Research Article

Global and Regional Patterns in Riverine Fish Species Richness: A Review

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We integrate the respective role of global and regional factors driving riverine fish species richness patterns, to develop a synthetic model of potential mechanisms and processes generating these patterns. This framework allows species richness to be broken down into different components specific to each spatial extent and to establish links between these components and the processes involved. This framework should help to answer the questions that are currently being asked by society, including the effects of species invasions, habitat loss, or fragmentation and climate change on freshwater biodiversity.

1. Introduction

The diversity of life, usually referred to as "biodiversity", is not evenly distributed throughout the globe. A considerable proportion is to be found in the tropics, while the poles are only home to a small fraction, and between the two extremes there is a whole diversity gradient. Ecologists, biogeographers, and paleontologists have studied the reasons for these differences, but the question remains open despite the dozens of hypotheses that have been put forward on the subject [1–5]. The present analysis is limited to one important aspect of biodiversity, species richness, which is defined as the number of species present at a given time in a given place. Species richness gradients can be examined across a variety of spatial extents (extent is the geographic separation between the furthest points) and grains (grain is the area of the sampling unit) [6]. But ecologists, who up to

the 90s preferred experimental approaches, mainly focussed on the factors and processes that influence species richness at fine grain sizes and spatial extents (based on published papers in *Ecology* between 1980 and 1986, cited by May [7]). However, it is now recognized that species richness patterns are directly influenced by processes working at much larger scales; that is, regional or even continental [8–12]. This gave birth to macroecology [13, 14], whose aim is to highlight the statistical properties that emerge from complex ecosystems, in order to identify general patterns at different space-time scales of observation, and particularly at the macroscopic scale. If we follow Brown's ([13, page 6]) definition of macroecology: *"it is a non-experimental, statistical investigation of the relationship between the dynamics and interactions of species populations that have typically been studied on small scales by ecologists and the processes of speciation, extinction, and expansion and contraction of*

ranges that have been investigated on much larger scales by biogeographers, paleontologists, and macroevolutionists. It is an effort to introduce simultaneously a geographical and a historical perspective in order to understand more completely the local abundance, distribution, and diversity of species, and to apply an ecological perspective in order to gain insights into the history and composition of regional and continental biotas." In fact, determining which factors and processes are responsible for the variation in species richness patterns is a crucial issue for conservation planning in the face of current and future global and regional anthropogenic impacts [15].

Here, we review patterns and predictors of riverine fish species richness at the drainage basin grain and at global and regional extents. The "freshwater fish" model is particularly well adapted to this type of study since drainage basins are separated from one another by barriers (oceans, or land) that are—for all practical purposes—insurmountable for strictly freshwater fishes, and thus form a kind of insular habitats. Like remote islands, drainage basins are not under equilibrium conditions, as they receive new colonists so rarely that immigration and speciation often occur on similar timescales. This absence of migration between river basins over large temporal scales implies that extinction and speciation processes are specific of each drainage basin [16]. Thus, river basins are, to some extent, independent entities that could be used in comparative analysis to explore the factors that shape overall fish community richness between them. Incidentally, a considerable amount of exploitable data is now available that enables the use of comparative approaches to test the main ecological hypotheses currently under consideration. In this chapter we will use this natural experiment framework to review and discuss the relative role of regional and continental features in determining river drainage basin diversity patterns.

Unless otherwise specified, the term "river drainage basin" will refer to rivers flowing into the ocean (including all their tributaries). For rivers that are part of a bigger drainage basin, the term "tributary" will be used. In this paper we will focus on two grains sizes (i.e., river drainage basin or tributary drainage basin) at two different extents (i.e., global to regional). The term species richness (or species diversity) describes here the total number of species encountered within a river basin or within a tributary.

2. Global Approach to Riverine Fish Species Richness

At the intercontinental scale, three major hypotheses that sum up the majority of different hypotheses proposed (see [3] for a review) have already been tested to explain the variability of riverine fish species richness.

The first, the area hypothesis [17, 18] refers to the existence of a positive relationship between the number of species present in a given area and the size of this area. This relationship has been described by a power function in the form $S = CA^Z$ (where S is the number of species, A is the (surface) area, and C and Z are constants to be fitted) [19, 20]. It suggests that size (the surface of a river drainage basin in the case of riverine fishes) limits the number of species an area can harbor, and, due to its universal application, almost serves as a law in community ecology [21]. Several nonexclusive explanations have been put forward to explain this species-area relationship (Schoener 2010) but three of them are most often invoked: (1) the size-dependent extinction rate [17, 18], (2) the size-dependent speciation rate [22], and (3) the diversity of the habitat [18]. According to the first explanation the probability of extinction of a species increases with a reduction in the size of the "island", due to a decrease in its population size. The second explanation suggests a positive effect of area on speciation rate by exposing species to greater ecological heterogeneity and/or geographical barriers [5]. The third explanation suggests that the heterogeneity of the habitat and the diversity of available food resources increase with the size of the "island" thus offering a large number of available niches and consequently favouring the coexistence of a large number of species [23].

