Global biogeographical regions of freshwater fishes

Article type: Research paper

Short title: Bioregions of freshwater fishes

Authors: Boris Leroy[1]*, Murilo S. Dias[1, 2], Emilien Giraud[1], Bernard Hugueny[3], Céline Jézéquel[3], Fabien Leprieur[4], Thierry Oberdorff[3], Pablo A. Tedesco[3]

[1] Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Muséum national d'Histoire naturelle, Université Pierre et Marie Curie, Université de Caen Normandie, CNRS, IRD, Sorbonne Universités, Paris, France.

[2] Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília (UnB), Brasília-DF, Brazil.

[3] UMR5174 EDB (Laboratoire Evolution et Diversité Biologique), CNRS, IRD, UPS, Université Paul Sabatier, F-31062 Toulouse, France

[4] UMR MARBEC (CNRS, IRD, IFREMER, UM), Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France.

Word count inclusive of abstract and references: 7825

Acknowledgements

We thank Céline Bellard and Philippe Keith for useful discussions, and Aldyth Nyth for English editing. Laboratoire Evolution et Diversité Biologique is part of the French Laboratory of Excellence projects "LABEX TULIP" and "LABEX CEBA" (ANR-10-LABX-41, ANR-10-LABX-25-01).

Abstract

Aim

To define the major biogeographical regions and transition zones for freshwater fishes.

Taxon

Strictly freshwater species of actinopterygian fish (i.e., excluding marine and amphidromous families of fish).

Methods

We based our bioregionalisation on a global database of freshwater fish species occurrence in drainage basins, which, after filtering (12 333 species in 2 916 basins). On the basis of this dataset, we generated a bipartite (basin-species) network upon which we applied a hierarchical clustering algorithm (the Map Equation) to detect regions. We tested the robustness of regions with a sensitivity analysis. We identified transition zones between major regions with the participation coefficient, which indicates the degree to which a basin has species from multiple regions.

Results

Our bioregionalisation scheme showed that the freshwater fish world is divided in half with two major kingdoms (Paleogeana and Neogeana). Nested within these two kingdoms lie six major regions (Nearctic, Neotropical, Palearctic, Ethiopian, Sino-Oriental and Australian) with extremely high degrees of endemism (above 96% except for the Palearctic). Transition zones between regions were of limited extent compared to other groups of organisms. We identified numerous subregions with high diversity and endemism in tropical areas (e.g. in the Neotropical), and a few large subregions with low diversity and endemism at high latitudes (e.g. in the Palearctic).

Main conclusions

Our results suggest that freshwater fish regions were shaped by events of vicariance and geodispersal which were similar to other groups, but with freshwater-specific processes of isolation that led to extremely high degrees of endemism, specific boundary locations, and limited extents of transition zones. The identified hierarchy of bioregions and transition zones of freshwater fish species probably reflect relatively recent processes of isolation from the late Miocene to the Pleistocene. The extremely high endemism and diversity of freshwater fish fauna raises many questions about the biogeographical consequences of current introductions and extinctions.

Key-words

Biogeographical regions, biogeography, bioregionalisation, bioregions, dispersal, freshwater fish, actinopterygians, vicariance, zoogeographical regions

Introduction

For almost two centuries, biogeographers have classified geographical areas of the world into distinct biogeographical regions on the basis of the distributions of organisms across the Earth (Wallace, 1876; Cox, 2001; Holt et al., 2013). Indeed, early biogeographers observed that many organisms share constellated distributions of endemics in particular regions. Furthermore, they observed that these patterns of endemism are often similar for distinct groups of organisms, which have resulted in very similar biogeographical regions. This marked similarity between biogeographical regions has led to the hypothesis that these regions reflect a shared history of diversification among taxa and have been conditioned by geography, geology and climate (Morrone, 2015; Lomolino, Riddle, & Whittaker, 2016).

The earliest classifications outlined six major biogeographic regions for birds (Sclater, 1858) and non-flying mammals (Wallace, 1876) (Nearctic, Neotropical, Palearctic, Ethiopian, Oriental and Australian). During recent years, these major regions have been confirmed by an upsurge in bioregionalisation studies. This upsurge was facilitated by the increase in quality and quantity of large-scale datasets, as well as the development of new analytical tools (Kreft & Jetz, 2010; Vilhena & Antonelli, 2015; Edler, Guedes, Zizka, Rosvall, & Antonelli, 2016). Consequently, multiple studies have tried to identify the major biogeographical regions for birds (Procheş & Ramdhani, 2012; Rueda, Rodríguez, & Hawkins, 2013; Holt et al., 2013), mammals (Kreft & Jetz, 2010; Procheş & Ramdhani, 2012; Rueda et al., 2013; Holt et al., 2013), amphibians (Procheş & Ramdhani, 2012; Rueda et al., 2013; Holt et al., 2013; Vilhena & Antonelli, 2015; Edler et al., 2016) and reptiles (Procheş & Ramdhani, 2012). The result of this upsurge was a debate on the precise limits of biogeographical regions. Indeed, some studies explicitly defined transition zones as distinct regions (e.g., Holt et al., 2013), whereas others included transition zones in major regions (Kreft & Jetz, 2010). This question of transition zones was settled to some extent in the major synthesis of Morrone (2015), proposing that transition zones should not be considered as distinct regions, but rather as transitional boundaries between major regions. Indeed, some regions share sharp boundaries, reflecting a long history of isolation by tectonics (Ficetola, Mazel, & Thuiller, 2017), whereas others share diffuse boundaries, reflecting recent interchanges, generally limited by orographic or climatic barriers (Morrone, 2015; Ficetola et al., 2017). Morrone (2015) proposed that five major transition zones have emerged from anterior works, which could be explained by a vicariance-dispersal model based on tectonic history. This synthetic model can be considered as a general framework to test for biogeographical regions.

However, the recent upsurge in bioregionalisation studies has concentrated exclusively on terrestrial vertebrates, which represent but a fraction of the continental organisms. There are other continental organisms with constraints to their dispersal and ecology that are fundamentally distinct from terrestrial vertebrates and for which one might expect distinct biogeogeographical regions. For example, plants are characterised by higher degrees of endemism than animals, because they do not have the dispersal, physiological and behavioural adaptations of animals to surmount climatic and other physical barriers (Lomolino et al., 2016). Hence, major phytogeographical regions were described as manifold

small regions (De Candolle, 1820, 1855; Takhtajan, 1986). However, Cox (2001) later proposed a handful of large floral regions comparable to biogeographical regions, thus suggesting that the major biogeographical regions are universal across the tree of life. A second example concerns microbes whose biogeography has also been shown recently to match terrestrial vertebrate biogeography (Murray et al., 2015). Another possibility concerns strictly freshwater organisms as they have lower dispersal abilities than terrestrial vertebrates, and are geographically isolated in drainage basins usually flowing to the oceans. Terrestrial boundaries and salt waters represent strong barriers to dispersal, hence drainage basins have been considered as 'island-like' systems for strictly freshwater organisms (Rahel, 2007; Hugueny, Oberdorff, & Tedesco, 2010; Tedesco et al., 2012; Dias et al., 2014). Dispersal can occur actively or passively via underground waters, stream captures, exceptional floods, glacier melting causing stream overflow, confluence during sea-level lowering, and displacement by other organisms or typhoons. However, such dispersal events are rare, therefore immigration and speciation presumably occur on similar time-scales (Oberdorff et al., 2011). Consequently, one might expect that, because of peculiarities of riverscape changes through geological times, strictly freshwater organisms have been subject to different histories of diversification from those of terrestrial vertebrates (Rahel, 2007) and thus have original biogeographical boundaries. Because dispersal is physically constrained, a higher degree of provincialism and endemism could be anticipated for such organisms, resulting potentially in smaller and more numerous biogeographic regions.

