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Ecole Doctorale Sciences de la Nature et de l’Homme – ED 227

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THESE

Pour obtenir le grade de

DOCTEUR DU MUSEUM NATIONAL D’HISTOIRE NATURELLE

Spécialité : **Ecologie (Macroecologie)**

Présentée et soutenue publiquement par

Murilo Sversut Dias

Le 24 juillet 2015

Speciation, extinction, and dispersal processes related to fragmentation of riverine networks: a multiscale approach using freshwater fishes

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Sous la direction de :

Thierry OBERDORFF et **Pablo A. TEDESCO**

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Place and date of oral defense: Paris, 24th July 2015

Abstract: Understanding factors driving the variation of diversity across the Earth is the main goal of ecology and biogeography. To reach this goal one needs to study the drivers of three main processes directly causing variation in diversity: speciation, extinction and dispersal. Speciation increases and extinction decreases diversity levels through time, whereas dispersal has a dual effect: it may increase or decrease diversity depending on the circumstances. Fragmentation, which stands by the emergence of natural or human-driven discontinuities on a given environment, is ubiquitous and has multiple ecological and evolutionary implications for the three diversity processes mentioned above (i.e., speciation, extinction and dispersal). Riverine fishes (i.e., strictly freshwater fishes) naturally experience fragmentation, as natural elements may disrupt connectivity of rivers (e.g., waterfalls) and river basins are separated from one another by barriers (oceans or land) which are insurmountable for these organisms. Riverine fishes thus constitute an ideal model for studying fragmentation effects. Here, I evaluated the effect of fragmentation on freshwater fish diversity by testing its effects on speciation, extinction, and dispersal processes at spatial and temporal scales ranging from a single river basin to worldwide rivers and from decades to million of years. In a first study, by analyzing endemism level of tributaries from the Orinoco river basin, I showed that tributaries highly fragmented by waterfalls have higher speciation probability and higher neo-endemism levels (i.e., species presumably originated by *in-situ* cladogenetic speciation) than their less fragmented counterparts. In a second study, I tested whether the historical connectivity between basins left an imprint on the global patterns of freshwater fish biodiversity. After controlling for contemporary and past environmental conditions, I found that palaeo-connected basins (those connected during the Last Glacial Maximum; 18-21 kya) displayed greater species richness but lower levels of endemism than did palaeo-disconnected basins. Palaeo-connected basins exhibited shallower distance decay of compositional similarity, suggesting that palaeo-river connections have favored the exchange of fish species. In a third study, I evaluated to what extent, if any, anthropogenic threats related to fragmentation (e.g., damming of rivers, agricultural practices) have been promoting fish extinctions in river basins. Focusing on Western Europe and North America, two strongly impacted regions, I showed that the percentage of cropland in the river basin and river fragmentation by dams are the main causes of present riverine fish species extinction. These extinctions, even if still reduced, correspond to extinction rates 40 times higher than background, natural rates. Overall, my results point for a prominent role of fragmentation as a driver of fish diversity through speciation processes and highlight the strong role played by history in explaining the global contemporary patterns of biodiversity via colonization processes. Moreover, they support the need of maintaining connectivity within river basins where human-made barriers have been created to avoid a substantial increase in species extinction rates.

Keywords: speciation; extinction; colonization; freshwater fish; river basins; richness, endemism, beta diversity; history effects; natural barriers, anthropogenic disturbances.

Résumé: Comprendre les facteurs qui contrôlent les variations de la biodiversité à travers la planète est un objectif central de la macroécologie et de la biogéographie. Pour atteindre cet objectif il est nécessaire d'étudier les facteurs structurant les trois processus qui contrôlent directement les variations de la biodiversité : la spéciation, l'extinction et la dispersion. La spéciation augmente la diversité au cours du temps alors que l'extinction la réduit. La dispersion, quant à elle fait augmenter ou diminuer la biodiversité selon les circonstances. La fragmentation, qui est définie comme l'émergence de discontinuités naturelles ou causées par l'homme sur un environnement donné, est omniprésente et a de multiples implications écologiques et évolutives sur les trois processus mentionnés plus haut (c.-à-d., la spéciation, l'extinction et la dispersion). Les poissons de cours d'eau (strictement d'eau douce) sont naturellement confrontés au phénomène de fragmentation car les bassins versant sont séparés les uns des autres par des barrières (eau de mer ou milieux terrestres) qui sont infranchissables pour ces organismes. Les poissons de cours d'eau constituent donc un modèle idéal pour étudier les effets de la fragmentation. Dans cette thèse, j'ai évalué les effets de la fragmentation sur les processus de spéciation, d'extinction et de colonisation des poissons d'eau douce à des échelles spatiales et temporelles allant du bassin versant à un échantillon représentatif des cours d'eau existantes sur la planète et de plusieurs décennies à quelques millions d'années. Dans une première étude, en analysant les niveaux d'endémisme des affluents du bassin versant de l'Orénoque, j'ai montré que les affluents très fragmentées par des chutes d'eau naturelles ont une probabilité plus élevée de spéciation et des niveaux plus élevés de néo-endémisme (c.-à-d., d'espèces probablement issues de la spéciation cladogénétique *in situ*) que leurs affluents homologues moins fragmentés. Dans une deuxième étude, j'ai testé si la connectivité historique entre bassins versants a laissé une empreinte sur les patrons mondiaux de biodiversité dans ses bassins. Après avoir contrôlé les conditions environnementales contemporaines et passées, j'ai montré que les bassins palaeo-connectés (ceux étant connectés pendant le dernier Maximum Glaciaire ; 18-21 ka) hébergent une plus grande richesse en espèces, mais des niveaux faibles d'endémisme en comparaison aux bassins palaeo-déconnectés. J'ai également montré que les niveaux de similarités des bassins palaeo-connectés décroissent plus légèrement avec la distance géographique entre bassins que les niveaux de similarités des palaeo-déconnectés, suggérant que les palaeo-connexions des bassins versants ont favorisé la colonisation des espèces. Dans un troisième temps, j'ai évalué dans quelle mesure la fragmentation liée aux activités anthropiques (par exemple la construction de barrages et les pratiques agricoles) a favorisé l'extinction d'espèces dans certains bassins versants. En focalisant sur l'Europe occidentale et l'Amérique du Nord, deux régions fortement touchées par les activités anthropiques, j'ai montré que le pourcentage des terres cultivées dans les bassins et la fragmentation de ces bassins par les barrages sont les principales causes de l'extinction actuelle des poissons d'eau douce. Ces extinctions, même si encore réduites, correspondent à un taux d'extinction 40 fois supérieur aux taux d'extinction naturels. Dans l'ensemble, mes résultats indiquent un rôle majeur joué par la fragmentation en tant que promoteur de la diversité de poissons via les processus de spéciation et mettent en évidence le rôle important de l'histoire pour expliquer les patrons contemporains de la biodiversité à l'échelle globale. En outre, ils supportent l'intérêt de maintenir une certaine connectivité au sein des bassins versants afin d'éviter une augmentation substantielle des taux d'extinction des espèces.

Mots clés: spéciation; extinction; dispersion; poissons d'eau douce; bassins versant; richesse spécifique; endémisme; diversité bêta; effets de l'histoire; barrières naturelles; perturbations anthropiques.

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“If we knew what we were doing, it wouldn't be called research...”
(Unknown)

“In principle, each of these phenomena [i.e., log normal distribution of population abundances, the theory of island biogeography, and tropical-temperate diversity gradients] *might have been revealed by detailed, reductionist studies of all the species involved, by studying their life history, enemies, competitors, other interactions, migration rates, and so on. But actually, put like that, the task is clearly hopeless! The patterns only emerge by ignoring the details.”*
Lawton (1999)

Contents

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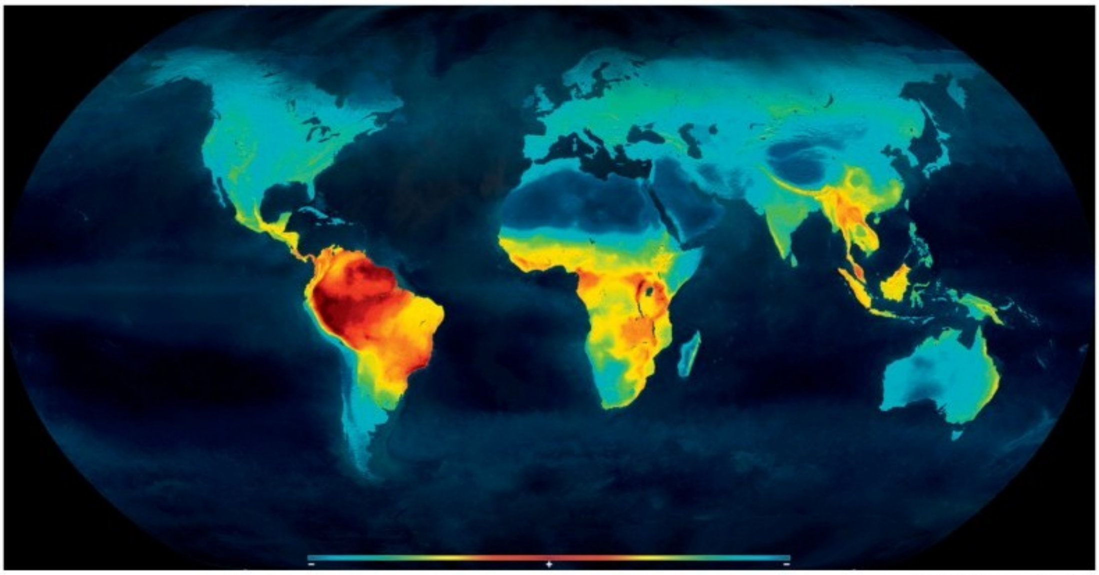
I) AN OVERVIEW

Introduction

Diversity of species is not homogeneous across the Earth. It is recognized since the XIX century that the number of species peaks around tropical regions and decreases toward the poles, i.e., the Latitudinal Gradient of species Diversity (LGD, hereafter). Indeed, many organisms such as mammals, birds, fish, trees, among others, show the same peak and the decreasing of diversity toward low latitudes (Rosenzweig 1995, Willig et al. 2003, Hillebrand 2004) (Figure 1). This global gradient in species diversity implies that diversity varies and all species are not everywhere. What determines the diversity patterns we observe? Why some areas are more diverse than others? What factors controls such variation on diversity? These are key questions for a fully understanding of nature and how life is structured on Earth. Understanding why differences exist in terms of species diversity, distribution and identity is the primary goal of ecology and biogeography. However, unifying the whole variation of biodiversity (i.e., in terms of genetics, population, species, and communities) in a single explicative theory is a great challenge (Heaney 2000, 2007, Ricklefs 2004, Mittelbach et al. 2007, Whittaker et al. 2007, 2008).

There have been many attempts to explaining global variation in species diversity (i.e., the total species richness), more precisely the LGD, and several hypotheses have been put forward. Overall, three major hypotheses that sum up the majority of different hypotheses proposed [see (Rohde 1992) for a review] can explain the variability of species richness at large extents (from continents to global). The first, the area hypothesis (MacArthur and Wilson 1967) refers to the existence of a positive relationship between the number of species present in a given area and the size of the area. It suggests that size limits the number of species an area can harbour and, due to its universal application, serves as a law in community ecology. Three non-exclusive explanations may explain this species-area relationship: 1) the size-dependent extinction rate (MacArthur and Wilson 1967) states that the probability of the extinction of a species increases with a reduction in the size of the “island”, which in turn, determines the total population size; 2) the size dependent speciation rate (Losos and Schluter 2000) suggests a positive effect of area on speciation rate by exposing species to greater ecological heterogeneity and/or geographical barriers (Rosenzweig 1995); and 3) the role of the habitat heterogeneity (MacArthur and Wilson 1967), suggesting that the heterogeneity of the habitat and the diversity of available sources of food increases with the size of the “island”, thus offering a large number of available niches and consequently favoring the coexistence of a large number of species (Rosenzweig 1995).



TRENDS in Ecology & Evolution

Figure 1: Distribution of extant terrestrial vertebrate species across the Earth (source: Mannion et al. 2014). Hot and cold colors indicates zones of high and low species richness, respectively.

Second, the species-energy hypothesis (Wright 1983, Wright et al. 1993) predicts a positive correlation between species richness and the energy available within the system. This hypothesis has received empirical support from a large number of studies carried out on different animal and plant assemblages [e.g., (Currie and Paquin 1987, Hawkins et al. 2003)]. This being said, there is still a certain ambiguity even in the way the hypothesis is expressed. In fact energy can influence richness by means of two different processes. Wright (1983) considers energy a factor that determines the availability of resources for a given biological community and thus as a productivity factor *per se*, whereas Turner et al. (1987) and Currie (1991), for example, consider energy as a determinant of species physiological limits. In the former, one would expect a variable such as net primary production to be an important predictor of species richness whereas in the latter variables linked with temperature or available solar energy would predominate (Hawkins et al. 2003).

Finally, the third hypothesis is linked to history, more precisely to the role of events occurring over geological time scales [e.g., (Haffer 1969, Araújo et al. 2008)]. It attempts to explain diversity gradients by differential extinctions coupled with the potential for diversification or re-colonization of systems and thus by the degree of maturity achieved since important historical events (Mittelbach et al. 2007). Some authors, for instance, argue that Latitudinal Gradient of Diversity have its roots up to 30 Million years ago (Mya) (Mannion et al. 2014), others relied on diversification burst after global climate changes during the Quaternary to explain tropical diversity (Haffer 1969). A parsimonious explanation, however, states that both events are influential (Rull 2011), and researchers now seem to agree that the historical context has a strong effect and must be considered when depicting current diversity patterns (Ricklefs 1987, 2004, Mittelbach et al. 2007).

An emerging consensus states that researchers should focus on quantifying the relative role of potential hypotheses rather than advocating for individual ones. Usually, studies have shown that climate and/or productivity and area play the most important role in determining species diversity gradients at large scales, whatever the habitats considered (terrestrial, marine or freshwater habitats) (Gaston 2000, Field et al. 2009, Tittensor et al. 2010, Tisseuil et al. 2013). History plays rarely a significant role, but this may reflect the difficulty of incorporating historical factors into regression models, and the collinearity between past and current climates, when past climate variables are used to evaluate the effect of history.

These approaches have mainly focused on testing the correlation between environmental variables associated to ecological hypotheses and patterns of richness, yet they have an important limitation as they do not directly address the processes that ultimately change species numbers (Ricklefs 2004, Wiens and Donoghue 2004). Indeed, an environmental variable cannot by itself change the number of species in a region or in a community. Instead, the processes that directly influence species numbers are speciation, extinction, and dispersal of taxa into or out of a region. To fully explain species richness patterns, we must determine how environmental factors (e.g., climate, area, natural barriers) interact with the evolutionary and biogeographic processes of speciation, extinction, and dispersal to create geographic gradients in species numbers (Wiens and Donoghue 2004, Wiens et al. 2006, Mittelbach et al. 2007, Rolland et al. 2014, Mittelbach and Schemske 2015).

Before delving into the processes, it is important considering the spatial scale at which ecological communities are studied (Cornell and Harrison 2014) and explaining the distinction of both local and regional communities. Overall, most field ecologists are used to deal with a set of species sampled in a sample of sites or locations, i.e., the local community. At this scale (sites), species richness, diversity, and composition are under the control of local processes such as predation, competition or disturbance regimes and subject to a series of ecological filters like water and prey availability, habitat structure, density of predators, among others. Such scale of analysis has dominated most of the ecological studies since the 1960s, but this deterministic and reductionist perspective [*sensu* (Maurer 1999)] is giving place to more integrative and dynamic frameworks (Hubbell 2001, Holyoak et al. 2005). Scaling up from local community, one deals with the pool of species of a given region (i.e., at broad spatial scales), which is defined as a set of organisms (i.e., species) capable of colonizing local/focal sites (Cornell and Harrison 2014). By definition, the local and regional pools of species are linked by dispersal processes, with the regional pool determining which group of species can potentially occur in local sites. Cornell and Harrison (2014) provide an enlightening discussion on the properties and advantages of considering the regional pool of species. The reason of detailing both scales here is that researchers now agree that only when studying the regional pool of species one can deal with the main three processes that indeed change species diversity (Ricklefs 1987, 2004, Mittelbach et al. 2007, Cornell and Harrison 2014, Mittelbach and Schemske 2015): extinction, dispersal, and speciation.

Three processes and the diversity of life

> *"...ecologists must now reject the parochial view of local determinism and recognize that ecology, evolution, geography, and history are different facets of a single set of processes and the patterns they generate."* Ricklefs and Schluter (1993), chapter 30, page 350.

Speciation, extinction, and dispersal are so important processes, and have so many peculiarities, that each one desires at least an entire book of description. These concepts have been discussed thoroughly elsewhere (Ricklefs et al. 1993, Rosenzweig 1995, Holyoak et al. 2005, Butlin et al. 2009, Losos and Ricklefs 2009) and my objective here is only introductory, focusing mostly on a few key concepts necessary to explain what I have done during my thesis.

Extinction is an important process because it reduces the number of species in a region and, as such, produces available niche and space for further colonization and speciation. One species is extinct when all its individuals are virtually dead. It might seem catastrophic but extinction is actually more frequent than we can imagine. Indeed, more than 99 % of organisms once inhabited the Earth are now extinct and at least five mass extinctions can be discriminated over the geological time (i.e., the "Big Five"; defined by the loss of more than 75 % of living species in a short period of time, ~2 million years) (Jablonski 1991, Jablonski and Chaloner 1994, Barnosky et al. 2011). As evidenced in geological records, these mass extinction events result from drastic changes in the environment, climate and from bolide impacts on the Earth surface (Barnosky et al. 2011). Species may though go naturally extinct over ecological time scales (from years to a few centuries): genetic and demographic phenomena may prevent individuals from coupling and breading; strong predation and competition among species may lead one to disappear; a disease may spread quickly and compromise all individuals from a given species; co-extinction of a group of interacting species may occur if one species disappears (e.g., mutualistic species); and environmental changes (e.g., climatic changes or marine incursion over land due to the sea level rise) may lead to extinction if individuals are not capable of dispersing to novel areas or coping with the new conditions. Notwithstanding, there is an increasing concern that humans are causing the Sixth Mass extinction (Barnosky et al. 2011) due to the large-scale destruction and pollution of natural habitats, the overexploitation of species, and the introduction of non-native species, jointly generating a reduction in local and regional diversity levels (McGill et al. 2015, Newbold et al. 2015). For this reason, extinction is thus a contentious issue in ecology and conservation biology (Lande 1993, Brook et al. 2008, Ladle 2009, De Vos et al. 2015).

Once available niches and space are created by extinction, species present in the regional pool may disperse and colonize new vacant areas. For the sake of simplicity, dispersal and migration are used hereafter as synonymous and I consider they refer to the ability of a species to move within an environment and reach a given location. Dispersal processes are important in connecting subpopulations of a given species, and enabling individuals to move according to their physiological requirements, cope with changing environments, and to rescue small subpopulations in isolated habitats (Brown and Kodric-Brown 1977). Together with extinction, dispersal is one core of the Island Biogeography theory (MacArthur and Wilson 1967) and researchers have been giving more importance to the processes of dispersal with the development of spatially-explicit, dynamic models (Hubbell 2001, Holyoak et al. 2005) and the recognition of the importance of the link between local and regional pools of species (Cornell and Harrison 2014). A key simulation study has shown, for instance, that the diversity level of a local community is directly related to the dispersion between regional and local communities, with differences in the species composition between local communities (i.e., beta diversity) decreasing with dispersal, and local diversity peaking at intermediate levels of dispersal (Mouquet and Loreau 2003).

Speciation is the last, though not less important, mechanism. Indeed, without speciation processes there would be only a single species (i.e., a directly descended organism from the first ancient life form) on the Earth (Adams 2009). It refers to the process whereby an ancestral species originates one or more “daughter” species (Turelli et al. 2001). Although there are many modes of speciation (Figure 2), allopatric speciation is historically viewed as the commonest one (Adams 2009). Overall, speciation in allopatry arises when a single species population is divided by the emergence of a barrier (e.g., a mountain, a river or two tectonic plates getting far apart) (i.e., classical allopatric speciation) or when part of the original population disperses to an isolated, peripheral environment (i.e., peripatric speciation) so that the levels of individual exchange, and hence the levels of gene flow, among the two populations are drastically reduced; as a consequence over the long term, the two isolated populations accumulate genetic distinctiveness that prevent inbreeding among them, hence generating two distinct species (Figure 2). Despite the fact that speciation is widely accepted as a process driving diversity and long lasting appeal of some researchers (Ricklefs 1987, Ricklefs et al. 1993), it has been only recently incorporated into ecological theoretical frameworks (Losos and Schluter 2000, Hubbell 2001, Losos and Ricklefs 2009). In short, allopatry and peripatry are primary modes of speciation explaining high diversity levels and are fueled by fragmentation levels settled by barriers and consequent isolation.

To summarize, these three processes (i.e. speciation, extinction and dispersal) generate diversity patterns (Figure 3) and understanding what, how, and to what extent environmental and biological factors drive them must be in the center of ecological and biogeographic research.

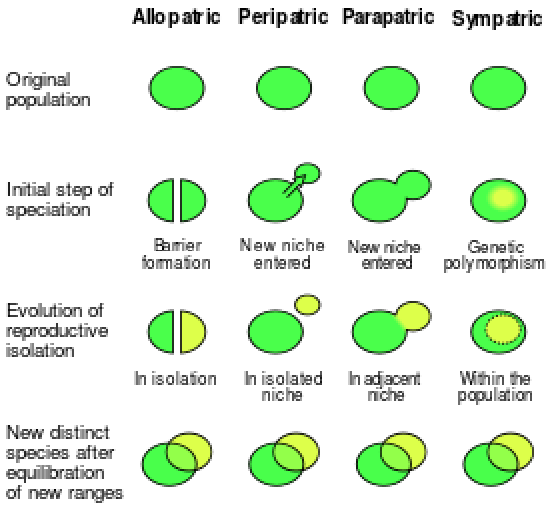


Figure 2: Speciation modes. Allopatric and Peripatric speciation: both modes are linked to the emergency of barriers or colonization of peripheral isolated habitat by part of original population in ways that exchange of individuals, and hence gene flow, is drastically reduced, leading to distinct species over the long term. Parapatric speciation: the whole population remains connected though range expansion leads to a decreasing contact (hence limited gene flow) among individual from extreme population edges so that local inbreeding promoted genetic distinctiveness and speciation event. Sympatric speciation: genetic variation accumulates, distinctiveness among individuals accentuates, barriers to reproduction emerge among individuals of the same population occupying geographically the same location so that two or more lineages are formed from the same ancestor. (source: Wikipedia, by Ilmari Karonen based on Dr. Dana Krempels).

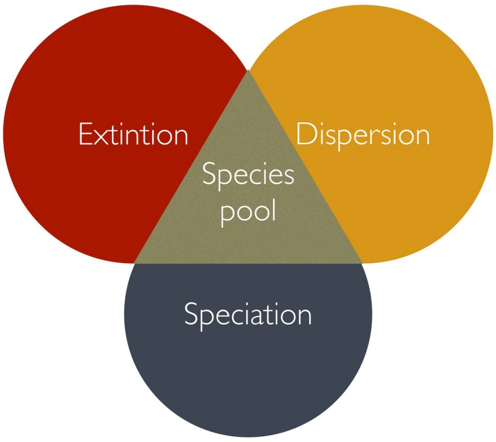


Figure 3: The species pool of a given area is ultimately the result of three ecological and evolutionary mechanisms: extinction, dispersal and speciation.

Fragmentation: a ubiquitous and important process?

Fragmentation stands by the emergence of discontinuities on an environment due to natural geological causes (e.g., volcanoes, mountains, oceans) or by human activities (i.e., anthropogenic fragmentation) (Ellis et al. 2010) such as land conversion to agriculture (Figure 4). Because fragmentation is a very common term in applied ecology and conservation biology (Fahrig 2003, Laurance et al. 2011), it is worth starting by the anthropogenic issue.

A biome like the Amazonian forest, for example, one of the biggest remnant primary forests on Earth, is said to be fragmented when its native vegetation is cleared in a patchy way by human in order to promote the development of urbanization and agriculture. For instance, the Amazon forests have historically reached levels of habitat loss up to 38,000 km^2/year leading to the fragmentation of natural habitats, though these rates have been considerably decreasing in the last years (~70 % reduction) (Nepstad et al. 2014). After fragmentation, the once unique block of forest gives place to a landscape composed of many forested patches surrounded by a matrix having distinct characteristics from the primary forest (e.g., mono-cultures, roads, pastures). Overall, the surrounding matrix is potentially a barrier to movements for some biological groups of birds, mammals, amphibians and insects [e.g., (Laurance et al. 2011)], but the matrix permeability varies considerably depending on the organisms.

The phenomenon of fragmentation may also naturally occur on a geological time scale. Tectonic is the most prominent example as thousands of islands compose the Earth surface and the continents themselves are large islands of varying degrees of connectivity (Figure 4a). The emergence of mountains, rivers formation (Figure 4b-c), glaciation events, geological faulting, major sea levels rise, volcanic activity, and climate oscillation are also examples of natural phenomena promoting fragmentation.

A direct consequence of habitat fragmentation is the reduction of habitat size *per se* since a continuous habitat is replaced by fragment of habitats. Besides decreasing the habitat surface, fragmentation acts on creating many isolated patches that vary considerably in size and shape (Fahrig 2003). Finally, the spatial heterogeneity of the habitat drastically increases since patches are isolated and distant from each other (Fahrig 2003). All these changes have consequences for diversity levels over both ecological (Lindenmayer and Fischer 2006) and geological time scales. The decreasing of habitat size by fragmentation processes initially determines a reduction in the number of species as small areas support fewer individuals, and hence less species, than large ones (MacArthur and Wilson 1967, Ferraz et al. 2003). Even if the habitat reduction is minimal, the isolation due to the spatial arrangement of patches reduces dispersal of individuals throughout the landscape and prevents small isolated populations from being rescued by large ones (Brown and Kodric-Brown 1977), thus increasing local extinction rates. For instance, fragments in eastern Amazonia (Figure 4d) are thought to locally lose up to 25 forest-dependent vertebrate species (i.e., mammals, birds, and amphibians) by 2050 (Wearn et al. 2012). On the other hand, highly isolated patches may experience an increase in diversity over geological time. On isolated oceanic islands, for instance, where the sea and distance from the continent (i.e., isolation) prevents most of the colonization events, the availability of niches may burst speciation events and increase diversity exponentially over time (Heaney 2000, Rosindell and Phillimore 2011). The most prominent examples are Darwin's finches and *Anolis* lizards from Galapagos and Caribbean islands, respectively, and cichlids from the East African Great Lakes (Gavrilets and Losos 2009), where a reduced number of descendants originate many species in a few million years or even less.

To summarize, fragmentation is a ubiquitous process and may have contrasting effects on biodiversity, both increasing and decreasing diversity levels depending on the temporal scale considered. Moreover, fragmentation issues have proven so important that new advances in ecological theory and concepts have emerged specially focusing on fragmented systems (Hanski et al. 2013). It seems therefore logic to consider the potential role of fragmentation in highly diverse, and naturally fragmented, environments such as riverine habitats.

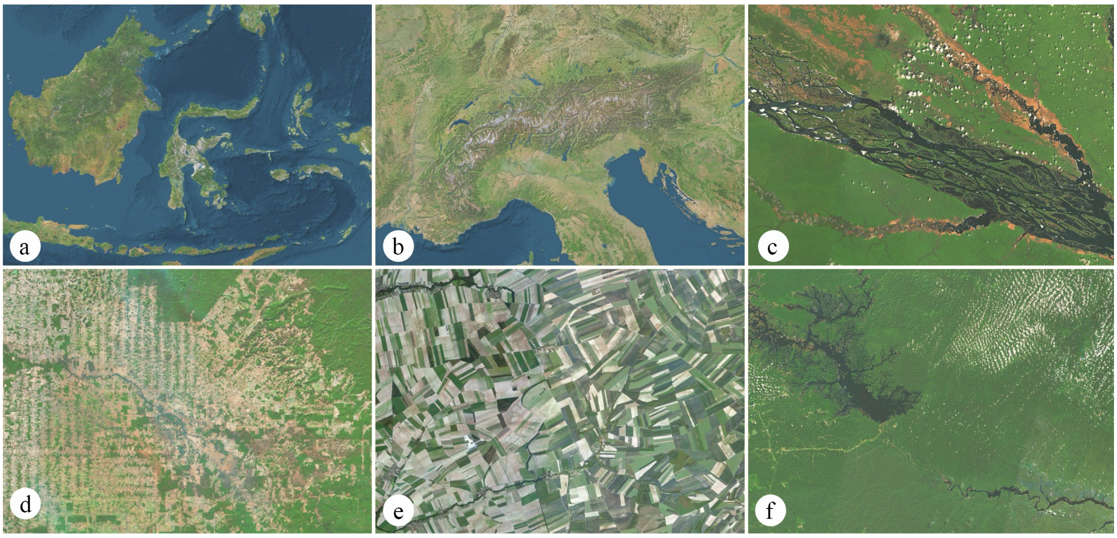


Figure 4: Natural and anthropogenic barriers are shown. (a) Islands and continents, (b) mountains, and (c) rivers separating blocks of forested habitat are all examples of naturally fragmented systems. (d) Fragments in western Amazonia, (e) agricultural landscape in France, and the (f) reservoir of Balbina dam in Uatuma River, central Amazonia.

Riverine networks: a fragmented, yet diverse, World

Inland waters represent only a small fraction of all available water on the planet. Most of the Earth is dominated by marine environments (around 75 % of the Earth surface) whereas all freshwaters cover only 0.8 % of the surface and rivers alone constitute no more than 0.3-

0.5 % of the surface (Downing et al. 2012). Yet, fresh water is a highly diverse environment in terms of living organisms. For instance, for fishes, which represent around 50 % of all described vertebrates, both marine and freshwaters have almost the same diversity, each homing around 15,000 described species (Lévêque et al. 2008, Carrete-Vega and Wiens 2012). Thus the question is: How freshwaters, covering such a small fraction of the Earth surface, can be as diverse as the marine environment for this group? Fragmentation seems to be one of the best candidates to explain this paradox (Tedesco et al. *in prep*).

For the sake of simplicity, I have focused my work on i) riverine systems, setting apart lakes and reservoirs whose dynamic differs from that of flowing waters, and ii) on strictly freshwater organisms, i.e., organisms restricted to freshwater pathways with impossibility to use terrestrial or marine environments.

Natural fragmentation

It is easy to recognize that streams and rivers are grouped within individual units called river drainage basins (Figure 5). A river drainage basin, or a catchment, may be defined as an extent of land drained by a river, or more precisely, an area where water from ice melting, rain, and underground water converges toward an end point of low altitude, which commonly corresponds to the sea (but see endorheic basins). Although there may be rare cases of flow exchanges (e.g., during high flood periods or connections such as river captures over geological time scales) (Benda et al. 2004, Burridge et al. 2008), drainage basins are overall well delineated by surrounding mountains and/or highlands. Such peculiarity leads researchers to consider drainage basins as “island-like” systems, wherein strictly aquatic organisms are isolated by barriers such as the marine environment (i.e., the sea) and a “sea” of terrestrial environments (Rosenzweig 1995, Rahel 2007, Hugueny et al. 2010, Heino 2011).

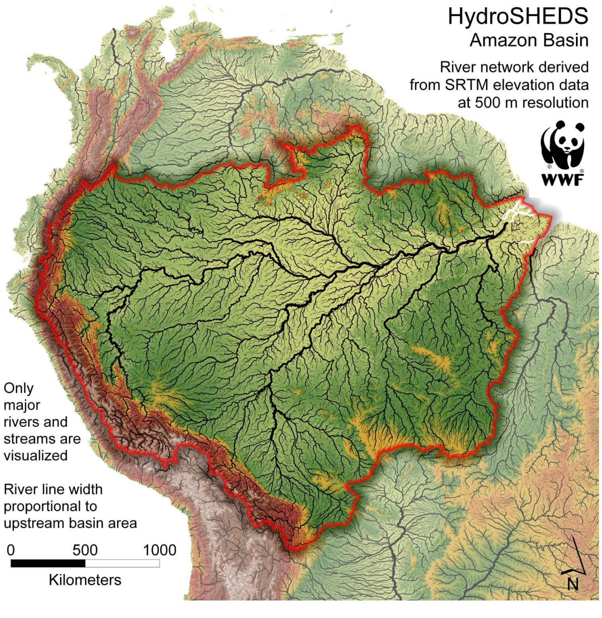


Figure 5: The Amazon basin. All rivers draining to a common end point (i.e., the sea) compose the drainage basin, and its limits are represented by a red line.

Scaling down to the local scale (i.e., within the same drainage basin), stream and rivers are dendritic networks that resemble the hierarchical branching pattern of trees (Figure 6) (Benda et al. 2004, Grant et al. 2007). This fact is of key importance because, compared to terrestrial systems where individuals move through various dispersal routes across the landscape, the movements of aquatic organisms are strictly limited to the river branches of the drainage network (i.e., rivers) and the connectivity between subpopulations is strictly dependent on the configuration of habitat patches present in these branches (Rahel 2007). Thus, geomorphological characteristics (e.g., waterfalls) or high hydrological variations due to climate seasonality (e.g., when rivers sections dry out and stop running) (Fagan et al. 2009) at the basin scale can dictate the permeability of fresh water bodies, since they constitute barriers limiting the dispersion of the species and/or individuals within the same drainage. As a result, the degree of longitudinal connectivity within a drainage basin must determine the spatial configuration of populations of aquatic organisms (e.g., fishes) and, therefore, the mechanisms that lead to speciation, extinction and species migration in evolutionary timescales. There has been a growing support for the hypothesis that riverine networks shape ecological processes for freshwater organisms (Fagan 2002, Muneepeerakul et al. 2008, Brown and Swan 2010, Grant et al. 2010, Bertuzzo et al. 2011, Grant 2011, Carrara et al. 2012, Yeakel et al. 2014).

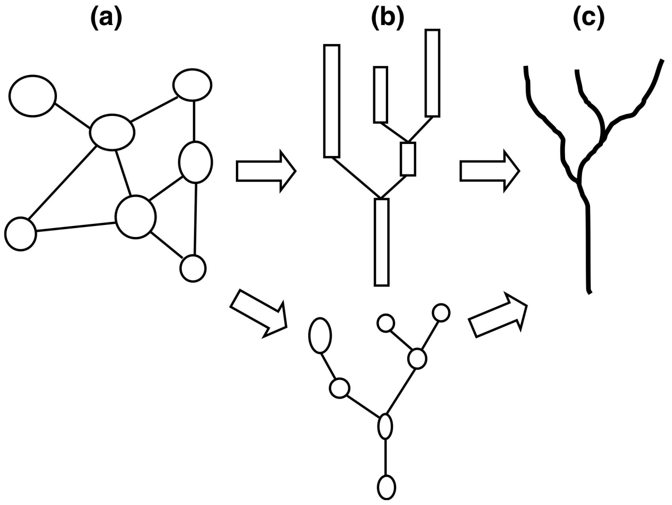


Figure 6: Topological differences between (a) terrestrial and (b-c) riverine networks (source: Grant et al. 2007). Networks are represented by nodes (circles) and links (connecting lines), where the former represent patches of habitat inhabited by organisms and the later represent possible pathways through which organisms move between patches. In stream and river networks, however, links do not represent only possible pathways but are important habitats through which movement of aquatic organisms occur.

Let me consider an empirical example (Figure 6) of how the barriers are more effective in decreasing connectivity within riverine drainage basins compared to terrestrial systems (Fagan 2002, Grant et al. 2010). Considering Figure 6a, most of the nodes have more than one link whereas only one node connects the network by a single link; in this case the presence of a barrier would eliminate some links yet individuals would be able to reach other nodes by using the remaining links. On the other hand, losing a few links in a riverine network would completely isolate branches from the entire network (Figure 6b), thus preventing exchanges of individuals from up- and downstream subpopulations.

Anthropogenic fragmentation

> *"The fate of the last* Acipenser sturio*:* A. sturio *is one of the most threatened European fish species, strictly protected at the national level in most countries, at the EU level and by a number of international agreements. Its protection depends largely on the efficiency and attention of those in charge of enforcing fisheries laws. It is interesting to record the fate of the last sturgeons... … in the Black Sea: The last known individual of* A. sturio *in the Black Sea basin was caught by a fishermen in 1991 in Georgia. It was recognized by scientists who tried to transport it alive to a research aquarium. On their way, they were stopped by a policeman, the fish was 'confiscated' and barbecued."* European Red List of Freshwater Fishes (2011)

Humans have changed all ecosystems on Earth and caused the extinction of hundreds of species (Barnosky et al. 2011). Fresh waters desire special attention within this biodiversity crisis as their biodiversity importance (9.5 % of global biodiversity in less than 1 % of Earth's surface) (Balian et al. 2008) clearly contrasts with the increasing exploitation rates of aquatic organisms and the degradation of aquatic resources (Strayer and Dudgeon 2010). In this human-driven scenario, large scale models predicting how freshwater biodiversity respond to anthropogenic threats should be established for guiding conservation practices (Pringle et al. 2000, Vörösmarty et al. 2010, Lehner et al. 2011).

Within the main causes of aquatic species loss, river fragmentation by dams and water pollution represent major threats due to the scale they have been affecting freshwater biodiversity (Malmqvist and Rundle 2002, Dudgeon et al. 2006). Since the last century, the demand of energy for both individual and industrial use has grown, promoting a worldwide increment in the number of dams. Indeed, over half of rivers worldwide is nowadays fragmented by these barriers (Nilsson et al. 2005, Lehner et al. 2011, Grill et al. 2015). Dams transform the dynamic of rivers by creating lentic systems where rapid waters and turbulent river sections predominated before impoundments, leading to structural changes that not only drastically shift local chemical water conditions (e.g., temperature, conductivity and oxygen levels) but also affect downstream areas (e.g., reduction in sediment deposition). As a result, regional changes in riverine ecosystems can be noted [e.g., (Poff et al. 2007)]. In the same way, water pollution also creates fragmentation (i.e., presence of unsuitable areas for aquatic organisms along the river course) and has been seen as a 'pandemic' problem [sensu (Dudgeon et al. 2006)] due to the growing of urban centers (Grimm et al. 2008, McDonald et al. 2011), pasture and crops across landscapes (Ramankutty et al. 2008); changes that have been boosting inputs of organic and inorganic compounds into riverine systems. For instance, the high levels of phosphorus and nitrogen input from traditional agricultural practices and the load of sewage from cities and industries have increased eutrophication in rivers in detriment of other natural processes (Carpenter et al. 1998, Smith and Schindler 2009). All these alterations have changed natural habitats and conditions for which physiological responses of organisms are adapted and decreased the availability and the permeability of natural habitats (Malmqvist and Rundle 2002, Bain and Wine 2010, Blanchet et al. 2010, Reidy-Liermann et al. 2012), increasing species extinctions (Fagan 2002, Morita and Yamamoto 2002, Perkin and Gido 2011) and ultimately promoting a simplification of aquatic communities (Relyea 2005, Walsh et al. 2005, Perkin and Gido 2012). Although dams and water pollution are modifying riverine habitats at the regional and continental scales, most of their effects on biodiversity have been evaluated at the local scale, thus promoting a growing demand for studies at larger spatial scales (Pringle et al. 2000, Duncan and Lockwood 2001), especially those aiming at guiding conservation strategies (Ziv et al. 2012).

