PRIMARY RESEARCH PAPER

Fish-SPRICH: a database of freshwater fish species richness throughout the World

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Abstract There is growing interest in large-scale approaches to ecology, for both plants and animals. In particular, macroecological studies enable examination of the patterns and determinants of species richness of a variety of groups of organism throughout the world, which might have important implications for prediction and mitigation of the consequences of global change. Here, we provide richness data for freshwater fishes, which, with more than 13,000

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Department of Physical Geography, Faculty of Geosciences, Utrecht University, Heidelberglaan 2, Room 106, P.O. Box 80.115, 3508 TC Utrecht, The Netherlands described species, comprise a quarter of all vertebrate species. We conducted an extensive literature survey of native, non-native (exotic), and endemic freshwater fish species richness. The resulting database, called Fish-SPRICH, contains data from more than 400 bibliographic sources including published papers, books, and grey literature sources. Fish-SPRICH contains richness values at the river basin grain for 1,054 river basins covering more than 80% of the earth's continental surface. This database is currently the most comprehensive global database of native, non-native and endemic freshwater fish richness available at the river basin grain.

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Introduction

The emergence of macroecology has led to an increase in the number of studies examining the patterns and determinants of species richness of different groups of organisms throughout the world (Brown, 1995; Gaston & Blackburn, 2000). Besides improving theoretical knowledge, macroecological approaches might have important implications for prediction and mitigation of the consequences of global change for organisms and ecosystem function (Kerr et al., 2007). Macroecological studies require global scale datasets. Such datasets have been published so far for only a few animal groups, namely birds (Davies et al., 2007), amphibians, and mammals (Orme et al., 2005; Grenyer et al., 2006). With regard to freshwater fish, since the nineties several studies have started investigating global (ca 200 river basins; Oberdorff et al., 1995; Guegan et al., 1998) and continental patterns of fish species richness (Hugueny, 1989; Oberdorff et al., 1997; Tedesco et al., 2005; Reyjol et al., 2007). This has enabled investigation of richness determinants of freshwater fishes, but it is still not sufficient to draw a detailed global map of fish richness, because of lack of coverage of the world's continental areas. Therefore, these original data were later combined and extended by making a detailed literature survey of more than 1,000 basins throughout the world. This gave rise to the Fish-SPRICH database that covers more than 80% of the earth's continental surface (excluding deserts). The Fish-SPRICH database hence enabled us to accurately map global species richness patterns of native (Oberdorff et al., 2011), endemic (Tedesco et al., 2012) and non-native (Leprieur et al., 2008) fish. However, the Fish-SPRICH database has never been published but could be of interest to many freshwater ecologists and global decision-makers (Seys et al., 2004; Kerr et al., 2007). Here, we make the Fish-SPRICH database publicly available. It contains species richness for native, non-native (or exotic), and endemic freshwater fish in 1,054 river basins distributed throughout the world, with the location, area, and altitude range of each basin.

Materials and methods

Data were collected from 2003 to 2008, as a joint collaboration between two French research institutes: the University Paul Sabatier, Toulouse (S. Brosse, O. Beauchard, F. Leprieur, and S. Blanchet) and the National Museum of Natural History (MNHN) in Paris (T. Oberdorff and P. A. Tedesco). During this period, we conducted an extensive survey of literature published from 1960 to 2008 on native, non-native, and endemic freshwater fish species richness at the river basin grain. Only counts of species-richness which considered the entire fish fauna in the river basin grain were retained, except for some large basins where we summed sub-drainage basin counts on the basis of species lists until we obtained complete coverage of the entire river basin. Sub-species were not considered, because of limited data availability. We used incomplete species counts or check lists, for example local inventories of a stream reach or inventories based solely on a given family, to complement our species lists and for cross-checking available species counts at the basin scale. Only freshwater fish were considered. Marine species occasionally occurring in freshwater and estuarine species with no freshwater life stage were discarded from our richness counts. The resulting database was gathered from more than 400 bibliographic sources including published papers, books, grey literature, and web-based sources. The complete list of references used to compile the Fish-SPRICH database is given as online supplementary material (ESM 1) and the original bibliography is stored at University Paul Sabatier, Toulouse, France, and at the National Museum of Natural History, Paris, France.