In this paper, we focussed on the global biogeography of strictly freshwater actinopterygian fishes (i.e., excluding marine and amphidromous families of fish), hereafter called freshwater fishes. While several studies delineated biogeographical regions of freshwater fishes at regional to continental scales (e.g., Unmack 2001; Oikonomou *et al*. 2014), almost none have been conducted at the global scale. One work hinted at nine potential freshwater fish biogeographic regions that covered the same biogeographical regions as terrestrial vertebrates (Matthews, 1998), but it was based on a coarse geographic scale (52 approximate drainage basins for the whole world) and a low taxonomic resolution (family level). In addition, Matthews, (1998) included marine and migratory fish families, which could conceal the effect of long-term isolation on freshwater fish endemicity patterns. Consequently, whether Sclater-Wallace's biogeographical regions are also applicable to freshwater fishes and to other freshwater organisms remains unresolved.

In this study, we aimed to define the major biogeographical regions for strictly freshwater fishes at the global scale. To delineate biogeographical regions, we capitalised on the recent development of the database on freshwater fish distributions in drainage basins of the world (Tedesco et al., 2017), a comprehensive dataset covering more than 80% of the Earth surface. First, we identified the large biogeographical regions of freshwater fishes using a recently developed hierarchical approach based on networks (Vilhena & Antonelli, 2015), recommended for bioregionalisation studies (Edler et al., 2016; Bloomfield, Knerr, & Encinas-Viso, 2017; Rojas, Patarroyo, Mao, Bengtson, & Kowalewski, 2017). Then, we mapped the transition zones between regions and investigate species that are distributed across region boundaries. Finally, we compared our biogeographical regions with terrestrial

150 vertebrate biogeographical regions and discussed our findings in light of the synthetic
151 vicariance-dispersal model proposed by Morrone (2015).

Methods

Distribution data

We based our bioregionalisation on the most comprehensive global database on freshwater fish species occurrence in drainage basins (Tedesco et al., 2017). This database comprises 110 331 occurrence records for 14 953 species in 3 119 drainage basins of the world. Species names in the database were validated according to FishBase (Froese & Pauly, 2017), and occurrence records were screened by the team developing the database (see Tedesco *et al.* 2017). We applied additional filters and corrections to the database. Since our aim was to describe the natural biogeographical regions resulting from long-term isolation of freshwater ichthyofaunas, we excluded documented records of introduced species, but included species considered to be recently extinct in their historical river basins. Additionally, to exclude most species that could disperse through marine waters, we retained only families having less than 10% of their species occurring in marine waters. This filter included all "primary" and almost all "secondary" families of fishes (only Pseudomugilidae and Fundulidae were not included), i.e. families with respectively no or limited salt tolerance species, as well as 22 families that had never been classified (based on Table 2 of Berra, 2007). It also included eight families with marine ancestors, seven of which had no species classified as tolerating salt water. Finally, we removed all diadromous species, according to FishBase. Additionally, we detected a few errors that were corrected in the database, mostly the native/introduced status for some species (the database used in this publication is available in Appendix S1 in Supporting Information). The resulting dataset included 75 692 records of 12 333 species in 2 916 basins (see Figure S2.1 in Appendix S2).

To define our bioregions, we worked at the species level and used the drainage basin as the geographical unit. Indeed, (1) in the absence of a unified phylogeny for actinopterygian fishes, species is the most standard unit available and (2) contrary to terrestrial vertebrates, for which gridded distribution data is available with reasonable quality, the most precise distribution data available for actinopterygian fishes is at the drainage basin unit. However, it is important to note that even if drainage basins are uneven in size, they are biogeographically meaningful for freshwater organisms because water bodies are generally connected within basins but not between basins (Hugueny et al., 2010).

Delineation of biogeographical regions

Until recently, the prevailing procedure for bioregionalisation has been based on hierarchical clustering methods applied to compositional dissimilarity (Kreft & Jetz, 2010; Procheş & Ramdhani, 2012; Holt et al., 2013). Since then, an approach based on biogeographical networks was introduced by Vilhena & Antonelli (2015), and has been recommended for delineating biogeographic regions (Edler et al., 2016; Bloomfield et al., 2017; Rojas et al., 2017). A network is composed of a series of *nodes* which can be connected to each other by *links* (or edges). In bioregionalisation, the network is composed of both sites (i.e., drainage basins) and species, which constitutes a *bipartite* network. When a taxon is known to occur at

a particular site, a link is drawn between the taxon and the site. A site cannot be connected to another site, and a taxon cannot be connected to another taxon. By definition, site-site and species-species links are not allowed in this type of analysis. Our final network had 13 876 nodes (11 295 species and 2 581 basins) and 59 373 links. We handled the network under Gephi 0.9.2, with the ForceAtlas2 algorithm. This software groups nodes that are tightly interconnected (such as groups of sites and species from the same biogeographical region) and separate groups of nodes that are not interconnected (distinct biogeographical regions). Such a graphical representation is useful for analysing and exploring the network.

We applied a community-detection algorithm to the entire network in order to group nodes into clusters (i.e. biogeographical regions). We applied the Map Equation algorithm (www.mapequation.org, Rosvall & Bergstrom, 2008) because it has been tested and recommended to identify biogeographical regions (Vilhena & Antonelli, 2015; Edler et al., 2016; Rojas et al., 2017) and it features hierarchical clustering. Clusters are identified by the algorithm as having high intra-group but low inter-group connectivity, which corresponds well to the definition of biogeographical regions, i.e. regions of distinct assemblages of endemic taxa. We ran Map Equation (version Sat Oct 28 2017) with 100 trials to find an optimal clustering. We ran the hierarchical clustering (i.e., multi-level) in order to discover whether larger regions have a nested hierarchy of subregions. We used the hierarchical structure identified by map equation to produce a radial tree of biogeographical regions with Evolview (He et al., 2016). We named the identified regions following Morrone (2015).

The biogeographical network approach presents several advantages over distance-based approaches that were instrumental in our choice. Foremost, species identities are not lost, i.e., they are not abstracted into dissimilarity matrices between sites. Consequently, the network approach allows one to map how sites are connected by individual species, which presents an unquestionable asset to investigate between- and within- regions structures, such as potential dispersal pathways or barriers. A second practical novelty is that the algorithm assigns each species to a specific bioregion, which enables species-level descriptions (e.g. for online databases such as FishBase) and analyses. Lastly, we found that the Map Equation algorithm was robust to differences in sampling intensities, and we did not need to filter our dataset, such as the removal of basins with low species richness. On the other hand, distance-based approaches have limitations (see e.g., Leprieur & Oikonomou, 2014) and can produce inconsistent results when transforming such large occurrence datasets into a single dimension during the clustering procedure.

Sensitivity analysis

We analysed the robustness of the identified regions by randomly extirpating a percentage (random value between 0.01 and 10.00% of the total number of species in the database) of species and running the whole bioregionalisation process. This process was repeated 200 times. Then, for each region, we evaluated its robustness by quantifying the percentage of simulations in which it was identified (e.g., a region that was identified 150 out of 200 runs has a robustness of 0.75).