The second hypothesis, the species-energy hypothesis [24, 25] 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 communities of animals and plants [24, 26–36]. 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 rather different processes. Wright [24] considers energy to be a factor that determines resources available for a given biological community and thus as a productivity factor *per se*, whereas Turner et al. [33] and Currie [27], for example, consider energy to be a factor that determines the physiological limits of the species. In the former, one would expect a variable such as net primary production to be an important predictor of species richness whereas in the later, variables linked with temperature or available solar energy would predominate [29].

Finally, the third hypothesis, the historical hypothesis [37], attempts to explain differences in richness gradients by the potential for recolonisation of systems and thus by the degree of maturity achieved since the last major climate change or by the degree of stability in past climatic conditions [38, 39]. This last hypothesis, which combines past environmental conditions with geographic contingencies regulating dispersal possibilities, has been relatively neglected compared to the others. Two main reasons can explain this gap: (i) in essence, past conditions are much more difficult to evaluate and accurately measure than present conditions and (ii) current and past conditions are globally highly correlated.

2.1. The Roles of Area and Energy. In the first global studies conducted in this topic Oberdorff et al. [40] and Guégan et al. [41] used data obtained for 292 drainage basins on 5 different continents to identify the factors responsible for variations in riverine fish species richness within the framework of the three above-mentioned hypotheses. The models resulting from these exploratory analyses tend to show that, at this spatial extent, the factors associated with the first two hypotheses (i.e., the area hypothesis and the species-energy
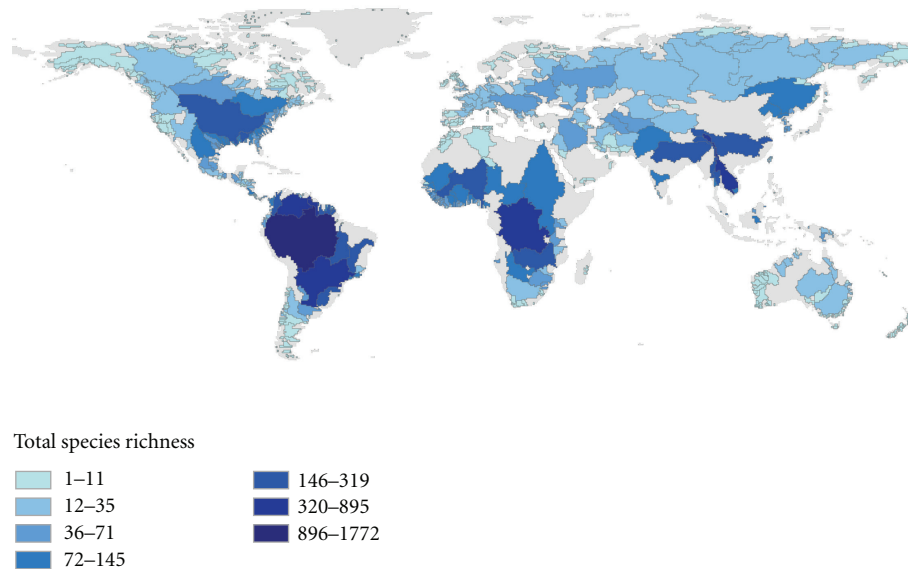
FIGURE 1: Global freshwater fish species richness patterns at the drainage basin grain.

hypothesis) predominate. Only taking into consideration three summary factors, that is, the total surface area of the river drainage basin, the mean flow at the river mouth and the net terrestrial primary productivity within the basin, those models explain between 78 and 93% (depending on the statistical model) of the natural variability of the river basin species richness, the mean annual river discharge explaining the greater part of the variance in species richness.

Based on a comprehensive species richness dataset (Figure 1) recently compiled (926 river basins analyzed, see [42, 43] and the Supplementary Appendix available online at doi: 10.1155/2011/967631 for further details on the database), we performed a spatial autoregressive model (SAR, see [44]) accounting for the spatial configuration of drainage basins. The final model explains 77.1% of the total variation in species richness. Results of this new analysis confirm previous findings concerning the effects of area-related and climate-related variables, but also reveal a significant influence of past climatic changes and geographic isolation of drainage basins on species richness patterns (see Table 1 and Figure 2). These historical effects have also been revealed in previous regional analyses (see [45–48] although on a different spatial grain) but, regarding freshwater fish, this is the first time that the effect of past climatic variability (from glacial periods of the Pleistocene to present day) on species richness patterns is detected at the global scale (but see [39] for an effect of climatic variability on beta diversity).

With respect to the area hypothesis, these results confirm those of several previous studies carried out at the regional scale that identified the size of the river drainage basin and/or the mean flow at the river mouth as important predictors of river basin species richness [46, 52–56]. Furthermore, according to our SAR model, habitat diversity still plays a significant role in explaining richness gradients after accounting for drainage area (Table 1). However these results do not fully answer the questions following from the area

hypothesis, that is, are species richness patterns due to area-dependant rates of extinction and/or speciation, or to an increase in habitat diversity, or both?