Four diversity descriptors were retained for each basin: native, non-native, endemic, and total richness. Native richness is the number of species that currently occur in the basin (Leprieur et al., 2008; Oberdorff et al., 2011). It takes into account both endemic and non-endemic species, but excludes non-native species that have been directly or indirectly (e.g. via artificial channels) introduced into the basin. It also excludes extirpated species that are currently absent from the basin. Exotic richness is the number of established non-native species occurring in each basin. We considered as non-native a species:

- 1. that did not naturally occur in a given basin, and
- 2. that is successfully established, i.e., maintains self-reproducing populations.

Endemic richness refers only to narrow endemic species that are native to a single river basin (i.e. "single-drainage endemics" by analogy with "single-island endemics" often applied to insular systems; Oberdorff et al., 1999; Tedesco et al., 2012). Total richness takes into account the total number of species established in a given basin; it is therefore the sum of native and non-native richness.

Data collection was completed in 2008 and data entries were carefully reviewed by the project contributors. Particular attention was given to cross checking the fish literature to avoid (or at least minimize) incomplete species counts. When fish lists were collected, we used FishBase (www.fishbase.org) to standardize the taxonomy and avoid bias arising from use of synonyms. Because occurrence data available in FishBase are often incomplete, FishBase was not used to collect richness data, solely to check that the species given in FishBase are present in the basins considered. The non-native or endemic status of each species was verified by using specific literature on endemism and introductions.

The location of each basin is characterized by the biogeographic realm to which it belongs (as described by Lévèque et al., 2008 and Balian et al., 2008), the latitude and longitude coordinates in decimal degrees at the river mouth, and the minimum, maximum, and median latitude and longitude of the watershed. Latitude and longitude were collected from the literature and from world atlases (Microsoft Encarta, 2001 and Google Earth, http://www.google.fr/intl/fr/earth/index.html). For each basin we indicated minimum and maximum altitudes and basin area, in accordance with Vörösmarty et al. (2000).

Results

The Fish-SPRICH database contains richness data for 1,054 river basins dispersed throughout the world (Fig. 1). These basins cover 80.7% of the world's continental surface area after excluding both cold and hot deserts where no perennial rivers exist (including deserts, the database covers 63.8% of total landmass). The number of basins included in the database is not balanced among the six biogeographic realms (i.e. the Afrotropical, Australian, Nearctic, Neotropical, Oriental, and Palearctic realms) (Table 1). Indeed, we collected species richness data in more than 200 river

basins in the Palearctic and Nearctic realms, whereas data were less abundant in the four remaining realms. This was particularly true for the Oriental region where we were unable to gather information on more than 59 basins (Table 1). Despite this, the overall realm surface area (excluding deserts) covered by the basins in the Fish-SPRICH database remained higher than 70% in all realms.

Basin altitudes also varied among realms, because of natural variations explained by the presence of high mountain ranges in some realms, for example the Himalayas in the Oriental realm or the Andes in the Neotropical realm. A similar pattern was found for basin surface area, obviously larger in regions with very large rivers, for example the Amazon in the Neotropics or the Congo in the Afrotropical realm. Nevertheless, altitudinal range and basin area vary substantially within each realm, testifying that the database covers a large range of basin sizes in each realm (Table 1). However, we cannot exclude a potential sampling bias between realms, because of limited data availability in some realms.

Total fish species richness per river basin ranged from 1 to more than 1,800 species, with a trend towards higher richness in tropical realms than in temperate realms. Indeed the mean species richness in Afrotropical, Neotropical, and Oriental realms was ca 60 species, whereas it was fewer than 40 species in Palearctic, Nearctic, and Australian realms. These total richness counts were mainly driven by the native species. Non-native species richness, although lower than native richness, varies substantially, ranging between 0 and 63 species per river basin. The mean number of non-native species was higher in the two temperate realms of the Northern hemisphere than in the rest of the world, with, on average more, than four non-native species per basin in the Nearctic and Palearctic realms, and fewer than three species per basin in the other realms. Finally, endemic richness was maximum in tropical realms with, on average, more than five endemic species per river basin in Afrotropical, Neotropical, and Oriental realms, whereas less than one was present per basin in the Palearctic, Nearctic, and Australian realms. Again, more detailed examination of the database reveals large variations between basins, as endemic species richness varies between 0 species (in more than 75% of the basins) to more than 800 species in the Amazon basin.