Such large scales studies have recently emerged for freshwater fishes but have faced many data deficiency problems preventing the establishment of the relative importance of distinct threats in causing the imperilment of species (Clavero et al. 2010, Reidy-Liermann et al. 2012). In this case, evaluating well known regions in terms of biological information and environmental impacts and focusing on threats supposed to have direct impacts on the freshwater biodiversity (e.g., dams, water pollution, introduced species) would shed light on the strength of stressors promoting species extinction and help disentangling their individual effects.

Riverine fish’s-eye view

The recognition of river basins as independent entities has lead researchers to assimilate them (river basins) as kind of biogeographic island in disequilibrium (Hugueny 1989, Rahel 2007, Hugueny et al. 2010, Oberdorff et al. 2011). The term 'disequilibrium', as conceptualized for highly isolated islands (Heaney 2000), comes from the extremely low probability of receiving new colonists from other river basins due to isolation provided by catchment divides and the sea (Hugueny et al. 2010).

Considering basins as biogeographic units for freshwater organisms enables the study of aquatic diversity over broad spatial scales (Hugueny et al. 2010). There are three good examples explaining patterns of distinct components of biological diversity (i.e., species richness, endemism and beta diversity) globally (Guégan et al. 1998, Leprieur et al. 2011, Tedesco et al. 2012). The first study has shown that up to 93 % of the variability in fish species richness in river basins can be explained by a combination of three variables: the drainage surface area, the river discharge at the river mouth, and the net terrestrial primary productivity within the basin (Guégan et al. 1998). These correlations suggest that the current climatic conditions and the surface area are the main drivers of fish species diversity, as suggested for other taxonomic groups (Hawkins et al. 2003). The second work has shown the distinct spatial distribution of two types of endemism (i.e., neo- and palaeo-endemism) (Tedesco et al. 2012). Neo-endemism, driven by *in-situ* cladogenetic speciation, is positively related to drainage surface area and negatively related to past climatic variability and species dispersal ability. Palaeo-endemism, related to range contraction and extinction processes due to isolation, is better predicted by geographic isolation, glacial history and the marine-derived origin of families (Tedesco et al. 2012). The third and final example has dealt with variation in species composition among drainage basins (i.e., beta diversity) and has shown that species turnover and nestedness components (Baselga 2010) differ geographically in their contribution to the freshwater fish beta diversity, a pattern that results from contrasting influences of Quaternary climate changes (Leprieur et al. 2011). More than depicting and explaining patterns of fish diversity and endemism, these papers are successful examples of how much we can gain in our understanding by considering large spatial scales and reinforce the reliability of studies using entire river drainage basins.

An important study for the context of fragmentation examined the spatial concordance in global diversity patterns for six freshwater taxa (i.e., aquatic mammals, aquatic birds, aquatic reptiles, fishes, crayfish and aquatic amphibians) in order to investigate the environmental factors driving these patterns at the river drainage basin grain (Tisseuil et al. 2013). These authors found that species richness and endemism patterns were overall well correlated among taxa, and that these patterns of cross-taxon congruence were often induced by common responses of taxa to their contemporary and historical environments (i.e., convergent patterns) (Tisseuil et al. 2013). A more interesting finding of this study, however, was that the surface of drainage basins was the major predictor for both patterns of fish species richness and endemism, contrarily to the other taxa, supporting the conclusions of several previous studies (Oberdorff et al. 1995, 2011, Tedesco et al. 2005, 2012). The explanation advanced by the authors was that, in contrast to the other taxa analysed (i.e., birds, aquatic mammals, reptiles, amphibians, crayfish), which have varying abilities to colonize other river systems by land or by sea, the dispersal options for strictly freshwater fishes are limited by their restriction to river drainage basins such that gene flow is limited in ways that can promote intra-basin diversification (Burridge et al. 2008, Tedesco et al. 2012, Tisseuil et al. 2013). Given the strong influence of isolation and geographical barriers in explaining diversity patterns, riverine fishes, as previously said, seem thus an ideal biological model to analyse the effects of fragmentation on speciation, extinction and dispersal processes for these organisms (Figure 7).

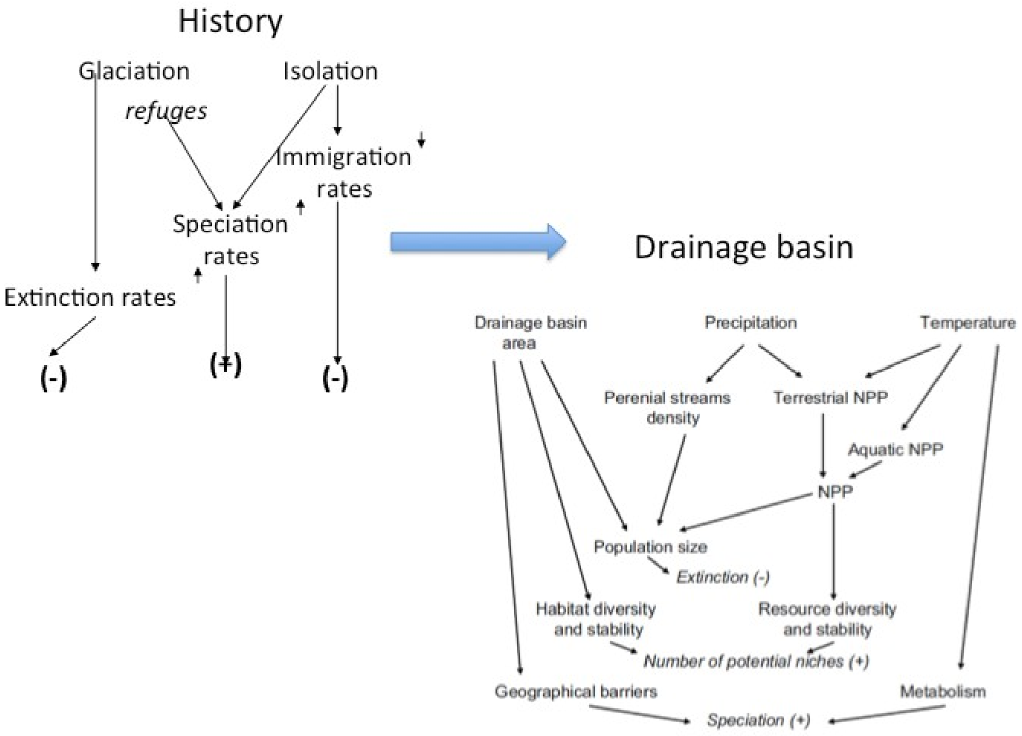


Figure 7: Potential causal pathways between environmental factors and processes increasing (+) or decreasing (–) species diversity of a river basin (source: adapted from Hugueny et al. 2010).

Objectives

Given the importance of fragmented habitats in increasing and decreasing biodiversity levels, I aimed at studying how fragmentation drives the outstanding diversity of freshwater fishes at broad spatial scales. In this sense, I studied to what extent habitat fragmentation from natural barriers (e.g., waterfalls), from historical sea level changes, and from current habitat conversion by human contributes in explaining the freshwater fish diversity patterns that we observe nowadays.

S*peciation driven by waterfalls*. In the first chapter, I showed how changes in connectivity due to the presence of waterfalls (generated by land uplift) have promoted speciation events and increased the diversity of freshwater fish in tributaries of the Orinoco river basin.

Dispersal events in palaeo-drainage basins. I evaluated in the second chapter how changes in the connectivity among drainage basins due to past sea level variations have contributed to freshwater riverine fish diversity patterns at the global scale.

Extinction rates of riverine fishes. Finally, I studied how habitat fragmentation by humans influences the recent extinction patterns of freshwater fish in Europe and North America (mainly USA).

Grain, extent and source of data

Studying multiple biological processes determining fish diversity necessitates data sources from distinct grains and extents. Grain is defined by the size of the smallest homogeneous unity used as samples in a given study and determines the resolution at which landscape is studied. Extent corresponds to the temporal and/or spatial limits over which samples are taken and for which inference is valid. I propose here a brief description of scales, grain and extent of each study and of the sources of biological data used.

The first study shows how natural fragmentation by waterfalls may drive freshwater fish diversification. In this case, the Orinoco river basin and its main tributaries represent respectively the extent and grain of the study (Figure 8). I used a published data set of fish species occurrence from the Orinoco drainage basin (Lasso et al. 2004). This dataset includes species lists for the main tributaries compiled from museum collections, taxonomic information and field work data (see references therein), providing the most updated fish species list registered for the Orinoco River basin. I considered the following 26 tributaries of the Orinoco River basin as sampling units: Alto Orinoco, Apure, Arauca, Aro, Atabapo, Bita, Capanaparo, Caris, Caroni, Cataniapo, Caura, Cinaruco, Cuchivero, Guaviare, Inirida, Manapiare, Meta, Morichal-Largo, Pao, Parguaza, Sipapo-Cuao, Suapure, Tomo, Ventuari, Vichada, and Zuata (Figure 8).

The second study describes the effects of reducing connectivity among river basins due to past sea level variations. The grain and extent of this study correspond to the river basin and the whole planet, respectively (Figure 8). The biological database contains the species occurrences of most of the freshwater fish species of the world described so far. This occurrence database was compiled from an extensive literature survey of fish species lists (including those considered recently extinct and excluding those introduced by recent human actions) obtained from published articles, books and gray literature. The survey yielded 14,717 species [nearly all freshwater fishes described so far; (Lévêque et al. 2008)] from 3,031 drainage basins. The resulting data set is an extended version of the information used in previous analyses (Brosse et al. 2013) and represents the most comprehensive database of native freshwater fish occurrences per drainage basin available so far.

The third chapter deals with extinction patterns of freshwater fishes related to anthropogenic fragmentation of rivers. All information has been gathered per drainage basin, which constitutes here the grain of the study (Figure 8). I compiled a comprehensive distributional dataset of fish extinction events in river basins from the western European continent (i.e., from Portugal to Petchora, Volga and Ural river basins in Russia) and North America (i.e., United States of America), and these two regions constitute the extent of my study. These two continents are highly impacted and benefits from numerous reports, books and papers that periodically update species extinctions. For Western Europe, the occurrence of fish species was assessed based on a comprehensive spatial data set on global freshwater fish distribution at the river basin grain (Brosse et al. 2013). I further incorporated registers of fish extinctions per river basin using information from Kottelat and Freyhof (2007) completed by data from unpublished reports, scientific papers and Red Lists (Freyhof and Brooks 2011). For North America, a comprehensive compilation of the status of native freshwater fishes was used as the main source of information (NatureServe 2010). In this case, species were considered extinct from a given basin when only historical records of their presence where reported throughout the hydrological units composing the river basin.

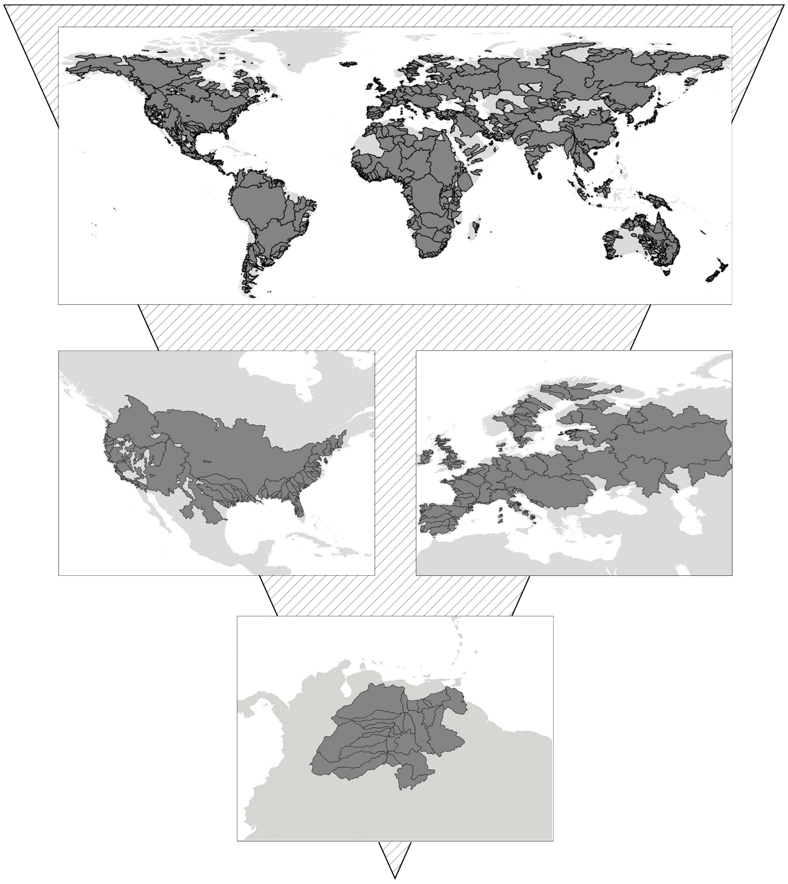


Figure 8: Grain and extent of studies. Spatial scale increases bottom-up. Top: river basins used for testing palaeo-connection effects of fish diversity. Center: drainage basin from European and North American continents using for studying the drivers of contemporary fish extinction. Bottom: Orinoco river basins and its main tributaries in which natural fragmentation by waterfalls was studied.

Natural fragmentation in river networks as a driver of speciation for freshwater fishes

Without any doubt, speciation is an important process for understanding diversity since it is directly responsible for generating the variety of forms we observe. Knowing that freshwater habitats are distinct from terrestrial environments by being naturally fragmented and isolated, it is possible that much of the fantastic diversity of freshwater fish is a result of allopatric speciation processes (Seehausen and Wagner 2014). Waterfalls and cascades are classical examples of fragmenting elements at the river basin grain (Rahel 2007). Large waterfalls constrain population movements of strictly aquatic species, and strongly prevent individual dispersal and gene flow within the river catchment (Martin-Smith and Laird 1998, Torrente-Vilara et al. 2011, Kano et al. 2012). Hence, this fragmentation pushes populations to evolve in separate evolutionary directions (Kano et al. 2012), thus creating distinct species in the long term. Understanding how barriers influence diversity patterns in river basins at large scales is a promising research area, and could help elucidating the question of the extraordinary freshwater fish diversity.

We studied here how natural fragmentation of riverine networks by waterfalls drive speciation of freshwater fishes. In this aim, we used the Orinoco river basin as it presents a large geographic variation in the number of waterfalls, and as it is one of the most diversified water bodies on the planet, with over 800 fish species (Lasso et al. 2004). Thanks to the knowledge on freshwater fishes accumulated by our scientific partners from South America, we were able to rely on a huge database describing the distribution of fishes in each major tributary of the Orinoco basin. Another challenge was to estimate the potential presence and position of waterfalls throughout the basin, for which we have relied on mapping and GIS techniques based on GIS layers of altitude. With these massive dataset in hand, we started testing our predictions on natural fragmentation largely based on the Island Biogeography theory (MacArthur and Wilson 1967).

Overall, our general hypothesis was that fish species diversity (i.e., species richness) and endemism (i.e., the number of endemic species, or endemic richness for short) were positively related to the level of fragmentation (i.e., the number of riverine patches with ≥ 13 km^2 of surface and defined by waterfalls ≥ 30 m in height) of each tributary. After controlling for other environmental predictors important for explaining fish diversity at broad spatial scales, we found no effect of fragmentation level on fish richness and endemism. This negative, though not totally unexpected, result may be due to the metrics themselves as, indeed, total and endemic species richness may not be good proxies for quantifying speciation (Chen and He 2009, Kisel and Barraclough 2010, Tedesco et al. 2012).

To circumvent this problem and generate better measures linked to speciation processes, we further considered the number of endemic species that presumably arose from *in-situ* (i.e., within a given subdrainage) cladogenetic speciation [hereafter called neo-endemics, *sensu* (Tedesco et al. 2012)] as a more accurate measure of the speciation intensity, i.e., neo-endemic species richness. To define neo-endemics we considered that the presence of two or more endemic species from the same genus should reflect *in-situ* diversification (i.e., neo-endemic species) (Coyne and Price 2000). Moreover, we applied another speciation metric following Kisel and Barraclough (2010). Based on Coyne and Price's method, these authors applied an index (or probability) of speciation as the number of genera with two or more endemic species divided by the number of genera with one or more endemic species (Kisel and Barraclough 2010, Tedesco et al. 2012). This last approach focuses on the ability of lineages to speciate rather than on what controls the size of radiations, which is better reflected by the richness of neo-endemic species.

After controlling for potential other factors influencing fish diversity, our results showed that both the neo-endemic species richness and the probability of cladogenetic speciation were positively linked, though to a different degree, to the number of patches (i.e., the fragmentation levels) in the tributaries of the Orinoco river basin. Overall, this supports the hypothesis that fragmentation by waterfalls generates cladogenetic speciation within sub-drainages, a process that similarly affects highly isolated islands and lakes, where local speciation has largely contributed to an increase in endemism richness over evolutionary timescales (Heaney 2000, Losos and Schluter 2000, Seehausen 2006, Barluenga et al. 2006, Algar and Losos 2011). This result has also implications at larger scales, as regions of high fish diversity, like South America and Africa, are those with high levels of natural fragmentation (i.e., waterfalls) (Figure 9) (Grill et al. 2015).

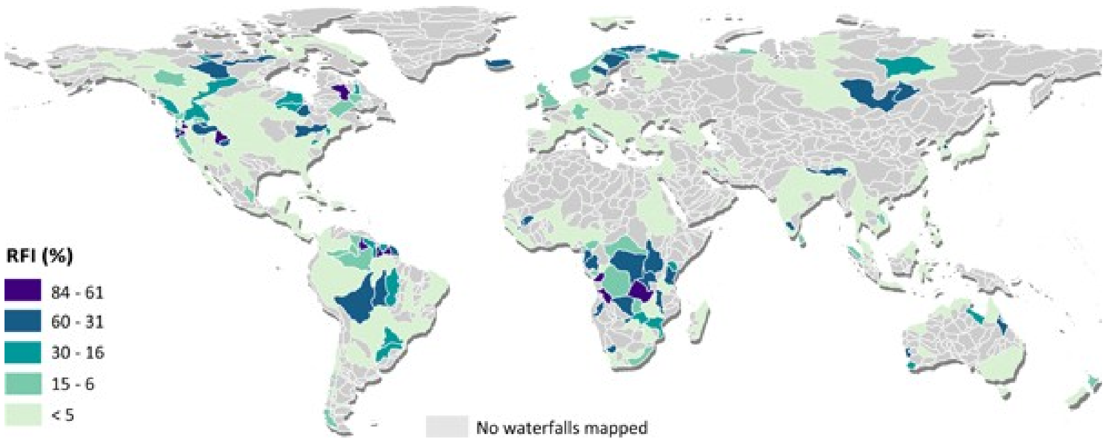


Figure 9: River Fragmentation Index: Worldwide fragmentation by waterfalls of river tributaries (source: Grill et al. 2015).

Perspectives

Numerous perspectives might be considered in future studies:

- one important limitation of our approach is that waterfalls were estimated by GIS techniques (Crosby and Whipple 2006) rather than empirically located. Although our estimation is valuable when studying a large drainage basin in a largely unknown region, such as the Orinoco river basin, one could argue that empirical data is necessary for confirming the linkage between waterfalls and fish speciation processes at the drainage scale. Fortunately, a recent study has shown how natural fragmentation by waterfalls varies in tributaries of major river basins at the global scale (Figure 9) (Grill et al. 2015). Such new data set is without any doubt a promising information source for further analyses;
- when identifying potential waterfalls, we adopted a height of 30 m as the minimal waterfall size for preventing individual exchange between up- and downstream sections. By doing so we took a conservative assumption and surely minimized the potential effect of fragmentation on speciation processes, as smaller waterfalls are also probably efficient barriers to dispersion for most of fish species (Torrente-Vilara et al. 2011, Kano et al. 2012). Identifying the minimal height size of waterfall leading to speciation is a natural next step;
- overall, our study use biological data from a megadiverse river basin for which there is no site-based fish occurrence detailed data; indeed, our fish data set was based on species occurrence lists per sub-drainages. Although we have been able to identify a possible link between the number of waterfalls and the speciation of freshwater fishes, a more efficient test of such hypothesis should include both detailed data sets of waterfall distribution and site-occurrence data for fishes. We are aware of two excellent initiatives from Grill et al. (2015) and the Faunafri project (www.poissons-afrique.ird.fr/faunafri), which, in combination, would enable testing the hypothesis of waterfall-related speciation as a factor generating neo-endemism. Using site scale data is thus an evident next step;
- finally, given that speciation rate is a direct function of surface area (Losos and Schluter 2000, Mittelbach et al. 2007), we could rely on more precise data sets (i.e., both waterfall and fish occurrence data) to evaluate the effect of patch size (i.e., the river section among two waterfalls) on neo-endemism diversity, and hence on diversification processes in naturally fragmented habitats.

Global imprint of historical connectivity on freshwater fish biodiversity

History provides an interesting case to test to what extent dispersal mechanisms explain current fish diversity patterns at broad spatial scales. Throughout the Quaternary, the Earth' climate fluctuated periodically, resulting in sea-level changes that reconfigured the connectivity between river systems (Voris 2000). During the Last Glacial Maximum, around 20,000 years before present, much of the water present on the planet was retained in the poles as ice sheet, due to the colder Earth temperatures. Such retention of water caused a drop in the sea level up to 120 m below the level observed today. As a consequence, rivers mouths progressed through kilometers of exposed marine shelves before reaching the ocean, which resulted in a connection (i.e., palaeo-connected drainage basins; green-colored drainages in Fig. 10a) or no connection (i.e., palaeo-disconnected river basins; red-, blue- and orange-coloured drainages in Fig. 10a) between previously isolated adjacent drainage basins. We tackled here the question of dispersion as a possible mechanism influencing contemporary fish diversity patterns at the global scale by evaluating the effect of palaeo-connections of river drainage basins generated by GIS techniques based on global bathymetric sea levels.

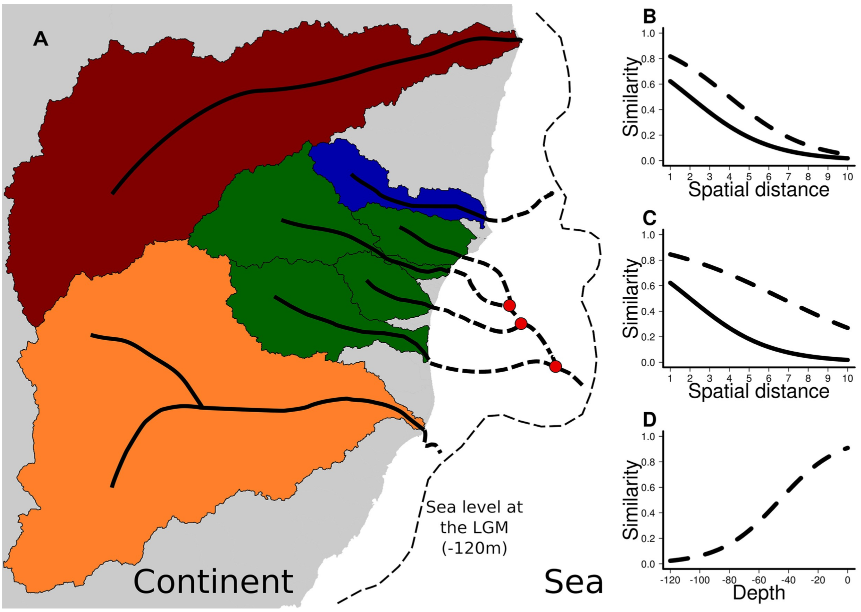


Figure 10: Coloured polygons (a) represent coastal drainage basins under current sea levels. The broken line represents the land expansion and river connections due to sea-level retraction during the LGM. The green basins are part of the same palaeo-drainage under the LGM conditions, while the other basins remained isolated. The expected effects of the palaeo-connection (broken line) and palaeo-disconnection (full line) on the distance–decay curves include (b) differences in the mean similarity for a given spatial distance if the dispersal limitation is similar for both groups and (c) changes in both the mean similarity and slope due to low dispersal limitation and homogenization of fish fauna within palaeo-connected drainages. Using the depth at which the palaeo-confluences occurred [red dots in (a)] as a proxy of the connection time (a greater depth indicates a longer period of connection), we should observe (d) an increase in the species similarity with decreasing depth.

We relied on a global data set containing the occurrence of over 14,700 fish species (nearly all freshwater fishes described until now) (Lévêque et al. 2008) in 3,031 drainage basins. A series of covariates were included to account for the global variation in current and historical climate and in habitat size and diversity (Hugueny et al. 2010, Leprieur et al. 2011, Oberdorff et al. 2011, Tedesco et al. 2012, Tisseuil et al. 2013), along with the spatial connectivity among each considered drainage basin (Hugueny and Lévêque 1994).

It is worth noting that all fish diversity measures were defined at the drainage basin grain (i.e., regional species pool). Hence, species richness stands for the total number of species present in a drainage basin. Endemism richness (or endemism level) in a drainage basin stands for the total number of endemic species, which are defined here as those species present in a single drainage basin (Oberdorff et al. 1999). Finally, distance decay of similarity stands for the negative relationship between compositional similarity [more precisely, a similarity measure of species composition turnover, i.e., 1-Bjtu *sensu* (Baselga 2010, 2012)] and neighborhood distance (i.e., a pairwise measure of geographical distance) among pairs of drainage basins (Leprieur et al. 2009). This negative relationship with geographical distance, the distance decay for short, was useful in our comparative framework because it gives a measure of dispersal limitation of the whole community (Nekola and White 1999) following palaeo-connection events.

Two predictions following past events of adjacent river basin connection are that i) palaeo-connected river basins should have overall higher species richness (as species were capable of reaching basins where they had been absent), and ii) should have lower endemism levels (as dispersion has potentially increased geographical ranges of species to the entire palaeo-drainage; green polygons in Figure 10a) compared to disconnected ones. Both predictions were supported by our models, but the strength of the relationship varied significantly depending on the biogeographic zone considered. For instance, the palaeo-connected and palaeo-disconnected drainage basins displayed similar species richness in the Indomalaya realm and similar levels of endemism in the Afrotropical, Palearctic and Nearctic realms [see Table 1 from (Dias et al. 2014)].

Thinking in terms of distance decay of compositional similarity, we expected an overall mean difference in similarity or changes in both mean similarity and slope due to the low dispersal limitation and homogenization of fish fauna within palaeo-connected drainages (Figure 10b-c). After controlling for covariates of climate, habitat size and diversity, we found both significant differences in mean similarity and in the slopes of the distance decay of similarity between the palaeo-connected and disconnected pairs of drainage basins (Figure 11) [see Table 2 from (Dias et al. 2014)], with the effects varying depending on the considered biogeographic zone.

As a final step, we investigated within the group of palaeo-connected river basins a possible effect of connection time on fish similarity. In this sense, we registered the depth at which palaeo-confluences took place (trough bathymetry sea maps) and used it as a proxy of connection duration. Our hypothesis was that shallower depth of connection should indicate a longer period of connection, and thus a greater faunal exchange between the palaeo-connected drainage basins (Figure 10d). This hypothesis was supported by a positive and significant effect of the palaeo-connection depth on the fish similarity for the Indomalaya and Neotropical realms [see Table 3 from (Dias et al. 2014)]. River basins from these two biogeographic zones are very diverse, have been completely remodeled due to climate variation and have not been directly affected by the ice sheet from the LGM, all factors that contribute to fish dispersal and range expansion through time.

Overall, our results are consistent with the predictions of past connectivity and fish dispersion for most of the chosen biological metrics. These results support the role of past climatic changes (i.e., history) in explaining the current biodiversity patterns (Araújo et al. 2008, Bonada et al. 2009, Hortal et al. 2011, Sandel et al. 2011, Tedesco et al. 2012, Pellissier et al. 2014), and that dispersal processes have at least as much importance as the niche-based processes in shaping the geographical distribution of species at the global scale.

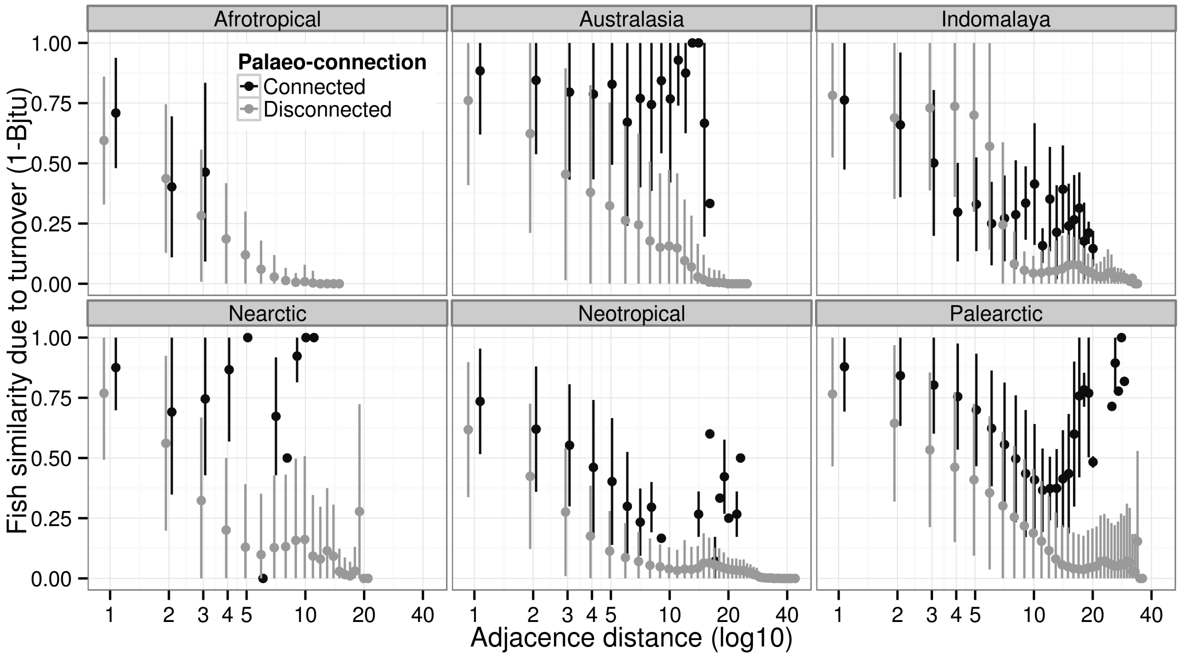


Figure 11: Distance decay of similarity due to turnover (1-ßjtu) between the drainage basins in each realm. The mean similarity (± 1 SD) per distance classis shown; black and gray correspond to similarities between pairs of palaeo-connected and disconnected drainage basins respectively.

Perspectives

A perspective may be advanced in this section:

- our study deals exclusively with changes in fish diversity under a taxonomic base (i.e., by using taxonomy to measure alpha and beta diversity). In order to increase predictability, however, many researchers have advocated the use of intrinsic components of form and function of species (i.e., 'species traits'), as these traits should have a direct influence on species performance and on how species respond to environment (Mcgill et al. 2006, Violle et al. 2007). As a consequence, we have seen many successful attempts to rebuild community ecology and biogeography under a trait-based perspective (Winemiller 2005, Mims et al. 2010, Lamanna et al. 2014, Violle et al. 2014, Whittaker et al. 2014, Sternberg et al. 2014). Under this perspective, we could evaluate which species groups were most involved in dispersal events during the Quaternary sea level changes. Species body size could be a good candidate, for instance, because large body size is often positively related to dispersal ability of fish species (Radinger and Wolter 2013). In this sense, we would expect no or weak relationship between community dissimilarity and distance decay for good dispersers (i.e., large-bodied species).

Anthropogenic drivers of riverine fish extinctions

Humans are causing the extinction of hundreds of species (Barnosky et al. 2011, Pimm et al. 2014). Therefore predicting species loss is critical for guiding conservation strategies aiming at maintaining biodiversity and resources in altered ecosystems. Most of the studies analyzing drivers of species extinction (Luck et al. 2004, Reynolds et al. 2005, Davies et al. 2006, Olden et al. 2007, Cardillo et al. 2008, Hutchings et al. 2012) suffer from data deficiency on the spatial distribution of extinctions and threats, and do not allow the assessment of the specific role of individual anthropogenic stressors in biodiversity loss (Clavero et al. 2010, Vörösmarty et al. 2010). When dealing with extinction it is also important considering the spatial variation of species loss because local populations of common species may be shrinking and are not accounted for in species-level analyses (Reynolds et al. 2005, Giam et al. 2011, Burkhead 2012). Moreover, integrating natural extinctions (i.e., background extinction rates) in extinction analyses is a bit more challenging and would be a key improvement for estimating human-driven extinction rates (De Vos et al. 2015). We circumvent these problems by i) analyzing patterns of fish species loss in two well-known regions (i.e., Western Europe and North America) for which much of the fish extinctions per river drainage basins is documented (Kottelat and Freyhof 2007, Jelks et al. 2008, NatureServe 2010, Freyhof and Brooks 2011, Burkhead 2012), ii) using detailed information on threats to freshwater biodiversity recently published (Vörösmarty et al. 2010), and iii) controlling for natural extinction rates independently of human land-use (Hugueny et al. 2011).

In order to evaluate the geographical variation in extinction, we computed the total native, resident and migratory species richness and the number of extinct fish species for each individual river basin (Brosse et al. 2013). To account for natural extinction rates, we used Observed/Natural Extinction ratios per river basin instead of direct percentages of species extinction. To obtain these ratios we relied on a highly accurate empirical riverine fish population extinction–area relationship previously established (Hugueny et al. 2011) for the Northern Hemisphere to (1) estimate the “background” (natural) extinction rates in river basins [see (Tedesco et al. 2013) for an application] and (2) calculate Observed/Natural Extinction ratios during the last 110 years, assuming that human-related extinctions started approximately 110 years ago (Miller et al. 1989, Burkhead 2012). Finally, we used an integrative index (i.e., the Incident Biodiversity Threat) and individual threat indices of freshwater biodiversity developed by Vörösmarty et al. (2010) as predictors of the Observed/Natural ratio in order to explain fish extinction patterns in Western Europe and North America.

A total of 1,050 species inhabiting 213 river basins were analyzed. The mean percentage of the total fish species extinction per river basin is 1.8 % (sd = 4 %; range = 0-36 %, 1st quartile = 0, 3rd quartile = 2.86, median = 0; Figure 12a). The Observed/Natural extinction ratios show that fish species extinctions in the last century are, on average, 40 times (sd = 124, range = 0-998; 1st quartile = 0, 3rd quartile = 17, median = 0) higher than expected under natural conditions, although many river basins have no extinct species recorded. The Colorado (998), Grande (720) and Mississippi (532) river basins in North America and the Danube (614), Dnepr (585) and Volga (499) river basins in Europe show the highest Observed/Natural extinction ratios (Figure 12b). These ratios were not predicted by the Incidence Biodiversity Threat index, suggesting that the IBT index is too broad to be a good proxy for predicting large scales riverine fish extinctions and minimizes the chances of potential synergistic feedbacks among anthropogenic stressors. Still, there are no mean differences in overall extinction ratios between continents, suggesting that fish species extinction rates per river basin are similar and are, on average, 40 times higher than natural extinction rates. Our estimates are lower than those obtained by other studies on freshwater fishes [between 130 (Tedesco et al. 2013) and 855 (Burkhead 2012) times higher than natural extinction rates] because numerous the river basins considered here had no documented extinct species despite of a highly modified environments.

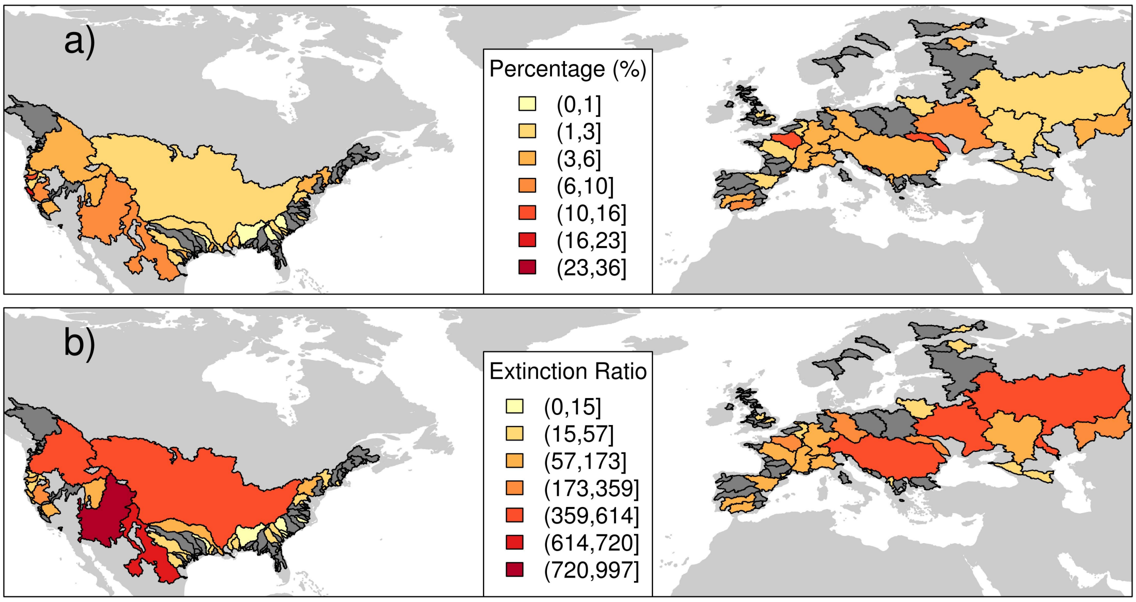


Figure 12: Percentage of extinction (a) and Observed/Natural extinction ratios (b) of total fish species per river basin for North America and Western Europe. Dark-gray polygons represent basins where no extinctions have been recorded.

Including individual threats shows that the number of dams on the main stem and the percentage of croplands in the river basin are the main determinants of fish extinctions (Figure 13). Observed/Natural extinction ratios for migratory fish were significantly predicted by the % of croplands in the river basin and marginally by the number of dams. Natural land clearance for agriculture (e.g., deforestation) jeopardizes terrestrial and aquatic communities at different spatial scales (Kerr and Cihlar 2004, Clavero et al. 2010, Giam et al. 2012, Lange et al. 2014, Mantyka-Pringle et al. 2014, Mendenhall et al. 2014, Leadley et al. 2014). Indeed, agricultural land use is tightly linked to modifications on forest cover, river structure and water quality. All of these factors alter local conditions (Allan 2004) and indirectly prevent species from migrating throughout the network, and ultimately increasing extinction risk.

Separating migratory and resident species showed that extinction ratios for resident species were higher in North America compared to Western Europe, and positively correlated to the number of dams on the main stem. Dams act directly on the degree of connectivity between species sub-populations by decreasing the permeability and availability of habitats within drainages (Luttrell et al. 1999, Rahel 2007, Pelicice et al. 2014), and eliminate the natural flow dynamics of rivers (Poff et al. 2007). These new conditions affect meta-population dynamics both directly and indirectly by decreasing the size of sub-populations (Alò and Turner 2005) and the overall genetic pool (Sterling et al. 2012), leading to species extinction (Hugueny et al. 2011, Perkin and Gido 2011). Recent studies have shown that centrality of riverine patches is essential for maintaining connectivity throughout river networks (Erős et al. 2011, Branco et al. 2014). Indeed, the main stem acts as a source of immigrants for tributaries (Grenouillet et al. 2004, Hugueny et al. 2010, Hitt and Roberts 2012); hence, damming the main course prevents fish from colonizing upstream reaches and, in the long term, contributes to the extinction of populations from the entire basin.