Transition zones and species shared between regions

We calculated the participation coefficient (Bloomfield et al., 2017) for each node of the biogeographical network. The participation coefficient indicates the degree to which a node is connected to different regions. A high participation coefficient for a given basin indicates that it contains species from different regions and can be assimilated to a transition zone between regions. A low participation indicates that all species in the basin belong to the same region. The participation coefficient of a node is calculated as follows:

$$P_i = 1 - \sum_{s=1}^{N_m} \left(\frac{k_{is}}{k_i}\right)^2$$

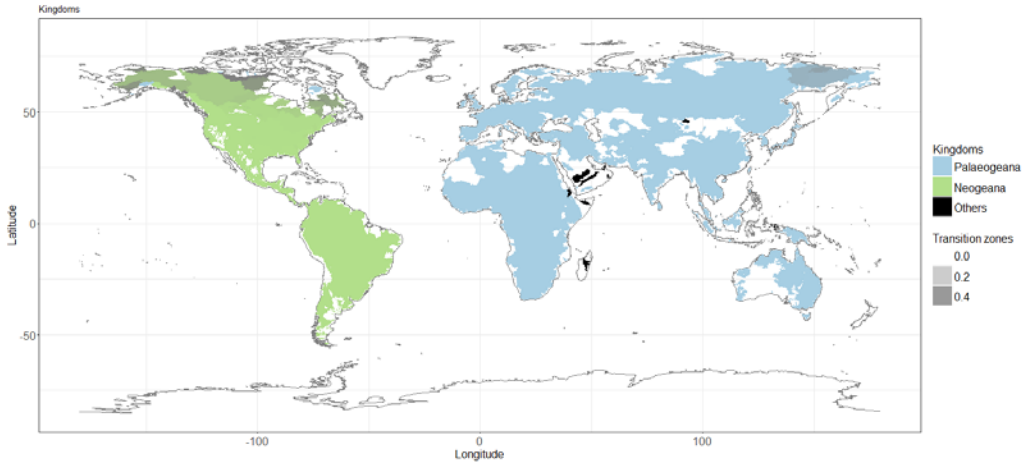
where P_i is the participation coefficient of node i, k_{is} is the number of links of node i to region s, k_i is the total number of links of node i, and N_m is the total number of regions. We calculated the participation coefficient at each level of the biogeographical structure identified by Map Equation.

We also summarised the list of species that were shared between the major regions (i.e., excluding tiny clusters) and their distribution characteristics.

Results

The Map Equation algorithm identified a hierarchy of biogeographical regions with up to six nested levels (Appendix S3). For this global-scale study, we investigated the first three levels, termed as Kingdoms, Regions and Subregions.

a. Kingdoms



b. Regions

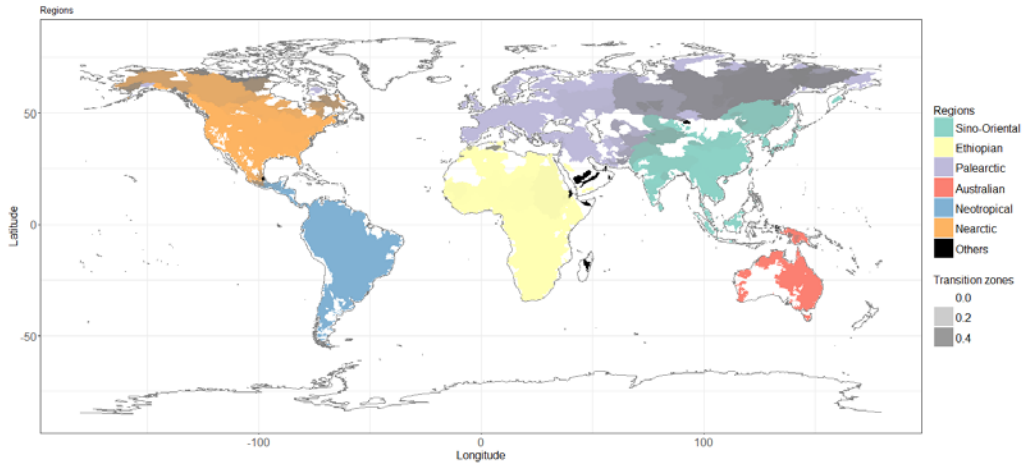


Figure 1. Biogeographical regions of freshwater fishes defined at the species level with the Map Equation clustering algorithm. We identified (a) two major kingdoms (Palaeogeana and Neogeana) and (b) six major regions (Nearctic, Palearctic, Neotropical, Ethiopian, Sino-Oriental, Australian), and a few drainage basins that do not share fish species with any other basin (called "Others"). We identified transition zones with the participation coefficient of each basin (i.e. the proportion of species in a basin that come from regions other than the region of this basin) which are superimposed with shades of

grey on the maps. The stronger the shade of grey of a basin, the more species it shares with distinct regions. Transition zones were only provided for major regions (i.e., excluding tiny regions not sharing any species with the main regions, called "Others" in the legend).

Kingdoms

At the first level, we found that the world of freshwater fishes was divided into two kingdoms that we named Palaeogeana (Eurasia, Africa and Australian) and Neogeana (Americas) following Sclater (1858) (Figure 1a). Each kingdom contained nearly half the world's 11 295 species with virtually 100% of endemic species (Table 1). Only two species occurred in both kingdoms (Figure 2 and Appendix S4): (1) *Esox lucius,* a Palaeogeana species that occurred in 32 basins of northern Neogeana, and (2) *Catostomus catostomus*, a Neogeana species that occurred in nine basins of northern Palaeogeana. These two kingdoms also hosted 99% of endemic genera and around 80% of endemic families. At this first level, we also found 14 tiny clusters of 49 basins (exclusively located in the Palaeogeana) that did not have endemic families and genera but had endemic species (40 species in total). These tiny clusters generally consisted of species-poor basins with high levels of endemism and were located in remote islands (e.g., Madagascar) or isolated arid areas (e.g., Arabian Peninsula).

Regions

At the second level, we found six major regions nested within the two kingdoms (Figure 1), that we named following Morrone (2015). In the Palaeogeana, we found four regions (Figure 1b). The richest one (Table 1) was the Ethiopian region with nearly 50% of Palaeogeana species, covering the entire African continent, including areas north from the Sahara, and a few basins in the Arabic peninsula. The second richest one was the Sino-Oriental region which included south-eastern Asia from India to Borneo, most of China and Mongolia, Korea and Japan. The third one was the Palearctic region with less than 10% of Palaeogeana species, covering Europe, Central Asia (up to Pakistan and Kazakhstan) and Siberia. The fourth one, the poorest, was the Australian region, with only 80 species in total, covering Australia, Tasmania and Papouasia-New Guinea. Within the Neogeana kingdom, we found two major regions. The first one was the Neotropical region, containing 85% of Neogeana species and 42% of the world's known freshwater fish species. The Neotropical region covered the whole of South America and Mesoamerica up to Southern Mexico. The second one was the Nearctic region, covering North America and northern Mexico. Finally, a tiny cluster composed of four basins of Central America was identified at this level, in addition to the other 14 tiny clusters already identified at level 1 (Table 1).

Most regions had very high degrees of endemism (Table 1b), above 96% for all regions except the Palearctic (88%). These high degrees of endemism are apparent on the biogeographical network through a low number of links between regions (Figure 2, Appendix S5). In other words, all regions shared only a very limited number of species (see Appendix S4). The

degree of endemism was lower for genera, ranging from 56% for the Palearctic to 98% for the Neotropical, and was much lower for families, with values below or equal to 50% for all regions except the Neotropical one.