With respect to the species-energy hypothesis, the results obtained by Oberdorff et al. [40] and Guégan et al. [41] tend to favour the hypothesis of an effect of energy on richness through an increase in available resources for the species. (Net Primary Productivity is an important predictors of species richness.) However, a difficulty in discussing further this last result is that these authors used estimates of terrestrial primary productivity from Lieth's models [57] instead of real aquatic primary productivity (data not available). Even if considering that terrestrial productivity gives a correct estimation of aquatic productivity (as food webs supporting fish are largely based on allochthonous inputs), using estimates of terrestrial primary productivity probably under-estimates true aquatic productivity (see [58] for a review). However, our SAR model also gives support to an indirect effect of energy through species physiological limits (positive effect of variables linked with temperature in the model, see Table 1).

The species-energy theory as developed by Wright et al. [25] posits a positive link between species richness and energy availability [59]. However, in plant and animal communities, a variety of patterns in species richness have been observed over productivity gradients, including positive, negative, and unimodal relationships [60–63]. It is not clear yet why richness shows these (apparently) contradictory relationships with productivity even if some explanations have already been proposed. For example, it has been suggested that all these noted relationships may just be incomplete segments of an overall hump-shaped, unimodal relationship over a broader range of productivity. Nevertheless, evidence for this possibility is currently limited at best [60, 63]. Results from Oberdorff et al. [40], Guégan et al. [41], and our SAR model support the view of

Table 1: Results from a spatial autoregressive model (SAR) relating species richness to environmental, climatic, and historical variables. Spatial analysis was performed with *R* statistical package [49] and *spdep* library [50] (see the Supplementary Appendix for further explanations). The spatial structure was implemented by a neighbourhood matrix of the drainage basins (see [46] and the Supplementary Appendix for further explanations) and assuming that the autoregressive process occurs in the error term (i.e., the "spatial error model" described by Dormann et al. [44]). Further methodological details on species richness, environmental variables computing, and modelling procedure are available in the Supplementary Appendix. Habitat heterogeneity was estimated by applying Shannon's diversity index to proportions of biomes (i.e., vegetation types associated with regional variations in climate) within drainage basins. Temperature anomaly represents the Quaternary climate variability measured as the change in mean annual temperature between the present and the Last Glacial Maximum (LGM, circa 21 thousand years ago). Following Oberdorff et al. [51] we also considered whether or not a drainage basin was on a land mass, a peninsula, or an island (LPI; continental mass = 0; peninsula = 1; island = 2). All other variables are fully explained in the Supplementary Appendix. The Moran's *I* value represents the remaining autocorrelation on the residuals of the model for the first distance class, that is, neighbour drainages (the values for the remaining distance classes are also nonsignificant).

Related hypothesis	Variable	Standardized estimates	Standard error	z value	P-value
Habitat size and diversity	Drainage area	0.548	0.032	17.123	<.0001
	Habitat heterogeneity	0.188	0.031	6.012	<.0001
	Altitudinal range	−0.208	0.194	−1.069	n.s.
	Altitudinal range^2	0.130	0.200	0.649	n.s.
	Runoff	0.784	0.091	8.628	<.0001
	Runoff^2	−0.761	0.098	−7.797	<.0001
Historical climatic stability and geographic isolation	Temperature anomaly	0.559	0.147	3.815	<.0001
	Temperature anomaly^2	−0.37	0.130	−2.857	.0043
	Land-Peninsula-Island (LPI)	−0.257	0.041	−6.349	<.0001
Climate/energy	Actual Evapotranspiration	0.073	0.049	1.493	n.s.
	Precipitation	0.376	0.058	6.464	<.0001
	Temperature	0.778	0.085	9.209	<.0001
	Temperature^2	0.195	0.047	4.176	<.0001
	Precipitation seasonality	0.009	0.040	0.227	n.s.
pseudo R^2		0.771			
AIC		1851.4			
Moran's I		0.0046			n.s.

a monotonically increase of riverine fish species richness with increasing productivity at the global scale (Figure 2).

At this spatial scale, the only direct historical factor significantly acting on species richness was past climatic variability (see Figure 2 and results of the SAR model in Table 1). It is thus tempting to conclude that history is a minor driver of diversity at the global scale. However we should keep in mind that all the variables used in the SAR model are interrelated to some extent and difficult to separate. This can be visualized in Figure 3, where the explained variance of a linear regression has been partitioned into three different groups of factors related to the area, energy and historical hypotheses. Currie [27], referring to land animals, put forward an explanation for the absence of influence of history on contemporary diversity patterns: that historical factors only influence species richness over relatively short periods, that is, less than the period of time since the last glacial maximum. Nevertheless this explanation seems inappropriate for riverine fishes. In their case, community saturation should be more difficult to reach than for land animals in the sense that their colonization depends on potential connections between river drainage

basins. It is thus logical to expect that the influence of historical events should still be detectable in riverine fish communities at the global scale and that the weak influence of this driver most often noticed comes preliminary from difficulties in defining the appropriate variables.