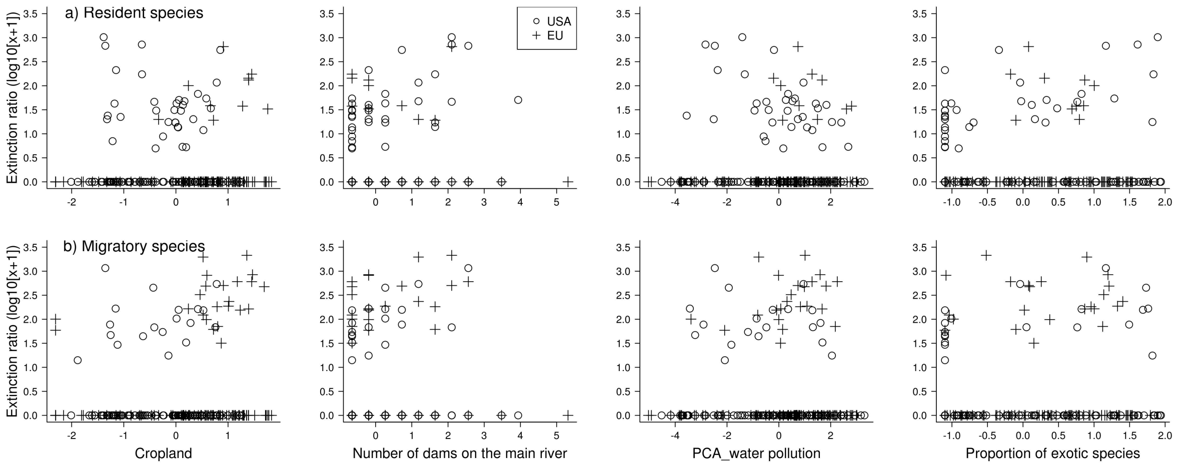


Figure 13: Fish extinction ratio for (a) resident and (b) migratory groups of species relating to individual threats. All threats are centered and reduced for improving coefficient interpretation during model fit.

Perspectives

A few perspectives desire further investigation:

- the dataset for each continent includes many small river basins for which no extinction has been documented (Figure 12). This may be due to the fact that small rivers are under-sampled compared to large and important rivers in both regions; as a consequence, extinction levels may be largely underestimated (i.e., false negative extinction rates). The fact of having many zeros in our dataset prevented the correct modeling of extinction levels; indeed, our models never had pseudo-R^2 (a measure of goodness-of-fit) higher than 10 %. One option to circumvent this analytical problem and increase the model performance is limiting the analysis to only large river basins (e.g., >10,000 km^2), which are usually better sampled.

- results obtained here show that extinction rates in river basins for resident species are related to the presence of dams on the main stem whereas migratory fish extinction is related to the percentage of cropland in each drainage basin. The odd absence of effect between migratory species and dams could be related to the measure of fragmentation we used here. One option for testing the robustness of our relationship could be integrating a more precise metric related to the loss of riverine habitat. For instance, quantifying the levels of free-flowing riverine section or discounting the fragmented area above dams from the total basin surface area;
- the threats we used here have a temporal bias because most of them correspond to a temporal window between 1990 and 2005 [see Supplementary Information from (Vörösmarty et al. 2010)]. Therefore, there might be a mismatch between the extinction events (mainly from 1900 to 1990) and the considered threats. Other data on habitat loss exist (Ellis et al. 2010), however adopting them would mean relating fish extinction to broad measures of landscape modification by humans rather than depicting individual threat' role as we have done here. Anyway, considering new data remains as an important perspective;

General conclusions

Results from my thesis show that habitat fragmentation is a key driver of speciation, extinction and species dispersal (Kisel *et al.*, 2011), and ultimately participates in generating differences in contemporary diversity patterns. Results obtained here also indirectly highlight the unambiguous role played by history in explaining the global contemporary patterns of biodiversity. In this sense, my thesis also brings a stone to the contentious debate on the extent to which the past environmental changes have shaped current global biodiversity patterns (Ricklefs 2004, Sandel et al. 2011). Habitat fragmentation influences the diversity of freshwater fish in at least two different ways: i) by promoting diversification (i.e., speciation) of some species groups, hence increasing diversity levels at large time scales (e.g., natural barriers like waterfalls in tributaries within a drainage basin) (Dias et al. 2013); ii) by increasing species extinction risk at short time scales (e.g., river fragmentation by dams and land conversion by humans since 1900 have increased extinctions) (Dias et al. *in prep.*). Habitat fragmentation seems to have thus conflicting consequences on biodiversity. Theory predicts that subsequent to isolation, extinction probabilities should increase in fragmented habitats, as isolated populations cannot be rescued by immigrants from neighboring areas (MacArthur and Wilson 1967). Conversely, lower genetic exchanges among populations of isolated habitats enhance diversification (Gavrilets and Losos 2009, Kisel and Barraclough 2010) [but see (Losos 2010)], promoting higher speciation rates at evolutionary time scales. Results obtained in my first two studies (Dias et al. 2013) (Dias et al. *in prep.*) reflect these conflicting effects of fragmentation and highlight the role of time in explaining these conflicting effects. At large temporal scale fragmentation of habitats and consequent isolation of populations seem to compensate extinctions rates by enhancing diversification. At contemporary time scales where speciation rates are around zero, only extinction probabilities influence diversity patterns.

My results also point to new avenues of research related to fragmentation processes beyond the scope of this thesis. Firstly, I showed that natural barriers like waterfalls promote fish speciation within tributaries and that dams in the main stem of rivers increase extinction probability by reducing connectivity among subpopulations. Knowing that dams may increase genetic divergence among subpopulation (Roberts et al. 2013, Fluker et al. 2014), a new avenue would be studying to what extent dams could promote diversification over ecological times scales (up to 200 years). Finally, past variation of the global sea levels due to natural climate changes played a strong role in structuring global fish diversity. Climate warming is in the short-term horizon and researchers now expect a sea level rise up to 2 m by 2100 with drastic consequences to biodiversity [e.g., see (Bellard et al. 2014) and references therein]. Knowing that the sea level rise will fragment river basins by isolating downstream tributaries and subsequently reducing the total surface area of the basins, what would be the impacts of future sea levels rise on freshwater fishes?

Overall, habitat fragmentation is likely to increase with the growing human population, therefore fragmentation will surely play a central role on ecological and evolutionary research over the next decades.

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II) PAPERS

Natural fragmentation in river networks as a driver of speciation for freshwater fishes

Murilo S. Dias, Jean-François Cornu, Thierry Oberdorff, Carlos A. Lasso, and
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Natural fragmentation in river networks as a driver of speciation for freshwater fishes

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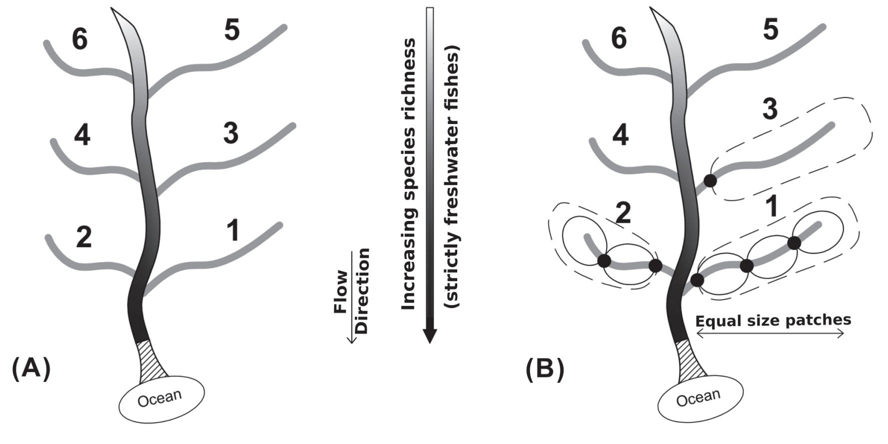
Although habitat fragmentation fosters extinctions, it also increases the probability of speciation by promoting and maintaining divergence among isolated populations. Here we test for the effects of two isolation factors that may reduce population dispersal within river networks as potential drivers of freshwater fish speciation: 1) the position of subdrainages along the longitudinal river gradient, and 2) the level of fragmentation within subdrainages caused by natural waterfalls. The occurrence of native freshwater fish species from 26 subdrainages of the Orinoco drainage basin (South America) was used to identify those species that presumably arose from in-situ cladogenetic speciation (i.e. neo-endemic species; two or more endemic species from the same genus) within each subdrainage. We related subdrainages fish diversity (i.e. total, endemic and neo-endemic species richness) and an index of speciation to our two isolation factors while controlling for subdrainages size and energy availability. The longitudinal position of subdrainages was unrelated to any of our diversity measures, a result potentially explained by the spatial grain we used and/or the contemporary connection between Orinoco and Amazon basins via the upstream Casiquiare region. However, we found higher neo-endemic species richness and higher speciation index values in highly fragmented subdrainages. These results suggest that habitat fragmentation generated by natural waterfalls drives cladogenetic speciation in fragmented subdrainages. More generally, our results emphasize the role of history and natural waterfalls as biogeographic barriers promoting freshwater biodiversity in river drainage basins.

Speciation is a key process in ecology and evolutionary biology because it generates biodiversity. The relative importance of factors contributing to diversification remains thus an active research area (Orr and Smith 1998, Losos and Schluter 2000, Rundle and Nosil 2005, Ricklefs and Bermingham 2007, Gavrilets and Losos 2009, Hortal et al. 2011). One of the earliest hypotheses advanced to explain how environmental factors could affect diversification rates was proposed by Cracraft (1982). This author hypothesized that speciation rates should increase with the number of natural barriers generating geographical isolation. Indeed, physical or climatic subdivisions of habitats limit gene flow in ways that can promote local diversification (Rahel 2007, Burridge et al. 2008, Boizard et al. 2009, Meeuwig et al. 2010). However, this fragmenting process also reduces the amount of available habitat, producing in fine smaller populations that may be subject to higher extinction rates (Fagan 2002, Morita and Yamamoto 2002, Hugueny et al. 2011).

Riverine networks represent overlooked systems offering an opportunity for testing these evolutionary hypotheses (Burridge et al. 2008). Compared to landscapes where individuals move through several dispersal routes, the movements of riverine organisms within drainage basins (i.e. strictly freshwater organisms) are restricted along the aquatic branches of the network. Then, the connectivity between organism's sub-populations strongly depends on the configuration of connections between habitat patches (Benda et al. 2004, Grant et al. 2007, Rahel 2007). As a consequence, the degree of connectivity within a river network should be an important mechanism driving speciation, extinction and immigration on evolutionary time scales. Waterfalls are natural barriers within the river network acting on the degree of connectivity and shaping the permeability and availability of habitats for populations of freshwater organisms (Rahel 2007, Cote et al. 2008). Besides decreasing colonization and increasing extinction rates, these barriers are also expected to increase speciation rates by promoting and maintaining population divergence (Losos and Parent 2009). Figure 1 depicts a river network under different configurations of habitat patches. Under a continuous river network configuration (Fig. 1A), immigration, extinction and speciation rates within subdrainages depend mostly on their size and position along the main river channel (Osborne and Wiley 1992, Oberdorff et al. 1997, Grenouillet et al. 2004, Hitt and Roberts 2012).



$$I_{1\,\&\,2} > I_{3\,\&\,4} > I_{5\,\&\,6}$$
$$E_{1,3\,\&\,5} < E_{2,4\,\&\,6}$$
$$S_{1\,\&\,2} < S_{3\,\&\,4} < S_{5\,\&\,6}$$

$$I_{1,2\,\&\,3} = 0;\ I_4 > I_5 = I_6$$
$$E_1 > E_2 > E_3 > E_4 = E_6 > E_5$$
$$S_1 > S_2 > S_3 > S_5 > S_6 > S_4$$

Figure 1. Importance of longitudinal position and waterfalls on immigration (I), extinction (E), and speciation (S) rates (i.e. per species per unit time) in subdrainages of a hypothetical drainage basin. There is usually an increase in species richness from upstream to downstream areas (Osborne and Wiley 1992, Oberdorff et al. 1997, Grenouillet et al. 2004, Hitt and Roberts 2012) with a level off at the river mouth (when the main channel reaches the ocean; dashed region). Following island biogeography theory, (A) subdrainages close to the zone having the highest number of potential colonists should have higher immigration and lower extinction and speciation rates compared to similar subdrainages distant from this zone; large subdrainages should have lower extinctions and higher speciation rates compared to small ones. (B) This pattern changes when considering waterfalls (black dots) within the same system; immigration should be minimal and extinctions should be greater in subdrainages containing waterfalls (1, 2 and 3) compared to non-fragmented ones (4, 5 and 6), while the isolation from the species pool should promote higher speciation rates on those subdrainages that have higher number of patches (circles within subdrainages; 1, 2 and 3).

Indeed, considering that upstream subdrainages are more isolated due to the unidirectional hydrological flow, they should receive new colonists less frequently and should display greater extinction and speciation rates than downstream ones (Fig. 1A, Oberdorff et al. 2011). Compared to non-fragmented subdrainages, the presence of natural barriers along the drainage network (Fig. 1B) should greatly modify the underlying evolutionary rates. The spatial configuration and waterfall distribution presented in Fig. 1B imply differential speciation, extinction and immigration rates for the different subdrainages. These rates should depend on a combination of subdrainages size and position but also on their degree of fragmentation supposed to prevent immigration and to gradually increase extinction rates (Fig. 1B). Everything else being equal (i.e. controlling for other factors known to affect diversity), if barriers promote speciation processes, higher speciation rates should be found in subdrainages benefiting from numerous patches isolated from each other by waterfalls (see case 1 in Fig. 1B).

Here we apply the framework conceptualized in Fig. 1 to subdrainages of a large tropical and fish species-rich drainage basin, the Orinoco River in South America (Fig. 2). We hypothesize that, after controlling for environmental factors already known to influence diversity patterns, the number of continuous freshwater 'patches' within subdrainages and the position of these subdrainages along the longitudinal river gradient should be positively related to the total number of endemic fish species inhabiting these subdrainages and particularly to the number of endemics originated by in-situ cladogenetic speciation (i.e. neo-endemic species; sensu Tedesco et al. 2012).

Methods

Biological data

We used a published data set of fish species occurrence from the Orinoco drainage basin (Lasso et al. 2004a). These authors compiled species lists for the main subdrainages (see below) from museums, taxonomic information and field work data (see references therein), providing the most updated fish species list registered for the Orinoco River basin. Only strictly freshwater species were considered in our analyses; all marine, euryhaline and introduced species were excluded based on information available in the original sources or in Fishbase (Froese and Pauly 2011). We considered 26 subdrainages of the Orinoco River basin as our sampling units: Alto Orinoco, Apure, Arauca, Aro, Atabapo, Bita, Capanaparo, Caris, Caroni, Cataniapo, Caura, Cinaruco, Cuchivero, Guaviare, Inirida, Manapiare, Meta, Morichal-Largo, Pao, Parguaza, Sipapo-Cuao, Suapure, Tomo, Venturi, Vichada, and Zuata (Fig. 2). The Casiquiare subdrainage was excluded because fish fauna exchanges with the Amazon River basin are known to frequently occur in this zone (Fig. 2, Willis et al. 2010). We registered for each subdrainage total and endemic (i.e. species unique to a single subdrainage) species richness. To guarantee that endemic species assigned to a subdrainage

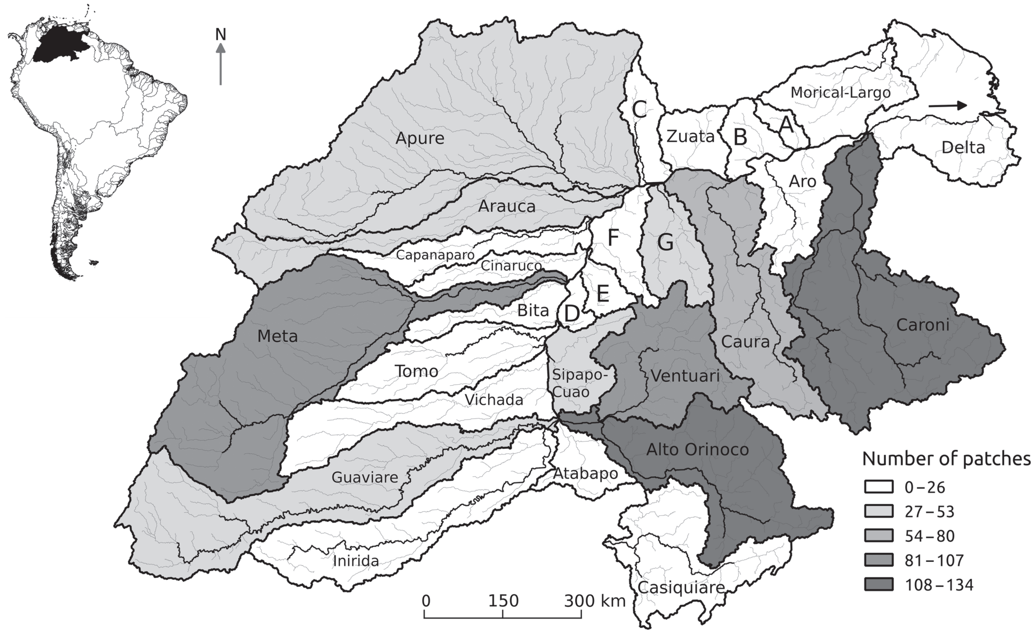


Figure 2. Number of patches within subdrainages of the Orinoco River basin. Names of small subdrainages: A = Caris, B = Pao, C = Manapire, D = Cataniapo, E = Parguaza, F = Suapure and G = Cuchivero. The arrow on the Delta region indicates the flow direction.

were not present in other South American river drainage basins, we searched for their distribution using information from Fishbase (Froese and Pauly 2011) and from the most comprehensive spatial database currently available on global riverine fish distribution (Brosse et al. 2013, Tedesco et al. 2012).

Speciation metrics

To examine the effects of the longitudinal gradient and of river network fragmentation due to waterfalls as drivers of fish speciation within subdrainages, we used first overall endemic species richness in each subdrainage as a substitute for speciation intensity. However, as overall endemic species richness may not be a good proxy to quantify speciation (Chen and He 2009, Kisel and Barraclough 2010, Tedesco et al. 2012), we further considered the number of endemic species that presumably arose from in-situ (i.e. within a given subdrainage) cladogenetic speciation (hereafter called neo-endemics, sensu Tedesco et al. 2012) as a more accurate measure of speciation intensity. To define neo-endemics we followed the method proposed by Coyne and Price (2000) considering that the presence of two or more endemic species from the same genus should reflect in-situ speciation (i.e. neo-endemic species). Finally, we applied a third speciation metric following Kisel and Barraclough (2010). Based on Coyne and Price's method, these authors quantified an index (or probability) of speciation as the number of genera with two or more endemic species divided by the number of genera with one or more endemic species (Kisel and Barraclough 2010, Tedesco et al. 2012). This last approach focuses on the ability of lineages to speciate rather than on what controls the size of radiations, which is better reflected by the number of neo-endemic species. Using only genera with endemic species also excludes lineages that have not been isolated or not been present long enough to speciate within subdrainages (Kisel and Barraclough 2010). Consequently, we excluded subdrainages for which no endemic species was recorded: Apure, Arauca, Bita, Capanaparo, Caris, Cuchivero, Manapiare, Pao, Vichada and Zuata. The index varies between 0 and 1, a value of 0 indicating no in situ speciation and a value of 1 indicating that all genera have undergone in situ speciation.

Environmental predictors

We used a set of environmental layers of 30-arcsec resolution (ca 1 × 1 km in the study zone) to estimate for each subdrainage variables related to isolation, energy availability and habitat size (see Supplementary material Appendix 1, Table A1 for a list of variables and sources). All these variables are known to be important predictors of total and endemic riverine fish species richness at large spatial grains and extents (Oberdorff et al. 2011). Energy availability and habitat size were measured using subdrainage mean annual net primary productivity (NPP, g carbon m^{-2}) and total surface area (area, km^2), respectively.

The degree of subdrainages isolation was estimated by using two measures acting at two different spatial extents. First, assuming an isolation gradient from upstream to downstream areas (Fig. 1), we used the distance from the confluence of each subdrainage with the main channel to the mouth of the Orinoco River (DistD) as a measure of subdrainage position along the longitudinal gradient. Second, natural waterfalls were considered as a surrogate for habitat fragmentation in each subdrainage. Based on elevation data at 3-arcsec resolution, we defined a waterfall as a slope greater than 30% between two adjacent grid cells (i.e. a difference in elevation of ca 30 m between two adjacent grid cells) along the river course (sensu knickpoints; Crosby and Whipple 2006). Since there is no consensus on which waterfall height can be considered as an insurmountable barrier for freshwater fishes, we considered such a threshold as a barrier high enough to prevent any upstream (and most downstream) fish dispersal. Then, we calculated the number of patches (continuous drainage area between two waterfalls) within each subdrainage. Assuming that small patches should prevent the establishment and maintenance of any fish population, we only considered patches having a surface area equal or greater than 13 km^2. According to Tedesco et al. (2012), this surface is the smallest area where a fish population can persist (i.e. the smallest drainage basin where a strictly freshwater fish species has been found so far).

Statistical analysis

We evaluated the effects of subdrainages' longitudinal position and fragmentation caused by waterfalls on total, endemic and neo-endemic species richness using multiple linear regression models. Area, number of patches, DistD and mean NPP values for each subdrainage were used as predictor variables in all models. When analyzing endemic and neo-endemic species richness, we added the total species richness as a covariate because this variable is known to partly explain endemic species richness (Oberdorff et al. 1999, Tedesco et al. 2012). Furthermore, in order to account for potential sampling biases present in our fish distribution dataset, we used a value ranging from one to four that broadly reflects the sampling intensity applied for each subdrainage. This last categorical variable was empirically established based on the experience and knowledge of several freshwater fish regional experts who assigned a 'sampling effort' value to each subbasin based on their own samplings and completeness of regional museum collections (Lasso et al. 2004b, p. 47); this variable was included in all models. Because the effects of fragmentation by waterfalls on species richness and endemism might vary with the location of subdrainages along the river main channel, we tested in all models the effect of an interaction term between these two variables. However, this interaction term neither produced a significant effect nor changed the effects of the other variables (results not presented). Except for the sampling intensity variable, all response and predictive variables were $\ln(x + 1)$-transformed to improve normality. To analyze the index of speciation we used a generalized linear model (GLM) with binomial distribution including all predictor variables except total richness and accounting for the number of genera having at least one endemic species. For comparative purposes, we estimated the fit (R^2) of the GLM model using null and residual deviances $[(\text{Null} - \text{Residual}) \times \text{Null}^{-1}]$. Multicollinearity in models was checked using a variance inflation factor (VIF) procedure but it revealed no strong collinearity among predictors (VIF: mean = 1.86, range = 1.23–2.97, standard deviation = 0.46).

After building full models, stepwise procedures were implemented to determine the most important variables in each model based on Akaike's information criterion (AIC). We applied a hierarchical partitioning procedure to determine the proportion of variance independently explained by each predictor (%PV) in the models, highlighting those that most contributed to the model fit. Finally, we ensured for the absence of spatial autocorrelation in model residuals using watercourse distances, Moran's I coefficients and correlograms. All analyses were carried out in R environment (R Development Core Team) using lm, glm, step, correlog and hier.part functions from stats, pgirmess (Giraudoux 2011) and hier.part (Walsh and Mac Nally 2008) packages, respectively.

Results

There are 874 species of strictly freshwater fishes listed so far for all subdrainages of the Orinoco River basin. From this species pool, 12% (107) are considered as endemics among which 25 were classified as neo-endemic species (Supplementary material Appendix 2, Table A2). The number of patches by subdrainage is highly variable, ranging from zero (i.e. no waterfalls fragmenting a subdrainage) to 134 (mean = 29, SD = 41, Fig. 2). Alto Orinoco, Caroni and Meta subdrainages have the highest number of patches (134, 118 and 100, respectively) while Meta and Caroni have the highest endemic richness values (endemic richness: 23 and 16, neo-endemic richness: 8 and 7, respectively) and also highest number of genus containing neo-endemic species (*Apistoloricaria*, *Astroblepus*, *Bryconamericus* and *Corydoras*; *Lebiasina*, *Neblinichthys* and *Trichomycterus*, respectively).

The model explaining total species richness accounts for 28% of the variability and it identifies sampling intensity as a positive and significant predictor, while subdrainage size has a marginally significant effect. The stepwise-selected model identifies these two variables as significant predictors and confirmed that the number of patches and longitudinal gradient position (as measured by DistD) of subdrainages are unrelated to total species richness (Fig. 3A, Table 1). The model explaining endemic species richness accounts for 70% of the variability and identifies subdrainage size and energy availability (as measured by NPP) as positive and significant predictors (Table 1), while sampling intensity shows a marginally significant effect. The stepwise procedure further identifies a marginally significant effect of total richness on endemic species richness (Table 1). We found no significant effect of the number of patches (Fig. 3B) or of the longitudinal gradient position on endemic species richness.

The neo-endemic species richness model explains 21% of the variance and indicates a marginally significant positive influence of the number of patches (Fig. 3C). This tendency is confirmed by the stepwise procedure, which identifies the number of patches as the only significant predictor of neo-endemic species richness in a model accounting for 37% of total variability (Table 1). Finally, the speciation index was not significantly related to any of the predictors. However, the model having the lowest AIC value only includes the number of patches, albeit not significantly (Table 1, Fig. 3D). Whatever the models, DistD was never identified as a significant predictor. Finally, spatial

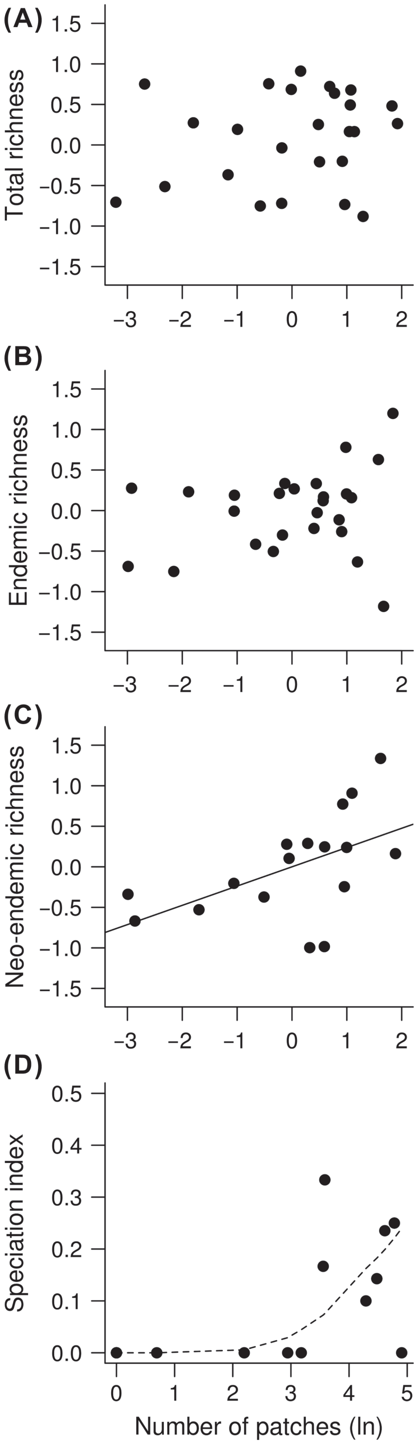


Figure 3. Partial-regression plots showing partial effects between the number of patches and (A) total, (B) endemics and (C) neo-endemic species richness extracted from full multiple linear models. Partial slopes (ß), %PV and p-values from full models are given in Table 1. (D) Relationship between the speciation index and the log-transformed number of patches. The solid line (C) represents a significant effect and the dashed line (D) shows a lowess (tension parameter = 0.6).

autocorrelation at the first distance class estimated from all model residuals shows non-significant Moran's I values (Supplementary material Appendix 1, Fig. A1).

Discussion

Habitat fragmentation has conflicting consequences on biodiversity. Theory predicts that subsequent to isolation, extinction probabilities increase in fragmented habitats where isolated populations cannot be rescued by immigrants from neighboring areas (MacArthur and Wilson 1967). Conversely, lower genetic exchanges among populations of isolated habitats enhance diversification (Gavrilets and Losos 2009, Kisel and Barraclough 2010, but see Losos 2010), promoting higher speciation rates at evolutionary time scales. Our study sheds light on the geomorphological features promoting diversification processes in a tropical species-rich aquatic realm, the Orinoco River basin. This riverine system became fully established after the rapid uplift of the Andean mountains about 7 Ma ago, a period since which some northern South American taxa (e.g. highland plants, bees, birds and rodents) have exponentially diversified producing the current outstanding biodiversity levels (Hoorn et al. 2010). Indeed, according to phylogenetic and fossil evidences, the major freshwater fish biogeographic patterns presently found in the Orinoco region probably originated during this period (Albert and Carvalho 2011).

As predicted by our schematic framework (Fig. 1), we found higher neo-endemism richness in fragmented subdrainages and a positive relationship with subdrainages fragmentation level (i.e. the number of patches created by natural waterfalls within subdrainages). Similarly, our speciation index also showed higher values in fragmented subdrainages and a clearly positive, albeit not significant, trend with fragmentation level. These findings support the hypothesis that fragmentation by waterfalls generates cladogenetic speciation within-subdrainages, a process that similarly affects highly isolated islands and lakes, where local speciation has largely contributed to an increase in endemism richness over evolutionary timescales (Heaney 2000, Losos and Schluter 2000, Barluenga et al. 2006, Seehausen 2006, Algar and Losos 2011). In our study, there was no significant relationship between overall or endemic fish richness and subdrainages fragmentation level (Fig. 3A, B). This result indicates that, even though new species may have been generated by cladogenetic processes, extinction rates could slightly overcome speciation rates, making total and endemic richness independent of the degree of subdrainages fragmentation.

Contrary to our expectations, none of our diversity descriptors was significantly affected by subdrainages position along the longitudinal gradient. This result suggests that the isolation of a subdrainage due to its position along the longitudinal river gradient is not an important factor driving diversity patterns, at least at the spatial scale applied here. This finding partly contradicts results of previous studies highlighting an increase in subdrainages species richness along the longitudinal gradient due to a longitudinal increase in the size of the species pool (Oberdorff et al. 1997). A possible explanation for this discrepancy is the existing link between the Orinoco and the Amazon River basins in the Casiquiare region (upstream region of the Orinoco River, Fig. 2). This natural waterway connecting the two river basins is considered as the Casiquiare River capture by the Negro River (Amazon basin) and acts as a

Table 1. Partial slope coefficients (ß), percentages of partitioned variance through hierarchical partitioning (%PV) and partial p-values [ß (%PV; p), respectively] from linear (total, endemic and neo-endemic species richness) and generalized linear models (speciation index) from subdrainages of the Orinoco River basin (see Methods for abbreviations). Both results from full models (using all predictors) and stepwise-selected variables (based on Akaike's information criterion) are presented. Significant p-values are given in bold.

	Partial coefficients [ß (%PV; p)]			
Variables	Total richness	Endemics	Neo-endemics	Speciation index
Full models				
Waterfalls				
Ln(Npatches)	0.0918 (17.5; 0.448)	0.0932 (21.3; 0.288)	0.2376 (51.4; 0.078)	0.6686 (63.1; 0.257)
Local				
Ln(DistD)	0.0964 (1.6; 0.616)	−0.0508 (0.9; 0.711)	−0.1256 (2.7; 0.484)	−0.2248 (1.6; 0.581)
Ln(Area)	0.3983 (42.5; 0.052)	**0.3806 (28.5; 0.021)**	0.1604 (27.1; 0.477)	−0.0066 (26.7; 0.995)
Sampling intensity	**0.3557 (35.8; 0.048)**	0.2440 (8.7; 0.080)	−0.0284 (2.7; 0.910)	−0.1808 (3.6; 0.723)
Ln(Total richness)	–	0.2670 (21.0; 0.108)	0.0264 (8.3; 0.938)	–
Current climate				
Ln(NPP)	−0.1089 (2.6; 0.845)	**0.9535 (19.6; 0.024)**	−0.2118 (7.7; 0.735)	−1.0693 (5.0; 0.532)
Adjusted R^2	0.2797	0.6977	0.2066	0.5416[#]
p-values	**0.0377**	**0.0000**	0.2199	–
AIC	69.59	52.32	42.53	29.60
Selected variables (stepwise)				
Waterfalls				
Ln(Npatches)			**0.2497 (100; 0.006)**	0.6921 (100; 0.134)
Local				
Ln(DistD)				
Ln(Area)	**0.4903 (64.5; 0.004)**	**0.4392 (36.4; 0.004)**		
Sampling intensity	**0.3133 (35.5; 0.034)**	**0.2615 (8.9; 0.039)**		
Ln(Total richness)	–	0.2908 (25.3; 0.069)		–
Current climate				
Ln(NPP)		**1.1904 (29.4; 0.001)**		
Adjusted R^2	0.3402	0.7082	0.3663	0.4731[#]
p-values	**0.0032**	**0.0000**	**0.0060**	–
AIC	64.90	50.00	35.60	22.30

[#] Estimated through model deviances [(Null − Residual) × Null^{-1}].

selective corridor for fish fauna exchanges from both river basins (Willis et al. 2007, 2010, Winemiller et al. 2008). Therefore, this connection can reduce the upstream-downstream isolation gradient created by the unidirectional hydrological flow and could explain the absence of a species richness gradient along the fluvial continuum.

In addition to the prominent role of fragmentation on shaping current freshwater fish diversity and in accordance with previous findings (Oberdorff et al. 1999, Tisseuil et al. pers. comm.), our results also show positive and significant effects of subdrainages size and energy availability on endemic species richness. These relationships have been attributed to two different non-exclusive evolutionary mechanisms (Hugueny et al. 2010, Oberdorff et al. 2011): 1) larger areas are more heterogeneous, promoting in fine higher speciation rates (Losos and Schluter 2000) and 2) energy availability increases resources available for a biological community favoring in fine specialization processes (Evans et al. 2005). However, as subdrainages size and energy availability were not significantly related to our other speciation descriptors (Table 1), we suggest that habitat size or energy availability per se are not conditioning speciation intensity in our system.

To conclude, our results corroborate the assumption that speciation processes are important factors determining biogeographic diversity patterns (Losos and Schluter 2000, Chen and He 2009, Schluter 2009) by showing that speciation processes have shaped in part the regional diversity patterns of endemic freshwater fishes of the Orinoco River basin, through natural fragmentation of the aquatic networks created by waterfalls.

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Supplementary material (Appendix E7724 at <www.oikosoffice.lu.se/appendix>). Appendix 1, 2.

Appendix A1

Dias, M.S., Cornu, J.-F., Oberdorff, T., Lasso, C.A., and Tedesco, P.A. 0000. Natural fragmentation in river networks as a driver of speciation for freshwater fishes. – Ecography 000: 000-000.

Table A1 Environmental variables utilized in this study, their abbreviation and reference sources.

Variables	Abbreviation	Sources
Mean annual net terrestrial primary productivity (g-Carbon m^{-2})	NPP	CIESIN layers (≈ 1x1 km resolution; sedac.ciesin.columbia.edu/es/hanpp.html)
Watercourse distances from the mouth of Orinoco river (km)	DistD	This study (≈ 1x1 km resolution)
Area of sub-drainages (km^2)	Area	HydroSHEDS layers (≈ 1x1 km resolution; hydrosheds.cr.usgs.gov)
Elevation data (m)	Elev	SRTM radar (≈ 90x90 m resolution) (Farr et al. 2007)
Number of patches (continuous drainage area between two waterfalls)	Npatches	This study (Elev data, above; knickpoints) (Crosby and Whipple 2006)
Sampling intensity	-	This study

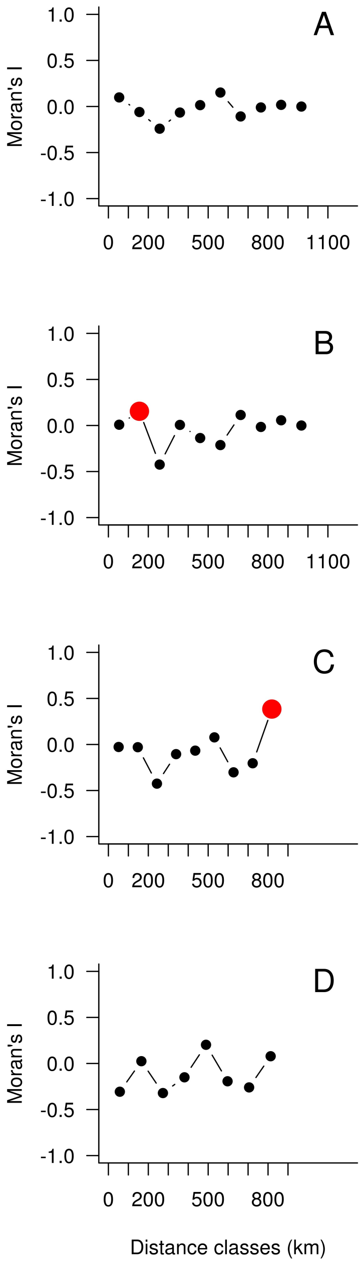

Figure A1 Correlograms of the model's residuals for (A) total, (B) endemic, (C) neo-endemic species richness and (D) speciation index. The numbers of classes were defined by Sturges' rule and red dots are significant values.

Supplementary literature cited

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Table A2 Endemic freshwater fishes distributed through the sub-drainages of the Orinoco River Basin.

