

REPORT

Patterns of endemism in riverine fish of the Northern Hemisphere

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Abstract

Loss of endemic species represents a symptom of general degrading ecosystem conditions that is the indirect result of biodiversity alteration. Here, we developed a predictive model relating species richness of endemic riverine fishes to measured biological, climatic, and historical variables using data from 118 rivers distributed all over the Northern Hemisphere. In a minimally adequate multiple general least square model, total riverine fish species richness, historical biogeography (Pleistocene glaciations), and contemporary climate accounted for 63% of the variability in endemic species richness; the strongest correlate being riverine fish species richness. Our findings suggest that (i) endemism and richness patterns are generally similar (fish diversity “hot-spots” areas sustain higher endemic species richness); (ii) glaciation in the Pleistocene have had a significant negative influence on endemic species richness in the more septentrional areas; and (iii) certain basins situated in desertic areas (subtropical dry-zone of deserts) have unusually high numbers of endemics. These last areas should not be overshadowed when setting conservation priorities.

Keywords

Climate, endemic richness, historical biogeography, Northern Hemisphere, riverine fishes, species richness

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INTRODUCTION

The accelerating rate of extinction of plants and animals due to anthropogenic loss or severe alteration of ecosystems is a world-wide crisis (Moyle & Yoshiyama 1994). The problem is particularly severe in freshwater habitats, which concentrate 25% of global vertebrate biodiversity (e.g. freshwater fishes) and are among the world's most threatened ecosystems (Groombridge 1992; Stiassny 1996; Myers 1997).

The effort to preserve this biodiversity is necessarily based on the comprehensive understanding of patterns of species richness on large scales (Oberdorff *et al.* 1995; Guégan *et al.* 1998). However, to develop conservation and management policies that ensure the preservation of biodiversity, we also need information about patterns of endemism (Pimm *et al.* 1995; Reid 1998).

Patterns of fish species richness in rivers at the global scale have previously been examined by addressing three of the most widely held hypotheses in community ecology: the species–area hypothesis (Preston 1962), in which species richness increases as a power function of surface area; the species–energy hypothesis (Wright 1983),

which predicts that species richness correlates with energy availability; and the historical hypothesis (Whittaker 1977), which explains richness gradients, on a global scale, by patterns of recolonization and maturation of ecosystems after glaciation. Factors related to components of river size (surface area and flow regime) and energy availability (net primary productivity) are essential for predicting fish diversity, whereas the role of other factors (e.g. contemporary climate and/or history) are of marginal importance (Oberdorff *et al.* 1995, 1997; Guégan *et al.* 1998).

We examine, here, the extent to which patterns of endemism in Northern Hemisphere rivers parallel patterns in overall species richness. Two questions are of prime importance in this approach: (i) when compared with more widespread species, are endemics a random subset of the biota with regard to abiotic and biotic factors?; and (ii) if not, what factors influence the degree of endemism? To answer these questions, we first assemble from published literature current information on total species richness, endemic species richness, and a range of ecological factors on 118 rivers distributed throughout the Northern Hemisphere. In a second step, we investigate the relationship between endemic species number and these



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explanatory variables in order to understand causes and patterns of endemism. We end by discussing predictions suggested by the results of our investigation.

MATERIALS AND METHODS

We used data from 118 rivers located as follows: 42 in Africa (36%), 47 in Europe (40%), 18 in North and Central America (15%), and 11 in Asia (9%); 38 rivers between 0° and 10° of latitude (32%), seven between 11° and 20° (6%), four between 21° and 30° (3%), 18 between 31° and 40° (15%), 33 between 41° and 50° (28%), 13 between 51° and 60° (11%), and five between 61° and 70° (4%).

As levels of endemism may be influenced by the same processes as overall species richness, we used the explanatory variables investigated in previous work dealing with global patterns of riverine fish species richness (Oberdorff *et al.* 1995, 1997; Guégan *et al.* 1998).

For each river, we determined the following variables.

Total species richness (TSR)

Endemism may be expressed as a percentage of all fish species present or as the absolute number of endemics in a river basin. The percentage approach emphasizes the generality of endemism in a biota, regardless of the total number of endemics. Counts of endemics become most significant when total richness and propensity for endemism are high (Hawksworth & Kalin-Arroyo 1995). To take into account both measurements, we introduced the total species richness in each basin as an explanatory variable in our model. Values for total species richness refer to the total number of riverine fish species collected from the entire drainage basin, which corresponds to the current community richness per river. We selected the most recent references and adjusted species numbers to account for extinction and introduction wherever possible. Only riverine fish species were included in the analyses, secondary or migratory euryhaline fishes being systematically withdrawn. Values for total riverine fish species richness were compiled from the literature (see Oberdorff *et al.* 1995 for details).

Endemic species richness (ESR)

Values for endemic species richness were compiled from the literature and refer to the total number of endemic fish species collected from the entire drainage basin (Appendix). Given the inconsistent use of the term endemism (Kruckberg & Rabinowitz 1985; Anderson 1994), the concept has become a relative one, and the endemic status of organisms can have varying biological significance depending on the size of the geographical area under consideration. Riverine fishes constitute an excellent group for defining unambiguously the units of measurement (i.e. the term

endemic for a species and the spatial scale considered) because of the insular nature of rivers for these organisms. Endemic species are therefore defined as those species inhabiting only one drainage basin (narrow endemic).

Total surface area of the drainage basin (km²) (SAD)

Values for this variable were compiled from literature or measured with a digital planimeter on 1:1,000,000 scale maps.

Mean latitude of river (degree and minutes) (LAT)

The values for mean latitude are for the centre of each river basin (weighted by the length of river reaches at various latitudes).