2.2. The Role of History. It is not always simple to separate effects linked to history from those linked to current environmental factors, but comparisons between similar environments in different regions could address variation in speciation and extinction caused by different history [66]. In order to highlight the potential influence of historical factors on species richness, Oberdorff et al. [65] studied rivers on two different continents, North America and Western Europe, which have comparable climatic and environmental characteristics but a rather different history (Figure 4). After having initially identified the main ecological factors responsible for variations in species richness on the two continents (i.e., factors related to river size, productivity, and climate), the second phase of the study integrated in the model factors presumed to reflect historical events (i.e., distance from the larger refugial area and surface area of
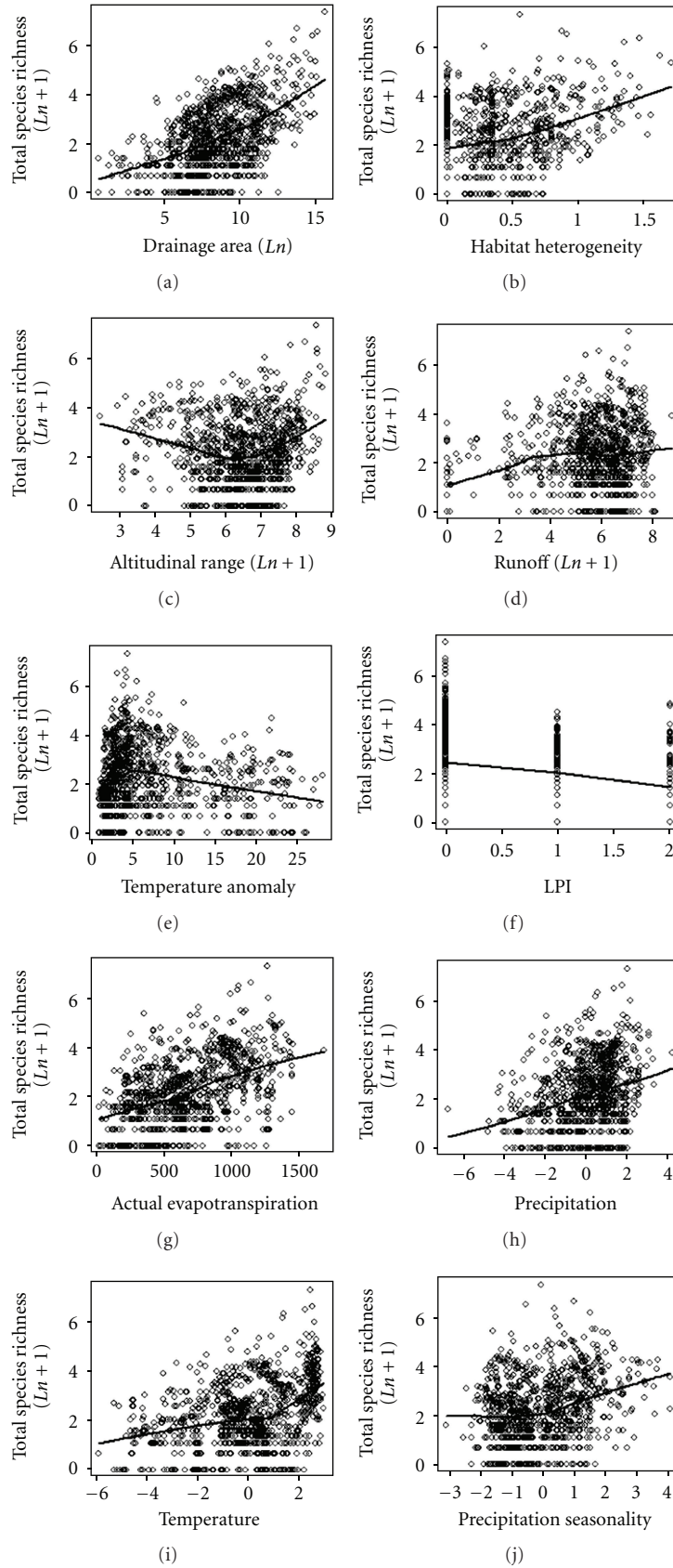
FIGURE 2: Fish species richness for each river basin as a function of drainage area (a), habitat heterogeneity (b), altitudinal range (c), runoff (d), temperature anomaly (e), LPI (Land-Peninsula-Island) (f), actual evapotranspiration (g), precipitation (h), temperature (i), and precipitation seasonality (j). See Table 1 for variables description.
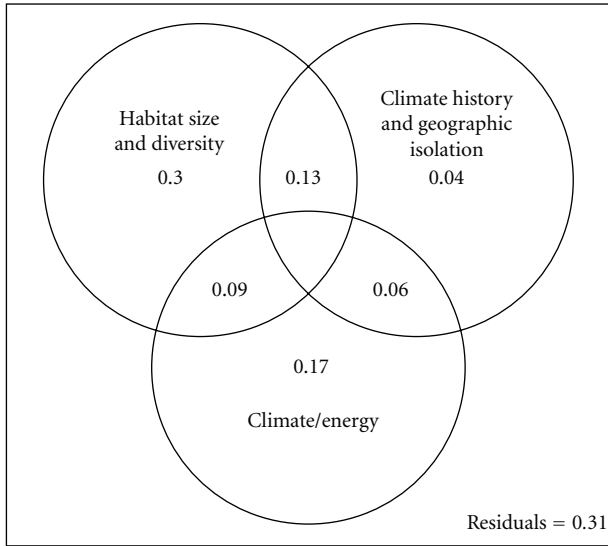
FIGURE 3: Variance partitioning in explaining species richness gradients between area-related, climate-related, and historical variables. The analysis was performed using the "varpart" function from the *vegan* R package [64] and grouping variables as in Table 1.
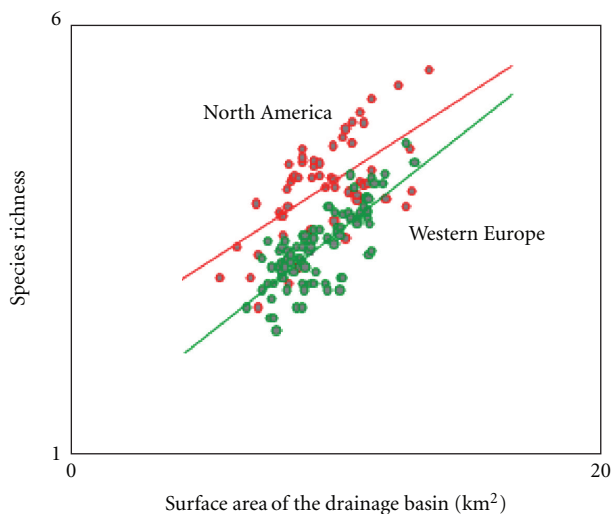