Order	Family	Species	Alto Orinoco	Ventuari	Atabapo	Inirida	Guaviare	Vichada	Sipapo-Cuao	Tomo	Cataniapo	Bita	Meta	Parguaza	Cinaruco	Suapure	Capanaparo	Arauca	Apure	Cuchivero	Manapiare	Zuata	Caura	Pao	Aro	Caris	Caroni	Morichal-Largo	Occurrence
Siluriformes	Loricariidae	Acestridium colombiensis				1																							1
Perciformes	Cichlidae	Aequidens chimantanus																									1		1
Characiformes	Anostomidae	Anostomoides atrianalis		1																									1
Perciformes	Cichlidae	Apistogramma guttata																										1	1
Perciformes	Cichlidae	Apistogramma iniridae				1																							1
Perciformes	Cichlidae	Apistogramma viejita											1																1
Siluriformes	Loricariidae	Apistoloricaria laani											1																1
Siluriformes	Loricariidae	Apistoloricaria listrorhinos											1																1
Gymnotiformes	Apteronotidae	Apteronotus galvisi											1																1
Gymnotiformes	Apteronotidae	Apteronotus apurensis																	1										1
Siluriformes	Astroblepidae	Astroblepus latidens											1																1
Siluriformes	Astroblepidae	Astroblepus mariae											1																1
Siluriformes	Astroblepidae	Astroblepus marmoratus	1																										1
Characiformes	Characidae	Astyanax superbus																	1										1
Cyprinodontiformes	Rivulidae	Austrofundulus transilis																	1										1
Characiformes	Characidae	Axelrodia riesei											1																1
Siluriformes	Heptapteridae	Brachyglanis magoi																									1		1
Siluriformes	Heptapteridae	Brachyrhamdia imitator																					1						1
Characiformes	Characidae	Brycon coquenani																									1		1
Characiformes	Characidae	Bryconamericus cristiani											1																1
Characiformes	Characidae	Bryconamericus loisae											1																1
Characiformes	Characidae	Bryconamericus singularis													1														1
Characiformes	Characidae	Bryconops imitator																					1						1
Characiformes	Characidae	Bryconops vibex									1																		1
Characiformes	Characidae	Bryconops colanegra																									1		1
Characiformes	Characidae	Bryconops collettei																					1						1
Perciformes	Cichlidae	Cichlasoma orinocense											1																1
Characiformes	Characidae	Charax apurensis														1													1
Siluriformes	Loricariidae	Cordylancistrus torbesensis																	1										1
Siluriformes	Callichthyidae	Corydoras boehlkei																					1						1
Siluriformes	Callichthyidae	Corydoras concolor												1															1
Siluriformes	Callichthyidae	Corydoras esperanzae											1																1
Siluriformes	Callichthyidae	Corydoras habrosus	1																										1

cont...																													
Order	Family	Species	Alto Orinoco	Ventuari	Atabapo	Inirida	Guaviare	Vichada	Sipapo-Cuao	Tomo	Cataniapo	Bita	Meta	Parguaza	Cinaruco	Suapure	Capanaparo	Arauca	Apure	Cuchivero	Manapiare	Zuata	Caura	Pao	Aro	Caris	Caroni	Morichal-Largo	Occurrence
Siluriformes	Callichthyidae	Corydoras loxozonus											1																1
Siluriformes	Callichthyidae	Corydoras melanotaenia											1																1
Siluriformes	Callichthyidae	Corydoras metae											1																1
Characiformes	Characidae	Creagrutus calai											1																1
Characiformes	Characidae	Creagrutus veruina									1																		1
Characiformes	Characidae	Creagrutus xiphos																					1						1
Perciformes	Cichlidae	Crenicichla zebrina		1																									1
Characiformes	Curimatidae	Cyphocharax meniscaprorus																							1				1
Perciformes	Cichlidae	Dicrossus gladicauda			1																								1
Siluriformes	Loricariidae	Dolichancistrus fuesslii	1																										1
Siluriformes	Aspredinidae	Ernstichthys anduzei																	1										1
Siluriformes	Auchenipteridae	Entomocorus gameroi																	1										1
Siluriformes	Loricariidae	Farlowella colombiensis											1																1
Perciformes	Cichlidae	Guianacara stergiosi																									1		1
Siluriformes	Loricariidae	Harttia merevari																					1						1
Siluriformes	Loricariidae	Hypancistrus contradens		1																									1
Siluriformes	Loricariidae	Hypancistrus debilittera			1																								1
Siluriformes	Loricariidae	Hypancistrus lunaorum		1																									1
Siluriformes	Aspredinidae	Hoplomyzon sexpapilostoma																	1										1
Characiformes	Characidae	Hemigrammus taphorni																					1						1
Siluriformes	Cetopsidae	Helogenes uruyensis																									1		1
Characiformes	Characidae	Hyphessobrycon albolineatum							1																				1
Characiformes	Characidae	Hyphessobrycon hildae							1																				1
Characiformes	Characidae	Hyphessobrycon saizi											1																1
Siluriformes	Heptapteridae	Imparfinis microps											1																1
Siluriformes	Trichomycteridae	Ituglanis guayaberensis					1																						1
Characiformes	Lebiasinidae	Lebiasina provenzanoi																									1		1
Characiformes	Lebiasinidae	Lebiasina taphorni																					1						1
Characiformes	Lebiasinidae	Lebiasina uruyensis																									1		1
Characiformes	Lebiasinidae	Lebiasina yuruaniensis																									1		1
Siluriformes	Loricariidae	Leporacanthicus triactis	1																										1
Characiformes	Anostomidae	Leporinus boehlkei											1																1
Characiformes	Anostomidae	Leporinus punctatus																					1						1
Siluriformes	Loricariidae	Lithogenes wahari							1																				1
Siluriformes	Loricariidae	Lithoxus jantjae		1																									1
Cyprinodontiformes	Rivulidae	Rachovia stellifer																	1										1

cont...																													
Order	Family	Species	Alto Orinoco	Ventuari	Atabapo	Inirida	Guaviare	Vichada	Sipapo-Cuao	Tomo	Cataniapo	Bita	Meta	Parguaza	Cinaruco	Suapure	Capanaparo	Arauca	Apure	Cuchivero	Manapiare	Zuata	Caura	Pao	Aro	Caris	Caroni	Morichal-Largo	Occurrence
Cyprinodontiformes	Rivulidae	Micromoema xiphophora		1																									1
Characiformes	Characidae	Moenkhausia schultzi							1																				1
Perciformes	Cichlidae	Nannacara sp.																										1	1
Siluriformes	Loricariidae	Neblinichthys roraima																									1		1
Siluriformes	Loricariidae	Neblinichthys yaravi																									1		1
Siluriformes	Doradidae	Oxydoras sifontesi																							1				1
Siluriformes	Heptapteridae	Phenacorhamdia anisura																							1				1
Siluriformes	Heptapteridae	Phenacorhamdia macarenensis					1																						1
Siluriformes	Heptapteridae	Pimelodella figueroai					1																						1
Siluriformes	Heptapteridae	Pimelodella pallida					1																						1
Siluriformes	Heptapteridae	Pimelodella metae											1																1
Siluriformes	Pimelodidae	Pimelodus garciabarrigai					1																						1
Characiformes	Characidae	Pristobrycon careospinus			1																								1
Siluriformes	Loricariidae	Lithoxancistrus orinoco								1																			1
Siluriformes	Loricariidae	Pseudancistrus reus																									1		1
Siluriformes	Loricariidae	Pseudancistrus yekuana		1																									1
Siluriformes	Pimelodidae	Pseudoplatystoma orinocoense																	1										1
Siluriformes	Auchenipteridae	Pseudepapterus gracilis																					1						1
Cyprinodontiformes	Rivulidae	Gnatholebias hoignei																	1										1
Cyprinodontiformes	Rivulidae	Renova oscari	1																										1
Gymnotiformes	Sternopygidae	Rhabdolichops zareti																	1										1
Gymnotiformes	Rhamphichthyidae	Rhamphichthys apurensis																	1										1
Cyprinodontiformes	Rivulidae	Rivulus altivelis				1																							1
Cyprinodontiformes	Rivulidae	Rivulus nicoi		1																									1
Cyprinodontiformes	Rivulidae	Rivulus tesselatus											1																1
Cyprinodontiformes	Rivulidae	Rivulus caurae																					1						1
Cyprinodontiformes	Rivulidae	Rivulus sape																									1		1
Characiformes	Characidae	Roeboides numerosus																	1										1
Siluriformes	Trichomycteridae	Schultzichthys gracilis					1																						1
Characiformes	Characidae	Schultzites axelrodi											1																1
Characiformes	Characidae	Serrasalmus nalseni																										1	1
Gymnotiformes	Apteronotidae	Sternarchorhynchus gnomus																									1		1
Cyprinodontiformes	Rivulidae	Terranatos dolichopterus																	1										1
Siluriformes	Trichomycteridae	Trichomycterus celsae																									1		1
Siluriformes	Trichomycteridae	Trichomycterus lewi																									1		1
Siluriformes	Trichomycteridae	Trichomycterus migrans					1																						1

cont...																													
Order	Family	Species	Alto Orinoco	Ventuari	Atabapo	Inirida	Guaviare	Vichada	Sipapo-Cuao	Tomo	Cataniapo	Bita	Meta	Parguaza	Cinaruco	Suapure	Capanaparo	Arauca	Apure	Cuchivero	Manapiare	Zuata	Caura	Pao	Aro	Caris	Caroni	Morichal-Largo	Occurrence
Siluriformes	Trichomycteridae	Trichomycterus dorsostriatus											1																1
Perciformes	Cichlidae	Uaru fernandezyepezi			1																								1

Global imprint of historical connectivity on freshwater fish biodiversity

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ECOLOGY LETTERS

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LETTER

Global imprint of historical connectivity on freshwater fish biodiversity

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Abstract

The relative importance of contemporary and historical processes is central for understanding biodiversity patterns. While several studies show that past conditions can partly explain the current biodiversity patterns, the role of history remains elusive. We reconstructed palaeo-drainage basins under lower sea level conditions (Last Glacial Maximum) to test whether the historical connectivity between basins left an imprint on the global patterns of freshwater fish biodiversity. After controlling for contemporary and past environmental conditions, we found that palaeo-connected basins displayed greater species richness but lower levels of endemism and beta diversity than did palaeo-disconnected basins. Palaeo-connected basins exhibited shallower distance decay of compositional similarity, suggesting that palaeo-river connections favoured the exchange of fish species. Finally, we found that a longer period of palaeo-connection resulted in lower levels of beta diversity. These findings reveal the first unambiguous results of the role played by history in explaining the global contemporary patterns of biodiversity.

Keywords

Alpha diversity, beta diversity, endemism, freshwater fish, global scale, history, Quaternary climate changes, richness, sea-level changes, species turnover.

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INTRODUCTION

Explaining the uneven distribution of species over large spatial scales is a major challenge in ecology and biogeography, and many ecological, evolutionary and historical mechanisms have been proposed to explain biodiversity patterns (e.g., Mittelbach *et al.* 2007; Field *et al.* 2009). However, the extent to which the past environmental changes have shaped current global biodiversity patterns remains a contentious issue and an active research area (Ricklefs 2004; Sandel *et al.* 2011). Until now, most large-scale studies testing the effect of historical imprints on current biodiversity patterns have focused on the impacts of temperature anomalies, glacial coverage or tropical aridity during the Quaternary period (e.g., Svenning & Skov 2007; Araújo *et al.* 2008; Hortal *et al.* 2011). However, these historical factors are highly correlated with the current climatic conditions, and separating their respective roles has therefore proven challenging (Kissling *et al.* 2012). We tackle this issue by evaluating the role of sea-level changes during the Last Glacial Maximum (LGM; 18-21 kya) in explaining the current biodiversity patterns of freshwater fishes, the most diverse group of all vertebrates. Specifically, we provide an unambiguous test of the role of history in shaping the current biodiversity patterns because the sea-level changes during the LGM are completely independent of the current climatic conditions.

River drainage basins are structured as dendritic networks with hierarchical branching ending in the sea, making them highly fragmented 'island-like' systems (Sepkoski & Rex 1974; Hugueny *et al.* 2010). Therefore, unlike vagile terrestrial organisms, the ability of strictly freshwater fish to move between drainage basins in response to climatic or geological changes is limited by the hydrological connectivity between these drainages. This implies that the opportunity for strictly freshwater fishes to expand their range across two or more drainage basins is only possible through two events: the geological/hydrological process of river capture or the confluence of river systems during low-sea-level periods due to climatic changes. Throughout the Quaternary period, the Earth's climate fluctuated periodically, resulting in sea-level changes that reconfigured the connectivity between river systems (Voris 2000). For instance, during the LGM drop in sea levels (i.e., up to 120 m), rivers mouths progressed through kilometres of exposed marine shelves before reaching the ocean, which resulted in a connection (i.e. palaeo-connected drainage basins; green-coloured drainages in Fig. 1a) or no connection (i.e., palaeo-disconnected river basins; red-, blue- and orange-coloured drainages in Fig. 1a) between previously isolated drainage basins.

In this study, we tested for the influence of palaeo-connections on the species richness, endemism and beta diversity of freshwater fishes using ocean bathymetry information to

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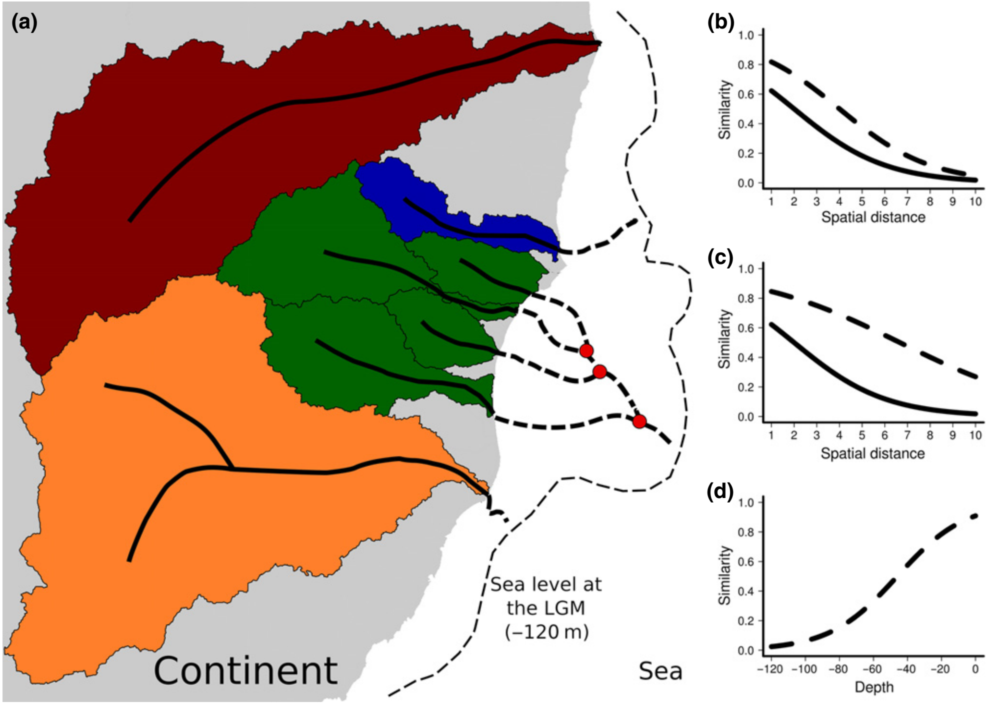

Figure 1 Coloured polygons (a) represent coastal drainage basins under current sea levels. The broken line represents the land expansion and river connections due to sea-level retraction during the LGM. The green basins are part of the same palaeo-drainage under the LGM conditions, while the other basins remained isolated. The expected effects of the palaeo-connection (broken line) and palaeo-disconnection (full line) on the distance–decay curves include (b) differences in the mean similarity for a given spatial distance if the dispersal limitation is similar for both groups and (c) changes in both the mean similarity and slope due to low dispersal limitation and homogenisation of fish fauna within palaeo-connected drainages. Using the depth at which the palaeo-confluences occurred [red dots in (a)] as a proxy of the connection time (a greater depth indicates a longer period of connection), we should observe (d) an increase in the species similarity with decreasing depth.

reconstruct the LGM palaeo-drainage basins worldwide. All factors being equal (i.e. controlling for other factors known to affect diversity), we expect the palaeo-connected drainage basins to host a higher number of fish species (compared with palaeo-disconnected ones) as a result of colonisation from other rivers within the same palaeo-drainage basin. We also expect lower levels of endemism (i.e. species restricted to a single drainage basin) in the palaeo-connected drainage basins because of the homogenising role of dispersal within palaeo-drainage basins (Tedesco *et al*. 2012). Furthermore, assuming that the differences between the drainage basins in both the past and current environmental conditions are comparable at similar geographical distances, we should observe (1) higher levels of the compositional similarity between pairs of basins that were connected through a palaeo-drainage basin compared with those that remained disconnected (Fig. 1b) or (2) higher mean levels of similarity combined with a shallower distance decay of the compositional similarity in palaeo-connected drainage basins (Fig. 1c), given that the breaching of the major marine dispersal barriers should favour the exchange of fish fauna. Finally, we evaluated the influence of the duration of the palaeo-connections between the drainage basins on fish compositional similarity. To test this assumption, we used the bathymetric levels (hereafter called depth) at which the palaeo-connections occurred (shown by red dots in Fig. 1a) as a proxy of the temporal window of the connection between the drainage basins, assuming that 'shallower' palaeo-connections persisted for a longer period of time. If a longer period allowed for a greater faunal exchange between the palaeo-connected drainage basins, we expect an increase in the similarity levels with a decrease in the depth of the palaeo-connection (Fig. 1d). Overall, our findings show that the historical connectivity between drainage basins caused by sea-level changes during the LGM left a marked worldwide imprint on the current alpha and beta diversity patterns of freshwater fish.

MATERIAL AND METHODS

Biological data

All diversity measures were based on a global data set that contained the occurrence of fish species in each drainage basin. This occurrence database was compiled from an extensive literature survey of fish species lists (including those considered recently extinct and excluding those introduced by recent human actions) obtained from published articles, books and gray literature. The survey yielded 14 717 species (nearly all freshwater fishes described until now; Lévêque *et al*. 2008) from 3031 drainage basins. The resulting data set is an extended version of the information used in previous analyses (Brosse *et al*. 2013) and represents the most comprehensive database of native freshwater fish occurrences per drainage basin available.

Assuming that drainage basins are isolated from each other by land and marine water (Hugueny *et al.* 2010), only native and strictly freshwater species were considered. Indeed, the migration of euryhaline or human-related species introductions would bias our distance–decay relationships. Endorheic drainage basins were excluded from the analysis because, by definition, past sea-level changes have not affected these drainages. Our final database consisted of 10 297 species and 2317 drainage basins (see Appendix S1).

All drainage basins were pooled into six broad biogeographic realms (i.e. Afrotropical, Australasia, Indomalaya, Nearctic, Neotropical and Palearctic; see Appendix S1 and Table S1). Such a procedure allows the regional effects of the historical connectivity between drainage basins to be evaluated while controlling for the uniqueness of regional species pools due to differences in the evolutionary history and/or taxonomic knowledge.

Alpha and beta diversity measures

The alpha diversity measures refer to the total number of native freshwater fish species and the number of endemic freshwater fish species; the latter corresponds to the number of species inhabiting a single drainage basin (sensu Oberdorff *et al.* 1999). By extension, the gamma diversity refers to the total richness of each biogeographic realm, and the beta diversity refers to changes in the species composition (i.e. compositional dissimilarity) between pairs of river basins within a given realm.

The compositional dissimilarity between drainage basins was estimated using the β_{jtu} index, a 'narrow-sense' measure of beta diversity that focuses on the compositional differences independent of the species richness differences (Baselga 2012). Recent studies have shown that richness gradients can distort species turnover patterns if the adopted dissimilarity measure (e.g. the Sørensen and Jaccard indices) incorporates the differences in species richness between localities (Baselga 2012). The β_{jtu} index is formulated as $\beta_{\text{jtu}} = [2 \times \min(b,c)]/[a + 2 \times \min(b,c)]$, where a is the number of species common to both drainages, b is the number of species occurring in the first drainage but not in the second and c is the number of species occurring in the second drainage but not in the first. Specifically, the β_{jtu} index measures the proportion of species that would be replaced among localities if both had the same number of species and therefore accounts for species turnover independent of differences in richness. The β_{jtu} index varies between 0 (total dissimilarity) and 1 (total similarity). To further assess the robustness of our results to other measures of beta diversity, we repeated the modelling framework described below (see Statistical analysis section) using the Sørensen and Simpson dissimilarity indices, which have been widely used in beta diversity studies (Graham *et al.* 2006; Soininen *et al.* 2007; Hortal *et al.* 2011).

Distance decay of similarity

The distance decay of similarity refers to the decrease in the compositional similarity between two localities as the geographical distance between them increases (Nekola & White 1999). The slope of the distance decay of similarity is widely used as a measure of species spatial turnover in ecological communities and can be interpreted as the rate of species replacement within the studied region (Nekola & White 1999). This pattern can be generated by two distinct, although not mutually exclusive, mechanisms (e.g., Soininen *et al.* 2007). First, the compositional similarity decays with geographical distance because of the decreasing similarity in environmental conditions combined with the differential ability of species to perform under those conditions (i.e. niche-based processes). Second, the spatial configuration of geographical barriers and organism dispersal abilities represent the dispersal constrains that limit species movements, resulting in decays of the compositional similarity with geographical distance (i.e., dispersal processes). By studying the effect of the LGM sea-level changes on freshwater fish assemblages, we focus on the second mechanism and account for the first (i.e. niche-based processes) by including the present and past environmental conditions in our models (see below).

Environmental data

The environmental factors known to explain freshwater fish alpha diversity patterns at the global scale (Tedesco *et al.* 2012; Tisseuil *et al.* 2013) were included in our modelling framework. These variables are related to the contemporary climate (i.e. temperature, precipitation, runoff, actual and potential evapotranspiration), habitat diversity/isolation (i.e. altitude, surface of the drainage basin, habitat diversity based on terrestrial biomes) and history (i.e. temperature anomaly from the LGM; Table S1) of the drainage basins. The mean values of all the variables were computed for each drainage basin using a Geographic Information System (see Table S1). The Quaternary climate stability (Jansson 2003) was defined as the change in the mean annual temperature between the present and LGM conditions (the average values based on two Global Circulation Models, Table S1).

A recent global-scale analysis showed that a particular set of environmental variables is a determinant of the turnover component of freshwater fish beta diversity (Leprieur *et al.* 2011). To account for the effect of environmental conditions on the compositional similarity of drainage basins, we used the same set of variables (Table S1) identified by Leprieur *et al.* (2011): temperature, precipitation, surface runoff, actual and potential evapotranspiration (i.e. current climatic effect); altitude (i.e. habitat diversity/isolation effect); and Quaternary climatic stability (i.e. historical effect). We computed Euclidean distance matrices for each of the three categories of environmental variables and used them as covariates in the models described below to control for their effect on the compositional similarity. The current climatic variables were previously scaled to a zero mean and unit SD to ensure equal weighting during the computation of the Euclidean distance matrix.

Geographic distance between drainage basins

We defined the geographical distance between drainage basins as the minimum number of drainage basin divides that would be crossed when travelling from one basin to another based on a neighbourhood graph, i.e. a connectivity matrix. By definition, a value of 1 corresponds to drainages that are contiguous (Fig. 1). This discrete distance proved useful when describing the distance–decay patterns of freshwater fish assemblages (Hugueny & Lévêque 1994) and allows the difficulty of defining the geographical Euclidean distances between river basins to be overcome. This geographical distance was computed for each realm based on a geo-referenced global river network (see Table S1), complemented by river networks and watershed polygons constructed for rivers beyond 60° N and 60° S (see Table S1).

Constructing palaeo-drainage basins

To generate the palaeo-drainages and their palaeo-connections, we applied a Flow Accumulation algorithm to the General Bathymetric Chart of the Oceans grid layer (GEBCO_08; www.gebco.net; 30-arc-second resolution). This data set consists of a global topographic map combined with bathymetric soundings of the sea floor from latitudes ranging from 80° N to 81° S. The Flow Accumulation starts with cells on land masses that have an upstream surface of at least 500 km^2 and progresses until sublittoral areas at -120 m below the current sea level (i.e. the sea level during the LGM; Voris 2000). The congruence between our drainage basins reconstruction and available data was evaluated for 328 drainage basins in six regions distributed in five realms. On average, we found 91% concordance between our palaeo-drainage reconstruction and the previous reconstructions reported in the literature, thus ensuring the accuracy of our bathymetric-based approach (see Fig. S1 for details). Finally, we estimated the bathymetric level at which two rivers were connected to each other during the LGM and used it as a proxy for the duration of connection time (Fig. 1d).

We exclusively considered the confluence of the river systems during the low-sea-level periods as a window of opportunity for strictly freshwater fishes to expand their ranges across the drainage basins and therefore did not account for other potential causes of past changes in river flow such as ice sheet barriers or isostatic depression and rebound during the retreat of ice sheets (e.g. Katz *et al.* 2011). To assess the robustness of our results regarding these potential biases, we repeated our analyses (see below) excluding drainage basins that were partially or entirely covered by ice sheets during the LGM (Tables S1–S3).

Statistical analysis

All models were performed separately for each realm. To test for differences in the species richness and endemism between drainage basins, we fitted Generalized Linear Models (GLM; Table S1) with Negative-Binomial error distributions to avoid overdispersion and because of high frequencies of small numbers and zeros. Both models comprised a binary variable that indicated the status of the basin during the LGM (palaeo-connected = 1, e.g. each green drainage from Fig. 1a; palaeo-disconnected = 0, e.g. orange, blue and red drainages from Fig. 1a) along with all of the covariates related to the current climate/available energy, habitat size/diversity and history. Some current climatic variables (i.e. temperature, precipitation and potential evapotranspiration) were excluded from the analysis to reach acceptable levels of multicollinearity among the predictors, which was measured using Variance Inflation Factors (VIF, Table S1) after model fitting. The surface area of the basin, elevation and runoff were log$_{10}$ transformed, and all of the covariates were standardised by centring and dividing by two SD. Finally, the log-transformed total native species richness was included in our models of endemism as a covariate to control for its effects on endemic species richness.

We hypothesised that pairs of basins connected during the LGM should have a higher faunal similarity than disconnected ones after accounting for the geographic distance and environmental dissimilarity. To test this hypothesis, we modelled the pairwise similarity (i.e. $1-\beta_{jtu}$) against the geographic distance (i.e. $\log_{10}[x + 1]$), the three environmental dissimilarity matrices (i.e. current climate, mean altitude and Quaternary climate stability) and a binary matrix that indicated whether (1) or not (0) a pair of basins were connected during the LGM. We opted for a GLM approach with a Quasi-Binomial error distribution with a *logit* link function. This framework has three advantages: (1) it accounts for values found between 0 and 1, (2) it handles similarity values of 0 (minimal similarity) and 1 (maximal similarity) without previous transformation and (3) it accounts for the usually curvilinear shape of the distance–decay plots. Within this framework, we expect the partial regression coefficient associated with the connectivity matrix to be positive. A problem caused by this type of analysis is that the cells of a similarity matrix are not statistically independent, making classic statistical tests invalid. The best way to test the significance of partial regression coefficients has been a matter of debate when the dependent and independent variables are distance matrices. The most comprehensive study conducted thus far on this topic (see the Appendix of Legendre & Fortin 2010) noted that some permutation methods provide good performance and are therefore recommended, while others lead to inflated Type I errors and should be avoided. In this study, we used one of the recommended methods that consisted on the permutation of the response variables (i.e. the rows and columns of the fish similarity matrix simultaneously) while the original order of the exploratory variables (i.e. the palaeo-connection, contiguity distance and covariate matrices) was held constant. Therefore, the statistical significance was assessed using the frequency at which the null simulated coefficients were higher and/or lower than the observed coefficients (i.e. unilateral or bilateral tests depending on the considered predictor; see Results). In the second step, we added an interaction term between the palaeo-connection factor and the adjacency distance to test for differences in the slope of the decay relationships between the palaeo-connected and disconnected drainage basins while accounting for the covariate effects (Fig. 1c).

Applying the same modelling procedure and accounting for the adjacency and environmental distances as covariates, we then focused only on pairs of drainage basins that were connected during the LGM to test the hypothesis of a positive relationship between fish community similarity and palaeo-confluence depth (as a proxy of connection duration; Fig. 1d). See Table S1 for references on the adopted statistical methods, programs and packages.

Table 1 Effects of the palaeo-connection and environmental descriptors on fish richness (a) and endemism (b)

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(a) Richness						
(intercept)	1.17 (±0.23)	1.01 (±0.07)	3.26 (±0.15)	2.34 (±0.12)	2.37 (±0.09)	2.41 (±0.06)
Historical factors						
Palaeo-connection	**0.30 (±0.10)**	**0.18 (±0.07)**	0.11 (±0.08)	**0.34 (±0.11)**	**0.21 (±0.08)**	**0.53 (±0.06)**
Mean Temp. Anomaly	**−2.87 (±0.60)**	**0.79 (±0.24)**	−0.04 (±0.33)	**0.40 (±0.15)**	−0.18 (±0.29)	0.18 (±0.09)
Current climate						
Mean AET	**1.36 (±0.16)**	**0.69 (±0.13)**	**0.23 (±0.09)**	**3.16 (±0.23)**	**1.60 (±0.17)**	**1.67 (±0.11)**
Mean runoff	0.08 (±0.15)	**0.21 (±0.10)**	**0.22 (±0.06)**	**−1.01 (±0.18)**	−0.10 (±0.11)	**−0.65 (±0.08)**
Habitat size/diversity						
Surface of drainage basin	**2.35 (±0.14)**	**1.58 (±0.10)**	**1.64 (±0.09)**	**1.67 (±0.19)**	**2.17 (±0.09)**	**1.14 (±0.07)**
Habitat diversity (IGBP)	**0.44 (±0.09)**	**0.18 (±0.08)**	**0.39 (±0.07)**	**0.30 (±0.14)**	**0.15 (±0.07)**	**0.57 (±0.06)**
Mean altitude	**0.33 (±0.16)**	**−0.54 (±0.10)**	**−0.40 (±0.10)**	−0.01 (±0.18)	**−0.64 (±0.08)**	−0.09 (±0.08)
N (number of basins)	219	367	346	158	372	850
AIC	1654	1303	2899	1099	2962	5351
Overdispersion parameter (k)	2.877	1242	3.102	3.361	2.458	2.599
Null deviance	1177.8	611.1	999.1	838.6	1628.3	1783.8
Residual deviance	220.7	284.4	367.7	158.4	390.3	870.9
Pseudo-R^2 † (%)	81.26	53.46	63.19	81.12	76.03	51.18
(b) Endemism						
(Intercept)	−5.82 (±1.20)	−6.68 (±1.24)	−7.34 (±0.91)	−9.03 (±1.07)	−5.69 (±0.48)	−5.65 (±0.66)
Historical factors						
Palaeo-connection	−0.16 (±0.35)	**−1.78 (±0.54)**	**−0.74 (±0.24)**	−0.23 (±0.38)	**−0.83 (±0.19)**	−0.64 (±0.35)
Mean Temp. Anomaly	−4.30 (±2.53)	**−5.53 (±2.52)**	−1.39 (±1.00)	**−3.55 (±0.88)**	0.12 (±0.81)	**−3.38 (±0.73)**
Current climate						
Mean AET	1.17 (±0.71)	0.98 (±1.18)	**2.37 (±0.43)**	−3.03 (±1.50)	−0.00 (±0.55)	0.08 (±0.89)
Mean runoff	0.26 (±0.65)	−0.52 (±1.10)	**−0.74 (±0.33)**	**2.35 (±0.83)**	−0.07 (±0.41)	**2.12 (±0.76)**
Habitat size/diversity						
Surface of drainage basin	**2.74 (±0.78)**	−1.20 (±1.01)	**1.76 (±0.49)**	0.73 (±1.34)	**0.83 (±0.39)**	**3.03 (±0.48)**
Habitat diversity (IGBP)	−0.19 (±0.34)	−0.35 (±0.70)	**0.68 (±0.30)**	−0.36 (±0.67)	0.31 (±0.16)	0.83 (±0.44)
Mean altitude	**3.33 (±0.97)**	**1.95 (±0.89)**	**1.27 (±0.42)**	**2.14 (±0.84)**	**1.61 (±0.28)**	0.32 (±0.55)
Species pool						
Total Richness [log(x + 1)]	0.37 (±0.25)	**1.69 (±0.51)**	**1.39 (±0.21)**	**2.45 (±0.43)**	**1.52 (±0.15)**	**1.30 (±0.23)**
AIC	368.0	160.6	527.8	209.2	686.1	427.5
Overdispersion parameter (k)	1.030	4.430	1.183	1.534	2.486	0.642
Null deviance	788.4	204.8	1091.7	567.1	3116.5	1058.0
Residual deviance	121.4	82.2	167.7	61.8	248.0	169.7
Pseudo-R^2 † (%)	84.60	59.85	84.64	89.11	92.04	83.96

†Estimated through model deviances: [(Null-Residual)/Null] × 100.

Bold values, $P < 0.05$.

Coefficients and standard errors (*log* link scale) are presented from the Generalized Linear Models with Negative-Binomial family distributions in which the total richness and endemism of strictly freshwater fish species were modelled against a binary variable indicating the drainage basin status at the LGM (palaeo-disconnected = 0, palaeo-connected = 1) and covariates of the current climate, habitat size/diversity and historical factors. Small values of the Variance Inflation Factor (VIF, mean = 3.26, SD = 1.94, range = 1.21–9.98) were found for all variables, indicating that multicollinearity did not affect our models.

RESULTS

The GLM results showed high values of pseudo-R^2 (ranging from 51 to 92%) and confirmed the importance of past and current environmental factors in explaining the present-day patterns of freshwater fish alpha diversity (Table 1). As expected from the increased dispersal possibilities under the LGM sea-level conditions (-120 m), the GLM results also showed overall higher total species richness and lower endemic species richness in palaeo-connected drainage basins compared with those that remained isolated (Table 1), with the exception of some realms. For instance, the palaeo-connected and palaeo-disconnected drainage basins displayed similar species richness in the Indomalaya realm and similar levels of endemism in the Afrotropical, Palearctic and Nearctic realms (Table 1).

Analysing the compositional similarity highlighted the significant effect of the palaeo-connection on the beta diversity patterns (Fig. 2). As expected, the GLM models identified a sharp decrease in fish compositional similarity (i.e. $1-\beta_{jtu}$) with increasing geographical distance between the drainage basins and significant, although less prominent, effects of the current climate, mean altitude and Quaternary climate stability. The models also revealed significant and positive effects of

Table 2 Effects of the palaeo-connection, distance between basins and environmental descriptors on assemblages' similarity

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(a) Without Interaction						
(intercept)	1.37 (±0.04)	**2.29 (±0.04)**	**3.85 (±0.08)**	**1.96 (±0.07)**	1.05 (±0.02)	**2.48 (±0.06)**
Palaeo-connection	−0.08 (±0.11)	**1.01 (±0.07)**	−1.34 (±0.11)	**1.36 (±0.27)**	**0.61 (±0.04)**	**0.93 (±0.08)**
Geographic distance	**−3.46 (±0.07)**	**−2.79 (±0.05)**	**−3.37 (±0.09)**	**−1.70 (±0.11)**	**−2.77 (±0.02)**	**−3.33 (±0.06)**
Interaction term	–	–	–	–	–	–
Covariates						
Temp. Anomaly (distance)	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.00 (±0.00)**	**−0.01 (±0.00)**	**0.00 (±0.00)**
Mean Altitude (distance)	0.00 (±0.00)	−0.00 (±0.00)	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**
Current Climate (distance)	**−0.12 (±0.01)**	0.00 (±0.01)	**−0.24 (±0.01)**	**−0.31 (±0.01)**	**−0.13 (±0.00)**	**−0.23 (±0.01)**
N (# of pairwise observations)	18337	35507	14602	12246	55630	160933
Null deviance	6714.8	32650.0	13846.0	8367.1	13681.1	90882.0
Residual deviance	3441.3	21857.0	6443.4	5882.4	6925.2	58402.0
Pseudo-R^{2} † (%)	**48.75**	**33.06**	**53.46**	**29.70**	**49.38**	**35.74**
(b) With Interaction						
(intercept)	1.37 (±0.04)	**2.35 (±0.04)**	**4.02 (±0.08)**	**1.99 (±0.08)**	1.07 (±0.02)	**2.54 (±0.06)**
Palaeo-connection	−0.09 (±0.14)	−0.13 (±0.13)	−2.43 (±0.16)	0.37 (±0.34)	0.20 (±0.06)	−0.11 (±0.21)
Geographic distance	**−3.46 (±0.07)**	**−2.86 (±0.05)**	**−3.62 (±0.10)**	**−1.75 (±0.11)**	**−2.80 (±0.02)**	**−3.40 (±0.07)**
Interaction term	0.15 (±0.72)	**2.17 (±0.24)**	**2.18 (±0.26)**	**2.70 (±0.76)**	**0.99 (±0.13)**	**1.44 (±0.27)**
Covariates						
Temp. Anomaly (distance)	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.03 (±0.00)**	**−0.00 (±0.00)**	**−0.01 (±0.00)**	**0.00 (±0.00)**
Mean Altitude (distance)	0.00 (±0.00)	−0.00 (±0.00)	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**	**−0.00 (±0.00)**
Current Climate (distance)	**−0.12 (±0.01)**	0.00 (±0.01)	**−0.21 (±0.01)**	**−0.31 (±0.01)**	**−0.13 (±0.00)**	**−0.23 (±0.01)**
Null deviance	6714.8	32650.0	13846.0	8367.1	13681.1	90882.0
Residual deviance	3441.3	21807.0	6372.7	5874.1	6916.2	58288.0
Pseudo-R^{2} † (%)	**48.75**	**33.21**	**53.97**	**29.80**	**49.45**	**35.86**

p bilateral: intercept, covariate distances, interaction term.

p unilateral: palaeo-connection, geographical distance and pseudo-R^{2}.

See Table 1 footnotes.

We fitted models without (a) and with (b) the interaction term between the palaeo-connection and geographic distance. Coefficients and standard errors (*logit* link scale) are presented from the Generalized Linear Models with Quasi-Binomial family distributions in which the beta diversity of strictly freshwater fishes due to species turnover ($1-\beta_{jtu}$, sensu Baselga 2012) was the response variable and the palaeo-connection (binary factor: connected = 1, disconnected = 0), geographic distance between the pairs of drainage basins, their interaction term and a series of environmental variables related to β_{jtu} (Leprieur *et al.* 2011) were the exploratory variables. Models were constructed for each realm, and significant factors were evaluated using Monte Carlo simulations (see Statistical analysis for details).

the palaeo-connection on the beta diversity values for the Australasian, Nearctic, Neotropical and Paleartic realms, showing that pairs of palaeo-connected drainages have higher levels of fish compositional similarity than do disconnected ones (Table 2a, Fig. 2). The pattern is particularly clear for the Australasia and Palearctic realms where the high similarity of the connected basins holds true at all geographical distance classes, while for the Neotropical and Nearctic realms, a discrepancy occurs for only one distance class. However, the Afrotropical and Indomalaya realms showed negative, although non-significant, differences between the palaeo-connected and palaeo-disconnected drainage basins. Including an interaction term between the palaeo-connection and the distance in the models confirmed the patterns observed in Fig. 2: significant differences in the slopes of the distance decay of similarity between the palaeo-connected and disconnected pairs of drainage basins (Table 2b). Indeed, the similarity values (i.e. $1-\beta_{jtu}$) decreased faster with an increasing distance between the pairs of palaeo-disconnected drainage basins in all realms, except for the Afrotropical one. Furthermore, it is worth noting that in some regions (e.g. Australasian, Neotropical and clearly in Palearctic; Fig. 2), the mean similarities per distance class in the palaeo-connected group tend to increase at geographic distances > 10. This is due to a decreasing number of palaeo-connected pairwise values at large distance classes and because the palaeo-connected basins from the concave-shaped regions tend to be similar in terms of their species composition but distant in terms of the adjacency distance metric (e.g. the 'U-shaped' regions formed between continental Europe and Scandinavia or between China and the Korean peninsula; Fig. 3 and Fig. S2).

Considering only pairs of palaeo-connected drainage basins and controlling for both the geographic and environmental distances, we found a positive and significant effect of the palaeo-connection depth on the fish similarity for the Indomalaya and Neotropical realms (Table 3).