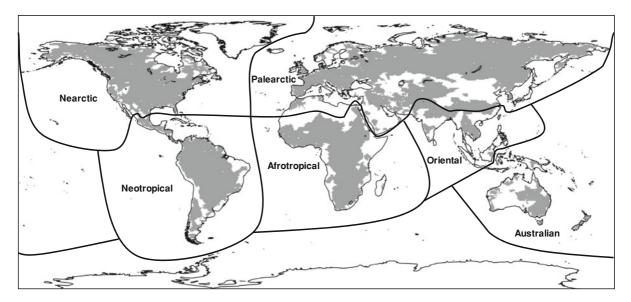


Fig. 1 Map indicating the area covered by the 1,054 river basins considered in the Fish-SPRICH database (grey). Note that some large areas where no basins were investigated correspond to deserts (both cold and hot) where there are no

perennial rivers (e.g. northern Africa, central Australia, polar zones). *Bold lines* indicate realm boundaries according to Lévèque et al. (2008) and Balian et al. (2008)

B realm	N basins	Fish species richness					Total number of species	
		Total	Native		Non-native	Endemic	(Lévèque et al., 2008)	
Afrotropical	108	59.33 (±96.50)	57.88 (±96.19)		1.45 (±2.74)	13.69 (±67.86)	3,272	
Australian	179	17.01 (±12.92)	14.74 (±11.78) 31.52 (±35.32)		2.26 (±2.76)	0.22 (±0.87)	580	
Nearctic	204	37.92 (±40.44)			6.40 (±10.06)	0.84 (±4.00)	1,741	
Neotropical	156	65.55 (±177.52)	64.50 (±	177.84)	1.47 (±2.58)	11.70 (±69.63)	4,231	
Oriental	59	60.10 (±108.99)	57.53 (±	105.11)	2.57 (±4.79)	6.69 (±27.51)	2,948	
Palearctic	348	25.12 (±28.25)	21.09 (±	25.90)	4.02 (±6.12)	0.86 (±8.35)	2,381	
B realm	N basi	ins Environme	Environmental descriptors					
		Altitudinal range		Basin area		Total informed area		% realm area
Afrotropical	108	913 (±7	913 (±740)		14 (±619,387)	18,248,935		97.4
Australian	179	617 (±4	617 (±452)		53 (±121,089)	4,655,187		72.7
Nearctic	204	822 (±8	822 (±815)		93 (±297,085)	15,406,333		91.6
Neotropical	156	1,405 (±1	1,405 (±1,257)		43 (±548,942)	14,826,588		81.5
Oriental	59	1,936 (±1,448)		91,005 (±235,129)		4,641,294		68.9
Palearctic	348	1,008 (±938)		81,764 (±314,701)		27,963,158		70.4

Table 1 Overall content of the Fish-SPRICH database for each of the six biogeographic realms (B realm)

N basins is the number of basins investigated. Values of species richness are mean numbers of species per river basin (\pm SD). The total number of species per realm recorded by Lévèque et al. (2008) is also indicated. Environmental descriptors are mean (\pm SD) altitude range from the source to the estuary, expressed in metres, mean (\pm SD) basin area, and total area covered in square kilometres. The percentage of each realm area covered by river basins contained in the Fish-SPRICH database is given for the total realm surface area after excluding desert and glaciated areas

The Fish-SPRICH data are given as online supplementary material to this article (ESM 2) and is also publicly accessible through the BioFresh data portal (http://www.freshwaterbiodiversity.eu/). The database is hence freely available pending citation of this paper.