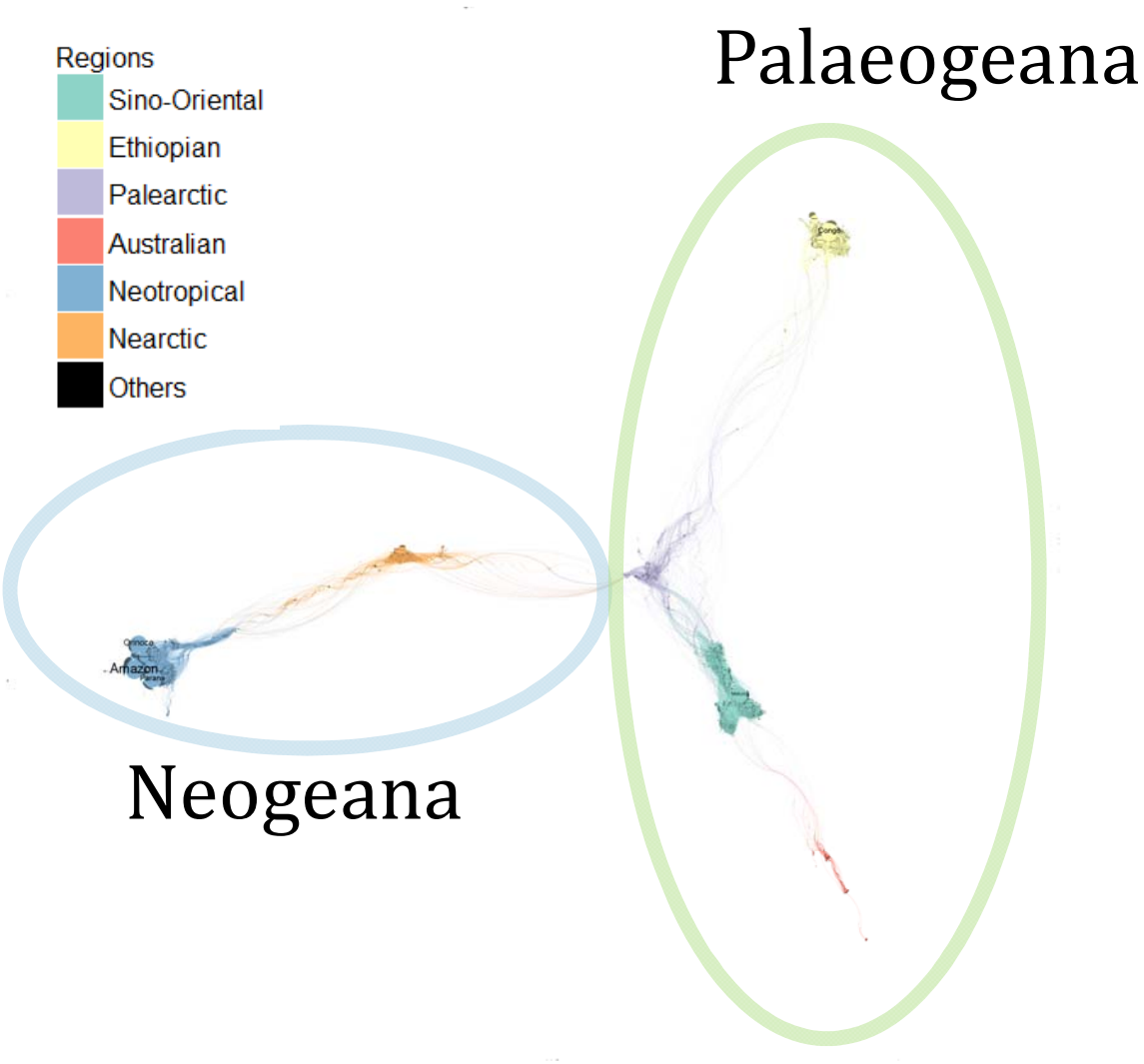


Figure 2. Global biogeographical network of freshwater fishes. In this network, both species and drainage basins are represented as nodes. When a species is known to occur in a drainage basin, a link between the species and the basin is drawn. The network is very complex because of the high number of nodes (13 909 nodes corresponding to 11 329 species and 2 580basins) and links (59 480 occurrences). We spatialised the network in Gephi with the ForceAtlas 2 (LinLog mode) algorithm in order to group nodes that are strongly interconnected (i.e., basins that share species in common) and spread away from all other nodes that are not interconnected (i.e., basins that have few or no species in common). We coloured species and basin nodes according to the regions identified with the Map Equation algorithm, and highlighted the two kingdoms (Neogeana and Palaeogeana) with coloured ellipses. A fully zoomable version is available in Appendix S5.

Table 1. Characteristics of the first two levels of biogeographical regions of freshwater fishes identified with the Map Equation algorithm.

	Total number of species	Number of species assigned to the region	Number of endemic species	Percentage of endemic species	Number of endemic genera	Percentage of endemic genera	Number of endemic families	Percentage of endemic families	Number of basins	Total basin area	Number of nested levels of complexity
a. Kingdoms											
Palaeogeana	5680	5679	5678	99.96%	846	99.30%	66	83.54%	1888	67 354 732.02	5
Neogeana	5577	5576	5575	99.96%	812	99.27%	54	80.60%	644	30 325 232.78	5
14 tiny clusters	40	40	40	100.00%	11	57.89%	2	25.00%	49	699803.609	3
b. Regions											
Sino-Oriental	2494	2465	2444	98.00%	399	88.86%	24	48.98%	718	14 961 835.97	5
Ethiopian	2680	2675	2671	99.66%	311	94.53%	17	50.00%	273	24 663 867.33	5
Palearctic	485	461	427	88.04%	65	55.56%	4	19.05%	515	23 036 751.72	5
Australian	80	78	77	96.25%	16	76.19%	4	40.00%	382	4 692 277.00	5
Neotropical	4760	4749	4738	99.54%	680	97.70%	41	75.93%	377	15 424 005.23	5
Nearctic	837	821	809	96.65%	117	85.40%	9	40.91%	263	14 881 955.51	5
15 tiny clusters	55	46	42	76.36%	11	42.31%	2	20.00%	53	719075.6526	3

Interestingly, our sensitivity analysis confirmed that most regions were stable to random extirpations of species (Appendix S6), except for the Sino-Oriental one, which split in two regions in half of the simulations. This split produced the Oriental and Sinean regions with respectively ~85% and ~72% of endemics. These two subregions are visible on the network with two apparent clusters of nodes in the Sino-Oriental cluster (Figure 2). We also observed other minor changes, such as some clusters of basins appearing as small distinct regions, e.g. in Central and southwestern North America and in Central Asia.

Subregions

At the third level, we observed different patterns among regions. Three regions (Sino-Oriental, Nearctic and Australian) had only two to three main subregions (Appendix S3) that were spatially coherent and had high degrees of endemism (68.7-91.5% of endemic species, Appendix S6). The other three regions (Ethiopian, Palearctic and Neotropical) were characterised by a high number of subregions (Appendix S3). These subregions were also generally spatially coherent (appendix S7). The Ethiopian and Neotropical subregions were generally characterised by a high number of species and endemics (Figures S7.3 and S7.9). The Palearctic subregions were characterised by a low number of species and generally low endemicity (Figure S7.5).