Our results are robust to the use of alternative beta diversity measures (Table S4) and to the potential effects of other geological events related to the presence of ice sheets during glacial periods and related isostatic movements that might have influenced the river basin connections (i.e. by excluding the drainage basins that were entirely or partially

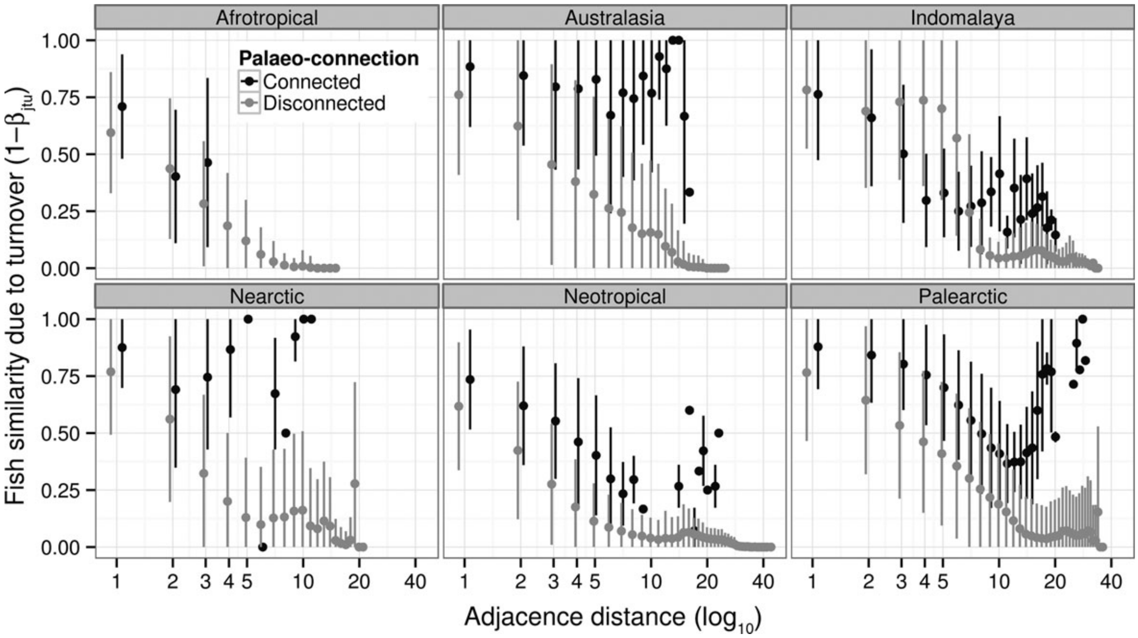

Figure 2 Distance decay of similarity due to turnover ($1-\beta_{\text{jtu}}$) between the drainage basins in each realm. The mean similarity (± 1 SD) per distance class is shown; black and gray correspond to similarities between pairs of palaeo-connected and disconnected drainage basins respectively.

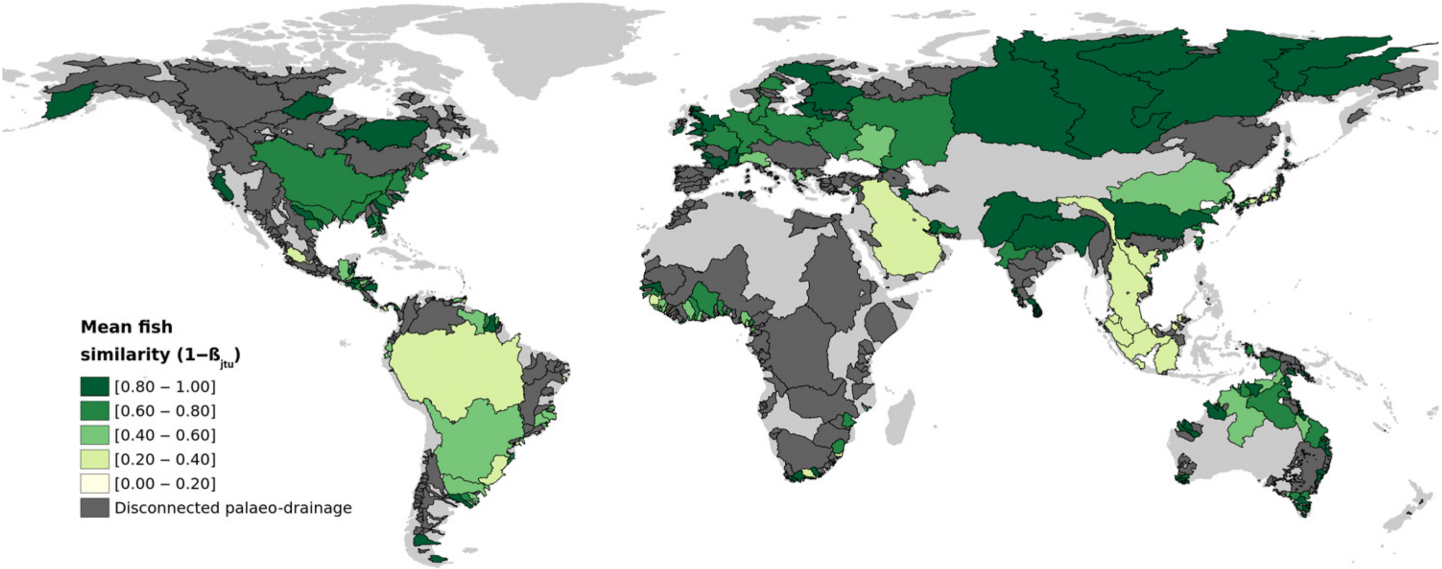

Figure 3 Mean similarity ($1-\beta_{\text{jtu}}$) of freshwater fish assemblages within palaeo-connected drainage basins. Dark gray areas indicate palaeo-disconnected drainages; light gray areas indicate no data or drainage basins that were not considered in this study.

covered by ice sheets during the LGM from our data set; Tables S2 and S3).

DISCUSSION

The imprint of palaeo-connections

The role of past climatic changes in explaining the current biodiversity patterns has been largely examined in both freshwater (e.g. Oberdorff *et al.* 1999; Bonada *et al.* 2009; Tedesco *et al.* 2012) and terrestrial ecosystems (e.g., Araújo *et al.* 2008; Hortal *et al.* 2011; Sandel *et al.* 2011; Baselga *et al.* 2012; Fitzpatrick *et al.* 2013). However, the historical factors used in these studies were most often highly correlated with the current climatic conditions, thus making it difficult to detect historical legacies in the present-day geographic patterns of biodiversity (Field *et al.* 2009; Kissling *et al.* 2012). Here, considering the influence of the past and current environmental factors that are already known to shape the large-scale alpha and beta diversity patterns of freshwater fishes (Leprieur *et al.* 2011; Tedesco *et al.* 2012; Tisseuil *et al.* 2013), our results clearly show an additional and unambiguous effect of the his-

Table 3 Effects of the palaeo-connection duration (i.e., depth, see Material and methods for details), geographic distance and environmental descriptors on the similarity of the drainage basin assemblages

Variables	Coefficients					
	Realms					
	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(intercept)	0.71 (±0.31)	**2.16 (±0.23)**	1.72 (±0.14)	1.52 (±0.48)	0.75 (±0.10)	**2.34 (±0.07)**
Depth	−0.01 (±0.00)	0.00 (±0.00)	**0.01 (±0.00)**	0.01 (±0.01)	**0.01 (±0.00)**	0.00 (±0.00)
Geographic distance	**−3.82 (±0.90)**	−0.66 (±0.29)	**−1.69 (±0.16)**	−1.13 (±0.75)	**−1.75 (±0.17)**	**−1.55 (±0.08)**
Covariates						
Temp. Anomaly (distance)	−0.01 (±0.02)	0.02 (±0.01)	0.00 (±0.01)	−0.00 (±0.01)	−0.01 (±0.01)	0.00 (±0.00)
Mean Altitude (distance)	0.00 (±0.00)	−0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	**0.00 (±0.00)**	0.00 (±0.00)
Current Climate (distance)	−0.01 (±0.14)	−0.31 (±0.09)	0.03 (±0.04)	0.18 (±0.08)	0.23 (±0.08)	**−0.52 (±0.03)**
N (# of connected pairwise observations)	88	995	735	94	602	4543
Null deviance	36.6	721.1	396.4	43.7	233.4	1924.5
Residual deviance	29.8	701.6	267.3	38.3	163.9	1292.3
Pseudo-R^2† (%)	18.53	2.71	**32.57**	9.31	**29.76**	**32.85**

p bilateral: intercept, covariates.
p unilateral: depth, geographic distance and pseudo-R^2.
see Table 1 footnotes
Coefficients and standard errors (*logit* link scale) are reported based on the results from the GLM (see Statistical analysis for details) using only the assemblages' similarity ($1-\beta_{jtu}$) from pairs of drainage basins that were inter-connected during the LGM as the response variable and the palaeo-connection depth as the exploratory variable, after controlling for geographic and environmental distances.

torical connectivity on these global-scale patterns. As expected from the greater dispersal possibilities among the drainage basins connected under the LGM sea-level conditions, we observed overall higher total species richness, lower endemism and higher levels of compositional similarity in these palaeo-connected basins compared with those that remained isolated.

Our results are in agreement with and extend the very few regional-scale studies showing that the palaeo-drainage rearrangements resulting from the Quaternary climate change have played a significant role in aquatic faunal diversification, species distribution and species diversity (Smith & Bermingham 2005; Swartz *et al.* 2007; Roxo *et al.* 2012; de Bruyn *et al.* 2013; Unmack *et al.* 2013). Furthermore, our results agree with recent findings suggesting that colonisation processes have played an important role in the regions affected by past climatic oscillations, partly determining the contemporary distribution of terrestrial organisms at large spatial scales (Hawkins & Porter 2003; Graham *et al.* 2006; Montoya *et al.* 2007; Araújo *et al.* 2008; Baselga *et al.* 2012).

Freshwater fish is not the only taxon whose distribution and diversity patterns have been modified by geological and climatic history. The existence of migration pathways among islands, regions, continents or oceans that are temporarily available in geological time have been invoked to explain the disjointed distribution patterns in a number of taxa (e.g. Floeter *et al.* 2008; Eiserhardt *et al.* 2011; Keith *et al.* 2013). Examples of the important geological and climatic events resulting in 'hard' barriers to dispersal are the formation of the Isthmus of Panama and the sea-level changes reshaping the Sunda and Sahul continental shelves. Aside from these obvious physical obstacles or bridges and depending on the taxon considered, permeable or 'soft' aquatic barriers such as large stretches of deep oceanic water (e.g. the mid Atlantic barrier), near-shore gradients in physical and chemical properties of sea water (e.g. the Amazon plume) or changes in the direction of sea currents have also affected the distribution of marine organisms (e.g. Floeter *et al.* 2008). These regional historical events have had important consequences for the connectivity between populations, shaping distributions and diversification patterns. For instance, in Southeast Asia, palm distribution patterns are prominently shaped by the long separation of the Sunda and Sahul shelves and in the Panamanian Isthmus, many clades are confined to either of the shelves or to one side of the Isthmus (Eiserhardt *et al.* 2011). Tectonic plates and mantle plume tracks have also been related to the patterns of coral diversity and composition in Southeast Asia (Keith *et al.* 2013), and the reef fish distribution patterns that we observe today have also been influenced by biogeographical filters (Mora *et al.* 2003; Floeter *et al.* 2008). Our results extend this general framework to a unique case where historical connectivity and its effects on species distribution and diversity patterns can be assessed at the global scale.

Differences between realms

Our findings suggest that the sea-level changes during the LGM and the associated drainage basin reconfigurations influenced the freshwater fish distributions in all regions of the world. However, our results also emphasise significant differences between realms. Indeed, the diversity patterns from the Afrotropical, Indomalaya and Nearctic realms do not conform to all of our expectations (Fig. 1). For instance, the narrow continental shelf of the Afrotropical realm resulted in a very limited number of palaeo-connected river systems under low-sea-level conditions (Figs. 2,3 and Fig. S1). This small number, combined with a particularly rich history of tectonic and climatic changes that rearranged drainage basins through inland river captures (Goudie 2005), may explain the absence of an overall significant difference in the endemism and compositional similarity levels between the palaeo-connected and palaeo-disconnected drainage basins. However, the distance–decay relationship observed for this realm shows higher average levels of compositional similarity in the palaeo-connected drainage basins for two of the three distance classes (Fig. 2). Furthermore, the higher total species richness and the lower levels of endemism observed (although non-significant) in the palaeo-connected basins suggest that dispersal through the palaeo-connection pathways most likely played a role in shaping the diversity patterns of African freshwater fishes. This finding has recently been confirmed by a phylogeographical study of fish assemblages in South Africa (Chakona *et al.* 2013).

In contrast, the Indomalaya realm has a prominent continental shelf that has exposed large extensions of land during low-sea-level periods (even larger than the current land surface in some parts of the realm), connecting very distant and relatively small-sized drainage basins (Fig. 3 and Fig. S1). In this case, faunal homogenisation related to the palaeo-connections has most likely been followed by extinction events of great magnitude caused by the rise in the sea level and the associated reduction in the surface of the drainage basins (Hugueny *et al.* 2011; Tedesco *et al.* 2013). These extinctions have reduced the total richness and compositional similarity of the palaeo-connected drainage basins. However, the less steep distance decay of similarity and lower endemism levels in the palaeo-connected drainage basins observed for this realm suggest that dispersal through the palaeo-connection pathways has played a significant role in the distribution patterns of freshwater fishes.

Although our observed patterns of distance decay in similarity and total species richness clearly support the significant role of the palaeo-connection pathways in shaping the current species diversity in the Nearctic realm, the results based on the endemic species richness do not support our hypothesis (Table 1b). A regional specificity that may account for this contrasting result is that most of the drainage basins that remained disconnected during low-sea-level periods are located in regions covered by ice sheets during the LGM (Fig. 3), reducing the potential occurrence of endemic species in these basins. A further explanation for this unexpected result is the disproportionate weight of the Mississippi drainage in our model regression coefficients. Indeed, the Mississippi served as a major Pleistocene refuge for North American fish fauna (Oberdorff *et al.* 1997) and thus harbours an exceptionally rich endemic fauna. Excluding this drainage basin from our analyses leads to the expected pattern of a decrease in the endemic richness in the palaeo-connected basins (results not shown).

The palaeo-connection time

The temporal window of connection between the drainage basins under low-sea-level conditions should logically influence the level of compositional similarity (Fig. 1d). However, this ‘time for colonisation’ hypothesis was only supported for the Indomalaya and Neotropical realms. For the remaining realms, the results suggest that the duration of the connection did not play a significant role or that all of the freshwater fish species able to migrate between the drainage basins through the palaeo-connection pathways rapidly achieved their range expansion. The periodical availability of the palaeo-connection pathways through the Quaternary period may strengthen the latter assumption by increasing the chances for successful migration through a gradual stepping-stone mechanism (Sepkoski & Rex 1974). The relatively low species richness found in the Australasian, Nearctic and Palearctic realms (Lévêque *et al.* 2008) may also contribute to the absence of a time effect on the similarity patterns, given that the exchange of fewer species is necessary to achieve high levels of similarity in these cases. Concerning the Afrotropical realm, the very narrow and steep continental shelf may explain the absence of a time effect.

Differential species dispersal capacity could also explain the different time effect results observed between the realms. Fish faunas from high latitudinal regions are dominated by large-bodied species (Blanchet *et al.* 2010), and this biological trait is known to be positively associated with the dispersal capacity of freshwater fishes (Tedesco *et al.* 2012; Radinger & Wolter 2013). The lack of a time effect on the fish compositional similarity in the palaeo-connected drainage basins from the Nearctic, Palearctic and Australasian realms (Table 3) may be thus explained by the large mean body sizes observed for fish assemblages in these realms (Blanchet *et al.* 2010), ensuring rapid faunal exchanges once the palaeo-connections were established. In contrast, the fish assemblages from drainage basins of the Indomalaya and Neotropical realms harbour smaller mean body sizes (Blanchet *et al.* 2010) and thus require more time for colonisation.

CONCLUSIONS

Our findings show that the historical connectivity between the drainage basins caused by the sea-level changes during the LGM left a marked worldwide imprint on the current freshwater fish alpha and beta diversity patterns. To our knowledge, this is the first study to unambiguously reveal the strength of the historical legacies in the current worldwide biodiversity patterns. In addition, this study emphasises that the dispersal processes have at least as much importance as the niche-based processes in shaping the geographical distribution of species, a topic being continuously debated among biogeographers and ecologists (e.g., Gilbert & Lechowicz 2004). Accounting for the dispersal-related species traits (e.g. body size, migratory behaviour, habitat specialisation and reproductive behaviour) appears to be the obvious next step to further understand the role played by the drainage basin historical connectivity in the contemporary freshwater biodiversity patterns and its differential effects on biogeographical realms.

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AUTHORSHIP

PAT, TO, BH and MSD conceived and designed the study. MSD performed the analyses with the help of FL. CJ and J-FC handled the environmental GIS data, and all authors contributed to the biological information. MSD, PAT and FL wrote the first draft of the manuscript, and all authors contributed substantially to finalising this manuscript.

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Title Global imprint of historical connectivity on freshwater fish biodiversity

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Appendix S1: Details on the exclusion of drainage basins and assignments to realms

The river basins from Madagascar were excluded because no palaeo-connected drainage basin occurred on this island during the LGM (as defined by our methods). Finally, drainage basins from the Pacific islands and Antarctica were excluded because the former had no palaeo-connected drainage basins during the LGM and there were no available biological data for the latter.

Minor corrections were made when assigning the drainage basins to the biogeographic realms; the entire Nile River basin was assigned to the Afrotropical realm because it shares most of its fauna with other western basins from Africa (Lévêque et al. 2008), some of the basins from Mexico (i.e., Papaloapan, Balsas, Tecolutla, Verde and two small drainages) were assigned to the Neotropical realm and all of the basins from Taiwan Island were assigned to the Indomalaya realm. These two last modifications were needed because the fine-scale limits of these realms would have separated small drainage basins from their expected palaeo-river drainage basins.

Table S1 Environmental variables and modeling components used in the modeling framework and reference sources. All variables were extracted over the surface of each drainage basin and then averaged to compose a single value per drainage.

Variables	Sources	Total & Endemic Richness*	Dissimilarity#
Mean annual actual evapotranspiration (mm)	CIAT-CGIAR, 1950-2000; http://csi.cgiar.org/Aridity/	X	X
Mean annual potential evapotranspiration (mm)	CIAT-CGIAR, 1950-2000; http://csi.cgiar.org/Aridity/		X
Mean Temperature (°C)	WorldClim, 1950-2000; http://www.worldclim.org/		X
Mean Precipitation (mm)	WorldClim, 1950-2000; http://www.worldclim.org/		X
Mean Temperature Anomaly	CCSM and MIROC3.2 MEDRES (data available from http://www.worldclim.org/)	X	X
Mean Annual Surface Runoff (mm/year)	UNH, Composite Runoff Field, Composite Runoff; http://www.grdc.sr.unh.edu/	X	X
Percentage cover of 15 terrestrial biomes in each drainage basin (transformed in habitat diversity by applying the Shannon index)	MOD12Q1, Boston University, igbp1_v5 (http://www-modis.bu.edu/landcover/page5/page5.htm)	X	
Current drainage basin surface (km²)	HydroSHEDS layers (≈ 1x1 km resolution; http://www.hydrosheds.cr.usgs.gov) (Lehner *et al.* 2006)	X	
River networks and on watershed polygons for rivers beyond 60°N and 60°S	(Jenson & Domingue 1988)		X
Mean Altitude (m)	San Diego University, SRTM30+ v6, NASA Shuttle Radar Topographic Mission	X	X
Quaternary climatic stability (1/10°C; i.e. temperature anomaly since LGM)	WorldClim, BioClim 1, Temperature, mean annual, LGM -21 000; models: CCSM et MIROC3.2 MEDRES; http://www.worldclim.org/	X	X
Adjacence distance	This study; HydroSHEDS layers (≈ 1x1 km resolution; http://www.hydrosheds.cr.usgs.gov)		X
Biogeographic realms	Six Realms adopted by (Olson *et al.* 2001)	X	X
Coverage (%) of drainage basins by the LGM Ice sheet	(Peltier 1994)		X

* (Oberdorff *et al.* 2011; Tedesco *et al.* 2012) ; # (Leprieur *et al.* 2011)

Modeling components	Sources	Total & Endemic Richness	Dissimilarity
Generalized Linear Models (GLM) with Negative Binomial distribution	(Zuur *et al.* 2009)	X	
Variance Inflation Factor (VIF)	(Zuur *et al.* 2010; Dormann *et al.* 2012)	X	
Generalized Linear Models (GLM) with Binomial distribution	(McCullagh & Nelder 1989)		X
Permutation procedure for testing parameters from GLM	(Lichstein 2007) which correspond to permutation Method 1 from (Legendre & Fortin 2010)		X
Centering and dividing covariates by 2sd's	(Gelman 2008)	X	
R program for statistics and graphs	(R Core Team 2013)	X	X
ArcGIS	ESRI. 2011 ArcGIS Desktop version 10. Redlands, CA: Environmental Systems Research Institute.	X	X

vegan package	http://cran.r-project.org/web/packages/vegan/vegan.pdf	X	X
betapart package	(Baselga & Orme 2012)		X
ggplot2 package	http://ggplot2.org/	X	X

Table S2. Coefficients and standard errors (on the link scale) from Generalized Linear Model with Quasi-Binomial family distribution in which beta diversity of strictly freshwater fishes due to species turnover (1-$ß_{jtu}$, sensu Baselga 2010, 2012) was the response variable and Palaeo-connection (binary factor: connected=1, disconnected=0), adjacency geographic distance among pair of river basins, their interaction term and a series of environmental variables related to $ß_{jtu}$ (Leprieur *et al.* 2011) were the exploratory variables. Models were constructed **excluding drainage basins covered (totally or partially) by ice sheets during the Last Glacial Maximum. Compared to the complete model detailed in the manuscript slight changes on regression coefficients are only observed for Neartic, Neotropical and Paleartic realms**. Factors significance was evaluated against 999 Monte Carlo simulations (see Analysis for details).

A Without Interaction

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(intercept)	1.37 (±0.04)	**2.29 (±0.04)**	**3.85 (±0.08)**	**2.29 (±0.10)**	0.99 (±0.02)	**2.26 (±0.02)**
Palaeo-connection	-0.08 (±0.11)	**1.01 (±0.07)**	-1.34 (±0.11)	0.09 (±0.22)	**0.65 (±0.04)**	**0.91 (±0.02)**
Geographic distance	**-3.46 (±0.07)**	**-2.79 (±0.05)**	**-3.37 (±0.09)**	**-2.85 (±0.20)**	**-2.71 (±0.02)**	**-3.13 (±0.03)**
Interaction term	-	-	-	-	-	-
Covariates						
Temp. Anomaly (distance)	**-0.03 (±0.00)**	**-0.03 (±0.00)**	**-0.03 (±0.00)**	**0.00 (±0.00)**	**-0.01 (±0.00)**	**-0.00 (±0.00)**
Mean Altitude (distance)	0.00 (±0.00)	-0.00 (±0.00)	**-0.00 (±0.00)**	**-0.00 (±0.00)**	**-0.00 (±0.00)**	**-0.00 (±0.00)**
Current Climate (distance)	**-0.12 (±0.01)**	0.00 (±0.01)	**-0.24 (±0.01)**	**-0.82 (±0.04)**	**-0.14 (±0.00)**	**-0.25 (±0.01)**
N (number of pairs)	18337	35507	14602	3321	50754	108615
Null deviance	6714.8	32650.0	13846.0	1576.5	12206.0	55347.0
Residual deviance	3441.3	21857.0	6443.4	628.4	6322.0	30388.0
Pseudo-R^2 †	**48.75%**	**33.06%**	**53.46%**	**60.14%**	**48.21%**	**45.10%**

B With Interaction

(intercept)	1.37 (±0.04)	**2.35 (±0.04)**	**4.02 (±0.08)**	**2.29 (±0.10)**	1.01 (±0.02)	**2.35 (±0.02)**
Palaeo-connection	-0.09 (±0.14)	-0.13 (±0.13)	-2.43 (±0.16)	0.10 (±0.29)	0.26 (±0.06)	-0.47 (±0.07)
Geographic distance	**-3.46 (±0.07)**	**-2.86 (±0.05)**	**-3.62 (±0.10)**	**-2.84 (±0.20)**	**-2.74 (±0.02)**	**-3.24 (±0.03)**
Interaction term	0.15 (±0.72)	**2.17 (±0.24)**	**2.18 (±0.26)**	-0.10 (±1.05)	**0.93 (±0.13)**	**1.89 (±0.09)**
Covariates						
Temp. Anomaly (distance)	**-0.03 (±0.00)**	**-0.03 (±0.00)**	**-0.03 (±0.00)**	**0.00 (±0.00)**	**-0.01 (±0.00)**	**-0.00 (±0.00)**
Mean Altitude (distance)	0.00 (±0.00)	-0.00 (±0.00)	**-0.00 (±0.00)**	**-0.00 (±0.00)**	**-0.00 (±0.00)**	**-0.00 (±0.00)**
Current Climate (distance)	**-0.12 (±0.01)**	0.00 (±0.01)	**-0.21 (±0.01)**	**-0.82 (±0.04)**	**-0.14 (±0.00)**	**-0.25 (±0.01)**
Null deviance	6714.8	32650.0	13846.0	1576.5	12206.3	55347.0
Residual deviance	3441.3	21807.0	6372.7	628.4	6313.9	30219.0
Pseudo-R^2 †	**48.75%**	**33.21%**	**53.97%**	**60.14%**	**48.27%**	**45.40%**

p bilateral: intercept, covariate distances, interaction term

p unilateral: paleoconnection, geographical distance and R^2

see Table S2 footnotes

Table S3. Effects of duration of palaeo-connection (i.e. depth, see methods for details), adjacency geographic distance and environmental descriptors on fish assemblages similarity. Coefficients and standard errors (logit scale) from Generalized Linear Model (see Statistical analysis for details) using assemblages similarity (1-$ß_{jtu}$) only from pairs of drainage basins inter-connected (N) during the LGM as the response variable and palaeo-connection depth as the exploratory variable, after controlling for geographic and environmental distances. **All drainage basins covered (totally or partially) by ice sheets during the Last Glacial Maximum were excluded for this analysis. Compared to the complete model detailed in the manuscript slight changes on regression coefficients are only observed for Neartic, Neotropical and Paleartic realms.**

	Coefficients					
	Realms					
Variables	Afrotropical	Australasia	Indomalaya	Nearctic	Neotropical	Palearctic
(intercept)	0.71 (±0.31)	**2.16 (±0.23)**	1.72 (±0.14)	1.60 (±0.57)	0.74 (±0.10)	1.55 (±0.06)
Depth	-0.01 (±0.00)	0.00 (±0.00)	**0.01 (±0.00)**	0.01 (±0.01)	**0.01 (±0.00)**	-0.00 (±0.00)
Geographic distance	**-3.82 (±0.90)**	**-0.66 (±0.29)**	**-1.69 (±0.16)**	-3.34 (±1.18)	**-1.72 (±0.17)**	**-1.30 (±0.08)**
Covariates						
Temp. Anomaly (distance)	-0.01 (±0.02)	0.02 (±0.01)	0.00 (±0.01)	0.03 (±0.02)	-0.01 (±0.01)	-0.00 (±0.00)
Mean Altitude (distance)	0.00 (±0.00)	-0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	**0.00 (±0.00)**	0.00 (±0.00)
Current Climate (distance)	-0.01 (±0.14)	**-0.31 (±0.09)**	0.03 (±0.04)	-0.61 (±0.46)	0.23 (±0.08)	**-0.47 (±0.03)**
N (number of connected pairs)	88	995	735	47	600	3586
Null deviance	36.6	720.3	396.4	23.3	231.1	1211.3
Residual deviance	29.8	701.0	267.3	10.9	161.7	812.6
Pseudo-R^2 †	**18.53%**	**2.68%**	**32.57%**	**9.31%**	**30.02%**	**32.91%**

p bilateral: intercept, covariates

p unilateral: depth, geographic distance and R^2

see Table S2 footnotes

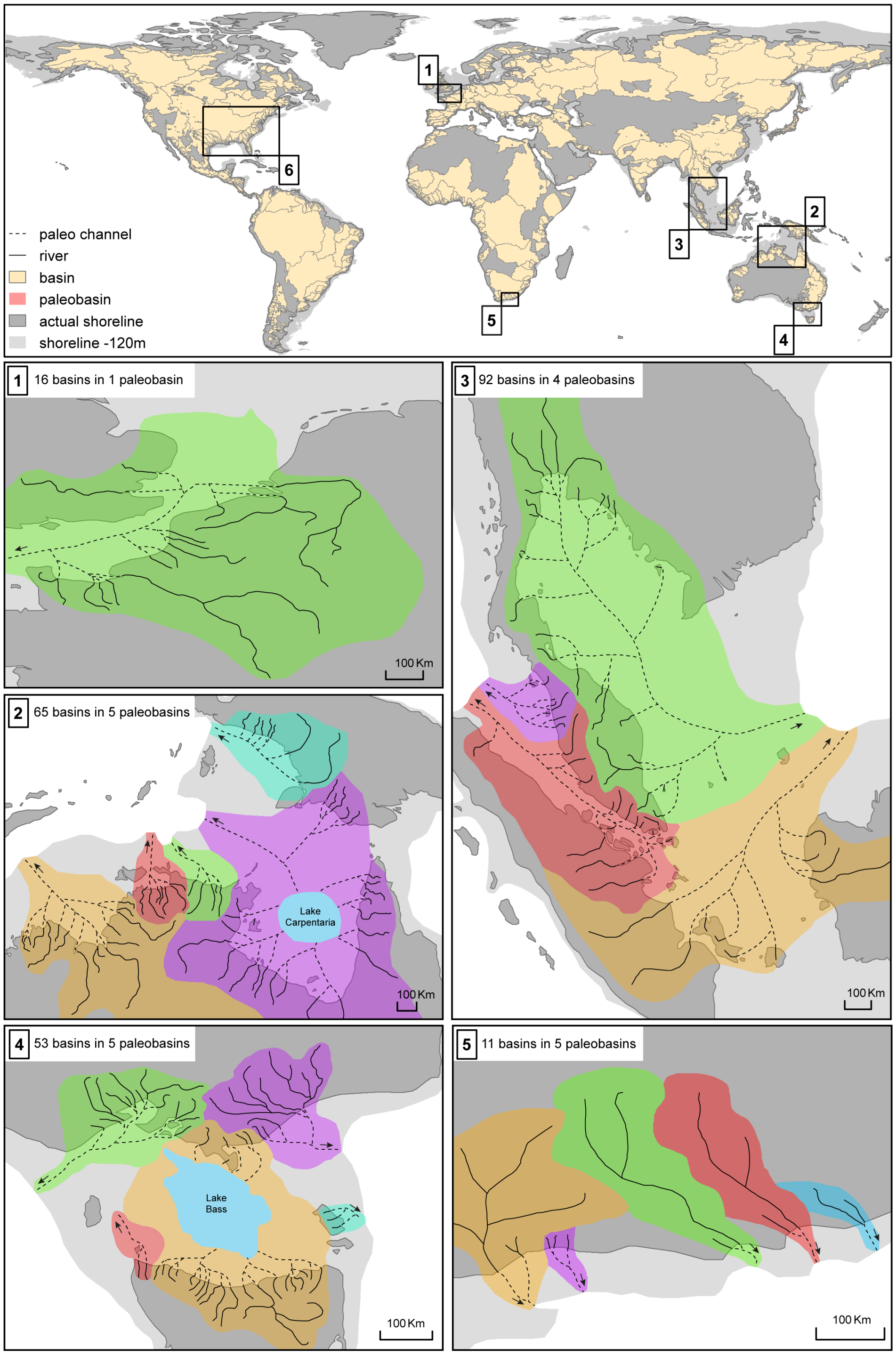
Table S4. Results from our modeling framework applying different beta diversity measures. A) Coefficients and standard errors (on the link scale) from Generalized Linear Models with Quasi-Binomial family distribution in which beta diversity **(Sørensen similarity: 1-ß$_{sor}$; and Simpson similarity: 1-ß$_{sim}$**; sensu Baselga 2010, 2012) of strictly freshwater fishes was the response variable and Palaeo-connection (binary factor: connected=1, disconnected=0), adjacency geographic distance among pair of river basins, their interaction term and a series of environmental variables related to ß$_{jtu}$ (Leprieur *et al.* 2011) were the exploratory variables. For each realm, factors significance was evaluated against 999 Monte Carlo simulations (see Statistical analysis section for further details). **Only palaeo-connection and its interaction effect with adjacency distance are shown for clarity.** B) Effects of the duration of palaeo-connection (i.e. depth, see methods for details), adjacency geographic distance and environmental descriptors on assemblages similarity for different similarity indices **(Sørensen similarity: 1-ß$_{sor}$; and Simpson similarity: 1-ß$_{sim}$**; sensu Baselga 2010, 2012). Coefficients and standard errors (logit scale) from GLM using similarities only from inter-connected pairs of drainage basins (N) during the LGM as the response variable and palaeo-connection depth as the exploratory variable, after controlling for geographic and environmental distances. **Only depth coefficients are shown for clarity**.

A)	$1\text{-}\beta_{sor}$			$1\text{-}\beta_{sim}$		
	Without Interaction	With Interaction		Without Interaction	With Interaction	
Realms	Palaeo-connection	Palaeo-connection	Interaction	Palaeo-connection	Palaeo-connection	Interaction
Afrotropical	-0.17 (0.07)	-0.33 (0.09)	1.77 (0.47)	-0.09 (0.13)	-0.12 (0.16)	0.18 (0.75)
Australasia	**0.54 (0.04)**	-0.15 (0.07)	**1.51 (0.14)**	**1.05 (0.08)**	-0.14 (0.14)	**2.22 (0.25)**
Indomalaya	-1.54 (0.40)	-2.21 (0.63)	**1.50 (1.06)**	-0.90 (0.07)	-2.29 (0.11)	**2.43 (0.17)**
Nearctic	**0.91 (0.18)**	0.32 (0.22)	**2.04 (0.55)**	**1.56 (0.31)**	0.31 (0.40)	**3.01 (0.85)**
Neotropical	**0.40 (0.03)**	0.02 (0.05)	**1.01 (0.10)**	**0.74 (0.04)**	**0.37 (0.08)**	**0.82 (0.15)**
Palearctic	**0.67 (0.09)**	-0.48 (0.20)	**1.73 (0.28)**	**1.13 (0.09)**	-0.29 (0.25)	**1.84 (0.32)**

B)	Depth effect	Depth effect
Afrotropical	-0.00 (0.00)	0.00 (0.00)
Australasia	-0.00 (0.00)	0.00 (0.00)
Indomalaya	**0.01 (0.00)**	**0.01 (0.00)**
Nearctic	0.01 (0.00)	0.01 (0.01)
Neotropical	0.00 (0.00)	**0.01 (0.00)**
Palearctic	0.00 (0.00)	0.00 (0.00)

Bold values, $p<0.05$ See Table S2 footnotes

Figure S1. Global distribution of drainage basins analyzed and examples of palaeo-drainage basins estimated through Flow Accumulation algorithm from bathymetric maps and compared to previous palaeo-drainage reconstructions in 6 regions distributed in 5 realms (no published data available concerning the Neotropical realm). Colored polygons represent individual palaeo-drainage basins grouping several current drainage basins. All regions show a good correspondence between our palaeo-drainage reconstruction and previous palaeo-drainage reconstructions found in the literature (between 77.8 to 100% of match).



1 16 basins in 1 paleobasin

2 65 basins in 5 paleobasins

3 92 basins in 4 paleobasins

4 53 basins in 5 paleobasins

5 11 basins in 5 paleobasins

Region 1: 100% of match. See Fig.1 from (Antoine *et al.* 2007).

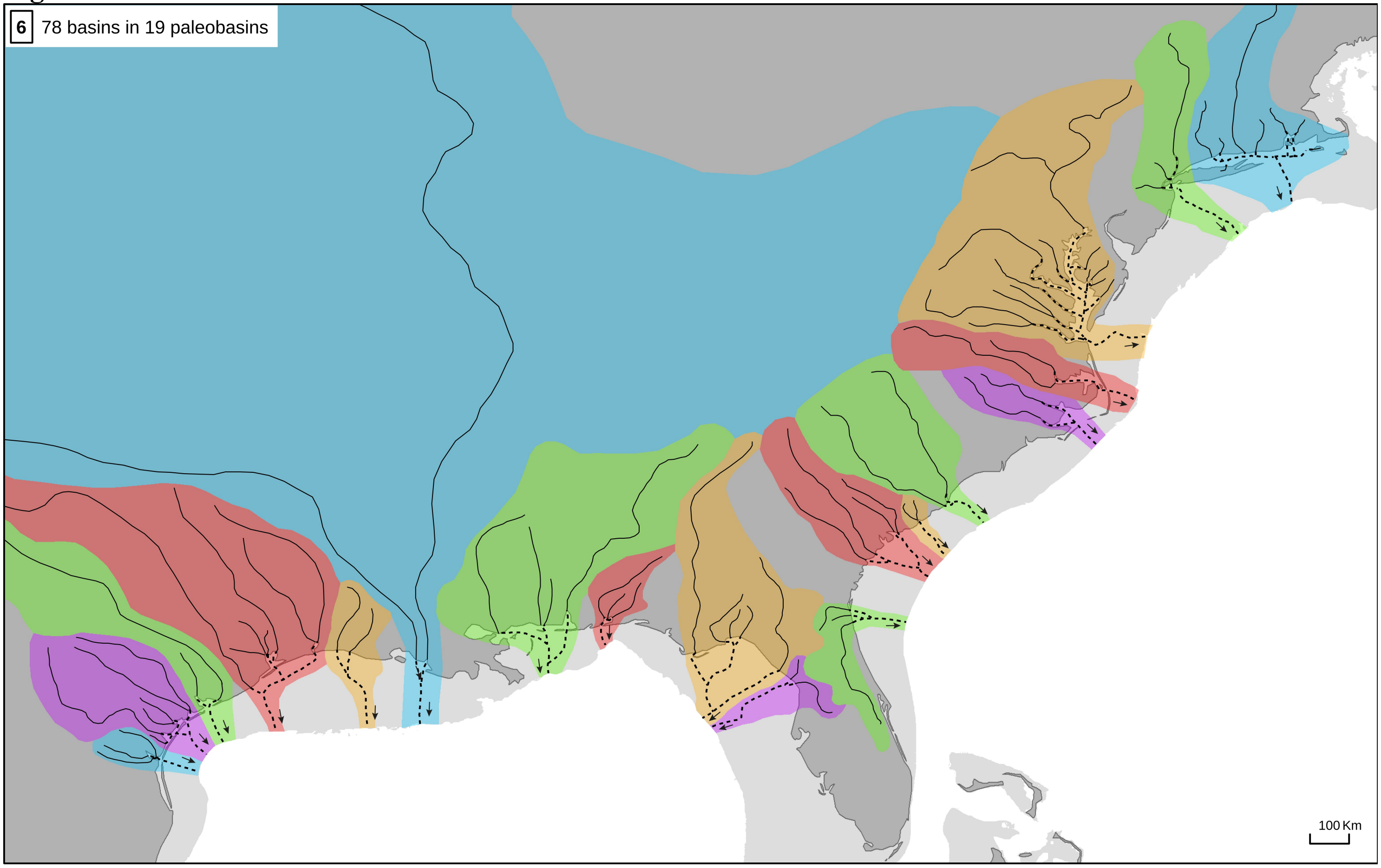
Region 2: 98.4% of match for palaeo-connected drainages. See Fig.1 from (Voris 2000).

Region 3: 95.5% of match. See Fig.1 from (Voris 2000).

Region 4: 94.4% of match. See Fig.3 from (Unmack *et al.* 2013).

