz et al. 2020; and references therein. <https://doi.org/10.1111/geb.13139>). Our results show that the niche breadth hypothesis (i.e. species using different habitats would be more widespread) seems not to apply for riverine fishes, as species with larger ranges were restricted, in our dataset, to lowland habitats where climatic and habitat conditions are more spatially stable (see chapter 2). However, the niche position (i.e. species utilizing widespread habitats should be more widespread), as well as the abundance/range size hypotheses still need to be tested. Another unexplored topic is the role of macroevolutionary processes in shaping freshwater fish species' range size. Even if we evaluated the effect of diversification on freshwater fish ranges through a coarse and timeless proxy (i.e. the total number of species within each genus; chapter 2), there is still a whole field to explore using the emerging phylogenies of

bony fishes (e.g. Rabosky et al. 2018, Bourgeaud et al. 2019), for example, testing the influence of speciation and extinction rates for which have been found mixed effect in terrestrial environments (e.g. Cardillo et al. 2003, Castiglione et al. 2017). Other relevant features that could be evaluated using these newly available phylogenies are the dynamics and constraints of geographic range size at evolutionary time scales. The hypotheses that we evaluated in this thesis assume that the interspecific difference in range size is at ‘static equilibrium’. However, geographic range size is highly dynamic at an evolutionary time scale (Warren et al. 2014), and ‘equilibrium’ hypotheses cannot explain why intrinsic factors (see chapter 1 for details) do not continuously evolve constraining the evolutionary dynamics of range size (Mayr 1963, Sheth et al. 2020). Phylogenetic reconstruction methods that explicitly incorporate historical shifts of species’ geographic range (e.g. Rolland et al. 2018) are a promising way to disclose these evolutionary dynamics and identify the factors that affect them. Furthermore, understanding the evolutionary dynamics of species range sizes is of utmost importance in the study of global environmental changes allowing us to better understand the response of species under changing environmental conditions and identifying the potential pathways to extinction (Tanentzap et al. 2020).

The findings of this thesis also demonstrated that fragmentation of geographic ranges by dams drastically increases the extinction risk of species (see chapter 4). Fragmentation by dams represents one of the greatest threats to freshwater fish biodiversity (Nilsson et al. 2005, Reid et al. 2019, Albert et al. 2020) by impairing movements between spawning and feeding areas (Freeman et al. 2007, Juracek 2015) and splitting populations into smaller units that reduce fish abundances (Alò and Turner 2005, Ziv et al. 2012, Carvajal-Quintero et al. 2017). Currently, about two-thirds of the large rivers (>1,000 km) are fragmented by dams (Grill et al. 2019) and thousands of major and small hydropower plants are under construction, planned, or in consideration (Zarfl et al. 2015, Couto and Olden 2018). Today, this higher hydropower expansion rate is concentrated in tropical regions (Zarfl et al. 2015), representing a great threat to the high diversity supported for tropical fresh waters. For example, the basins of Mekong, Amazon and Congo support about one-third of the world’s freshwater fish species, much of them endemic, and about 1,300 large dams currently fragment or are planned to fragment the water courses of these three large rivers (Winemiller et al. 2016). In addition to biodiversity losses, the construction and operation of hydropower plants also carry social impacts on local human communities related to food and water availability (Richter et al. 2010, Orr et al. 2012), emissions of greenhouse gas (Gibson et al. 2017), deterioration in

water quality (Wei et al. 2009), changes in hydrology and sediment transport (Constantine et al. 2014), and spread of water-associated diseases and invasive species (Lerer and Scudder 1999, Johnson et al. 2008).

Several calls for reducing the multiple impacts of future dams have raised the need for basin-scale planning of hydropower development (e.g. [Kareiva 2012](#), [Ziv et al. 2012](#), [Opperman et al. 2015](#), [Winemiller et al. 2016](#), [Latrubesse et al. 2017](#)). Currently, our knowledge on impacts of dams is largely focused in local and post-dam-construction studies. However, to achieve a holistic view of the impacts of new hydropower projects, assessments must go beyond by accounting and forecasting synergies with existing and other planned dams, as well as land cover changes and likely climatic shifts (Castello and Macedo 2016, Poff et al. 2016, Winemiller et al. 2016). The lower limit of the macroecological relationship between the geographic range and body size represents a valuable tool to attain these purposes. In this thesis, we showed through this lower limit how we can be used to evaluate changes in species vulnerability due to shifts in species geographic range (see chapter 3), and at the same time, assess how the cutting of geographic ranges into smaller pieces induced by hydropower development in a tropical basin (i.e. effects of current and planned dams) heighten the extinction risk of species (see chapter 4). Recent studies have started to use this limit to also assess the additive effects of dam fragmentation and other human-related stressors (e.g. dam fragmentation + climate change, Herrera et al. in press), supporting the high potential of this macroecological limit as a tool to guide the sustainable management of hydropower development, and overall, to quantify and forecast how the reshaping of species range size occurring in the Anthropocene affects and will affect the persistence of species.