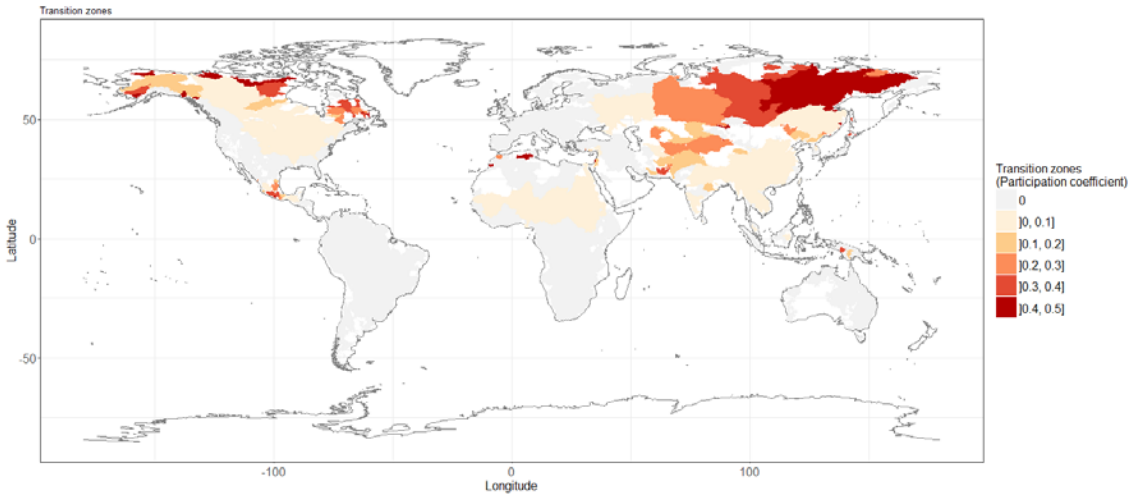


Figure 3. Map of transition zones characterised by the participation coefficient of basins, i.e the proportion of species in a basin that come from regions other than the region of this basin. Transition zones were only provided for major regions (i.e., excluding tiny regions not sharing any species with the main regions).

Transition zones and species shared between regions

At the kingdom level, we obtained participation coefficients of basins between 0.0 and 0.5, with transition zones (i.e., basins with high participation coefficients) located in north-

eastern Siberia as well as in northern North America (Figure 1a, figure 3). At the regional level, we observed participation coefficients also ranging from 0.0 to 0.5 (Figure 1b, figure 3). Unsurprisingly, we found the same transition zones between the Nearctic and the Palearctic as for kingdoms. However, the major transition zones were located at the boundaries between the Palearctic and Sino-Oriental regions: the high participation coefficients of basins at their boundaries indicated that they were diffuse (Figure 3). These diffuse boundaries are reflected on the network by the high number of links between multiple species and multiple basins from both regions (Figure 2, Appendix S5). We identified another transition zone between the Nearctic and the Neotropical regions, with high participation coefficients of basins at their boundary (Figure 3). A dozen species of each region also incurred in the other region with similar distribution patterns (Appendix S4).

Overall, the species that were distributed across boundaries could be separated in two broad categories (Appendix S4). First, we found that the majority of shared species had restricted distributions close to regional boundaries with occasional occurrences beyond. For example, the two spot livebearer *Heterandria bimaculata* has a distribution endemic to Central America at the northernmost part of Neotropical, and incurred in two basins of the Nearctic. Second, we found a limited number of species with large spatial distributions that were able to incur in multiple basins of other regions. The best example is the Northern pike *Esox lucius* which is one of the two species distributed across both kingdoms. Another example is the Eurasian minnow *Phoxinus phoxinus* that is widespread in the Palearctic with multiple occurrences in the Sino-Oriental region.

On the other hand, we found almost no transition zones at the boundaries of the Ethiopian or the Australian regions. For the Ethiopian region, only a few basins in northern Africa and the Middle East shared species between the Ethiopian and Palearctic regions (Figure 3) as illustrated by the limited number of links on the network (Figure 2). Only nine species were shared between these two regions (Appendix S4). For the Australian region, only four species dispersed through the Wallace-Huxley boundaries (Figure 2, Appendices S4 and S5): two species assigned to the Oriental region (*Aplocheilus panchax* and *Datnioides polota*) occur in Papuasia, and one species assigned to the Australian region (*Ophisternon bengalense*) was distributed in Australia, Papuasia and Southeastern Asia.

Discussion

Summary of findings

Here, we have provided the first global bioregionalisation of freshwater fishes based on a quantitative analysis of species distributions. We found that the freshwater fish world is first divided into two kingdoms, the Paleogeana and Neogeana. These two kingdoms are then divided into six major biogeographical regions with very high degrees of endemism: Paleogeana was divided in the Sino-Oriental, Ethiopian, Palearctic and Australian regions, whereas Neogeana was composed of the Neotropical and Nearctic regions. Each of these major biogeographical regions was then subdivided into subregions with varying degrees of endemism. Some regions had a few large subregions, while others had numerous subregions with heterogeneous size, species diversity and endemism. We found transition zones between the Nearctic and Neotropical regions, and between the Palearctic, Sine-Oriental regions, but almost no transition zones for the Ethiopian and Australian regions. The fish species that were distributed between regions were of two types: (i) species with restricted ranges close to regional boundaries that occasionally crossed and (ii) species with large distributions that expanded their range beyond boundaries.

Our results compellingly contradict our initial hypothesis that freshwater fish would have biogeographical regions which were different from the terrestrial vertebrate scheme of Sclater-Wallace because of their restricted dispersal abilities and the specificic spatial-temporal dynamics of riverscapes. Indeed, we found a total of six major biogeographical regions that were similar in size and location to the six biogeographical regions identified by Wallace (1876). The only differences were the locations of several boundaries. More surprisingly, our regions were also similar to the coarse biogeographical regions based on freshwater fish families identified by Matthews (1998), that also included migratory fish species. Our Neotropical region is the only major difference to Matthews (1998): he identified a distinct cluster south to the Andes. This difference may be explained by the fact that this area was mostly colonised by the family of Galaxiidae that migrate between freshwater and oceans, which were included in Matthews' analysis, but not in ours. In addition, we also identified transition zones broadly following the bioregionalisation model of Morrone (2015), suggesting that freshwater fish regions were shaped by vicariance and geodispersal events similar to other groups. However, we observed extremely high rates of endemism for each region, more than 96% of endemic species for all regions except the Palearctic. Therefore, freshwater fishes are likely to have the highest rates of endemism per region among continental vertebrates, although a direct comparison with other groups is not feasible as endemism rates were not reported in previous bioregionalisation studies.

The two major "kingdoms" we identified might seem to contradict Morrone's biogeographical model (2015). Indeed, Morrone (2015) hypothesised that three major kingdoms could be derived from formerly disconnected land masses (Holarctic, Holotropical, Austral). This apparent contradiction rather indicates that our analyses at the species level reflect more recent processes of isolation than the ancient vicariant processes of Morrone's kingdoms. To

test the ancient processes suggested by Morrone (2015), a dated phylogenetic tree of actinopterygian fishes is required to unravel the evolutionary origins of biogeographic regions (e.g., Daru et al., 2017).