FIGURE 4: Plot of fish species richness as a function of the surface area of drainage basins for West European and North American rivers. Variables expressed in logarithmic values (Ln): redrawn from Oberdorff et al. [65].

drainage basin covered by the ice sheet during the last Pleistocene glaciation) in order to examine their relative contribution in explaining species richness gradients.

Results showed that ecological factors (particularly the size of the river and to a lesser extent available energy) explain a large part of variations in species richness between the two continents, while one historical factor (distance from the larger refugial area) appears to be more marginal though significant, while the other (surface area of drainage basin covered by the ice sheet during the last Pleistocene glaciation) is invariably rejected. These results thus seem to

agree with conclusions reached at the global scale, suggesting a marginal role of history in driving contemporary diversity patterns. This is rather surprising if one accepts the low dispersion capacity generally attributed to fish communities. A preliminary explanation is that the most northern regions of Western Europe and North America are mainly populated with euryhaline species that could have rapidly recolonised rivers via coastal fringes. At the same time, the fact that a "continental" effect is highly significant in the final model leads to think that other historical factors not taken into account in the study are perhaps involved in differences between rivers on the two continents, like, for example, differences in the process of speciation which seem to occur more often in North American refuge zones [67]. In fact, some North American genera such as *Notropis* have radiated at a rate not encountered in any of the European genus [67]. If speciation rate is assumed to be inversely related to body size [68], a low speciation rate is also suggested by body size distribution of European fish with dominance of medium and large species, conversely to North America were small fish predominate [67, 69, 70]. A complex array of factors is probably involved in this pattern, but speciation events seem to have occurred more frequently in North American refugial areas than in West European ones [67]. Moreover, the data analysed by Oberdorff et al. [65] also show that after river size and net primary productivity have been factored out, North American rivers are still 1.7 times as rich as European ones.