We identify two future steps in the use of the lower limit of the range – body size relationship. The first step is to scale up the basin- and regional-scales assessments of changes in species extinction risk (e.g. Carvajal-Quintero et al. 2017, Herrera et al. in press) building a global picture of the additive and/or synergetic impacts of human stressors on freshwater fish fauna. Thus, we will be able to forecast potential scenarios of changes in species diversity by identifying hotspots of species extinction risk. As a second step, we propose to integrate the range – body size relationship with temporal dynamics of extinction to better understand and quantify the species' extinction debt across the planet. For example, relating the number of nonviable species predict through the range – body relationship with known rates of species loss (e.g. (Hugueny 2017)). By addressing this second step, we will be able to go beyond the geography of species extinction risk, determining regions with the fastest rates and shortest

delays in species extinction. From an applied view, the results of these two steps could be directly used to set our conservation priorities and inform where actions are needed.

In regions identified as a priority for conservation the connectivity of watercourses must be restored and safeguarded. The findings of this thesis show that the branching architecture of river networks intrinsically constrain the movements of freshwater fishes (see chapter 2) that highly restricts their ability to respond to environmental changes (Olden et al. 2010). Therefore, the effect of human-origin fragmentation has more severe impacts on freshwater than for terrestrial ecosystems, by reducing drastically metapopulation persistence (Fagan 2002). The extent of the effect of fragmentation in freshwater environments depends on the size of the remaining fragment, showing higher species vulnerability as fragment size decreases (Fagan 2002, Carvajal-Quintero et al. 2017). Similarly, Roberts et al. (2013) showed that the effects of climate change on freshwater fishes are more profound in small fragments, highlighting that the greatest conservation need is for management to increase fragment lengths to forestall species extinction risk because of climate change. There is large evidence showing that restoration of river connectivity recovers populations (Lovett 2014, O'Connor et al. 2015) and increases the diversity of freshwater communities (Paillex et al. 2009, Magilligan et al. 2016). Besides, the restoration of river connectivity also brings great economic and social benefits. For example, by removing old dams we can save the great costs of their maintenance, which can exceed up to three times the cost of removal (Born et al. 1998). Also, it has been reported that only a few months after dam removals, different species that sustain fisheries stocks spawn in tributaries that were inaccessible before, increasing abundance of their populations in the newly available habitats (O'Connor et al. 2015). In this way, we call for the reorganization of the management and development of hydropower across the world, by restoring connectivity in places where hydroelectric production is not greater than the environmental and social benefits and favouring construction of new hydropower plants in places where others already exist leaving the rest of the hydrological network with full connectivity. This is a research topic where efforts should be focused on to reduce the degradation of freshwater ecosystems.

Finally, we consider that the database RivFishTIME (see chapter 5) represents valuable information to tackle further challenges in the study of the geographic ranges of freshwater fishes, bringing the opportunity to understand the spatio-temporal dynamics of different characteristics of the distribution of freshwater fishes (e.g. local occurrence, extent of occurrence, geographic range), and also connect them with population features (e.g.

abundance and occupancy). For example, we could use this database to evaluate patterns in the variation of abundance across the species' geographic range (e.g. Osorio-Olvera et al. 2020) as well as temporal trends in the extent of occurrence of species across the globe (e.g. Comte et al. 2014). RivFishTIME can also be used as a 'backbone' to integrate information from different aspects of biodiversity and evaluate trends and interactions between them, something that has not been explored at large spatial and temporal scales.