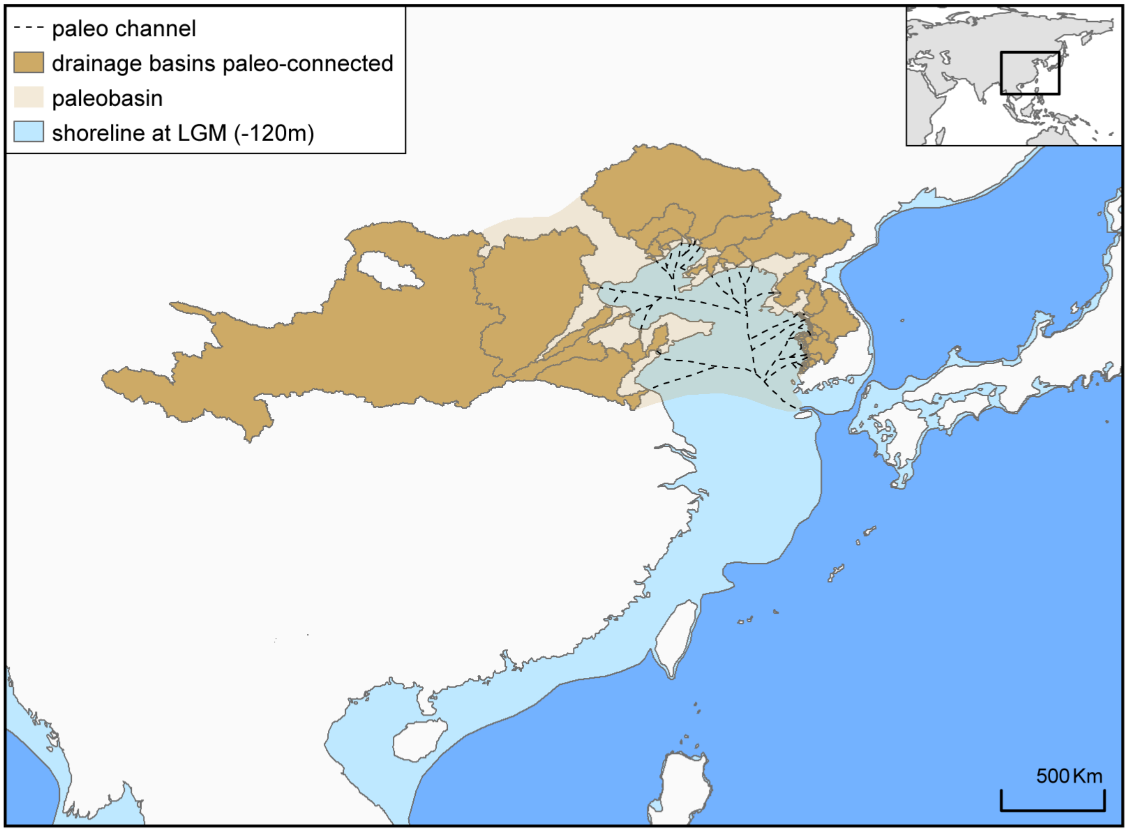
Region 5: 77.8% of match. See Fig.2 from (Swartz *et al.* 2007).

Figure S1. Continuation...



Region 6: 77.9% match. See palaeo-drainage basins from http://www.peter.unmack.net/gis/sea_level/index.html

Figure S2. Example of a 'U-shaped' palaeo-drainage basin where high assemblage similarity (1-$ß_{jtu}$) between distant pairs of basins may occur when using adjacency distances. We focused here on the Korean peninsula. Large adjacency distances separate pairs of basins at both limits of the palaeo-drainage but fish assemblages similarity between present-day basins may be high due to the palaeo-connection.



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Anthropogenic drivers of riverine fish extinctions

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In prep.

Title: Anthropogenic drivers of riverine fish extinctions

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Summary

1. Human activities are often implicated in the extinction of contemporary species. Riverine fishes are a well-studied and emblematic group that have experienced much fragmentation and flow regulation due to the damming of rivers, abstraction and pollution of water, degradation of habitat, and the introduction of non-native species. However, few studies have evaluated the role of each of these threats on fish extinction at large spatial scales.

2. Focusing on western Europe and North America, two of the most heavily impacted regions, we quantify contemporary fish species loss per river basin by controlling for natural extinction levels to evaluate the role that these threats have played on fish extinction.

3. We show that mean fish extinction rates during the last 110 years in both continents is ~ 40 times higher than background (i.e., natural) extinction rates.

4. The number of dams on the main stem together with the alteration of basin drainage (i.e., % of croplands) appear to be the main drivers behind fish species extinction. These extinctions have occurred for both migratory and resident fish species.

5. *Policy implications*. Individual threats such as the number of dams on the main river stem and the percentage of cropland are good proxies for predicting migratory and fish species loss at broad spatial scales. The negative effects of dams and croplands in the river basin on fish biodiversity highlighted here have important conservation implications as the number of large dam constructions and natural land clearance for agriculture are strongly increasing in tropical regions where much of the world's freshwater ichthyofauna is concentrated.

Keywords: anthropogenic threats; background extinction; cropland; dams; extinction rate; freshwater fish; fragmentation; river basins.

Introduction

Humans have modified ecosystems on Earth and have been responsible for the extinction of hundreds of species (Barnosky *et al.* 2011). Predicting to what extent large-scale anthropogenic alterations have resulted in species loss is thus critical for guiding conservation strategies aiming to maintain biodiversity and resources in altered ecosystems. Many recent studies that have analyzed drivers of species extinction have generally used surrogates of extinction risk (e.g., human population density, economic activity, the extent of agricultural and urban land-area; Luck *et al.* 2004; Davies *et al.* 2006), or have tried to identify the most vulnerable groups of organisms through non-spatial frameworks (i.e., through correlations with species life-history traits; Reynolds, Webb & Hawkins 2005; Olden, Hogan & Zanden 2007; Cardillo *et al.* 2008; Hutchings *et al.* 2012). However, these approaches, mainly applied because of the deficiency of data on the spatial distribution of extinctions and threats, do not allow the specific role of individual anthropogenic stressors in biodiversity loss to be assessed (Clavero *et al.* 2010; Vörösmarty *et al.* 2010).

Riverine ecosystems are extraordinarily diverse (Balian *et al.* 2007; Tisseuil *et al.* 2013) and are some of the most threatened habitats on Earth (Jenkins 2003; Vörösmarty *et al.* 2010). Extinction risk of riverine fishes, for instance, is thought to be higher than that of terrestrial organisms (Ricciardi & Rasmussen 1999) and recent extinction rate estimates of North American fish species range from being 130 to 855 times higher than background extinction rates (Burkhead 2012; Tedesco *et al.* 2013). For terrestrial organisms, estimating geographic variation in species loss is a challenging task mainly due to the lack of discrete boundaries on the landscape, but the extinction of fish populations from distinct river basins (i.e., closed systems; Hugueny, Oberdorff & Tedesco 2010) provides an opportunity to highlight the underlying drivers of geographical variation in species loss. Two types of extinction can occur in riverine systems: regional or global extinctions (Burkhead 2012). Regionally extinct species, also called extirpated species, are those that have disappeared from one or more river basins but still maintain natural populations elsewhere. Globally extinct species are those that have disappeared from their full natural range (i.e., from all river basins worldwide). We refer herein to these two types as ‘extinct’ species.

The multiple abiotic threats to fish biodiversity are widely known and include habitat fragmentation and homogenization in stream flow dynamics due to the damming of rivers, introduction of non-native species, dumping of nutrient or organic loadings increasing eutrophication processes, accumulation of toxic pollutants, degradation of the riverine habitat and water abstraction for human and agricultural consumption (Sala *et al.* 2000; Nilsson *et al.* 2005; Vörösmarty *et al.* 2010). However, there are few studies that have elucidated the role of each of these threats on fish extinction at large spatial scales (Clavero *et al.* 2010). In this sense, the intercontinental comparison of highly impacted regions containing independent extinction histories may shed light on the main drivers of fish species loss (Kerr, Kharouba & Currie 2007).

In this study, we use a set of spatially explicit freshwater abiotic threats recently developed to a global extent (Vörösmarty *et al.* 2010), together with a uniquely comprehensive database of freshwater fish extinctions at the river drainage basin grain, to estimate fish species loss in North American and western European river basins. By doing so, we evaluate to what extent each of the main biotic and abiotic threats have promoted fish extinctions in these two well-studied regions where high-quality records of fish extinctions are available. Because migratory and resident species may have differential sensitivity to anthropogenic threats, and hence different responses in terms of species extinction, we analyzed these two components of fish communities separately. For instance, diadromous fishes, migrating from fresh- to salt-water and vice versa, are thought to face increased extinction risk as rivers become fragmented (e.g., through fragmentation by dams; Reidy-Liermann *et al.* 2012), whereas resident fish species should be more sensitive to local habitat alterations (e.g., (Giam *et al.* 2011).

Materials and methods

Biological data

Western Europe and North America benefit from well-documented information on the extinction status of fish species (Kottelat & Freyhof 2007; Jelks *et al.* 2008; NatureServe 2010; Freyhof & Brooks 2011; Burkhead 2012). Freshwater fish extinctions were assessed by using multiple complementary sources. For western Europe (i.e., from Portugal to Petchora, Volga and Ural river basins in Russia), the occurrence of fish species was assessed based on a comprehensive spatial data set on global freshwater fish distribution at the river basin grain (Brosse *et al.* 2013). We further incorporated registers of fish extinctions per river basin using information from Kottelat & Freyhof (2007) completed by data from unpublished reports, scientific papers and Red Lists. For North America (i.e., the United States of America), a comprehensive compilation of the status of native freshwater fishes was used as the main source of information (NatureServe 2010). In this case, species were considered extinct from a given basin when only historical records of their presence where reported throughout the hydrological units composing the river basin. False zero extinction values are a potential bias inherent in this kind of data, mainly affecting small and under-studied rivers. In order to minimize this potential bias, river basins containing less than 10 species were withdrawn from our dataset. Lacustrine species were not considered. For all species, we compiled information on their migratory (i.e., anadromous, catadromous, potamodromous and amphidromous species) or non-migratory (i.e., resident species) status based on FishBase (Froese & Pauly 2011).

Computing fish extinction ratio

We computed the total native, resident and migratory species richness for each river basin (Brosse *et al.* 2013); we further calculated percentages of extinction as the number of extinct fish species divided by fish species richness for each group and each river basin for mapping purposes. However, when analyzing recent human induced extinctions, it is important to first control for natural extinction rates. Otherwise, estimates of ongoing natural and anthropogenic extinction rates could be confounded. To circumvent this problem, we thus decided to use Observed/Natural Extinction ratios per river basin in our modeling process, instead of direct percentages of extinction. To obtain these ratios we relied on a highly accurate empirical riverine fish population, extinction–area relationship previously established by Hugueny, Movellan & Belliard (2011) for the Northern Hemisphere to (1) estimate the "background" (natural) extinction rates in river basins [see Tedesco *et al.* 2013 for an application] and (2) calculate Observed/Natural Extinction ratios during the last 110 years, assuming that human-related extinctions started approximately 110 years ago (Miller, Williams & Williams 1989; Burkhead 2012).

The population extinction–area relationship extracted from Fig. 5 in Hugueny, Movellan & Belliard (2011) allows calculation of the expected natural extinction rate per species per year, e, as a function of river drainage area, A (in km²):

$$e = f(A) = 1 - [1/\exp(cA^b)] \qquad \text{(eqn 1),}$$

where $c = 0.0073$ and $b = 0.6724$. For a given drainage basin area A, assuming species are identical with regard to extinction risk and no colonization process, the expected background number of extinct species over t years is given by:

$$E = SR_o - SR_o\,[1 - e]^t \qquad \text{(eqn 2),}$$

with e given by equation (1) and SR_o being the initial species richness (see Tedesco *et al.* 2013) for further details). Applying equation 2, we obtained the number of species extinctions expected under natural conditions over the last 110 years for each river basin. Finally, background extinctions E were used to compute the ratio of Observed/Natural Extinctions. We then used this ratio as a response variable for testing a set of aquatic stressors (see below).

Although the extinction–area relationship from equation 1 was developed without accounting for life-history trait differences among species (Hugueny, Movellan & Belliard 2011), we assumed here similar natural extinction rates for migratory and resident species and consequently applied the same procedure for both groups. We then compared Observed/Natural Extinction ratios between these two groups during the last 110 years to identify which group experiences more human disturbance and which predictors better explain species extinctions in these groups.

Environmental predictors

In a recent analysis of global threats to river biodiversity, Vörösmarty *et al.* (2010) developed a set of spatially explicit variables (30 arc-second resolution) reflecting the main stressors of freshwater organisms (Table 1). Based on the expertise of freshwater specialists, these authors also weighted the contribution of those freshwater stressors to obtain a synthetic Incident Biodiversity Threat index (hereafter IBT). We first used the IBT index to evaluate the potential link between overall aquatic threat and the pattern of fish extinction in river basins. In a second step, we extracted individual maps of stressors related to Catchment Disturbance, Pollution, and Water Resource Development (Table 1) from Vörösmarty *et al.* (2010) at the sub-drainage scale (Lehner, Verdin & Jarvis 2006) and then computed a mean value per drainage basin weighted by each sub-drainage surface area. This surface-related weighting procedure assures better estimates of mean threats per drainage basins when heterogeneity in threat level is important among sub-drainages (e.g., without weighting by sub-drainage surface, a small, highly-impacted sub-drainage would contribute most to the overall drainage threat mean). All stressor values vary between 0 and 1 (see Supplementary Information from Vörösmarty *et al.* 2010).
Concerning Biotic Factors, we directly used the percentage of non-native species present in each river basin provided by Leprieur *et al.* (2008) as the metrics developed by Vörösmarty *et al.* (2010) were based on that information. We then applied the Cumulative Distribution Function standardization to rescale the percentages ($\log_{10}$-transformed excluding zeros) on an index varying between 0 and 1 (see Supplementary Information from Vörösmarty *et al.* 2010).

We intend to explore the relationships between freshwater biodiversity stressors related to Catchment Disturbance, Pollution, Water Resource Development and Biotic Factors reported by Vörösmarty *et al.* (2010) and fish extinctions in river basins. However, these stressors are highly correlated with each other, particularly within each stressor category. Hence, we selected stressors within each category with weights > 0.10, which measures the importance of each threat based on the expertise of a set of freshwater researchers (Vörösmarty *et al.* 2010; see Table 1). We then retained those stressors showing the lowest mean Pearson correlation ($r < 0.30$). This procedure selects a parsimonious subset of the most important stressors keeping low collinearity between variables to allow the individual effects of each stressor on fish extinction patterns to be evaluated. Based on this procedure, the following environmental stressors were selected: % of croplands in the river basin, nitrogen loading, phosphorus loading, sediment loading, organic loading, water temperature alteration, conservation water loss, flow disruption, river fragmentation by dams, and the percentage of non-native species.

Because river fragmentation by dams is a major concern, we investigated the effects of two stressors related to different processes of river fragmentation. First, the ranges of both resident and migratory species may decrease due to the reduction of available riverine habitat caused by the accumulation of dams on river systems. This mechanism was evaluated by the inclusion of the River Fragmentation threat developed by (Vörösmarty *et al.* 2010; see Table 1). However, migratory species need free pathways to complete their life cycle in marine and fresh waters; hence, dams positioned in the mainstem (main river channel) should drastically reduce river connectivity between freshwater and marine habitats and increase the extinction risk of these species. As a proxy for this threat, we used the number of large dams (i.e., > 50 m in height) in the main stem of each drainage basin derived from a global scale dams database (Lehner *et al.* 2011).

Data analysis

In order to further reduce multicollinearity among the selected predictors and create synthetic drivers, we performed Principal Component Analyses with variables from the Pollution and Water Resource Development groups. Nitrogen, Phosphorus, Sediment, Organic loadings and water Temperature Alteration were reduced to a single PCA axis accounting for 71% of the variability. In the same way, Conservation Water loss and Flow Disruption were reduced to a single PCA axis accounting for 60% of the variability. Therefore, both axes represent proxies for water pollution, water use and flow regulation.

We first mapped the percentage of fish extinction and the observed/natural extinction ratio per river basin for both continents. We further modeled the observed/natural extinction ratios against our selected stressors using Ordinary Least Square (OLS). The Observed/Natural extinction ratios were $\log_{10}$-transformed before modeling. A binary covariate distinguishing North American (0) and European (1) river basins was included to assess differences in fish species loss among continents. Multicollinearity was assessed with the Variance Inflation Factor (VIF); although there is no rule of thumb, VIF values < 10 are acceptable and indicate low multicollinearity among predictors (Dormann *et al.* 2012). Models were built considering all species and then separating migratory from resident species to investigate differences in extinction rates, stressors and continental effects for both groups of species. All analyses and graphics were performed in R (R Core Team 2013).

Results

A total of 1050 species inhabiting 213 river basins were analyzed (see Table S1 in Supporting Information). Among all river basins (mean = 0.78 species extinction by river; sd = 1.49; range = 0-9), 73 have suffered, at least one species extinction (mean = 2.3 extinctions; sd = 1.75; range = 1-9). The highest numbers of species extinction are found in the Mississippi (8), Grande (7) and Pearl (6) river basins of North America; and in the Dnestr (9), Seine (5), Dnepr (5), and Danube (5) river basins for western Europe. IBT values vary from 0.15 to 0.99 (mean = 0.81; sd = 0.13), showing that all river basins analyzed are somehow disturbed and many of them highly altered by human activities.

The mean percentage of total fish species extinction per river basin is 1.8 % (sd = 4 %; range = 0-36 %, 1st quartile = 0, 3rd quartile = 2.86, median = 0; Fig. 1a). The Observed/Natural extinction ratios show that fish species extinctions in the last century are, on average, 40 times (sd = 124, range =

0-998; 1st quartile = 0, 3rd quartile = 17, median = 0) higher than expected under natural conditions, although many river basins have no recorded species extinctions. Among the 73 river basins with non-zero extinction values, the Colorado (998), Grande (720) and Mississippi (532) river basins in North America and the Danube (614), Dnepr (585) and Volga (499) river basins in Europe show the highest Observed/Natural extinction ratios (Fig. 1b). These ratios were not related to the Incidence Biodiversity Threat index (Table 2). This last result suggests that the IBT index is too broad to be a good proxy for predicting large scale riverine fish extinctions and minimizes the chances of potential synergistic feedbacks among anthropogenic stressors. However, our model including individual threats suggests that the number of dams on the main stem and the % of croplands in the river basin are the main determinants of extinctions (Table 2; Fig. 2). Higher Observed/Natural extinction ratios were observed for migratory (mean = 65; sd = 245, range = 0-2138, median = 0) than for resident species (mean = 26; sd = 115, range = 0-1024, median == 0). Finally, migratory Observed/Natural extinction ratios were significantly predicted by the % of croplands in the river basin and marginally by the number of dams, whereas resident Observed/Natural extinction ratios were higher in North America compared to western Europe and significantly positively correlated to the number of dams on the main stem (Table 2).

Discussion

We estimated spatially explicit riverine fish extinctions per river basin from two distinct and highly-impacted regions, while controlling for natural extinction rates. Three main conclusions can be drawn from our results: (1) fish species extinction rates per river basin are similar between both continents and are, on average, 40 times higher than natural extinction rates; (2) there is no link between the Incident Biodiversity Threat (IBT) index developed by Vörösmarty *et al.* (2010) and the loss of riverine fish diversity, suggesting that this index is too broad and synthetic to predict fish extinctions at the drainage basin grain; and (3) migratory and resident fish extinctions respond differently to human threats, though not as expected (i.e., resident species are more sensitive to fragmentation by dams and migratory species are more sensitive to drainage alteration).

The average 40-fold increase of extinction rates observed here includes all river basins; i.e., those affected by species extinctions as well as those with no recorded extinctions. For this reason, the average increase in extinction rate is lower compared to recent estimates for the Nearctic fish fauna made by Burkhead (2012) and Tedesco *et al.* (2013) (respectively 855 and 130 times higher than natural extinction rates). Contrary to our study, Tedesco *et al.* (2013) considered only river basins affected by species extinctions, while Burkhead (2012) did not use river basins as spatial sample units. Our estimated average increase in fish extinction rates is thus clearly conservative compared to the estimates made by these authors. Indeed, when focusing only on drainage basins impacted by species extinctions, our extinction rate estimates increased and reached similar levels (up to 998 times; Fig 1b).

After accounting for natural extinction rates, the number of dams on the main stem and the percentage of cropland in the river basin were found to play a significant role in explaining current patterns of fish extinction. Dams act directly on the degree of connectivity between species sub-populations by decreasing the permeability and availability of habitat within drainages (Luttrell *et al.* 1999; Rahel 2007; Pelicice, Pompeu & Agostinho 2014). Furthermore, dams eliminate the natural flow dynamics of rivers (Poff *et al.* 2007) to which freshwater fish assemblages are tightly adapted (Olden, Poff & Bestgen 2006; Mims & Olden 2012). These new conditions affect meta-population dynamics both directly and indirectly by decreasing the size of sub-populations (Alò & Turner 2005) and the overall genetic pool (Sterling *et al.* 2012), leading to species extinction (Hugueny, Movellan & Belliard 2011; Perkin & Gido 2011). Moreover, we showed that the number of dams on the main stem is by far more important for predicting the Observed/Natural fish extinction ratios than the fragmentation level of the whole basin (i.e., the river fragmentation index). These contrasting results suggest that the position of dams within the drainage (i.e., in the river main stem) has a greater impact than the global reduction in riverine habitat availability. Recent studies have shown that centrality of riverine patches is essential for maintaining connectivity throughout river networks (Erős, Schmera & Schick 2011; Branco *et al.* 2014). Indeed, the main stem acts as a source of immigrants for tributaries (Grenouillet, Pont & Hérissé 2004; Hugueny, Oberdorff & Tedesco 2010; Hitt & Roberts 2012; Dias *et al.* 2013); hence, damming the main course prevents fish from colonizing upstream reaches and, in the long term, contributes to the extinction of populations from the entire basin.

Interestingly, our findings challenge the common idea that migratory rather than resident fish species should be the most affected by dams through the creation of physical barriers that make accessing spawning and feeding grounds difficult (Reidy-Liermann *et al.* 2012). A possible explanation is that most anadromous and catadromous species (representing 77% of our migratory species pool) could overcome, at least partially, such fragmentation levels by crossing dams through fish passage devices (Rechisky *et al.* 2013) or by reproducing in remnant free-flowing river sections, as suggested by theoretical population models (Jager *et al.* 2001). Conversely, resident species, which tend to be more restrictive in their habitat requirements, may be shrinking as a result of damming of the main stem, which, in turn, creates barriers to movement and isolates populations in different sub-basins.

Natural land clearance for agriculture (e.g., deforestation) jeopardizes terrestrial and aquatic communities at different spatial scales (Kerr & Cihlar 2004; Clavero *et al.* 2010; Giam *et al.* 2012; Lange *et al.* 2014; Mantyka-Pringle *et al.* 2014; Mendenhall *et al.* 2014; Leadley *et al.* 2014). Our results show that the percentage of croplands in the drainage basin is positively related to migratory fish extinction. This finding is consistent with other studies showing that the presence, abundance of individuals (Lange *et al.* 2014) and juvenile production (Jonsson, Jonsson & Ugedal 2011) of a migratory species (brown trout, *Salmo trutta* Linnaeus, 1758) is dependent on the intensity of farming at the basin scale. Indeed, agricultural land use is tightly linked to modifications on forest cover, river structure and water quality. All of these factors alter local conditions (Allan 2004) and indirectly prevent species from migrating throughout the network.

Other stressors considered to be important in the loss of aquatic diversity (e.g., consumptive water loss, flow disruption and non-native species) were not related to our Observed/Natural extinction ratios. For instance, contrary to the expectation that the introduction of non-native species outside their native range is one of the leading threats to contemporary biodiversity (Sala *et al.* 2000), non-native species introduction showed no significant effect on extinction rates in our model. Although non-native species may contribute to the homogenization and reduction of diversity via several ecological and evolutionary mechanisms (Olden *et al.* 2004), their role in promoting fish species extinction might not be detectable at the inter-continental scale applied here (but see Light & Marchetti 2007 for a significant effect of non-native species on species extinction at the regional scale). Indeed, for strictly freshwater fishes, river basins can be considered as non-equilibrated islands in which species extinctions (related to historical events) are not fully balanced by colonization from neighbouring river basins (Hugueny, Oberdorff & Tedesco 2010). The implication is that river basins are most often unsaturated with species and thus more susceptible to the establishment of non-native species without systematically generating native species extinction because ecological space should be less densely packed and interspecific competition should be less intense in these systems (Leprieur *et al.* 2009). However, we should keep in mind that human-mediated non-native species introduction and extinction processes act at different time scales and species extinctions might take many decades to millennia to come to completion (Sax & Gaines 2008).

Water pollution, water use for consumptive purposes and changes in natural river flow were not significantly related to extinction patterns. As their potential role in depleting freshwater biodiversity is well understood (Carpenter *et al.* 1998; Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010), this negative result is surprising but might be attributed to differences in spatial resolution and quality of the original data, limiting the use of these threats as predictor variables (see Suppl. Inform. from Vörösmarty *et al.* 2010). Furthermore, the temporal range used to quantify these threats (1990-2005; Vörösmarty *et al.* 2010) may not reflect the environmental conditions during which extinction events occurred over the last 110 years (i.e., the majority of extinctions occurred before 1990). Indeed, the North American and

European fresh waters have benefited from significant improvements in water quality and habitat riverine conditions over the last few decades (Vörösmarty *et al.* 2010). Therefore, historical measures of water quality and habitat riverine conditions before 1990 are required to determine their potential contribution to patterns of fish species loss. Interestingly, the rationale that fish extinctions and threats are temporally separated does not hold for stressors like dams that have been present in rivers since the last 110 years, even if their number increased markedly over the past 60 years (Lehner *et al.* 2011).

The negative effects of dams and drainage basin alteration (i.e., percentage of croplands in the river basin) on fish biodiversity highlighted here have important conservation implications as the number of large dam constructions and natural land clearance for agriculture are strongly increasing in tropical regions (Lehner *et al.* 2011; Finer & Jenkins 2012; Ziv *et al.* 2012) where much of the world's freshwater ichthyofauna is concentrated (Oberdorff *et al.* 2011; Tedesco *et al.* 2012). As stated previously, many river basins in our study had no recorded species extinction even if they were highly altered by human activities. In addition to the problem of false zero extinction values due to a poor knowledge (monitoring) of some rivers, we have to keep in mind that a species extinction event often takes several decades to millennia to unfold. These are timescales (at least for millennia) beyond our study. Such time-lags could create a large extinction-debt (Reidy-Liermann *et al.* 2012) undetectable in the present study that will be paid in the future.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Fish extinction levels, composed and individual threats to aquatic biodiversity and river basin features used in this paper.

Table 1. List of stressors developed by Vörösmarty *et al.* (2010) that were used as predictors in our models and their effects on aquatic biodiversity.

Theme Driver	**Abbrev.**	**Weight ***	**Used**	**Overall effects**
Catchment disturbance				
Croplands	Crop	0.31	X	Degrades and fragments local riparian habitats
Impervious Surfaces	ImpSurf	0.25		Degrades local riparian and floodplain habitats, increases variability of flow
Livestock Density	LivDens	0.18		Degrades local riparian and floodplain habitats, soil compaction, distorts flow patterns
Wetland Disconnectivity	WDisc	0.26		Leads to losses of habitat, nutrient processing and retention, and organic matter inputs, distorts flow patterns
Pollution				
Soil Salinisation	SSalin	0.08		Causes osmoregulatory and ionic stress that can lead to chronic sub-lethal stress or mortality
Nitrogen Loading	Nitr	0.12	X	Fosters eutrophication (and oxygen depletion)
Phosphorus Loading	Phosph	0.13	X	Fosters eutrophication (and oxygen depletion), causes blooms of N-fixing cyanobacteria that can be toxic to aquatic animals
Mercury Deposition	Mercu	0.05		Jeopardises animal development and health, particularly in top predators following bioaccumulation within food web
Pesticide Loading	Pestic	0.10		Imposes acute or chronic toxicity through a variety of mechanisms depending upon specific pesticide and dose, has indirect effects on species interactions and ecosystem processes
Sediment Loading	Sedim	0.17	X	Increases water turbidity, alters benthic physical structure, interferes with respiration, breeding and vision of aquatic animals
Organic Loading	Organ	0.15	X	Changes trophic state of rivers, fosters oxygen deficits, potentially releases toxic chemicals and nutrients
Potential Acidification	PotAcid	0.09		Lethal and sub-lethal effects opn sensitive taxa, increases solubility of certain toxic chemicals, has indirect effects on food availability for pH-insensitive taxa
Thermal Alteration	TAlt	0.11	X	Alters habitat conditions, excludes native species, encourage invasion by non-native species, enhances susceptibility to eutrophication and oxygen depletion
Water Resource Development				
Dam Density	DamD	0.25		Inundates riparian ecosystems, eliminates turbulent reaches, facilitates invasion by lentic biota, blocks animal movements, retains nutrients and sediment that contribute to downstream river and floodplain productivity
River Fragmentation	RFrag	0.30	X	Reduces population sizes and gene flow of aquatic species, restrics animal migrations
Consumptive Water Loss	CWLoss	0.22	X	Decreases contaminant dilution potential, reduces habitat area, distorts flow patterns
Human Water Stress	HWStr	0.04		Decreases contaminant dilution potential, reduces habitat area, distorts flow patterns
Agricultural Water Stress	AWStr	0.07		Decreases contaminant dilution potential, reduces habitat area, distorts flow patterns
Flow Disruption	FlowDis	0.12	X	Retains nutrients, organic material, and fine particles, alters hydrological and thermal regimes
Biotic Factors				
Non-Native Fishes	%Exot	0.26	X	Competes with and/or preys upon native species, alters structure and functioning of ecosystems,

(%)			may contribute to degradation of water quality
Non-Native Fishes (#)	#Exot	0.21	Competes with and/or preys upon native species, alters structure and functioning of ecosystems, may contribute to degradation of water quality
Fishing Pressure	FishPres	0.34	Alters community structure and can give rise to trophic cascades, induces behavioral changes, may contribute to degradation of water quality
Aquaculture Pressure	AquaPres	0.19	Degrades water quality through concentrated chemical pollution, may alter habitat structure and flow, provides a source of non-native species

* see Suppl. Inform. from Vörösmarty *et al.* 2010)

Table 2. Summary of Least Square models relating extinction ratios to anthropogenic threats in North American and European river basins. Models were fitted for total, migratory and resident species. Small values of the Variance Inflation Factor (VIF) were observed for all variables, indicating that multicollinearity did not affect our models.

	Extinction ratio §					
	Combined threats			**Individual threats**		
Predictor	**Total**	**Migratory**	**Resident**	**Total**	**Migratory**	**Resident**
(intercept)	0.50±0.38	0.36±0.39	0.12±0.31	0.57±0.06	0.43±0.06	0.34±0.05
Incident BD Threat	0.09±0.46	0.09±0.48	0.27±0.38	-	-	-
Catchment disturbance						
Crop	-	-	-	**0.21±0.10**	**0.27±0.11**	0.06±0.08
				(P = 0.031)	**(P = 0.012)**	
Pollution						
PCA1 (+Nitr, Phosph, Sedim, Organ, TAlt)	-	-	-	-0.07±0.06	-0.09±0.06	0.00±0.05
Water Resource Development						
PCA1 (+CWLoss, FlowDis)	-	-	-	-0.05±0.06	-0.06±0.07	0.00±0.05
RFrag	-	-	-	0.08±0.06	0.07±0.07	0.06±0.05
# Dams on the main river	-	-	-	**0.19±0.06**	*0.12±0.07*	**0.15±0.05**
				(P = 0.003)	*(P = 0.081)*	**(P = 0.005)**
Biotic factor						
%Exot	-	-	-	0.08±0.06	0.05±0.07	0.03±0.05
Continent	0.00±0.06	**0.14±0.06**	**-0.13±0.05**	-0.06±0.06	0.07±0.07	**-0.15±0.5**
(Europe = 1, USA = 0)		**(P = 0.029)**	**(P = 0.009)**			**(P = 0.005)**
Mean VIF±sd	-	-	-	1.90±1.06	1.90±1.06	1.90±1.06
R-squared (%)	00	02	03	12	09	11
Residual standard deviation	0.87	0.90	0.71	0.82	0.88	0.69
N (# of basins)	213	213	213	213	213	213

§ Estimated as $\log_{10}$[(Obs/Est)+1]

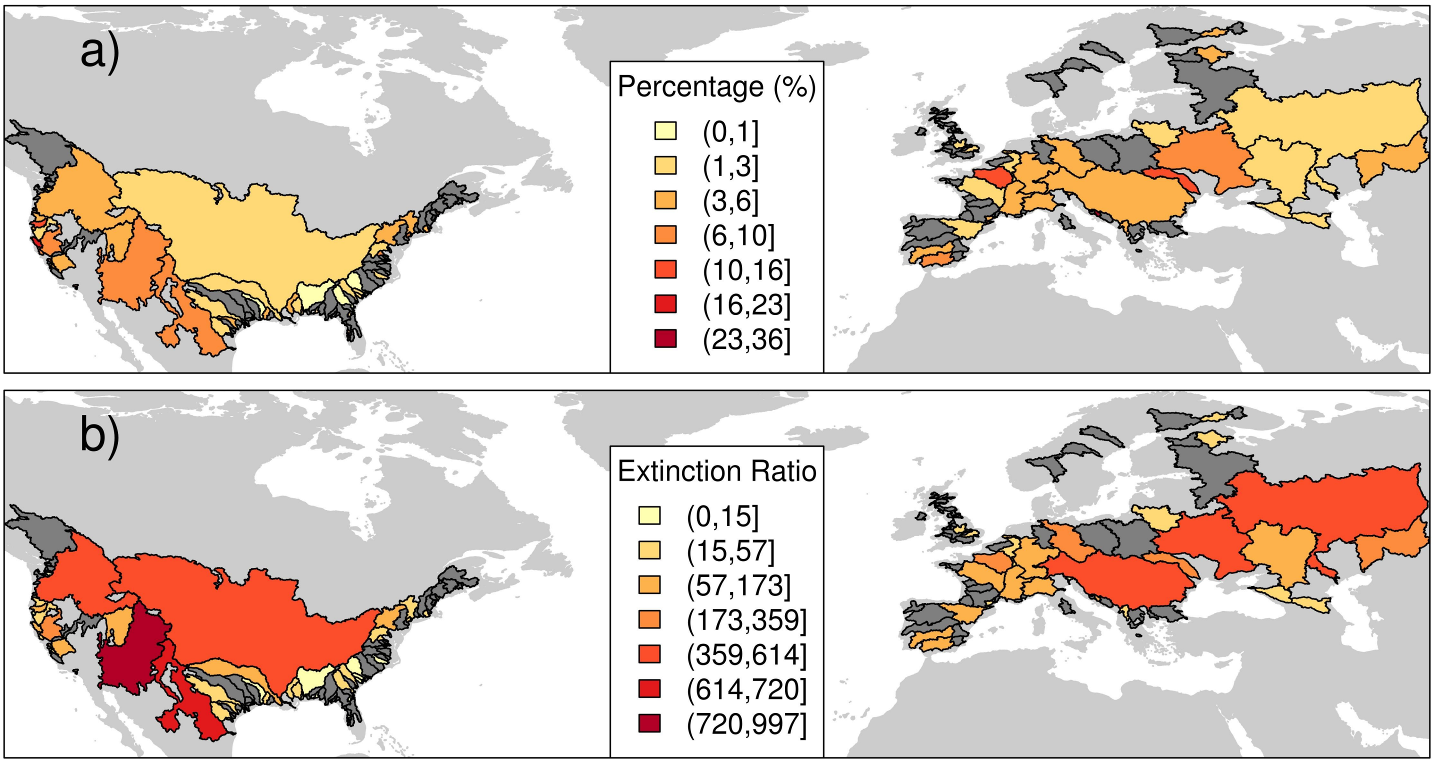

Figure 1. Percentage of extinction (a) and Observed/Natural extinction ratios (b) of total fish species per river basin for North America and western Europe. Dark-gray polygons represent basins where no extinctions have been recorded.

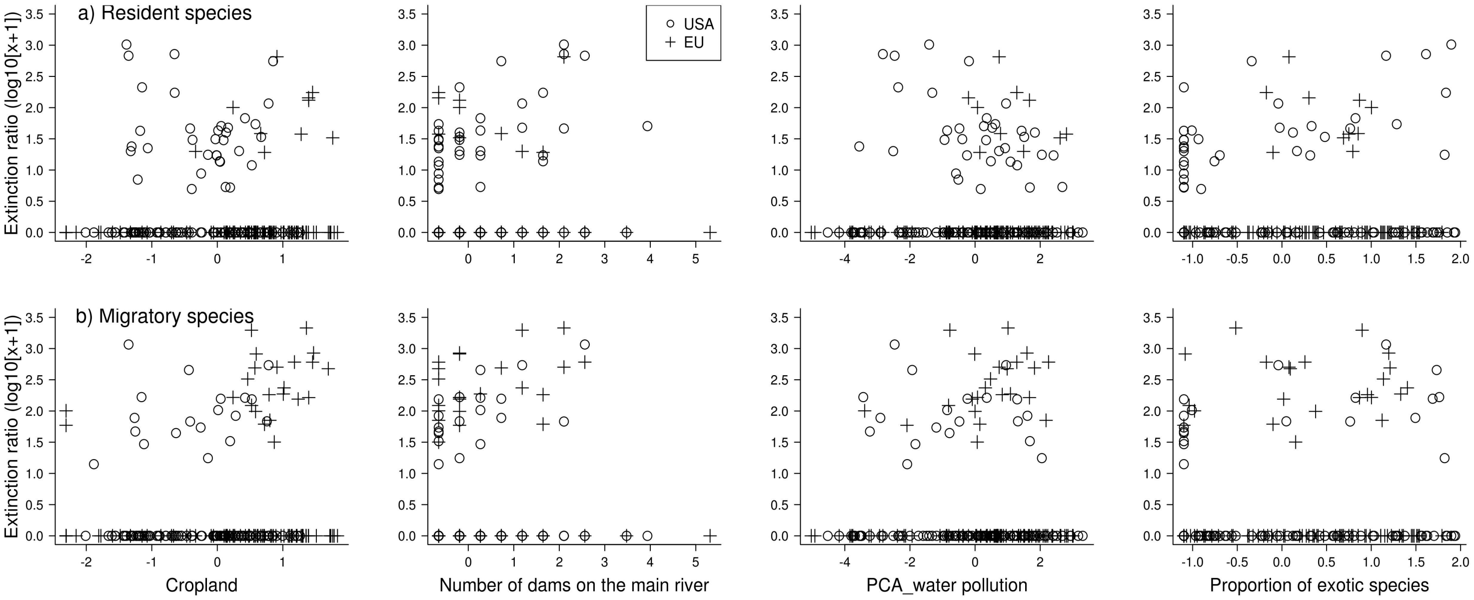

Figure 2. Fish extinction ratio for (a) resident and (b) migratory groups of species relating to individual threats. All threats are centered and reduced for improving coefficient interpretation during model fit.

Table S1. Fish extinction levels, composed and individual threats to aquatic biodiversity and river basin features used in this paper.