Consistent with this, other recent studies trying to evaluate the role of history in shaping riverine fish diversity patterns at regional and intercontinental scales found a significant influence of history in forging riverine species richness patterns [45–48]. For example, Tedesco et al. [46] have analyzed the effect of rain forest refuges at the last glacial maximum (LGM) on tropical freshwater fish diversity patterns in three different regions, that is, Tropical South America, Central America, and West Africa. At the end of the most recent glacial period (Last Glacial Maximum, LGM; 18,000 years BP), while ice sheets in the Northern Hemisphere extended from the Arctic southward to cover most of North America and central Asia to approximately 45°N latitude, African, and Amazonian rain forests contracted in response to glacial aridity [71]. Following this scenario, in the Northern Hemisphere, high fish species extinctions should have occurred in the rivers totally or partially glaciated, while few extinctions should have occurred in the few refuge zones representing remnants of preglaciation habitats. At the same time, in the tropical zone of the Southern Hemisphere, overall reduced precipitation should have led to high extinction rates in river basins affected by the drought (through a decrease in river basins discharge and active surface area), and few or no extinctions in river basins having kept their characteristic natural (e.g., precipitation patterns and vegetation conditions). Indeed, Tedesco et al. [46] found that both river drainage area and contact (or absence of contact) with LGM rain forest refuges explained the greatest proportions of variance in the geographical pattern of riverine species richness. In the three examined regions, highest richness was found in drainages that were connected to the rain forest refuges (Figure 5). However, they
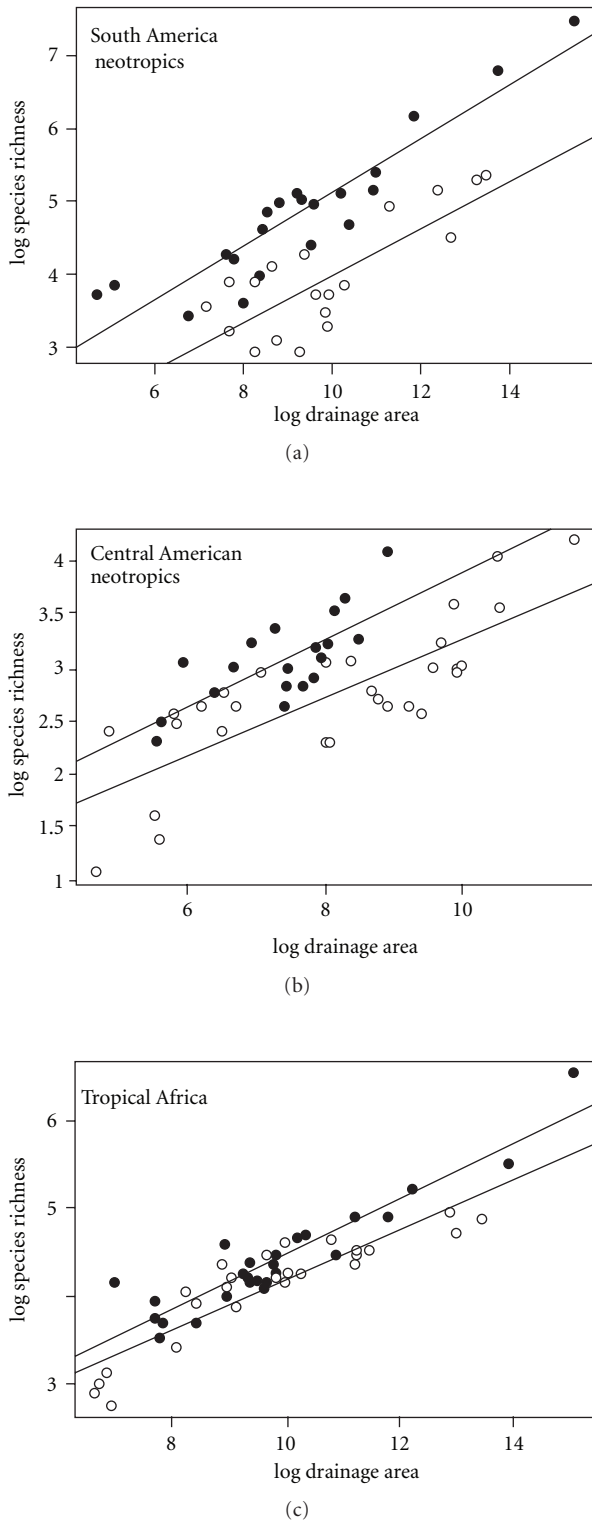
(a)

(b)

(c)

Figure 5: Plot of species richness as a function of total surface area of the drainage for river basins from tropical South America, Central America and tropical Africa. Black circles represent the basins that were in contact with a rain forest refuge zone during the LGM; white circles represent basins completely isolated from rain forest refuges. Lines correspond to simple linear regressions for each group. Variables are expressed in logarithmic values (Ln): redrawn from Tedesco et al. [46].

also found that, at the continental scale, South American rivers were more species rich than their African and Central American counterparts, respectively. Therefore, a historical signal seems to persist even when the regional historical effect (climate at the LGM) has already been accounted for. These results suggest that from the LGM to the present day (a time scale of 18,000 years), extinction processes should have played a predominant role in shaping the current diversity pattern. By contrast, the continental effects could reflect historical contingencies explained by differences in speciation and extinction rates between continents at larger time scales (millions of years). Despite these few studies, the role of historical processes in shaping present-day distribution patterns of diversity is still the subject of considerable debate, stressing the difficulties of testing historical processes based on current species distributions. More refined tests of historical factors involving intercontinental comparisons are needed to better assess the relative importance of ecological and historical processes in shaping contemporary diversity patterns. In this context, endemic species have always been fascinating because they should reflect the roles of speciation, extinction, and dispersal ultimately responsible for their restricted geographic distribution. They are then good candidates for analysing the role of historical processes in present-day distribution patterns of diversity.