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Evaluating determinants of freshwater fishes geographic range sizes to inform ecology and conservation

Abstract: Understanding the geographic distribution of species across space and time is one of the long-standing challenges in ecology and evolution. Among the major components of species distribution, the species' geographic range size has been studied across several taxonomic groups and has been related to multiple ecological and evolutionary factors. The geographic range size of species is also of paramount importance in conservation strategies because it consistently emerges as a key correlate of extinction risk, where species occupying smaller geographic ranges are assumed to have a higher risk of extinction. Results concerning these fundamental and applied aspects of geographic range size have largely neglected freshwater fish, commonly focusing on the usual vertebrate groups (e.g. mammals, birds). However, freshwater fish, the most diverse vertebrate group, can provide novel insights about the geographic range size determinants and threats because of the unique dendritic shape and reduced amount of their habitat (i.e. river networks) compared to other terrestrial and marine ecosystems.

In this PhD work, we analyzed for the first time the global patterns of geographic range size in freshwater fish species and tested previous hypotheses proposed to explain the variation of geographic range size in other taxonomic groups. Our findings showed that current and historical connectivity are the most important factors driving the geographic range size of freshwater fishes, contrasting with the main determinants reported for terrestrial and marine taxa. From an applied point of view, we focused on the usually observed macroecological relationship between the species' geographic range size and body size. This relationship would allow estimating the minimum geographic range size needed by species for long-term persistence. Based on ecological theory of species temporal fluctuations of abundances, we provide a mechanistic validation of this relationship, supporting its use to identify vulnerable species and their changes in extinction risk through reduced geographic ranges induced by anthropogenic factors. Using a tropical river basin as a case study, we used this macroecological relationship to quantify changes in species extinction risk due to the fragmentation of their ranges caused by hydropower development. The results and the data compiled in this thesis represent useful information to guide and inform conservation in freshwater fish and give the opportunity to continue filling theoretical gaps.

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TITRE : Évaluation des déterminants de l'aire de répartition de poissons d'eau douce pour éclairer leur écologie et conservation

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Résumé : Comprendre la répartition géographique des espèces dans l'espace et le temps est un défi de longue date en écologie et évolution. Parmi les principales composantes de la répartition des espèces, la taille de l'aire de répartition géographique a été étudiée dans plusieurs groupes taxonomiques, et liée à de multiples facteurs écologiques et évolutifs. La taille de l'aire de répartition géographique des espèces est également liée au risque d'extinction, où les espèces occupant des aires géographiques plus petites présentent un risque d'extinction plus élevé, et relève donc d'une importance primordiale dans les stratégies de conservation. Les résultats concernant ces aspects fondamentaux et appliqués de la taille de l'aire de répartition géographique ont largement négligé les poissons d'eau douce, se concentrant généralement sur d'autres groupes de vertébrés (p.ex. les mammifères, les oiseaux). Cependant, les poissons d'eau douce, le groupe de vertébrés le plus diversifié, peuvent fournir de nouvelles perspectives sur les déterminants de la taille de l'aire géographique et sur l'impact des perturbations anthropiques en raison de la forme dendritique unique et la taille réduite de leur habitat (des réseaux fluviaux) par rapport aux autres écosystèmes terrestres et marins.

Dans ce travail de doctorat, nous avons analysé pour la première fois les patrons globaux de la taille de l'aire géographique des espèces de poissons d'eau douce et testé les hypothèses explicatives précédemment proposées pour d'autres groupes taxonomiques. Nos résultats ont montré que la connectivité actuelle et historique sont les facteurs les plus importants qui déterminent la taille de l'aire de répartition géographique des poissons d'eau douce, contrastant avec les principaux déterminants signalés chez les vertébrés terrestres et marins. D'un point de vue appliqué, nous nous sommes concentrés sur la relation macroécologique communément observée entre la taille de l'aire géographique et la taille corporelle des espèces. Cette relation permettrait d'estimer la taille minimale de l'aire géographique nécessaire aux espèces pour leur persistance à long terme. En se basant sur les fluctuations temporelles des abondances des espèces, nous fournissons une validation mécaniste de cette relation, confortant son utilisation pour identifier les espèces vulnérables et leurs changements de risque d'extinction face aux réductions de l'aire géographique induites par des facteurs anthropiques. En utilisant un bassin fluvial tropical comme étude de cas, nous avons utilisé cette relation macroécologique pour quantifier les changements dans le risque d'extinction des espèces en raison de la fragmentation de leurs aires de répartition due au développement de l'hydroélectricité. Les résultats et les données compilés dans cette thèse représentent des informations utiles pour guider et informer la conservation des poissons d'eau douce et fournir des éléments pour continuer à combler les lacunes théoriques.

MOTS-CLÉS : Macroécologie; Répartition géographique des espèces; Vulnérabilité; Réseaux fluviaux; Évaluation du risque d'extinction; Synchronie de la population; Base de données

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