Discussion

Although the Fish-SPRICH database contains fish richness values for more than 80% of the earth's continental surface, some geographical discrepancies remain between biogeographic realms. The discrepancy between temperate and tropical regions is well known in ecology (Jackson & Sweeney, 1995; Blanchet et al., 2009), and emphasises the urgent need for more studies in the tropical areas (Tedesco et al., 2005) that host the highest biodiversity but are also facing severe human disturbance (MEA, 2005; Dudgeon et al., 2006).

Despite the potential bias inherent in data availability, the overall richness patterns derived from Fish-SPRICH are consistent with those found in the literature (Lévèque et al., 2008). The average richness was maximum in the Afrotropical, Neotropical, and Oriental realms (ca 60 species per basin), which are known to host the highest fish diversity with 3,000 to 4,500 species per realm (Table 1; Lévèque et al., 2008). In the same way, the average number of species per basin was minimum for the Australian realm (ca 17 species per basin), which also hosts the lowest overall number of species (Table 1; Lévèque et al., 2008). These differences in species richness are explained by different habitat availability, climate, and geographical isolation of realms (Oberdorff et al., 2011). Finally, the average non-native and endemic species richness per basin was also consistent with that found in the literature, with high endemism in tropical regions and a high incidence of invasion in highly anthropised realms (Moyle & Cech, 2004; Lévèque et al., 2008).

Although the Fish-SPRICH database provides an overall realistic image of fish richness patterns throughout the world, potential bias could affect the data. First, the richness per basin given in the Fish-SPRICH data is derived from data published between 1960 and 2008. Recent species descriptions or taxonomic revisions might, hence, affect the number of species. This might, for example, be so for European fish data, where the number of European freshwater fish species varies between 256 (Maitland, 2000) and 546 (Kottelat & Freyhof, 2007) species, depending on the source. This factor of two difference is, however, mainly because of splitting of some widely distributed species into several local species, leading to only slight changes in terms of basin richness. In France, Brosse & Blanchet (unpubl. data) found that richness did not change for most river basins (i.e. the richness difference never exceeded two species). Second, recent fish extirpations or invasions might affect richness patterns. As shown by Villeger et al. (2011), extirpations remain rare compared with invasions. As a consequence, non-native richness would be the most affected by recent non-native species establishment, which in turn would increase the total richness count. To deal with these potential biases, regular updating of the database might be of interest. This could be performed in relation to ongoing international projects and databases on freshwater biodiversity, for example BioFresh (http://www.freshwaterbiodiversity. eu/), FADA (http://fada.biodiversity.be), or FishBase (http://www.fishbase.org). We should, however, be aware that increasing the data collection time span can also introduce bias, because of the high variability of ecological inventory updates across the world. Indeed, richness counts from basins located in developing countries and/or remote areas often arise from single studies that can be updated or cross-checked only with difficulty, because of the lack of recent or confirmatory literature.

Already, the Fish-SPRICH database has enabled us to investigate global patterns of freshwater fish species richness and to quantify the relative importance of basin area, energy, and historical processes in determining fish species richness at the basin grain (Oberdorff et al., 2011). A similar approach revealed spatial patterns and determinants of endemic species richness throughout the world (Tedesco et al., 2012). Focussing on non-native richness also enabled demonstration that human activity, by increasing the rate of species introduction and by disturbing the environment, is the main driver of the establishment of nonnative species throughout the world, thus explaining why economically developed areas host the highest richness in non-native freshwater fish (Leprieur et al., 2008; Blanchet et al., 2009).

Apart from these studies on a global scale, we hope that the Fish-SPRICH database will lead to new research opportunities, for example cross-taxon congruence analysis of global richness patterns. In the same way, the Fish-SPRICH database could be of interest for regional studies on fish diversity, for example biodiversity gradient approaches or species– area investigations. Such macroecological work might have important implications for prediction and mitigation of the consequences of global changes (Kerr et al., 2007). Freshwater ecosystems are currently recognised as the most affected ecosystems on earth (MEA, 2005; Dudgeon et al., 2006), we therefore hope that the Fish-SPRICH data will help to develop global conservation programmes and contribute to largescale aquatic ecosystem management.

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