3. Regional Approach to Riverine Fish Species Richness

Changing the spatial extent we now consider variations in richness in rivers and tributaries of comparable size that flow in the same biogeographical region. In other words, we will now control for the effects highlighted at the intercontinental scale (i.e., energy and history) and focus on factors that intervene at this regional scale. Two main explanations can be put forward to explain differences in species-area relationships at this scale: (1) the area-dependent extinction rates hypothesis and (2) the habitat diversity hypothesis. In order to distinguish effects specific to each hypothesis, Hugueny [54] proposed considering two types of rivers: tributaries, which can be freely colonized by species present throughout the basin and completely isolated river drainage basins. According to the hypothesis of size-dependent extinction rates, tributaries should harbor overall a higher number of species than river drainage basins of similar size, since the immigration rate of the former is higher than zero while the immigration rate of the later is actually zero. Conversely, according to the hypothesis of habitat diversity, the same number of species is to be expected in both categories (tributaries and river drainage basins) as long as they are of comparable size. In order to test the hypothesis of the size-dependent extinction rate Hugueny [54] and Belkessam et al. [72] compared the species richness of river drainage basins and tributaries of similar size within bio-geographical regions (West Africa and North-west France, resp.). The results of these comparisons showed that species richness of river drainage basins was overall lower than that of tributaries of comparable size (Figure 6). These results thus suggest that regional species richness is regulated in part by
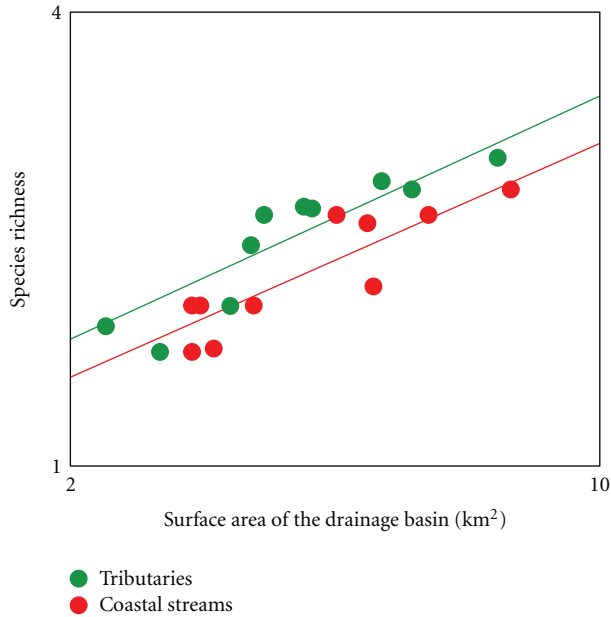
FIGURE 6: Relationship between species richness and total surface area of the drainage basin for tributaries and coastal rivers of North-Western France: redrawn from Belkessam et al. [72].

processes of extinction and immigration and that *a priori*, the threshold of species richness is not only determined by habitat diversity. Two other studies analysing colonisation patterns of introduced species in several watersheds of North America supported these previous results [73, 74]. These studies show that fish communities are not saturated and are thus capable of achieving higher species richness if the pool of potential colonisers is artificially increased by the introduction of other species. Another study of freshwater fish communities brought into contact by the opening of the Panama Canal in 1914 also supports this view. Smith et al. [75] analyzed data on communities from Caribbean and Pacific river basins sampled in 1911 and 2002. Numerous species migrated through the canal and have reached similar relative abundances in their new basin. Furthermore, it appears that no species has gone extinct, hence increasing species richness in both basins. The authors concluded that the communities were unsaturated and that community composition and richness were not regulated by interspecific competition at least over ecological time scales (10–100 generations), but rather by regional processes of dispersal.

4. Concluding Remarks and Future Directions

At this stage, by synthesizing results presented above, we can develop a preliminary integrated framework that provides a potential mechanistic explanation for riverine fish species richness patterns at the global scale (Figure 7). Although each one of the processes involved in the framework outlined in Figure 7 still needs to be refined, it may be helpful in predicting how current and future changes should alter species richness patterns at large spatial scales. Invasion of exotic species, habitat loss and fragmentation and global climate

change held to be the primary causes of endangerment to riverine fish species [76]. Below we focus on how the results detailed in this paper could help us to forecast the consequences of these changes on fish species richness.

4.1. Introduction of Exotic Species. Knowledge of the degree of saturation of a community provides an important basis for understanding how the community reacts or will react to the introduction of new species. In this context, understanding to what extent freshwater fish introductions have long-term consequences for biodiversity is crucial to the adoption of sound and effective conservation strategies. As previously said, for strictly freshwater fishes, river basins (flowing into the ocean) can be considered as nonequilibrated islands in which species extinctions (related to historical events) are not fully balanced by colonization from neighbouring river basins [16, 46, 54, 72]. The implication is that river basins are very likely to be unsaturated with species and thus more susceptible to the establishment of nonnative species because ecological space should be less densely packed and interspecific competition should be less intense [75]. An implication is that species introductions might have impacts on fish communities that are smaller than would be expected if the saturation point had already been reached [42, 43, 77, 78].