Regions and transition zones

The Neotropical and Nearctic regions of freshwater fishes are very similar to the Neotropical and Nearctic regions highlighted for terrestrial mammals, amphibians and bird species (Kreft & Jetz, 2010; Procheş & Ramdhani, 2012; Holt et al., 2013). These two regions are therefore in agreement with the synthetic world biogeographical regionalisation of Morrone (2015). As for other groups of organisms, we identified a Mexican transition zone between Nearctic and Neotropical. The identification of this Mexican transition zone (Morrone, 2015) for freshwater fishes suggests that these organisms were affected by biotic interchange between the Americas, but to a much lesser extent than terrestrial vertebrates (Bussing, 1985; Smith & Bermingham, 2005). Indeed, we found that only 25 species with restricted distributions were shared between Nearctic and Neotropical, as illustrated by the restricted area of the transition zone (Figure 3). These species belong to both primary and secondary freshwater families, which colonised Mesoamerica separately, as suggested by molecular analyses (Smith & Bermingham, 2005). Secondary freshwater fishes probably dispersed through Mesoamerica before the formation of the Panama isthmus, during periods of high runoff leading to temporary freshwater or brackish-water bridges in marine waters coupled with northward discharge of the proto-Amazon during the Miocene ~18-15 Ma (Smith & Bermingham, 2005; Hoorn et al., 2010). Later, primary freshwater families dispersed through Mesoamerica during the Isthmus formation via landscape diffusion (Smith & Bermingham, 2005). Subsequent changes in the landscape led to increasing isolation of basins within Mesoamerica as well as occasional connectivity events, which in turn shaped the regional patterns of dispersal and diversification (Smith & Bermingham, 2005; Dias et al., 2014) that probably drove the restricted extent of the Mexican transition zone for freshwater fishes.

The Ethiopian region of freshwater fish resembles the Ethiopian regions of terrestrial vertebrates except for its northern limit. We found that this region expanded beyond the limits of the Sahara up to the Mediterranean sea, similarly to flightless terrestrial mammals (Kreft & Jetz, 2010). However, flightless terrestrial mammals were also found to expand their Ethiopian boundary beyond the Arabian Peninsula into Central Asia, which was not the case here. Moreover, most studies for terrestrial vertebrates located the northern boundary of the Ethiopian region south of the Sahara (Procheş & Ramdhani, 2012; Rueda et al., 2013; Holt et al., 2013; Vilhena & Antonelli, 2015). This discrepancy may be explained by several factors. First, most studies on vertebrates identified the Sahara and the northern coast of Africa as transition zones between the Palearctic and Ethiopian regions (Holt et al., 2013; Morrone, 2015). This transition zone was not identified in our analyses: Palearctic fishes only anecdotally crossed the Mediterranean Sea, while their African counterparts merely ventured into the Middle-East. Therefore, we can hypothesise that the Mediterranean Sea was an insurmountable barrier for freshwater fishes, contrary to terrestrial vertebrates that could

disperse through Straits of Gibraltar. Dispersal during the desiccation of the Mediterranean Sea during the Messinian salinity crisis about 6 Ma had been proposed with the Lago Mare hypothesis (Bianco, 1990). This hypothesis stated that, during the refilling of the Mediterranean Sea, a freshwater or brackish phase occurred which would have permitted large scale dispersal of freshwater fishes across the basin. However this hypothesis received limited support in the light of phylogenetics studies (Levy, Doadrio, & Almada, 2009; Perea et al., 2010). Hence, freshwater fish dispersal during the Messinian salinity was not the same as that of other groups (e.g., Veith *et al.* 2004; Agustí *et al.* 2006). A probable dispersal pathway for freshwater fishes was through diffusion (*sensu* Lomolino et al., 2016) between the Nile and Mediterranean basins of the Middle East (illustrated by the distributions of *Clarias gariepinus* and four African cichlid species). This Middle-East dispersal pathway to some extent corroborates the Saharo-Arabian transition zone proposed by Morrone (2015). This dispersal pathway had been identified for early colonisation of Cyprinidae from the Sino-Oriental to Ethiopian (Gaubert, Denys, & Oberdorff, 2009). Second, drainage basins north of the Sahara are extremely poor in freshwater fish species, notably because of their arid nature. Northernmost basins were probably colonised by Ethiopian species during repeated periods of aquatic connectivity across the Sahara region, the most recent being the Holocene African Humid period (~11 to 8ka) (Drake, Blench, Armitage, Bristow, & White, 2011).

The Sino-Oriental region is a major originality of freshwater fishes, for two reasons. Firstly, the northern boundary between Sino-Oriental and Palearctic is different from other groups of organisms. This boundary is located beyond the Himalayas and the Gobi desert to the North-West, and goes up to the Stanovoï mountains located north of China, whereas all other groups are limited to a boundary extending longitudinally from the Himalayas to the Chinese sea (Cox, 2001; Procheş & Ramdhani, 2012; Rueda et al., 2013; Holt et al., 2013; Morrone, 2015). Secondly, this region is composed of two major subregions that were frequently identified as distinct regions in our sensitivity analysis. In particular, the Sinean subregion hosting a rich freshwater fish fauna (963 species) with 72% of endemics seems unique to freshwater fishes, and has been identified more as a transition zone for other groups (Procheş & Ramdhani, 2012; Holt et al., 2013; Morrone, 2015). We can speculate that the originality of the Sino-Oriental region for fishes arose from several factors. Firstly, the entire region was prone to fish radiation since the Eocene (55My), probably because of the very high diversity of aquatic habitats combined with the repeated rearrangement of rivers through capture and glaciation melting (Dias et al., 2014; Kang et al., 2014; Kang, Huang, & Wu, 2017; Xing, Zhang, Fan, & Zhao, 2016). For example, the Cyprinidae family, which accounts for 45% of Sino-Oriental species, originated from the Indo-Malaysian tropical region and has likely radiated into Asia since the Eocene (Gaubert et al., 2009). Secondly, the northern boundary is located farther North than from other groups, suggesting that orographic barriers were more important in defining boundaries for fishes than for other groups, whose boundaries appeared to be defined more by a combination of tectonics and climate (Ficetola et al., 2017). Consequently, the fish transition zone between Sino-Oriental and Palearctic is not located near areas of recent tectonic merging as reported for other groups (Morrone, 2015). In

addition, this transition zone is asymmetrically distributed towards the Palearctic (Figure 3) and possibly exceeding the asymmetry reported for other groups (Sanmartín, Enghoff, & Ronquist, 2001), probably because of the extreme differences in fish richness between both regions. Given the orographic constraints of the boundary, dispersal pathways probably emerged at river confluences when the sea level dropped (Dias et al., 2014), both at the Northeastern part and Southwestern parts of the Sino-Oriental boundaries (Gaubert et al., 2009).

The Australian region is the most depauperate of all fish regions, probably owing to the combination of the complete isolation of this region for the last 60 million years (Scotese, 2016) and the dryness of the Australian continent. The boundary between Australian and Sino-Oriental encompasses the entire Wallacea: the Sino-Oriental extends to the limits of the Sunda shelf, whereas the Australian extends to the limits of the Sahul shelf (Lomolino et al., 2016). Only three species occur on both sides of the boundary: *Aplocheilus panchax* and *Datnioides polota* are Sino-Oriental species known from one drainage basin of the Australian region, and *Ophisternon bengalense* is distributed in 10 and 11 basins of Australian and Sino-Oriental respectively. *O. bengalense* lives in estuaries and is tolerant to brackish waters, and thus may have progressively dispersed through Wallacea. On the other hand, the distributions of the other two species are more surprising, and the absence of data in all islands of Wallacea makes hypotheses highly speculative. These apparent disjoint distributions could be linked to exceptional dispersal events –such events have happened between Nearctic and Neotropical before the formation of the Panama isthmus (Smith & Bermingham, 2005), undocumented introductions, or that these are in fact two species misidentified as single species.