Column names	**Description**
id	row identification
River_basin	name of river basin
Continent	continent on which basin is located
E_Extinct	Number of all extinct species
C_Current	Number of all extant species (not extinct)
E_Migratory	Number of migratory extinct species
C_Migratory	Number of migratory extant species (not extinct)
E_Resident	Number of resident extinct species
C_Resident	Number of resident extant species (not extinct)
Exotic	Number of exotic species
proportExotic_Exotic/(E+C+Exot)	Proportion of exotic species
proportExotic.ecdf	Proportion of exotic species standardized by Cumulative Distribution Function (see Suppl Mat, Vörösmarty et al. 2010)
Surface_basin_km	Surface are of drainage basin in Km
e	Expected natural extinction rate per species per year (see Methods; Hugueny et al 2010; Tedesco et al. 2013)
NaturalExt	The expected Background Extinction over the last 110 years
ratioTOTAL	Ratio between percentage of extinct species and the NaturalExt
ratioMIGRATORY	Ratio between percentage of migratory extinct species (E_Mig/(E_Mig+C_Mig)) and the NaturalExt
ratioRESIDENT	Ratio between percentage of resident extinct species (E_Res/(E_Res+C_Res)) and the NaturalExt
Incbdthreat	The Incident Biodiversity Threat Index (combined threats; see Vörösmarty et al. 2010)
cons_watloss	Consumptive Water Loss
cropland	Percentage of Croplands
thermal_alt	Thermal Alteration
nitrogen_load	Nitrogen Loading
organic_load	Organic Loading
phosphor_load	Phosphorus Loading
sediment_load	Sediment Loading
riv_fragm	River Fragmentation
flow_disrupt	Flow Disruption
Ndams_main stem	Number of dams on the main river stem

id	River_basin	Continent	E_Extinct	C_Current	E_Migratory	C_Migratory	E_Resident	C_Resident	Exotic	proportExotic_Exotic/(E+C+Exot)	proportExotic.ecdf	Surface_basin_km	e	NaturalExt
1	Adour	Europe	0	26	0	11	0	15	13	0.3333333333	0.6948356808	16861.2687386	1.05559292845614e-05	0.0011604845
2	Alabama	USA	1	203	0	14	1	189	19	0.0852017937	0.1267605634	112050.976877	2.95414661788396e-06	0.0003249038
3	Alafia	USA	0	40	0	3	0	37	24	0.375	0.7464788732	1105.06652146	6.59585455803358e-05	0.0072294204
4	Alemeda.creek	USA	2	22	1	11	1	11	39	0.619047619	0.9201877934	1898.53647193	4.58396102298586e-05	0.0050297808
5	Aliakmon	Europe	0	30	0	10	0	20	4	0.1176470588	0.1737089202	6580.65394385	1.98724467547207e-05	0.0021836033
6	Alsea	USA	0	20	0	14	0	6	17	0.4594594595	0.8356807512	1164.40561521	6.36791730923569e-05	0.0069804547
7	Altamaha	USA	1	86	0	10	1	76	21	0.1944444444	0.3990610329	37545.2463734	6.16208488357639e-06	0.0006776017
8	Apalachicola	USA	0	120	0	12	0	108	24	0.1666666667	0.3286384977	50797.5362504	5.02863460394298e-06	0.0005529982
9	Appomattox	USA	0	57	0	8	0	49	28	0.3294117647	0.6713615023	4168.87518363	2.70117797417369e-05	0.0029669259
10	Aransas	USA	0	16	0	3	0	13	6	0.2727272727	0.5821596244	2290.90922669	4.04000308138475e-05	0.0044342328
11	Argens	Europe	0	26	0	10	0	16	14	0.35	0.7183098592	2761.64680567	3.56295697437892e-05	0.003911652
12	Ashley	USA	0	49	0	10	0	39	17	0.2575757576	0.5399061033	1035.42735158	6.89093833472487e-05	0.0075516354
13	Aucilla	USA	0	56	0	3	0	53	4	0.0666666667	0.0938967136	2503.33354552	3.8061641719489e-05	0.0041781076
14	Aude	Europe	2	30	0	11	2	19	13	0.2888888889	0.6150234742	5226.38705848	2.32025648265743e-05	0.0025490574
15	Aulne	Europe	0	17	0	8	0	9	1	0.0555555556	0.0704225352	1686.59974459	4.96370657645517e-05	0.0054453329
16	Avon.Eng	Europe	0	21	0	7	0	14	4	0.16	0.3098591549	2229.18414573	4.11488307644481e-05	0.0045162355
17	Awe	Europe	0	11	0	8	0	3	0	0	0	851.291644138	7.86064172988432e-05	0.0086097676
18	Axios	Europe	0	34	0	10	0	24	5	0.1282051282	0.2300469484	24397.027784	8.23403360550312e-06	0.0009053374
19	Bann	Europe	0	12	0	11	0	1	10	0.4545454545	0.8262910798	5810.96754002	2.16060023766618e-05	0.0023738639
20	Bear.river	USA	1	19	0	1	1	18	33	0.6226415094	0.9248826291	122525.615512	2.78186084523568e-06	0.0003059583
21	Blackstone	USA	0	21	0	3	0	18	18	0.4615384615	0.8403755869	1662.03700482	5.0129120344411e-05	0.0054991654
22	Blavet	Europe	0	23	0	11	0	12	10	0.303030303	0.6431924883	2056.93604735	4.3435085233634e-05	0.0047665668
23	Bollin	Europe	0	20	0	7	0	13	5	0.2	0.4084507042	2404.24421864	3.91094112881518e-05	0.0042928785
24	Brazos	USA	0	74	0	5	0	69	14	0.1590909091	0.3004694836	109375.697259	3.00253962448593e-06	0.0003302253
25	Buyuktchekmedje	Europe	0	22	0	8	0	14	1	0.0434782609	0.0469483568	637.347812726	9.54940413320227e-05	0.0104498629
26	Calcasieu	USA	4	82	0	5	4	77	4	0.0444444444	0.0516431925	10158.1346073	1.48413988616536e-05	0.0016312341
27	Cape.Fear	USA	0	91	0	15	0	76	21	0.1875	0.3661971831	22786.3285113	8.62100031184809e-06	0.0009478646
28	Cedar	USA	0	29	0	16	0	13	31	0.5166666667	0.882629108	1532.19088513	5.29473092353294e-05	0.0058074295
29	Cedar.Bayou	USA	0	25	0	5	0	20	6	0.1935483871	0.3943661972	611.58924213	9.81799606121214e-05	0.0107422117
30	Cetina	Europe	4	7	0	2	4	5	3	0.2142857143	0.441314554	3868.93222751	2.84025498338281e-05	0.0031194492
31	Charente	Europe	0	28	0	12	0	16	12	0.3	0.6384976526	9526.29970024	1.549629032771e-05	0.0017031531
32	Chehalis	USA	0	28	0	16	0	12	17	0.3777777778	0.7558685446	5462.82208238	2.25224509255995e-05	0.002474431
33	Choctawhatchee	USA	0	95	0	10	0	85	5	0.05	0.0563380282	11879.8081321	1.33584174042412e-05	0.0014683566
34	Clyde.Scotland	Europe	0	18	0	12	0	6	14	0.4375	0.8075117371	2971.93065542	3.39141706663382e-05	0.0037236719
35	Cocheco	USA	0	35	0	14	0	21	13	0.2708333333	0.5680751174	2507.35411536	3.80205936215683e-05	0.004173611
36	Colorado.Texas	USA	1	64	0	5	1	59	18	0.2168674699	0.4507042254	106550.786826	3.05583574167212e-06	0.000336086
37	Colorado.USA	USA	4	35	0	1	4	34	92	0.7022900763	0.9436619718	620529.083893	9.3455809113685e-07	0.0001027962
38	Columbia	USA	3	56	0	17	3	39	52	0.4684684685	0.8544600939	653050.002772	9.03003823604642e-07	9.93255323370468e-05
39	Combahee	USA	2	63	0	10	2	53	0	0	0	4351.47834483	2.62442802995144e-05	0.0028827456
40	Connecticut	USA	0	45	0	16	0	29	31	0.4078947368	0.779342723	29001.3419794	7.3304097326643e-06	0.000806023
41	Conon	Europe	0	14	0	11	0	3	0	0	0	1189.85555812	6.27601265621447e-05	0.0068800539
42	Cooper	USA	0	55	0	11	0	44	0	0	0	1861.40923113	4.64523845437048e-05	0.0050968478
43	Cosumnes	USA	0	20	0	9	0	11	35	0.6363636364	0.9295774648	5888.74380876	2.14137082670263e-05	0.002352761
44	Coyote.creek	USA	0	21	0	10	0	11	0	0	0	1704.43961413	4.92871362626213e-05	0.0054070476

conti...														
id	**River_basin**	**Continent**	**E_Extinct**	**C_Current**	**E_Migratory**	**C_Migratory**	**E_Resident**	**C_Resident**	**Exotic**	**proportExotic_Exotic/(E+C+Exot)**	**proportExotic.ecdf**	**Surface_basin_km**	**e**	**NaturalExt**
45	Crni.Drim	Europe	2	50	1	11	1	39	10	0.1612903226	0.3145539906	13067.6169104	1.25292937809274e-05	0.0013772816
46	Dane	Europe	0	20	0	7	0	13	10	0.3333333333	0.6948356808	1422.57054466	5.56571355753155e-05	0.0061037513
47	Danube	Europe	5	89	1	22	4	67	22	0.1896551724	0.3708920188	802041.215885	7.86462004298549e-07	8.65071125355499e-05
48	Dee.Scotland	Europe	0	12	0	8	0	4	0	0	0	2115.43695524	4.26237341546454e-05	0.0046777358
49	Dee.Wales	Europe	0	21	0	14	0	7	13	0.3823529412	0.7605633803	1928.21850015	4.53639495171521e-05	0.0049777175
50	Delaware	USA	0	73	0	15	0	58	29	0.2843137255	0.6009389671	28599.4371168	7.39951727768418e-06	0.0008136187
51	Deschutes	USA	0	24	0	14	0	10	0	0	0	448.246730727	0.0001209911	0.0132216406
52	Dnepr	Europe	5	68	5	15	0	53	10	0.1204819277	0.1830985915	512383.084766	1.06298712687636e-06	0.0001169218
53	Dnestr	Europe	9	63	5	14	4	49	13	0.1529411765	0.2910798122	72531.5100922	3.95768060956758e-06	0.000435251
54	Don.Russia	Europe	1	63	1	15	0	48	15	0.1898734177	0.3755868545	429402.712567	1.19707463419605e-06	0.0001316696
55	Dordogne	Europe	0	32	0	15	0	17	13	0.2888888889	0.6150234742	23902.4532429	8.34820747985798e-06	0.0009178851
56	Douro	Europe	0	22	0	11	0	11	14	0.3888888889	0.7746478873	97420.9167662	3.24555756547884e-06	0.0003569482
57	Earn	Europe	0	19	0	13	0	6	4	0.1739130435	0.3568075117	974.014935216	7.18013576901377e-05	0.0078673222
58	Ebro	Europe	1	29	1	10	0	19	21	0.4117647059	0.7887323944	85613.608325	3.54011377734498e-06	0.0003893374
59	Eden	Europe	0	21	0	9	0	12	3	0.125	0.2253521127	2321.57193284	4.00404693710055e-05	0.0043948541
60	Edisto	USA	1	64	1	5	0	59	0	0	0	7431.64944518	1.83120975538742e-05	0.0020123217
61	Eel	USA	4	13	4	10	0	3	21	0.5526315789	0.9014084507	9371.06304692	1.56684319957412e-05	0.0017220566
62	Elbe	Europe	3	46	3	15	0	31	13	0.2096774194	0.4272300469	143657.315362	2.49960882547917e-06	0.0002749195
63	Escambia	USA	0	99	0	9	0	90	7	0.0660377358	0.0892018779	10987.8620783	1.4078185272437e-05	0.0015474128
64	Escatawpa	USA	1	70	0	6	1	64	4	0.0533333333	0.0610328638	2798.50846202	3.53133271717709e-05	0.0038769995
65	Evros	Europe	0	35	0	12	0	23	6	0.1463414634	0.2629107981	53026.3171158	4.88551832855677e-06	0.000537264
66	Fraser	USA	0	16	0	10	0	6	0	0	0	231742.134988	1.81229966700336e-06	0.0001993333
67	Garonne	Europe	0	29	0	12	0	17	24	0.4528301887	0.8215962441	55704.1032189	4.72633170200965e-06	0.0005197626
68	Glen	Europe	0	23	0	8	0	15	6	0.2068965517	0.4178403756	1590.03235029	5.16443940566935e-05	0.0056649235
69	Glomma	Europe	0	17	0	6	0	11	6	0.2608695652	0.5492957746	41911.4871428	5.72271040188976e-06	0.0006293019
70	Grande.USA	USA	7	72	1	6	6	66	42	0.347107438	0.7136150235	474891.784782	1.11870937757885e-06	0.0001230505
71	Green	USA	0	26	0	16	0	10	0	0	0	1187.87713786	6.2830389529922e-05	0.0068877301
72	Greens.Bayou	USA	0	39	0	2	0	37	13	0.25	0.5258215962	2676.11673485	3.63912914523867e-05	0.0039951131
73	Guadalquivir	Europe	2	25	1	11	1	14	11	0.2894736842	0.6197183099	57053.8963132	4.65085197598469e-06	0.0005114641
74	Guadalupe	USA	2	51	0	3	2	48	17	0.2428571429	0.4976525822	15752.8546325	1.10497639169704e-05	0.0012147423
75	Guadiana	Europe	1	26	1	11	0	15	12	0.3076923077	0.6478873239	67064.4929461	4.17181660161692e-06	0.0004587955
76	Herault	Europe	0	28	0	9	0	19	14	0.3333333333	0.6948356808	2624.57664279	3.68702698494427e-05	0.0040475908
77	Hillsborough	USA	2	49	1	5	1	44	0	0	0	1791.29395461	4.76672415877788e-05	0.0052297983
78	Housatonic	USA	0	30	0	7	0	23	27	0.4736842105	0.8591549296	4999.16173184	2.39065060709809e-05	0.0026262923
79	Hudson	USA	3	80	1	20	2	60	32	0.2782608696	0.5868544601	34885.6404888	6.47414946008951e-06	0.0007119052
80	Humboldt	USA	0	10	0	1	0	9	26	0.7222222222	0.9530516432	53639.639329	4.84788636212485e-06	0.0005331266
81	Imandra	Europe	1	21	1	11	0	10	0	0	0	12275.1904495	1.30675551973658e-05	0.0014364078
82	Indalsalven	Europe	0	27	0	12	0	15	0	0	0	25839.1620463	7.92213128208985e-06	0.0008710583
83	James	USA	0	60	0	6	0	54	0	0	0	18268.0360509	1.00022104972952e-05	0.0010996436
84	Jucar	Europe	0	24	0	10	0	14	14	0.3684210526	0.7323943662	21555.4395024	8.94899319392461e-06	0.0009839093
85	Kemijoki	Europe	0	26	0	10	0	16	1	0.037037037	0.0375586854	52513.2111117	4.91756501697083e-06	0.0005407872
86	Kennebec	USA	0	43	0	18	0	25	15	0.2586206897	0.544600939	24600.9313353	8.18808173530527e-06	0.0009002872
87	Klamath	USA	1	33	1	16	0	17	28	0.4516129032	0.8169014085	31126.559346	6.98999535952982e-06	0.0007686066

conti...

id	River_basin	Continent	E_Extinct	C_Current	E_Migratory	C_Migratory	E_Resident	C_Resident	Exotic	proportExotic_Exotic/(E+C+Exot)	proportExotic.ecdf	Surface_basin_km	e	NaturalExt
88	Koutno	Europe	1	25	1	12	0	13	1	0.037037037	0.0375586854	30903.3284115	7.02390628615213e-06	0.000772334
89	Krka	Europe	0	15	0	4	0	11	3	0.1666666667	0.3286384977	2549.42467506	3.7597578885995e-05	0.0041272707
90	Kuban	Europe	1	65	1	18	0	47	19	0.2235294118	0.4647887324	52689.9475809	4.90646780049175e-06	0.0005395672
91	Lavaca	USA	0	24	0	2	0	22	3	0.1111111111	0.1690140845	5886.41432723	2.14194059099393e-05	0.0023533863
92	Leven	Europe	0	14	0	10	0	4	5	0.2631578947	0.5539906103	814.731157461	8.09610543587302e-05	0.0088665349
93	Little.Manatee	USA	0	37	0	4	0	33	0	0	0	531.464751369	0.0001079015	0.0117996324
94	Loire	Europe	1	34	1	16	0	18	22	0.3859649123	0.765258216	116982.925541	2.86981295138933e-06	0.0003156301
95	Los.Angeles	USA	1	9	0	5	1	4	0	0	0	2024.41459758	4.39030283413411e-05	0.0048177961
96	Manatee	USA	0	29	0	1	0	28	0	0	0	602.002080677	9.92285238162749e-05	0.0108563194
97	Mattaponi	USA	0	53	0	10	0	43	31	0.369047619	0.7370892019	2314.27478163	4.01253155961623e-05	0.0044041464
98	Meherrin	USA	0	90	0	13	0	77	16	0.1509433962	0.2769953052	11997.9006401	1.32698651531538e-05	0.00145863
99	Mermentau	USA	0	63	0	6	0	57	0	0	0	7466.81143068	1.82540698208111e-05	0.0020059514
100	Merrimack	USA	0	37	0	13	0	24	18	0.3272727273	0.6666666667	13072.5734243	1.2526099347876e-05	0.0013769307
101	Meuse	Europe	1	46	1	18	0	28	24	0.338028169	0.6995305164	32047.5883539	6.85427436597497e-06	0.0007536886
102	Minho	Europe	0	16	0	12	0	4	8	0.3333333333	0.6948356808	16985.470048	1.05039665437845e-05	0.0011547751
103	Mission	USA	0	13	0	3	0	10	0	0	0	2576.27784203	3.73336259017476e-05	0.0040983542
104	Mississippi	USA	8	415	0	17	8	398	66	0.1349693252	0.2394366197	3009004.66497	3.23272057012325e-07	3.55592997722809e-05
105	Myakka	USA	0	39	0	5	0	34	16	0.2909090909	0.6244131455	1279.61430061	5.97649848587123e-05	0.0065527811
106	Nassau	USA	0	59	0	9	0	50	4	0.0634920635	0.0845070423	1109.04009502	6.5799554154311e-05	0.0072120565
107	Neches	USA	1	100	0	8	1	92	8	0.0733944954	0.1079812207	27384.1647205	7.61874523780293e-06	0.0008377141
108	Nehalem	USA	0	18	0	13	0	5	0	0	0	2221.62903885	4.12428688320032e-05	0.0045265334
109	Nene	Europe	0	25	0	10	0	15	7	0.21875	0.4600938967	2432.97444071	3.879827860509e-05	0.0042587989
110	Neretva	Europe	0	16	0	5	0	11	3	0.1578947368	0.2957746479	13122.0966522	1.24942928834137e-05	0.0013734368
111	Ness	Europe	0	11	0	8	0	3	0	0	0	1852.45450926	4.66032489778723e-05	0.0051133589
112	Nestos	Europe	0	27	0	9	0	18	2	0.0689655172	0.0985915493	6218.27050682	2.06439044178053e-05	0.0022682765
113	Neuse	USA	1	79	1	9	0	70	17	0.175257732	0.3615023474	11691.7381129	1.35025235679098e-05	0.0014841851
114	Neva	Europe	0	47	0	15	0	32	1	0.0208333333	0.0093896714	279587.415576	1.59742682970254e-06	0.0001757017
115	Niemen	Europe	1	47	1	17	0	30	10	0.1724137931	0.3521126761	95925.7719913	3.27948583056514e-06	0.000360679
116	Nisqually	USA	0	28	0	17	0	11	0	0	0	1874.88243943	4.62276679222828e-05	0.0050722535
117	Nith	Europe	0	16	0	10	0	6	5	0.2380952381	0.4929577465	1229.05704454	6.14070443000214e-05	0.0067322187
118	Nueces	USA	1	45	0	4	1	41	11	0.1929824561	0.3849765258	43637.2311475	5.56953050967479e-06	0.0006124624
119	Ochlockonee	USA	0	70	0	6	0	64	6	0.0789473684	0.1126760563	5676.73404036	2.19482116347036e-05	0.0024114176
120	Odra	Europe	0	55	0	17	0	38	16	0.2253521127	0.4694835681	118939.61769	2.8379816833235e-06	0.0003121297
121	Ogeechee	USA	0	63	0	7	0	56	4	0.0597014925	0.0798122066	11460.9982221	1.36847108340721e-05	0.0015041961
122	Orb	Europe	0	29	0	11	0	18	10	0.2564102564	0.5352112676	1556.43811287	5.23912706088536e-05	0.0057466154
123	Oulujoki	Europe	0	29	0	12	0	17	1	0.0333333333	0.0234741784	24241.8087055	8.26944672494001e-06	0.0009092293
124	Ouse	Europe	1	32	0	16	1	16	12	0.2666666667	0.5633802817	8442.82870155	1.68068220882667e-05	0.0018470581
125	Pajaro	USA	1	15	0	6	1	9	0	0	0	3357.25249485	3.12450582532486e-05	0.0034311103
126	Pascagoula	USA	3	111	0	10	3	101	0	0	0	21728.859435	8.90090577931879e-06	0.0009786248
127	Passaic	USA	3	37	0	7	3	30	0	0	0	2448.57803364	3.86318619435277e-05	0.0042405702
128	Patuxent	USA	1	50	0	9	1	41	0	0	0	1676.81687788	4.98315969912344e-05	0.0054666156
129	Peace	USA	0	43	0	5	0	38	0	0	0	5803.69361735	2.16242066150008e-05	0.0023758616
130	Pearl	USA	6	126	1	9	5	117	5	0.0364963504	0.0281690141	21804.9268051	8.88001511611947e-06	0.0009763291

conti...														
id	**River_basin**	**Continent**	**E_Extinct**	**C_Current**	**E_Migratory**	**C_Migratory**	**E_Resident**	**C_Resident**	**Exotic**	**proportExotic_Exotic/(E+C+Exot)**	**proportExotic.ecdf**	**Surface_basin_km**	**e**	**NaturalExt**
131	Peedee	USA	0	102	0	12	0	90	25	0.1968503937	0.4037558685	46104.7758446	5.36729974776051e-06	0.0005902303
132	Penboscot	USA	0	39	0	18	0	21	7	0.152173913	0.2863849765	21964.1173928	8.83668797235782e-06	0.0009715677
133	Perdido	USA	0	74	0	8	0	66	0	0	0	2266.96570276	4.06864454336464e-05	0.0044655995
134	Petronila.creek	USA	0	13	0	2	0	11	0	0	0	2694.15673038	3.62272670880737e-05	0.0039771417
135	Po	Europe	2	41	2	12	0	29	22	0.3384615385	0.7042253521	71328.1765232	4.00245189979831e-06	0.0004401737
136	Potomac	USA	2	56	0	10	2	46	35	0.376344086	0.7511737089	30377.1064912	7.10548985838333e-06	0.0007813013
137	Presumpscot	USA	2	29	2	11	0	18	0	0	0	1704.26816074	4.92904701550057e-05	0.0054074124
138	Puyallup	USA	1	28	0	16	1	12	0	0	0	2645.05247701	3.66781131192484e-05	0.0040265381
139	Quinebaug	USA	2	36	2	15	0	21	0	0	0	4753.35873591	2.47308589508277e-05	0.0027167311
140	Rappahannock	USA	3	37	2	3	1	34	0	0	0	5024.17595933	2.38264091708684e-05	0.0026175046
141	Raritan	USA	0	41	0	6	0	35	0	0	0	2833.96885026	3.50156117630007e-05	0.0038443761
142	Red	USA	5	153	1	7	4	146	32	0.1684210526	0.3333333333	185998.121345	2.10107598197506e-06	0.0002310919
143	Rhine	Europe	2	43	2	14	0	29	26	0.3661971831	0.7276995305	160223.473298	2.3227443181062e-06	0.0002554695
144	Rhone	Europe	2	43	1	16	1	27	21	0.3181818182	0.661971831	96620.4780645	3.26361215563509e-06	0.0003589335
145	Ribble	Europe	0	22	0	9	0	13	6	0.2142857143	0.441314554	1941.147408	4.51605700855229e-05	0.0049554559
146	Roanoke	USA	0	98	0	15	0	83	30	0.234375	0.4788732394	25374.2950875	8.01943018713391e-06	0.0008817519
147	Rogue	USA	4	20	0	10	4	10	0	0	0	13360.7959764	1.23437588326336e-05	0.0013569004
148	Russian	USA	2	19	2	10	0	9	0	0	0	3863.91715934	2.84273317914252e-05	0.0031221668
149	Sabine	USA	0	90	0	7	0	83	7	0.0721649485	0.103286385	26590.3552698	7.77094024706493e-06	0.0008544415
150	Saco	USA	0	30	0	13	0	17	0	0	0	4419.75206561	2.59709942521669e-05	0.0028527696
151	Sacramento	USA	3	30	3	12	0	18	38	0.5352112676	0.8920187793	70938.1632788	4.0172348813039e-06	0.0004417991
152	Sainte.Croix	USA	0	31	0	12	0	19	0	0	0	3934.16987117	2.80850007705613e-05	0.0030846262
153	Saint.Jean.USA	USA	0	29	0	10	0	19	5	0.1470588235	0.2723004695	55070.5438277	4.7628242182407e-06	0.0005237747
154	Saint.Johns	USA	0	77	0	17	0	60	26	0.2524271845	0.5305164319	24659.3367164	8.17503661154628e-06	0.0008988535
155	Saint.Marks	USA	0	58	0	4	0	54	0	0	0	2265.93908832	4.06988389781704e-05	0.0044669567
156	Saint.Mary.s	USA	1	54	0	7	1	47	0	0	0	3322.89465979	3.14619178339859e-05	0.0034548835
157	Salinas	USA	0	14	0	6	0	8	0	0	0	11049.3719591	1.40254409843887e-05	0.0015416198
158	San.Antonio	USA	0	40	0	4	0	36	15	0.2727272727	0.5821596244	10860.5557995	1.41889339909662e-05	0.0015595764
159	San.Bernard	USA	0	17	0	4	0	13	2	0.1052631579	0.1455399061	2581.65066602	3.72813654597737e-05	0.0040926289
160	San.Jacinto	USA	0	59	0	3	0	56	0	0	0	7398.11148867	1.83678746079607e-05	0.002018445
161	San.Joaquin	USA	1	23	1	11	0	12	25	0.5102040816	0.8779342723	53514.0285942	4.85553477547196e-06	0.0005339675
162	Santee	USA	1	105	0	11	1	94	29	0.2148148148	0.4460093897	39787.4946978	5.92637150009789e-06	0.0006516904
163	Satilla	USA	0	46	0	5	0	41	0	0	0	8820.48484272	1.63195093018098e-05	0.0017935503
164	Savannah	USA	4	113	0	15	4	98	24	0.170212766	0.338028169	27228.813031	7.6479458348544e-06	0.0008409235
165	Schelde	Europe	0	32	0	11	0	21	10	0.2380952381	0.4929577465	18949.2789624	9.75897769195377e-06	0.0010729168
166	Segura	Europe	0	16	0	9	0	7	12	0.4285714286	0.8028169014	14985.3243007	1.1427187953772e-05	0.0012562082
167	Seine	Europe	5	28	5	9	0	19	18	0.3529411765	0.7230046948	75990.665857	3.83562149453009e-06	0.0004218302
168	Severn.UK	Europe	0	25	0	16	0	9	21	0.4565217391	0.8309859155	11381.6790947	1.37487635307743e-05	0.0015112313
169	Siuslaw	USA	1	21	0	13	1	8	0	0	0	2000.55348058	4.42544336588524e-05	0.0048562654
170	Skagit	USA	0	24	0	17	0	7	0	0	0	8210.23980313	1.71254969072443e-05	0.0018820475
171	Skokomish	USA	0	23	0	13	0	10	0	0	0	622.157792007	9.70554586537942e-05	0.0106198258
172	Smith	USA	1	17	1	14	0	3	0	0	0	1857.47897776	4.65184496064586e-05	0.0051040782
173	Snohomish	USA	0	29	0	18	0	11	0	0	0	4545.24666601	2.54866409199472e-05	0.0027996399

conti...														
id	**River_basin**	**Continent**	**E_Extinct**	**C_Current**	**E_Migratory**	**C_Migratory**	**E_Resident**	**C_Resident**	**Exotic**	**proportExotic_Exotic/(E+C+Exot)**	**proportExotic.ecdf**	**Surface_basin_km**	**e**	**NaturalExt**
174	Sperchios	Europe	0	16	0	7	0	9	1	0.0588235294	0.0751173709	1385.33070823	5.6658740719473e-05	0.0062132554
175	Spey	Europe	0	11	0	8	0	3	1	0.0833333333	0.1220657277	3061.10952267	3.32466275407839e-05	0.0036505105
176	Stillaguamish	USA	0	24	0	17	0	7	0	0	0	1752.02643964	4.83829701327654e-05	0.0053081174
177	Stour	Europe	0	26	0	11	0	15	7	0.2121212121	0.4319248826	877.892258024	7.69968880406369e-05	0.0084342145
178	Susquehanna	USA	3	79	1	13	2	66	33	0.2869565217	0.6056338028	71074.4756962	4.01205270306182e-06	0.0004412293
179	Suwannee	USA	0	72	0	10	0	62	3	0.04	0.0422535211	26450.7238243	7.79849969023694e-06	0.0008574705
180	Tagliamento	Europe	1	24	1	7	0	17	6	0.1935483871	0.3943661972	2609.87426604	3.70097986994722e-05	0.0040628773
181	Tagus	Europe	0	31	0	12	0	19	12	0.2790697674	0.5915492958	71203.7732658	4.00715254511574e-06	0.0004406905
182	Tar	USA	0	73	0	9	0	64	10	0.1204819277	0.1830985915	8102.70294994	1.72779916637333e-05	0.0018987905
183	Tay	Europe	0	18	0	13	0	5	5	0.2173913043	0.455399061	4927.68315847	2.41391250489498e-05	0.0026518135
184	Tees	Europe	0	24	0	11	0	13	5	0.1724137931	0.3521126761	1792.11419089	4.76525711444742e-05	0.0052281929
185	Teifi	Europe	0	19	0	11	0	8	3	0.1363636364	0.2441314554	995.665558628	7.07477933363787e-05	0.0077523271
186	Terek	Europe	1	59	1	15	0	44	2	0.0322580645	0.0187793427	56525.3773251	4.68004730802551e-06	0.0005146739
187	Tet	Europe	2	21	0	6	2	15	9	0.28125	0.5962441315	1379.97609118	5.68064689504544e-05	0.0062294054
188	Tevere	Europe	0	19	0	7	0	12	25	0.5681818182	0.9107981221	17861.2549331	1.01548135889029e-05	0.0011164115
189	Thames.UK	Europe	0	28	0	13	0	15	13	0.3170731707	0.6572769953	13513.9488495	1.22495210925777e-05	0.0013465482
190	Trent	Europe	1	31	0	15	1	16	12	0.2727272727	0.5821596244	10392.7477275	1.46152781107523e-05	0.0016064007
191	Trinity	USA	0	74	0	6	0	68	9	0.1084337349	0.1502347418	45873.9193282	5.38544660122486e-06	0.0005922253
192	Truckee	USA	0	10	0	1	0	9	28	0.7368421053	0.9577464789	7169.79923351	1.87591342660776e-05	0.0020613965
193	Tweed	Europe	0	15	0	13	0	2	12	0.4444444444	0.8122065728	5074.47766912	2.36673421086797e-05	0.0026000524
194	Tyne	Europe	0	21	0	8	0	13	4	0.16	0.3098591549	2886.39878455	3.4586662806313e-05	0.0037973704
195	Umealven	Europe	0	26	0	11	0	15	0	0	0	26939.0690018	7.70315873721561e-06	0.0008469918
196	Umpqua	USA	1	27	1	14	0	13	0	0	0	12093.5878826	1.31991756887606e-05	0.0014508654
197	Ural	Europe	2	48	2	11	0	37	1	0.0196078431	0.0046948357	253148.961883	1.70776958297036e-06	0.0001878372
198	Var	Europe	0	17	0	4	0	13	5	0.2272727273	0.4741784038	2818.56612828	3.51441590916712e-05	0.0038584624
199	Vashon.Island	USA	0	23	0	14	0	9	0	0	0	112.823302554	0.0003058865	0.0330927154
200	Veleka	Europe	0	15	0	5	0	10	0	0	0	1068.82277868	6.74541893672664e-05	0.0073927493
201	Vilaine	Europe	0	27	0	13	0	14	14	0.3414634146	0.7089201878	10490.5404907	1.45235281532319e-05	0.0015963242
202	Volga	Europe	2	65	2	15	0	50	28	0.2947368421	0.6291079812	1392013.74544	5.42842379380737e-07	5.97108951726488e-05
203	Voronia	Europe	0	16	0	9	0	7	0	0	0	9494.69724743	1.55309524583203e-05	0.0017069595
204	Waccasassa	USA	0	53	0	6	0	47	0	0	0	1667.78532677	5.00128809451938e-05	0.0054864486
205	Wear	Europe	0	24	0	11	0	13	3	0.1111111111	0.1690140845	1163.35563252	6.37178112794512e-05	0.0069846755
206	Weser	Europe	0	28	0	10	0	18	5	0.1515151515	0.2816901408	45211.0428162	5.43841280187252e-06	0.0005980481
207	West.river	USA	0	24	0	7	0	17	0	0	0	424.345659421	0.0001255318	0.0137144523
208	Wisla	Europe	0	50	0	12	0	38	18	0.2647058824	0.558685446	193895.872117	2.04314045459952e-06	0.0002247204
209	Withlacoochee	USA	0	50	0	5	0	45	0	0	0	4746.24235543	2.4755785615671e-05	0.0027194657
210	Wye	Europe	0	19	0	12	0	7	12	0.3870967742	0.7699530516	4144.98301024	2.71163718035261e-05	0.0029783971
211	Yellow	USA	2	85	0	10	2	75	0	0	0	3506.31401737	3.03455837213917e-05	0.0033324997
212	York.USA	USA	0	57	0	11	0	46	0	0	0	3804.88088656	2.87231587799974e-05	0.0031546066
213	Zrmanja	Europe	0	11	0	2	0	9	0	0	0	853.131529479	7.8492393116969e-05	0.0085973319

id	ratioTOTAL	ratioMIGRATORY	ratioRESIDENT	lncbdthreat	cons_watloss	cropland	thermal_alt	nitrogen_load	organic_load	phosphor_load	sediment_load	riv_fragm	flow_disrupt	Ndams_main stem
1	0	0	0	0.8486846072	0.4844715063	0.6599278359	0.3889259158	0.812078924	0.6863525711	0.8320050271	0.6991299007	0.1361040183	0.1284032657	0
2	15.0874214272	0	16.1991261639	0.828469002	0.2872283754	0.528777275	0.4933726853	0.6712788292	0.4969076821	0.7067298167	0.5427927858	0.7346813374	0.4009086643	5
3	0	0	0	0.8675410151	0.9188500047	0.7145159841	0.7464810014	0.909439981	0.8597009778	0.960875988	0.1829189956	0.1597370058	0.6814479828	2
4	16.5679851787	16.5679851787	16.5679851787	0.9393349886	0.9027469754	0.4989179969	0.6226599813	0.7280070186	0.8548920155	0.9708269835	0.845426023	0.0514086001	0.6766219735	1
5	0	0	0	0.852221	0.720238	0.766208	0.235935	0.835083	0.659999	0.844554	0.659556	0.335912	0.946249	3
6	0	0	0	0.7109310031	0.2806659937	0.1610530019	0.4256410003	0.1380389929	0.1758739948	0.3455829918	0.2073120028	0.9376779795	0.4553000033	0
7	16.9631393027	0	19.1661444069	0.8423764414	0.4021773814	0.6084800754	0.53084112	0.7685822435	0.6296087302	0.8010216521	0.6521705301	0.5451543957	0.3296069913	2
8	0	0	0	0.834603117	0.3597039201	0.5936539725	0.5530500553	0.7210928068	0.5744480194	0.7938570925	0.595723747	0.6308439221	0.416363574	9
9	0	0	0	0.8531489968	0.3298169971	0.6043800116	0.2539420128	0.8044570088	0.5964570045	0.7519649863	0.6862620115	0.5776079893	0.2277130038	1
10	0	0	0	0.9358959794	0.4791939855	0.7871580124	0.7929559946	0.9812949896	0.8561059833	0.9628069997	0.9028480053	0.3462449908	0.8733440042	0
11	0	0	0	0.830093	0.638387	0.424098	0.309783	0.784025	0.646383	0.840499	0.698194	0.552121	0.530929	0
12	0	0	0	0.8877609968	0.6298400164	0.388139993	0.9716960192	0.8508499861	0.788827002	0.9118509889	0.7976350188	0.3652670085	0.6413999796	0
13	0	0	0	0.794219017	0.1490309983	0.5322499871	0.6565480232	0.8081730008	0.5538820028	0.7480199933	0.5682780147	0.2939999998	0.2421060055	0
14	24.5188676062	0	37.3620839714	0.897054	0.734769	0.684376	0.242291	0.848796	0.712907	0.836768	0.701771	0.470109	0.413627	3
15	0	0	0	0.861545	0.629272	0.812031	0.231863	0.82225	0.626486	0.911112	0.529935	0.4217	0.124326	0
16	0	0	0	0.956309	0.752836	0.809469	0.365119	0.900071	0.858619	0.972399	0.802073	0.470859	0.1076	0
17	0	0	0	0.720663	0.390782	0.226236	0.0696096	0.62027	0.0844898	0.556775	0	0.656749	0.293123	1
18	0	0	0	0.9244562388	0.7888017644	0.7233234717	0.6407567012	0.8647001203	0.85651466	0.8930860329	0.8317724666	0.5509499997	0.7071724235	1
19	0	0	0	0.8754615238	0.5711304714	0.5876247808	0.4586291874	0.8472510301	0.6763460717	0.8807019903	0.3846865768	0.3709719669	0.0982	0
20	163.4209608833	0	172.0220640877	0.7462863335	0.6998100609	0.3818779705	0.299429064	0.7680425805	0.3518067824	0.6966326355	0.1368661791	0.6960666207	0.4797403511	5
21	0	0	0	0.7779170275	0.7375680208	0.3878679872	0.5723350048	0.6339510083	0.7522580028	0.9085950255	0	0.3223780096	0.083148703	0
22	0	0	0	0.873854	0.596704	0.843658	0.151639	0.848929	0.666444	0.918486	0.644187	0.29372	0.222149	0
23	0	0	0	0.931591	0.813726	0.644683	0.726276	0.878152	0.870934	0.98175	0.106628	0.494439	0.126096	0
24	0	0	0	0.9082866515	0.7539494589	0.7614153649	0.578560054	0.9426398697	0.753704401	0.8716061186	0.8210309604	0.75535414	0.4941067049	3
25	0	0	0	0.774222	0.870028	0.755948	0.37332	0.910938	0.967396	0.981544	0.882115	0	0.5591	1
26	28.5131536398	0	30.2732248521	0.8176494609	0.354597979	0.5251268126	0.5575090875	0.6785905467	0.4419644632	0.7040156748	0.4495848094	0.6067064047	0.1509311948	0
27	0	0	0	0.8929517031	0.4722678333	0.5958384418	0.7219386955	0.7764276981	0.6981653124	0.8584251354	0.7204907781	0.4493856413	0.2827320929	2
28	0	0	0	0.8204650283	0.525282979	0.2357169986	0.3279269934	0.1027190015	0.5279359818	0.7961959839	0.425992012	0.553161025	0.2090580016	1
29	0	0	0	0.9581032857	0.5543562586	0.6241326361	0.9587745304	0.8883795753	0.8497732728	0.9648517834	0.84713945	0.7031999826	0.6255172199	0
30	116.5706947361	0	142.4752935663	0.725322	0.566735	0.852784	0.153773	0.68232	0.598603	0.800497	0.614607	0.034	0.7019	0
31	0	0	0	0.9485884658	0.5273349095	0.8800452743	0.3962772249	0.89582509	0.7702696803	0.9045511291	0.7475978334	0.3696712981	0.1500845347	1
32	0	0	0	0.7133690119	0.2806040049	0.3705160022	0.4698950052	0.1642930061	0.3406189978	0.6504909992	0.3013890088	0.5531759858	0.3689329922	0
33	0	0	0	0.7625741953	0.2780427318	0.6176433797	0.4130800137	0.7256295161	0.5106259835	0.7305638328	0.5370610394	0.5040118448	0.1013067667	0
34	0	0	0	0.93782	0.614488	0.666155	0.327407	0.835056	0.7302	0.955751	0.372645	0.519228	0.147149	0
35	0	0	0	0.8003301478	0.5007955928	0.2814397384	0.5968666285	0.5954561552	0.6060325209	0.7693291948	0	0.6077073435	0.3432597068	0
36	45.775835397	0	49.5904883467	0.7567074432	0.6836921458	0.5455206673	0.3837426192	0.8201828003	0.5812368495	0.7345282189	0.6247610412	0.6084716747	0.5616693193	10
37	997.7426041562	0	1023.9989884761	0.6877428762	0.4249360572	0.2124348246	0.2983539021	0.6956070593	0.4025325167	0.6191525648	0.243665547	0.6541070734	0.4453767392	6
38	511.9273607774	0	719.1360544255	0.7672000232	0.4301790138	0.3812186158	0.1632834976	0.556282424	0.2430687689	0.4966462499	0.1007916157	0.8441838925	0.5859234767	6
39	10.6735851929	0	12.6142370461	0.8252254703	0.186549999	0.541746657	0.5700264242	0.8054143808	0.6587121765	0.8326497307	0.6919244396	0.0363145216	0.3882895107	0
40	0	0	0	0.8327215661	0.3383351157	0.3514398889	0.5290383113	0.5621498967	0.4342761018	0.6351414804	0.0474868499	0.7170099123	0.2715315963	7
41	0	0	0	0.627578	0.00202707	0.0353231	0.0209794	0.694624	0.075969	0.629471	0	0.601599	0.536309	1
42	0	0	0	0.7370895858	0.48777395	0.3192181078	0.3390637799	0.7367115705	0.6440463137	0.7608319722	0.6279243908	0.2083675548	0.6831924813	1
43	0	0	0	0.8581860849	0.6113228734	0.4420638999	0.5332762664	0.4507234938	0.5073400853	0.736360089	0.4480613572	0.6018605035	0.6375992694	0
44	0	0	0	0.9245179892	0.84770298	0.325466007	0.5784419775	0.7037950158	0.8426920176	0.9684820175	0.7751410007	0.1058899984	0.6121850014	2

conti...