4.2. Fish Species Facing Habitat Loss and Fragmentation. Habitat loss and fragmentation is one of the greatest threats to biodiversity worldwide, and this certainly holds true for riverine fishes. One of the conclusions of the present paper is that extinction processes are quite important in setting contemporary riverine fish species richness. It is thus almost certain that disturbances, generated for example by dams, weirs, reservoirs for water supply, diversion for irrigation and industrial purposes (creating physical barriers blocking normal migrations and movements of the biota or decreasing habitat availability), flow modification, industrial pollution, and eutrophication, all creating direct or indirect decreases in habitat availability, will endanger or extinguish many freshwater fish species in the future. The global scale models described above, by including factors related to the size of the river basin (i.e., surface area of the drainage basin, river discharge) could be of use to predict patterns of extinction due to this type of disturbance. Nevertheless, we should keep in mind that there is an important time lag between habitat loss and species loss [79, 80]. For example, Morita and Yamamoto [81] have estimated that the probability of extinction of a salmonid species (*Salvelinus leucomaensis*) in an isolated stream basin of 1 km^2 is equal to 0.8 after 50 years and is equal to 0.1 for an isolated stream basin of 10 km^2 for the same time lag. That means that the processes involved are rather slow, even for small rivers. This fact will be further discussed in the next paragraph.

4.3. Future Richness Patterns under Global Climate Changes. Changes in global climate are expected in the twenty first century. At this point it is difficult to make precise predictions about how these changes will affect rivers. The changes may be varied and large, involving diverse characteristics as
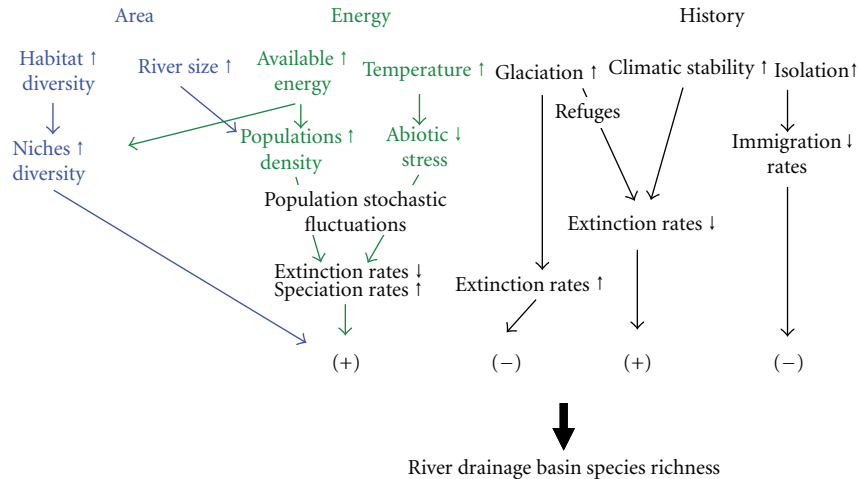
FIGURE 7: Potential causal pathways between environmental factors and processes affecting positively (+) or negatively (−) the species richness of a river basin.

temperature, hydrology, and water level (through changes in rainfall patterns) and consequently productivity within the systems. The long-term effects of such changes are largely a matter of speculation but by combining results obtained by computer-driven General Circulation Models (GCMs) and global models detailed here, a gross estimation of the potential effects of global warming on river basin species richness could be realised. For example, Xenopoulos et al. [82] and Xenopoulos and Lodge [83] have developed global scenarios of future losses in river discharge from climate change and have applied these results to known relationships between fish species and discharge to build gross scenarios of losses of riverine fish richness at global and regional scales. In rivers with hypothesized reduced discharge (about 30% of the world rivers), these authors predicted fish losses up to 75%. However, this species-discharge-based model only projects the fraction of species "committed to extinction", primarily resulting from decreases in river flow. While such extrapolations are useful for assessing rivers vulnerability to climate change, the lag time between being "committed to extinction" and actually going extinct may range from decades to many millennia suggesting that the realized extinction rates, at a given time, are likely to be lower and perhaps much lower than the projected species "committed to extinction" percentages [84]. New approaches quantifying real extinction rates (i.e., the number of extinctions divided by the time over which extinctions occurred) are now critically needed to start organizing sound-effective remedial conservation actions. In this sense, a promising way is the use of empirical relationships established from historical data (prehuman) between species extinction rates and area of occupancy (extinction-area relationships) to predict true extinction rates (integrating the time lags to extinction) due to future habitat loss. Hugueny et al. [85] provided an empirical extinction-area relationship for riverine fishes by (i) estimating population extinction rates since the fragmentation of paleorivers due to sea level rise at the end of the Pleistocene and (ii) by combining this information with

rates estimated using population surveys and fossil records. The use of this empirical extinction-area relationship (EAR) to project riverine fish extirpation rates under future global climate change may be a future fruitful approach.
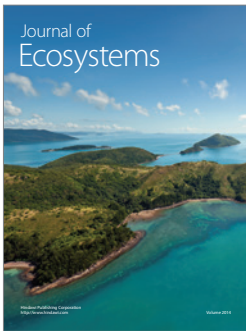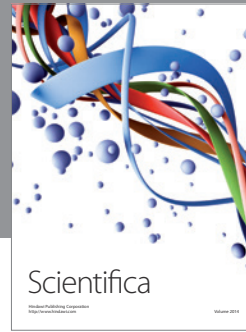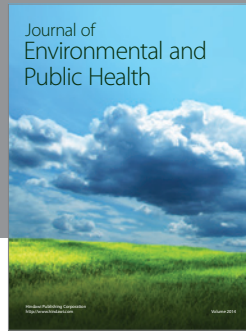
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