Subregions

The differences in number and endemism of subregions among major regions may be explained by the combination of habitat size and diversity, past climate change, and paleoconnectivity during the last glacial maximum (LGM, see Leprieur *et al.* 2011; Tedesco *et al.* 2012; Dias *et al.* 2014). Past climate change had an enormous impact on high-latitude regions, such as the Nearctic and northern parts of the Palearctic (Leprieur et al., 2011). Most of these areas were covered by ice during the LGM. These Northern areas were colonised after the LGM (e.g., Rempel & Smith 1998) by species from refuges that were located in the southernmost parts of these regions (Mississipi basin for the Nearctic, Danube basin for the Palearctic). Consequently, the relatively recent colonisation of these regions explains these wide species-poor subregions. On the other hand, such climate events were less extreme in tropical regions (Tedesco, Oberdorff, Lasso, Zapata, & Hugueny, 2005) thereby allowing lineages to thrive for a long period. The combination of this prosperity with the high diversity and size of habitats in tropical regions, as well as the long-term isolation of drainage basins during the Pleistocene (Dias et al., 2014) probably generated conditions favourable to divergence and radiation in tropical subregions. This hypothesis would explain the numerous subregions with high diversity and endemism in tropical regions. The only apparent contradiction could arise from the two large subregions with high endemism of the Sino-

Oriental. However, this intermediate level probably reflects the uplift of the Tibetan plateau that led to the isolation of these two subregions (Kang et al., 2014). In turn, these two subregions included numerous smaller regions with high diversity and endemism (Figure S7.10) similar to the other tropical regions.

Robustness of findings

This first global quantitative analysis of the biogeography of freshwater fishes is based on a large scale database compiling occurrence data from thousands of sources and is thus inevitably subject to errors and incomplete data (Tedesco et al., 2017). To minimise errors, a careful screening and correction procedure has been implemented for this database (see Tedesco et al., 2017). Reassuringly, our sensitivity analysis suggests that the regions we identified are robust to changes in species occurrence data. Furthermore, regions were all spatially coherent (even though no spatial information was provided at any stage of the process) for the first two levels, with high degrees of endemism, indicating the quality of both the dataset and the bioregionalisation approach. The only discrepancies were for several basins of North America that were attributed to the Palearctic region. These were composed of only one or two species, including the pike *Esox lucius*. Since *E. lucius* has been assigned to the Palearctic region, less-documented basins of North American basins where it is the only reported species (or with a single species of lower occurrence) were attributed to the Palearctic. Generally, this species assignation to regions is a major asset of networks, as explained in the methods. However, one major caveat needs to be acknowledged. Species are assigned to the region where their present-day distribution is largest – this region is not necessarily the region where they originated from. A perfect example is the Characidae family at the transition between Nearctic and Neotropical: *Astyanax mexicanus* was assigned to the Nearctic, although its lineage is assumed to have colonised Mesoamerica during the Panama Isthmus formation (Smith & Bermingham, 2005).

Our results at subregional and finer scales have several limits. Firstly, species introductions are relatively well documented between major continents or regions. However, at regional scales, we can expect that some human-assisted translocations of species among basins have not been documented, thereby blurring subregional patterns of endemism. Secondly, heterogeneity in land topology led to vast differences in size and number of drainage basins within different geographical areas of the world. For areas with numerous small basins, species lists were not necessarily available for all basins, and thus identification of provinces beyond the subregional scale would be speculative. Likewise, fine-scale data was not available in similar quantity or qualitywithin different regions of the world, and for example, remote areas of Africa or Papuasia remain poorly sampled compared to other regions. Last, the Map Equation is expected to identify transition zones as distinct clusters (Vilhena & Antonelli, 2015; Bloomfield et al., 2017). We did not observe this pattern at large scales, except for a few basins at the transitions between Nearctic and Neotropical or between Sino-Oriental and Palearctic or Australian. However, at subregional and finer scales, transitions are likely to stand out as separate zones (Bloomfield et al., 2017), which may not necessarily be an appealing property since the participation coefficient is informative enough to describe

transition zones. For all these reasons, we deemed preferable not to investigate our results below the third level, because such fine-scale provinces would be better studied in regional studies (e.g., Smith & Bermingham, 2005; Kang et al., 2014).

Concluding remarks

This first quantitative study of freshwater fish bioregions revealed that their biogeography was probably shaped by the same major drivers as other continental groups of organisms, with peculiar exceptions such as the Sino-Oriental region. These regions identified with species distributions probably reflect relatively recent processes of dispersal and isolation, whereas more ancient processes will be explored in the future when dated phylogenies with a large taxonomic coverage of freshwater fishes become available.

We found that freshwater fishes, in addition to being the most diverse group of continental vertebrates, have extremely high rates of endemism, above 96% for all regions except the Palearctic. Furthermore, we found that tropical regions have a myriad of subregions with very high endemism and richness. These figures compellingly bespeak that freshwater fishes ought to be considered in hotspot analyses, and raise many questions about the biogeographical consequences of the current colossal global rates of freshwater fish introductions and extinctions.

Agustí, J., Garcés, M., & Krijgsman, W. (2006). Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *238*(1–4), 5–14.

Berra, T. M. (2007). *Freshwater fish distribution*.

Bianco, P. G. (1990). Potential role of the palaeohistory of the Mediterranean and Paratethys basins on the early dispersal of Euro - Mediterranean freshwater fishes. *Ichthyological Exploration of Freshwaters*, *1*(6), 167–184.

Bloomfield, N. J., Knerr, N., & Encinas-Viso, F. (2017). A comparison of network and clustering methods to detect biogeographical regions. *Ecography*, (November 2016), 1–10.

Brosse, S., Beauchard, O., Blanchet, S., Dürr, H. H., Grenouillet, G., Hugueny, B., ... Oberdorff, T. (2013). Fish-SPRICH: a database of freshwater fish species richness throughout the World. *Hydrobiologia*, *700*(1), 343–349.

Bussing, W. (1985). Patterns of distribution of the Central American Icthyofauna. In G. G. Stehli & S. D. Webb (Eds.), *The Great American Biotic Interchange* (pp. 453–473). New York: Plenum Press.

Cox, B. (2001). The biogeographic regions reconsidered. *Journal of Biogeography*, *28*, 511–523.

Daru, B. H., van der Bank, M., & Davies, T. J. (2017). Unravelling the evolutionary origins of biogeographic assemblages. *Diversity and Distributions*, *2*, 313–324.

De Candolle, A. P. (1820). *Essai Elémentaire de Géographie Botanique*. F. Levrault.

De Candolle, A. P. (1855). *Géographie botanique raisonnée*. Paris: Librairie de Victor Masson.

Dias, M. S., Oberdorff, T., Hugueny, B., Leprieur, F., Jézéquel, C., Cornu, J. F., ... Tedesco, P. A. (2014). Global imprint of historical connectivity on freshwater fish biodiversity. *Ecology Letters*, *17*(9), 1130–1140.

Drake, N. A., Blench, R. M., Armitage, S. J., Bristow, C. S., & White, K. H. (2011). Ancient watercourses and biogeography of the Sahara explain the peopling of the desert. *Proceedings of the National Academy of Sciences*, *108*(2), 458–462.

Edler, D., Guedes, T., Zizka, A., Rosvall, M., & Antonelli, A. (2016). Infomap Bioregions: Interactive Mapping of Biogeographical Regions from Species Distributions. *Systematic Biology*, *66*(2), syw087.