id	ratioTOTAL	ratioMIGRATORY	ratioRESIDENT	lncbdthreat	cons_watloss	cropland	thermal_alt	nitrogen_load	organic_load	phosphor_load	sediment_load	riv_fragm	flow_disrupt	Ndams_main stem
45	27.9256890797	60.5056596726	18.1516979018	0.8521302394	0.2824206179	0.6977675223	0.6199875189	0.6918331658	0.6797982647	0.5583059567	0.6342935112	0.5143707482	0.597932546	5
46	0	0	0	0.948961	0.825436	0.661366	0.954854	0.929564	0.916938	0.991275	0.138088	0.397412	0.3108	0
47	614.8799538286	502.5975274773	651.2531341959	0.9120542668	0.5853303762	0.741589982	0.4544859929	0.8103684841	0.7679578547	0.6746574648	0.7045873842	0.8225530384	0.3884795294	6
48	0	0	0	0.803474	0.348163	0.561847	0.241751	0.826104	0.416062	0.843178	0.302403	0.162405	0.177801	0
49	0	0	0	0.875067	0.573762	0.518329	0.720231	0.837633	0.731184	0.887837	0.429694	0.424258	0.227452	1
50	0	0	0	0.9333691457	0.5118202421	0.5714644673	0.5748431321	0.6563621576	0.6202346002	0.8045038013	0.647186207	0.650367138	0.3647979604	2
51	0	0	0	0.8027219772	0.5760700107	0.4243429899	0.5317389965	0.2264579982	0.3740310073	0.70529598	0.3192070127	0.6913679838	0.4593220055	0
52	585.803029894	2138.1810591132	0	0.8547670959	0.617553773	0.8451098297	0.2734003879	0.8923330623	0.8224856933	0.8839069354	0.5071742192	0.5890919466	0.1303016448	6
53	287.1906231943	604.6118383037	173.3981121173	0.8839998899	0.6740507513	0.8668380339	0.3087238533	0.8338579112	0.8298739408	0.8772259908	0.7359610992	0.5521748652	0.455776718	0
54	118.6682248699	474.6728994794	0	0.8457006679	0.7460336652	0.9220679567	0.206837206	0.8748235648	0.8000327132	0.9004706346	0.5934904012	0.5670828787	0.1792689127	0
55	0	0	0	0.9056673914	0.406036443	0.5556766193	0.2477273608	0.8490361696	0.6487945509	0.8140111622	0.7410716014	0.5274636884	0.4618978865	4
56	0	0	0	0.9464400639	0.6122454219	0.785089339	0.3843508071	0.8608240779	0.6438545793	0.8373521263	0.6501612056	0.7504903332	0.6860570898	13
57	0	0	0	0.883321	0.542796	0.63063	0.465057	0.755134	0.396526	0.874122	0.217786	0.660016	0.179391	0
58	85.6155455552	233.4969424232	0	0.9342786386	0.6060838113	0.7663707441	0.3459983011	0.8132875	0.5749692663	0.7918076667	0.611048102	0.7341206594	0.627401449	4
59	0	0	0	0.852592	0.386226	0.575417	0.288498	0.766299	0.459619	0.762159	0.173447	0.656073	0.239451	0
60	7.6452065886	82.8230713764	0	0.8823132847	0.5721602966	0.5963875352	0.7001098533	0.8294380219	0.7136185289	0.8507937357	0.746112381	0.1393033833	0.6520259124	0
61	136.6355325451	165.9145752333	0	0.6544830567	0.0964588117	0.2653984033	0.0949884142	0.3454121961	0.1941138779	0.4522563214	0.2297521727	0.4795992317	0.3317963444	1
62	222.6996847337	606.2380306639	0	0.9736263043	0.6605607721	0.8031168435	0.6764986258	0.9020823911	0.8186505315	0.9330374775	0.7973397047	0.7368802697	0.6011903422	7
63	0	0	0	0.6765549167	0.1161908998	0.5179757312	0.289222535	0.6811982725	0.4412385683	0.6618860003	0.5072500566	0.1523363754	0.402631545	0
64	3.6328369203	0	3.968175713	0.8016800284	0.4120720029	0.441967994	0.9239529967	0.677734971	0.4521380067	0.6615440249	0.4835500121	0.5181379914	0.4018760026	0
65	0	0	0	0.9050256915	0.8088783802	0.7378739399	0.3279601403	0.8128868445	0.8116191186	0.8768107953	0.8120313072	0.7275303521	0.769582188	2
66	0	0	0	0.5076890785	0.0473385162	0.0687575857	0.0460165893	0.2790587847	0.0577405827	0.3604767167	0.0171987078	0.6299838324	0.298585082	0
67	0	0	0	0.9118296933	0.3782121285	0.697368688	0.2724884113	0.7854823515	0.5739725173	0.7549094882	0.6041064429	0.625009034	0.383251444	1
68	0	0	0	0.987579	0.72092	0.94264	0.693095	0.956752	0.930888	0.98668	0.769489	0.699012	0.48736	0
69	0	0	0	0.6214154616	0.1462933898	0.1633620999	0.0042522551	0.5843483036	0.2639641654	0.4228199237	0.0551833351	0.442492456	0.5436165544	3
70	720.0911335826	1160.9632561842	677.2285661074	0.4506806522	0.2695208743	0.2197929952	0.1669323834	0.4815646305	0.3794197936	0.4610132798	0.3087962821	0.4255702399	0.2488263123	7
71	0	0	0	0.8087080121	0.5878379941	0.2466160059	0.2480259985	0.0968051031	0.4062550068	0.7199090123	0.3688130081	0.6669049859	0.3214299977	1
72	0	0	0	0.9767100215	0.7783849835	0.6451089978	0.9714400172	0.9361199737	0.8730840087	0.9664319754	0.8889679909	0.6998670101	0.5957210064	0
73	144.8275239458	162.930964439	130.3447715512	0.9679765713	0.8655982196	0.853201097	0.2974346752	0.9050715518	0.7978743164	0.9212272388	0.8761676311	0.6832906816	0.8748423255	1
74	31.0648995613	0	32.928793535	0.8573001592	0.7472961437	0.6860785984	0.2282868688	0.9464753169	0.7870227094	0.8903166422	0.8589714604	0.5089935737	0.7777839622	1
75	80.726678161	181.6350258623	0	0.8495885234	0.6716351601	0.7137594011	0.2049654765	0.8390483126	0.7277494012	0.8179714623	0.8060044477	0.6448411105	0.733094377	5
76	0	0	0	0.928154	0.793254	0.58822	0.602818	0.908343	0.781519	0.872578	0.777475	0.347577	0.552918	0
77	7.4985083814	31.8686606209	4.2491547495	0.8618549705	0.8550549746	0.5768659711	0.5970489979	0.8994960189	0.8486220241	0.9553499818	0.4155400097	0.0132964998	0.6401619911	0
78	0	0	0	0.8531155696	0.5945218151	0.3748999209	0.5520310919	0.5806868328	0.6360996677	0.8253826385	0.3957429091	0.6201675147	0.3832094311	0
79	50.77161572	66.8895889644	45.3123022017	0.8872205182	0.3789856533	0.4363212522	0.4935291522	0.6342071899	0.4950261745	0.7106196726	0.4336819069	0.7435113123	0.3646519751	6
80	0	0	0	0.4891995474	0.5141328822	0.1727921016	0.1381063153	0.5051520719	0.1376640511	0.4212652624	0.0479565294	0.4831080357	0.1316655615	0
81	31.6445957471	58.015092203	0	0.5021851041	0.3600816742	0	0.1068465762	0.4929181246	0.3911413314	0.5539787272	0.4279083385	0.4779291916	0.4974025711	1
82	0	0	0	0.510933239	0.0436536907	0.0004953772	0.0627932437	0.5690516595	0.1620774787	0.2385100049	0.1089881668	0.539433463	0.6624663556	1
83	0	0	0	0.8752120554	0.2552963523	0.5756515352	0.5132147171	0.7016430052	0.4717225784	0.6628021323	0.6059572701	0.6005558035	0.2841469328	0
84	0	0	0	0.7657958794	0.708317611	0.5929716482	0.3829275903	0.787602032	0.7082402761	0.7419244594	0.749790387	0.4708255592	0.796370365	5
85	0	0	0	0.4938417824	0.0489873711	0	0.1179828743	0.4985443817	0.0931479221	0.2139609777	0.0730046136	0.5420369438	0.5497454221	7
86	0	0	0	0.7083246627	0.152561292	0.2590641125	0.3852844474	0.4961459429	0.2414679026	0.4462314998	0	0.6751534289	0.3852769689	6
87	38.2663418381	76.5326836762	0	0.7455372678	0.2856702074	0.240806184	0.1922826889	0.5082951223	0.2360659831	0.4296872843	0.2195044866	0.6601900662	0.5522538718	3

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id	**ratioTOTAL**	**ratioMIGRATORY**	**ratioRESIDENT**	**Incbdthreat**	**cons_watloss**	**cropland**	**thermal_alt**	**nitrogen_load**	**organic_load**	**phosphor_load**	**sediment_load**	**riv_fragm**	**flow_disrupt**	**Ndams_main stem**
88	49.7991003806	99.5982007612	0	0.3214796274	0.1749404109	0	0.0005269381	0.5343072566	0.1277746454	0.5571033413	0	0.0800484243	0.0201376148	0
89	0	0	0	0.733909	0.566182	0.830402	0.573304	0.719074	0.618174	0.719059	0.598628	0.207145	0.225101	0
90	28.0808695944	97.544073328	0	0.7742406676	0.5654880685	0.6663578211	0.2201411393	0.6944602138	0.6106016786	0.763679404	0.7081051972	0.3697911079	0.096830152	1
91	0	0	0	0.8374586652	0.7520225345	0.8027923945	0.5318739067	0.949682356	0.7149586564	0.8564520888	0.8084270773	0.3422403888	0.7876897612	0
92	0	0	0	0.790462	0.431642	0.285116	0.287262	0.646899	0.236791	0.644566	0.0394883	0.687899	0.153075	0
93	0	0	0	0.8360999823	0.9100000262	0.725399971	0.7085999846	0.9024000168	0.8532000184	0.9609000087	0	0	0.6463999748	1
94	90.5218879845	186.3685929092	0	0.926094106	0.4979214872	0.7638644355	0.419669701	0.8586839309	0.7030616207	0.8602946093	0.6653867528	0.3923334074	0.2025136294	2
95	20.7563784495	0	41.512756899	0.7155320048	0.9068920016	0.2605749965	0.784825027	0.9153029919	0.9395679832	0.4962710142	0.7155820131	0	0.6092000008	0
96	0	0	0	0.8203499913	0.9008719921	0.696762979	0.5274180174	0.8850129843	0.8285520077	0.9495469928	0	0	0.5513859987	1
97	0	0	0	0.8830080032	0.6335809827	0.6149460077	0.8400989771	0.744189024	0.6848310232	0.8703669906	0.6784480214	0.2319879979	0.4293949902	0
98	0	0	0	0.8647877255	0.186198938	0.6480697845	0.4558334497	0.7430541078	0.5819532241	0.7666737184	0.6361319897	0.5054584781	0.490210498	0
99	0	0	0	0.7620886106	0.3516670478	0.7093308633	0.3191884799	0.6366017327	0.4543487447	0.6862589376	0.2582786025	0.4321351238	0.0662263249	0
100	0	0	0	0.8217044236	0.4797131653	0.2946856557	0.6614869069	0.5364790959	0.5688004433	0.7367194598	0.00061752	0.6454302038	0.2664083894	3
101	28.2299557084	69.8319956996	0	0.9512894994	0.6773005025	0.7166148482	0.6937346574	0.8920506349	0.7812187324	0.9681766959	0.7320152965	0.4983521098	0.1882063972	0
102	0	0	0	0.8425420353	0.4276357268	0.3708375406	0.3119031535	0.5810771714	0.4838840585	0.724437729	0.43258807	0.6156986341	0.4154820796	5
103	0	0	0	0.9112020135	0.4516060054	0.7398639917	0.9003599882	0.9783040285	0.9032530189	0.9767240286	0.9366000295	0.4561829865	0.7678099871	0
104	531.8588856345	0	554.1288389738	0.8798369054	0.503254013	0.7279944522	0.4077005094	0.82373614	0.4950517361	0.7084498399	0.4600411137	0.9086544936	0.4613527915	3
105	0	0	0	0.7750869989	0.8746399879	0.6144679785	0.0067566098	0.8350480199	0.7577189803	0.9169229865	0	0	0.2783429921	0
106	0	0	0	0.7721300125	0.5014939904	0.2291489989	0.8125240207	0.8007389903	0.6622210145	0.8315330148	0.5054150224	0.1448509991	0.2624999881	0
107	11.8190564246	0	12.8357494504	0.8695563123	0.2589995795	0.5400432681	0.5471848102	0.7689677577	0.5816338784	0.7546660428	0.6218406717	0.7099529874	0.7350065653	5
108	0	0	0	0.6722800136	0.2457890064	0.3500210047	0.0442979001	0.2096869946	0.2779439986	0.5418040156	0.3282760084	0.5251290202	0.6835610271	0
109	0	0	0	0.985726	0.710611	0.927431	0.815125	0.953168	0.935274	0.992467	0.780326	0.622883	0.214749	1
110	0	0	0	0.79359	0.533497	0.690166	0.209103	0.715373	0.676216	0.740084	0.668858	0.430604	0.482435	1
111	0	0	0	0.626727	0.000161724	0	0	0.683462	0.0842423	0.329875	0	0.437356	0.453994	2
112	0	0	0	0.824831	0.779991	0.510185	0.283406	0.776947	0.769304	0.826991	0.809023	0.515628	0.788356	2
113	8.4221299476	67.3770395804	0	0.8858463694	0.6187945555	0.7063245326	0.6103043884	0.7792050078	0.7001272412	0.8689079752	0.7086806659	0.3219474184	0.3524262578	1
114	0	0	0	0.5845384405	0.2818081549	0.2671276529	0.2078866331	0.6015321102	0.3307027843	0.5773897132	0.006415898	0.7508999905	0.3954251477	0
115	57.7614302936	154.0304807829	0	0.8303279943	0.5229511508	0.8160920913	0.2257357457	0.8337466905	0.7460423098	0.8170362745	0.1401946002	0.4937303179	0.319056373	1
116	0	0	0	0.8017969728	0.4191789925	0.292708993	0.240733996	0.3426840007	0.2789190114	0.696649015	0.2275529951	0.8556650281	0.4894930124	1
117	0	0	0	0.886668	0.402275	0.592376	0.361761	0.7352	0.481199	0.794352	0.29017	0.185063	0.163435	0
118	35.4946350257	0	38.8750764567	0.8349074368	0.7687196214	0.5626232677	0.3103899446	0.9848610385	0.8018135275	0.9241147436	0.848121203	0.2875722177	0.3169566112	1
119	0	0	0	0.7609570026	0.3666130006	0.5550929904	0.3406130075	0.7636870146	0.5319880247	0.7473649979	0.565162003	0.1379089952	0.4176479876	1
120	0	0	0	0.9110519996	0.6608062742	0.8520772608	0.654531207	0.9050615443	0.8532654988	0.9196658672	0.5260791172	0.5082043862	0.4944469954	1
121	0	0	0	0.8061043811	0.2230144369	0.66840994	0.4739944545	0.8267265898	0.5973516396	0.7483097779	0.6167817518	0.2226228783	0.6161425799	0
122	0	0	0	0.920931	0.814755	0.642854	0.602832	0.913438	0.743877	0.849583	0.732227	0.483815	0.577612	1
123	0	0	0	0.5300837782	0.0861723901	0.1904424831	0.344819559	0.5826239752	0.3031134158	0.3704372456	0	0.2895700309	0.2734063879	1
124	16.4061060743	0	31.8471470854	0.9462314079	0.8344702673	0.9376829565	0.5429874496	0.9656498904	0.9441591688	0.9853369161	0.8105967107	0.0987870451	0.2651317814	1
125	18.2156776434	0	29.1450842294	0.9126756725	0.8454016916	0.5537977287	0.3805733653	0.7319733574	0.569290596	0.8053732883	0.6885674212	0.4699551129	0.4421982222	0
126	26.8905802718	0	29.4762129902	0.7094790809	0.2106747712	0.4446894654	0.3368588013	0.6405625343	0.4402923882	0.6559325276	0.474858333	0.2517177888	0.1456994486	1
127	17.6863008483	0	21.4379404221	0.9318450093	0.5537779927	0.2872300148	0.781916976	0.6621000171	0.6199550033	0.8420559764	0.5874869823	0.7896460295	0.4378930032	0
128	3.5868340625	0	4.3554413616	0.8977149725	0.8296129704	0.5609350204	0.8750320077	0.8323630095	0.8620049953	0.9714679718	0.8243139982	0.2308969945	0.348751992	2
129	0	0	0	0.8913090719	0.9368226856	0.6864892761	0.4892987849	0.9038457819	0.8048228495	0.885945215	0.3823079426	0.3904086375	0.6929487902	1
130	46.5565825908	102.4244816997	41.9772465982	0.7561515965	0.223938873	0.5347273195	0.2976959116	0.6502200345	0.4632162533	0.693381201	0.4563158304	0.5550415324	0.4882236331	2

conti...

id	ratioTOTAL	ratioMIGRATORY	ratioRESIDENT	lncbdthreat	cons_watloss	cropland	thermal_alt	nitrogen_load	organic_load	phosphor_load	sediment_load	riv_fragm	flow_disrupt	Ndams_main stem
131	0	0	0	0.9112174914	0.4533195847	0.6489919457	0.5667423973	0.7553936814	0.6589039971	0.8129171061	0.6716448329	0.5577493905	0.302603643	3
132	0	0	0	0.6709634138	0.0726104436	0.2014276198	0.2622299204	0.5018222136	0.1637780947	0.3408140279	0	0.6739539967	0.4659175327	7
133	0	0	0	0.7439739704	0.4410569966	0.5173490047	0.2789959908	0.6580910087	0.5060470104	0.7633270025	0.4624609947	0.0598431006	0.4120000005	0
134	0	0	0	0.8547080159	0.80943501	0.8226829767	0.3369570076	0.9790809751	0.8532000184	0.9559090137	0.9326599836	0.00399026	0.3400999904	0
135	105.6665345349	324.5472132144	0	0.9128662625	0.5398925405	0.6386426414	0.5076875325	0.7255449121	0.6353103258	0.8254075736	0.5100515172	0.5717252205	0.2292414433	0
136	44.1350337225	0	53.3298324147	0.8997057376	0.391896548	0.6659957914	0.4801516298	0.75222083	0.6095287537	0.7776998379	0.7285992241	0.4124878169	0.2964871675	0
137	11.9310540011	28.4509749257	0	0.7052845817	0.4188999954	0.2739246826	0.3193019773	0.5338587934	0.4578202331	0.6646820149	0	0.375528869	0.3167827759	2
138	8.5638724203	0	19.1040230914	0.7959180503	0.5370573501	0.2273554748	0.2332249369	0.2065863468	0.338549554	0.6554642837	0.3053351311	0.7330427789	0.2910434112	1
139	19.3731277646	43.3046385326	0	0.7705204093	0.632723304	0.3865647246	0.4014239526	0.5394658321	0.6647583388	0.8197646895	0.0110331886	0.3553772544	0.1694495769	0
140	28.6532450144	152.8173067437	10.9155219103	0.9364373105	0.6059248428	0.6531893445	0.5723389957	0.8106526937	0.6912680356	0.842359078	0.7532895326	0.5840827648	0.28768149	0
141	0	0	0	0.9396209717	0.6663219929	0.5765650272	0.6303139925	0.627572	0.711360991	0.8962389827	0.6772999763	0.5999330282	0.3883909881	0
142	136.9393315347	540.910359562	115.3942100399	0.9120603435	0.5526415858	0.7120820259	0.4430654345	0.8809658281	0.6598240591	0.8052743464	0.6822397034	0.9384885626	0.558916884	4
143	173.9716034982	489.2951348387	0	0.9463217695	0.6107886887	0.6639227276	0.7609391234	0.821567308	0.7504571013	0.9116146943	0.6672113396	0.6156687508	0.2504623407	3
144	123.8236207328	163.8842039111	99.5011238031	0.8934959071	0.4271954191	0.5869953948	0.4432536941	0.7308645023	0.5565012344	0.7746183032	0.5166531576	0.6634070335	0.2950365749	1
145	0	0	0	0.893098	0.679509	0.613104	0.412817	0.795435	0.737522	0.944063	0.0544575	0.503151	0.0688877	0
146	0	0	0	0.9150243668	0.4373259709	0.6381944369	0.2690772761	0.7465507855	0.624554137	0.8015003626	0.7024327149	0.6579506608	0.5132417317	5
147	122.8289586432	0	210.5639291027	0.727865822	0.2404961708	0.2672441054	0.2180373318	0.3762566647	0.321633728	0.5701601044	0.3638521096	0.5812778542	0.4107434928	1
148	30.5038458717	53.3817302755	0	0.7374839783	0.6926689744	0.4733229876	0.5973380208	0.2789820135	0.4484519959	0.686973989	0.4623700082	0.000233773	0.3191150129	0
149	0	0	0	0.8802574598	0.3378743364	0.5586270824	0.4784531961	0.7731594889	0.6084710016	0.7941364607	0.6324825584	0.6775001932	0.5482319092	3
150	0	0	0	0.7623291335	0.3263105121	0.2468056555	0.379851555	0.4928021173	0.4403566093	0.6118316922	0	0.5921803948	0.445753501	4
151	205.7702027475	452.6944460445	0	0.8336717593	0.53563231	0.4318284836	0.3985836975	0.527569123	0.2945709928	0.571177721	0.2717763989	0.7153183105	0.5811059089	2
152	0	0	0	0.6328349579	0.0813593597	0.2280215073	0.1264973107	0.4952162799	0.2040055338	0.4085772024	0	0.5144956903	0.4689191461	4
153	0	0	0	0.6225604882	0.1456517809	0.275335781	0.1231611748	0.4815682195	0.1869585177	0.4326930715	0.0155119232	0.4853866151	0.1590103863	1
154	0	0	0	0.8457603967	0.6761105958	0.3959063997	0.5229543179	0.815568657	0.7548199539	0.8932000258	0.5971302787	0.5083039878	0.3650924245	1
155	0	0	0	0.781513989	0.4034039974	0.4054050148	0.6162970066	0.7660629749	0.574500978	0.7906050086	0.6008459926	0.0744258985	0.2540369928	0
156	5.2626428978	0	6.0301116537	0.6921520233	0.3215500116	0.2520099878	0.2800849974	0.7681990266	0.5601279736	0.7144110203	0.3534750044	0.2780730128	0.2624999881	0
157	0	0	0	0.8353427897	0.7021622473	0.5571009139	0.2460982673	0.6304548496	0.4605505586	0.6759284616	0.6318069309	0.574263676	0.5429396701	1
158	0	0	0	0.8980892374	0.7986620211	0.6818592767	0.4229245739	0.9738009672	0.8903691097	0.9507966269	0.9324848173	0.4817906903	0.8686081104	1
159	0	0	0	0.8618990183	0.709273994	0.8125839829	0.7075729966	0.9384469986	0.7471489906	0.8523460031	0.781826973	0.146739006	0.4944629967	0
160	0	0	0	0.9263089748	0.6731558342	0.5743878707	0.4422819894	0.8576875465	0.8251418839	0.9277604245	0.8390756447	0.7198248217	0.7335136752	2
161	78.0322132737	156.0644265474	0	0.895450316	0.6769672893	0.5437958851	0.4966634283	0.6646301927	0.5115515095	0.7369650728	0.4793275464	0.7899710091	0.6660014658	3
162	14.4761422392	0	16.15232713	0.934707131	0.7222272372	0.529742144	0.6048295022	0.8944577228	0.8707538012	0.9429670123	0.8966383447	0.6705220972	0.4520205763	2
163	0	0	0	0.7460607741	0.2759867864	0.583247523	0.2199784451	0.7817125724	0.5329058613	0.7230719566	0.5013402909	0.1781404101	0.1378753712	0
164	40.6553447773	0	46.6340719505	0.8767571345	0.3640642364	0.5695632946	0.6171627072	0.6994517885	0.589128565	0.7793088638	0.6144893022	0.6129530779	0.6548677031	4
165	0	0	0	0.955012988	0.8483459058	0.8334344189	0.8458025922	0.9522824316	0.9131156832	0.9873233665	0.6944623913	0.4605027	0.050049383	0
166	0	0	0	0.1511775193	0.1572540432	0.1147663482	0	0.1544876258	0.1461563916	0.1523768332	0.1549833422	0.1295418959	0.1599085248	2
167	359.1851871957	846.6507983898	0	0.9287659403	0.5592349857	0.8702441188	0.5714422516	0.8816752912	0.7314075052	0.8888616203	0.7088631234	0.443380816	0.3636025368	1
168	0	0	0	0.9402614854	0.651985214	0.7810112497	0.6955760865	0.9102157437	0.844898779	0.9660122437	0.6479338146	0.3561832156	0.1714590986	0
169	9.3599795846	0	22.8799500956	0.7000240088	0.2047660053	0.230460003	0.2427320033	0.1770959944	0.2116809934	0.4335469902	0.2301400006	0.8169000149	0.122552	0
170	0	0	0	0.6465433375	0.2189634901	0.1734253026	0.0269287101	0.2210601547	0.1468373679	0.4256303126	0.1044646328	0.4945315513	0.6191202623	2
171	0	0	0	0.6083289981	0.1375129968	0.2373189926	0	0.0999754965	0.2621420026	0.5466610193	0.1998540014	0.6111459732	0.5176410079	1
172	10.884542442	13.0614509304	0	0.6931080222	0	0.0977502987	0.4259620011	0.494738996	0.266328007	0.5711190104	0.2275409997	0.5485709906	0.3725549877	0
173	0	0	0	0.7112502737	0.5544209867	0.1490854403	0.036474268	0.1157773085	0.2658728972	0.4956754331	0.2412158118	0.5764150144	0.3612715764	0

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id	**ratioTOTAL**	**ratioMIGRATORY**	**ratioRESIDENT**	**lncbdthreat**	**cons_watloss**	**cropland**	**thermal_alt**	**nitrogen_load**	**organic_load**	**phosphor_load**	**sediment_load**	**riv_fragm**	**flow_disrupt**	**Ndams_main stem**
174	0	0	0	0.884436	0.825468	0.672902	0.0879767	0.868861	0.678442	0.86667	0.777759	0.654025	0.841119	0
175	0	0	0	0.673035	0.164249	0.122449	0	0.785134	0.302809	0.695762	0.105241	0.0949472	0.374531	0
176	0	0	0	0.694791019	0.2788259983	0.2548100054	0.0780598	0.2106750011	0.1771530062	0.4878480136	0.1527500004	0.3817000091	0.4122180045	0
177	0	0	0	0.948363	0.889563	0.9544	0.439054	0.97875	0.966465	0.987845	0.886314	0	0.7188	0
178	82.9168979242	161.8853721377	66.6586826449	0.9305146674	0.4457539032	0.6291546867	0.6081696778	0.6836555099	0.5502146251	0.740038147	0.6639799466	0.6797450483	0.3161289141	2
179	0	0	0	0.7338801581	0.2612275465	0.5577080732	0.3984703041	0.7715048292	0.5259161525	0.7142334518	0.4794284113	0.136679501	0.2162643753	0
180	9.8452395193	30.7663734977	0	0.829494	0.503002	0.732128	0.41944	0.681899	0.536291	0.85132	0.49796	0.636591	0.119688	0
181	0	0	0	0.9611886304	0.7073460455	0.728981635	0.5208946689	0.8950412716	0.777057565	0.8891892042	0.7767886273	0.7967062374	0.8664034775	9
182	0	0	0	0.8875795644	0.4259082877	0.7132890942	0.5412042111	0.7441864553	0.6376540262	0.8174702528	0.6740307062	0.4488379247	0.6573625544	0
183	0	0	0	0.7621641291	0.2813196815	0.3333146234	0.074860199	0.6823885497	0.1333096568	0.796799146	0.0725505423	0.6254225098	0.2792970992	1
184	0	0	0	0.886156	0.603496	0.674643	0.378147	0.839231	0.643552	0.907253	0.120062	0.572557	0.261486	1
185	0	0	0	0.662906	0.296862	0.43595	0.267419	0.711656	0.435475	0.722968	0.425676	0	0.2686	0
186	32.3829634043	121.4361127662	0	0.6913447325	0.6525774085	0.6522641229	0.1066339642	0.6560255934	0.607222506	0.6482225596	0.5582782855	0.2259165233	0.1107681505	0
187	13.9590404765	0	18.8857606446	0.830936	0.716634	0.455394	0.796225	0.77562	0.676684	0.825129	0.739298	0.434524	0.404186	4
188	0	0	0	0.9464588449	0.7393231001	0.7950687839	0.52026415	0.8910003687	0.8268631844	0.925075404	0.8043722486	0.3963172103	0.5766896346	2
189	0	0	0	0.9666638298	0.8470191842	0.7856525427	0.8308058473	0.9527000737	0.9293744739	0.9883006024	0.7923592464	0.3317984484	0.1372653091	0
190	19.4534278313	0	36.6182170943	0.975993332	0.8470586684	0.8265814911	0.8731086503	0.9257118321	0.9081087145	0.9842259912	0.684563012	0.6276422627	0.2659485053	0
191	0	0	0	0.9231835764	0.5379941	0.7138896058	0.6704543358	0.9001367347	0.7910895413	0.8949388019	0.8307875283	0.8069748498	0.6660752491	5
192	0	0	0	0.8164668418	0.5895659161	0.207075446	0.603206877	0.5025443907	0.4607850625	0.7332716473	0.171148074	0.5845813907	0.4474270793	0
193	0	0	0	0.8500587811	0.4242211251	0.7190832599	0.6822360962	0.8582859419	0.6488473942	0.8424893484	0.5284185021	0.1529041231	0.2723833521	0
194	0	0	0	0.835579	0.343961	0.566896	0.374241	0.811364	0.508651	0.822137	0.157234	0.51772	0.303359	1
195	0	0	0	0.4638113831	0.0051673318	0	0.001152693	0.4386861804	0.0597574322	0.124064071	0.0013430524	0.6114732943	0.5863690663	0
196	24.6158507327	45.9495880344	0	0.6433989756	0.0450375763	0.2434264389	0.0744549824	0.3180568242	0.2543636665	0.4695275828	0.3071550712	0.4963352028	0.1731333078	0
197	212.9503963651	819.0399860196	0	0.6565490104	0.4976494952	0.6686398832	0.2600920047	0.815707635	0.6847715913	0.7680941833	0.3611149316	0.3744066049	0.3346586535	1
198	0	0	0	0.793123	0.657631	0.377944	0.425103	0.754672	0.559222	0.757048	0.600452	0.613741	0.5708	0
199	0	0	0	0.9005309939	0.6830040216	0.4060199857	0.5119360089	0.1699070036	0.7430379987	0.9410129786	0.6724029779	0.5822650194	0.2810559869	0
200	0	0	0	0.736695	0.760789	0.56476	0.439169	0.759323	0.68056	0.801094	0.664551	0.411612	0.333181	0
201	0	0	0	0.9233076054	0.6569579282	0.9308745012	0.5402284167	0.9195375354	0.8254209927	0.9456249886	0.7784640009	0.0434215205	0.1044973858	0
202	499.9212653293	1970.2779280626	0	0.7928678711	0.5075470099	0.651853718	0.1542096449	0.7183353413	0.5722602426	0.747899055	0.3111751848	0.6830998663	0.192244301	4
203	0	0	0	0.3636928806	0.373552514	0	0	0.5253514686	0.0204513412	0.5123565786	0.0122538702	0.1328749262	0.42582407	0
204	0	0	0	0.7107319832	0.0384163	0.477824986	0.0969578028	0.7386299968	0.5169309974	0.675590992	0.4478470087	0.0067020701	0.3111999929	0
205	0	0	0	0.906117	0.694487	0.695205	0.474697	0.847982	0.683594	0.938456	0.0208277	0.591704	0.293094	0
206	0	0	0	0.9069347274	0.7210849321	0.792005611	0.7603531529	0.9156058004	0.8366783154	0.9484718662	0.7126256472	0.3476283241	0.4254700491	0
207	0	0	0	0.8194950223	0.5183320045	0.3293839991	0.7180539966	0.6019279957	0.6110550165	0.8199539781	0.2846629918	0.676699996	0.351669997	0
208	0	0	0	0.9097764726	0.6403771052	0.8442995551	0.5272560563	0.9012867615	0.8476615399	0.9051658166	0.5553690798	0.5380210138	0.362050394	1
209	0	0	0	0.909431994	0.698258996	0.5212829709	0.6140909791	0.8549029827	0.7978429794	0.8976640105	0.7065510154	0.5805400014	0.4553509951	1
210	0	0	0	0.8659411015	0.3740250237	0.6419219393	0.4448215126	0.8666326121	0.6987434904	0.9378861333	0.700181052	0.1010723254	0.1304467795	0
211	6.8982768876	0	7.7941570028	0.7215349617	0.2722039452	0.4749104844	0.4001301881	0.6982273245	0.4451627991	0.6823933693	0.5027423568	0.2965949274	0.0507010531	0
212	0	0	0	0.9081082934	0.6014355929	0.6244283271	0.8180691182	0.75214608	0.6369968545	0.8178451236	0.6725623157	0.409198786	0.272842713	0
213	0	0	0	0.707751	0.542716	0.831111	0.165483	0.735273	0.519274	0.551278	0.510692	0.170063	0.2026	0

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Abstract: Understanding factors driving the variation of diversity across the Earth is the main goal of ecology and biogeography. To reach this goal one needs to study the drivers of three main processes directly causing variation in diversity: speciation, extinction and dispersal. Speciation increases and extinction decreases diversity levels through time, whereas dispersal has a dual effect: it may increase or decrease diversity depending on the circumstances. Fragmentation, which stands by the emergence of natural or human-driven discontinuities on a given environment, is ubiquitous and has multiple ecological and evolutionary implications for the three diversity processes mentioned above (i.e., speciation, extinction and dispersal). Riverine fishes (i.e., strictly freshwater fishes) naturally experience fragmentation, as natural elements may disrupt connectivity of rivers (e.g., waterfalls) and river basins are separated from one another by barriers (oceans or land) which are insurmountable for these organisms. Riverine fishes thus constitute an ideal model for studying fragmentation effects. Here, I evaluated the effect of fragmentation on freshwater fish diversity by testing its effects on speciation, extinction, and dispersal processes at spatial and temporal scales ranging from a single river basin to worldwide rivers and from decades to million of years. In a first study, by analyzing endemism level of tributaries from the Orinoco river basin, I showed that tributaries highly fragmented by waterfalls have higher speciation probability and higher neo-endemism levels (i.e., species presumably originated by *in-situ* cladogenetic speciation) than their less fragmented counterparts. In a second study, I tested whether the historical connectivity between basins left an imprint on the global patterns of freshwater fish biodiversity. After controlling for contemporary and past environmental conditions, I found that palaeo-connected basins (those connected during the Last Glacial Maximum; 18-21 kya) displayed greater species richness but lower levels of endemism than did palaeo-disconnected basins. Palaeo-connected basins exhibited shallower distance decay of compositional similarity, suggesting that palaeo-river connections have favored the exchange of fish species. In a third study, I evaluated to what extent, if any, anthropogenic threats related to fragmentation (e.g., damming of rivers, agricultural practices) have been promoting fish extinctions in river basins. Focusing on Western Europe and North America, two strongly impacted regions, I showed that the percentage of cropland in the river basin and river fragmentation by dams are the main causes of present riverine fish species extinction. These extinctions, even if still reduced, correspond to extinction rates 40 times higher than background, natural rates. Overall, my results point for a prominent role of fragmentation as a driver of fish diversity through speciation processes and highlight the strong role played by history in explaining the global contemporary patterns of biodiversity via colonization processes. Moreover, they support the need of maintaining connectivity within river basins where human-made barriers have been created to avoid a substantial increase in species extinction rates.

Keywords: speciation; extinction; colonization; freshwater fish; river basins; richness, endemism, beta diversity; history effects; natural barriers, anthropogenic disturbances.