Ficetola, G. F., Mazel, F., & Thuiller, W. (2017). Global determinants of zoogeographical boundaries. *Nature Ecology & Evolution*, *1*(March), 89.

Froese, R., & Pauly, D. (2017). FishBase.

Gaubert, P., Denys, G., & Oberdorff, T. (2009). Genus-level supertree of Cyprinidae (Actinopterygii: Cypriniformes), partitioned qualitative clade support and test of macro-evolutionary scenarios. *Biological Reviews*, *84*(4), 653–689.

He, Z., Zhang, H., Gao, S., Lercher, M. J., Chen, W. H., & Hu, S. (2016). Evolview v2: an online visualization and management tool for customized and annotated phylogenetic trees. *Nucleic Acids Research*, *44*(W1), W236–W241.

Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., ... Rahbek, C. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, *339*(6115), 74–78.

Hoorn, C., Wesselingh, F. P., Ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., … Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, *330*(6006), 927–931.

Hugueny, B., Oberdorff, T., & Tedesco, P. A. (2010). Community Ecology of River Fishes: A Large-Scale Perspective. In K. B. Gido & D. A. Jackson (Eds.), *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques* (pp. 29–62). Bethesda, USA, USA: American Fisheries Society Symposium 73.

Kang, B., Deng, J., Wu, Y., Chen, L., Zhang, J., Qiu, H., … He, D. (2014). Mapping China's freshwater fishes: Diversity and biogeography. *Fish and Fisheries*, *15*(2), 209–230.

Kang, B., Huang, X., & Wu, Y. (2017). Palaeolake isolation and biogeographical process of freshwater fishes in the Yellow River. *PLoS ONE*, *12*(4), 1–15.

Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, *37*, 2029–2053.

Leprieur, F., & Oikonomou, A. (2014). The need for richness-independent measures of turnover when delineating biogeographical regions. *Journal of Biogeography*, *41*(JANUARY), 417–420.

Leprieur, F., Tedesco, P. A., Hugueny, B., Beauchard, O., Dürr, H. H., Brosse, S., & Oberdorff, T. (2011). Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, *14*(4), 325–334.

Levy, A., Doadrio, I., & Almada, V. C. (2009). Historical biogeography of European leuciscins (Cyprinidae): Evaluating the Lago Mare dispersal hypothesis. *Journal of Biogeography*, *36*(1), 55–65.

Lomolino, M. V, Riddle, B. R., & Whittaker, R. J. (2016). *Biogeography 5th edition* (5th ed.). Sinauer Associates, Oxford University Press.

Matthews, W. J. (1998). *Patterns in freshwater fish ecology*. *Chapmann & Hall* (Vol. 80).

Morrone, J. J. (2015). Biogeographical regionalisation of the world: A reappraisal. *Australian Systematic Botany*, *28*(3), 81–90.

Murray, K. A., Preston, N., Allen, T., Zambrana-Torrelio, C., Hosseini, P. R., & Daszak, P. (2015). Global biogeography of human infectious diseases. *Proceedings of the National Academy of Sciences*, *112*(41), 12746–12751.

Oberdorff, T., Tedesco, P. A., Hugueny, B., Leprieur, F., Beauchard, O., Brosse, S., & Dürr, H. H. (2011). Global and Regional Patterns in Riverine Fish Species Richness: A Review. *International Journal of Ecology*, *2011*, 1–12.

Oikonomou, A., Leprieur, F., & Leonardos, I. D. (2014). Biogeography of freshwater fishes of the Balkan Peninsula. *Hydrobiologia*, *738*(1), 205–220.

Perea, S., Böhme, M., Zupančič, P., Freyhof, J., Šanda, R., Özulu, M., … Doadrio, I. (2010). Phylogenetic relationships and biogeographical patterns in Circum-Mediterranean subfamily Leuciscinae (Teleostei, Cyprinidae) inferred from both mitochondrial and nuclear data. *BMC Evolutionary Biology*, *10*(1), 1–27.

Procheş, Ş., & Ramdhani, S. (2012). The World's Zoogeographical Regions Confirmed by Cross-Taxon Analyses. *BioScience*, *62*(3), 260–270.

Rahel, F. J. (2007). Biogeographic barriers, connectivity and homogenization of freshwater faunas: It's a small world after all. *Freshwater Biology*, *52*(4), 696–710.

Rempel, L. L., & Smith, D. G. (1998). Postglacial fish dispersal from the Mississippi refuge to the Mackenzie River basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(4),

893–899.

Rojas, A., Patarroyo, P., Mao, L., Bengtson, P., & Kowalewski, M. (2017). Global biogeography of Albian ammonoids: A network-based approach. *Geology*, *45*(7), 659–662.

Rosvall, M., & Bergstrom, C. T. (2008). Maps of random walks on complex networks reveal community structure. *PNAS*, *105*(4), 1118–1123.

Rueda, M., Rodríguez, M. Á., & Hawkins, B. A. (2013). Identifying global zoogeographical regions: Lessons from Wallace. *Journal of Biogeography*, *40*(12), 2215–2225.

Sanmartín, I., Enghoff, H., & Ronquist, F. (2001). Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, *73*(4), 345–390.

Sclater, P. L. (1858). On the general Geographical Distribution of the Members of the Class Aves. (Continued.). *Journal of the Proceedings of the Linnean Society of London. Zoology*, *2*(8), 137–145.

Scotese, C. R. (2016). PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project. Retrieved from http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/

Smith, S. A., & Bermingham, E. (2005). The biogeography of lower Mesoamerican freshwater fishes. *Journal of Biogeography*, *32*(10), 1835–1854.

Takhtajan, A. (1986). *Floristic Regions of the World*. Berkeley: University of California Press.

Tedesco, P. A., Beauchard, O., Bigorne, R., Blanchet, S., Buisson, L., Conti, L., … Oberdorff, T. (2017). A global database on freshwater fish species occurrence in drainage basins. *Scientific Data*, *4*(October), 170141.

Tedesco, P. A., Leprieur, F., Hugueny, B., Brosse, S., Dürr, H. H., Beauchard, O., … Oberdorff, T. (2012). Patterns and processes of global riverine fish endemism. *Global Ecology and Biogeography*, *21*(10), 977–987.

Tedesco, P. A., Oberdorff, T., Lasso, C. A., Zapata, M., & Hugueny, B. (2005). Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography*, *32*(11), 1899–1907.

Unmack, P. J. (2001). Biogeography of Australian freshwater fishes. *Journal of Biogeography*, *28*(9), 1053–1089.

Veith, M., Mayer, C., Samraoui, B., Barroso, D. D., & Bogaerts, S. (2004). From Europe to Africa and vice versa: Evidence for multiple intercontinental dispersal in ribbed salamanders (Genus Pleurodeles). *Journal of Biogeography*, *31*(1), 159–171.

Vilhena, D. A., & Antonelli, A. (2015). A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, *6*, 6848.

Wallace, A. R. (1876). *The geographical distribution of animals; with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface*. New York: Harper & Brothers.

Xing, Y., Zhang, C., Fan, E., & Zhao, Y. (2016). Freshwater fishes of China: Species richness, endemism, threatened species and conservation. *Diversity and Distributions*, *22*(3), 358–370.

Biosketch

Boris Leroy is lecturer at the Muséum National d'Histoire Naturelle of Paris. He is interested in the biogeography of aquatic organisms and how it is or will be impacted by global changes such as climate change and invasive alien species.