Net primary productivity (kg⁻²y⁻¹) (NPP)

As net aquatic primary productivity data were not available for the rivers, we used mean annual air temperature and mean annual rainfall to estimate average values of terrestrial primary productivity from Lieth's (1975) models (see Oberdorff *et al.* 1995 for details).

Climatic zones (CLZ)

The climatic zone assigned to each river corresponds to the largest climatic area drained by the river. The rivers studied fall into the following zones (MacNally *et al.* 1982): zone I, the equatorial zone with very high annual precipitation (36 rivers); zone II, the tropical summer-rainfall zone with heavy rains in the summer and extreme drought during the cooler season (19 rivers); zone III, the subtropical dry-zone of deserts with very low rainfall (seven rivers); zone IV, the Mediterranean transition zone with winter rainfall (15 rivers); zone V, the warm-temperate climate zone with high humidity in summer (two rivers); zone VI, the temperate climate zone with moderate humidity (28 rivers); zone VII, the arid temperate climate zone of continental regions with low rainfall (two rivers); and zone VIII, the cold-temperate or boreal climate zone with high precipitation (14 rivers). Climatic zones were entered in multiple-regression analyses as dummy (qualitative) variables.

Drainage basin covered by glaciers during the last Pleistocene glaciation (GLA)

This variable considers whether or not a river basin has been glaciated or not during the Pleistocene (uncovered = 0; partially or totally covered = 1; entered in multiple-regression analyses as dummy variables).

Land mass, peninsula, or island (LPI)

We considered whether or not a river drainage was on a land mass, a peninsula, or an island (continental mass = 0; peninsula = 1; island = 2; entered in multiple-regression analyses as dummy variables), postulating that for

peninsulas or islands, colonization rates should be sufficiently low to favour the formation of endemic populations (Case & Cody 1987).

Continent (CON)

Each river was assigned to one of the following land masses: Africa, North and Central America, Europe, and Asia (entered as dummy variables).

All variables (except dummy variables and mean latitude) were log-transformed in order to minimize effects of non-normality.

In a first step, we performed simple regression analyses of endemic species richness on the explanatory variables listed above (except dummy variables) and checked for evidence of curvilinearities. The only variable showing evidence of curvilinearity was mean latitude. We thus incorporate the quadratic term LAT^2 into the regression. Correlation analysis showed reasonable independence of explanatory variables ($r < 0.65$ for all combinations). In a second step, we used stepwise multiple regressions (both forward and backward procedures) to distinguish the relative effects of total species richness and of ecological and historical factors on endemic species richness. Firstly we determined the contribution of the independent ecological and historical variables to the between-river variation in total species richness. Secondly, we analysed the contribution of the different independent variables (included total species richness) to the between-river variation in endemic species richness. With this procedure factors acting on total species richness can be separated from factors specifically acting on endemic species richness. At each iteration, the variable showing the highest partial correlation with the dependent variable was included into the model only if its correlation was significant at the 5% level. When no variable could be added to the model, the procedure was finished.

All statistical analyses were performed using Systat 5 version 5.2.1., Evanston, IL for the Macintosh (Wilkinson *et al.* 1992).

RESULTS

The simple regression models show that total species richness is the strongest significant predictor of the number of endemic species (Fig. 1), followed by total surface area of the drainage, mean latitude (curvilinear relationship), and net primary productivity (Table 1). Two distinct models are generated by stepwise multiple regression procedures. Model A analyses total species richness as a function of the different independent ecological and historical variables (Table 2). Using this approach, surface area of the drainage, net primary productivity, climatic zones, and continent together

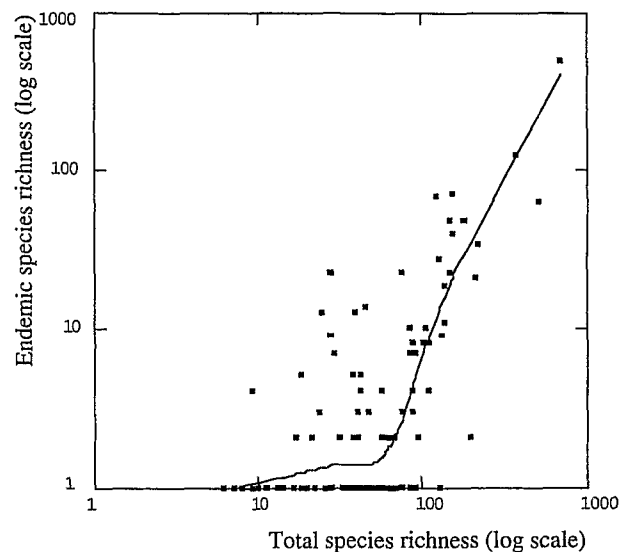


Figure 1 Log-log plot of endemic riverine fish species richness (ESR) as a function of total riverine fish species richness (TSR) for 118 river basins of the Northern Hemisphere. Line is fit using the lowest method for local regression (Cleveland 1979).

Table 1 Simple regression coefficients between endemic riverine fish species richness (log scale) and eight independent ecological and historical variables ($n = 118$)

Variables	r	P
TSR (log scale)	0.652	<0.001***
SAD (log scale)	0.465	<0.001***
NPP (log scale)	0.230	<0.05*
LAT	0.391	<0.001***
LPI (dummy variable)		<0.001***
CLZ (dummy variable)		<0.001***
GLA (dummy variable)		<0.01**
CON (dummy variable)		<0.05*

TSR, total species richness; ESR, endemic species richness; SAD, total surface area of the drainage basin; NPP, net primary productivity; LAT, mean latitude of river; GLA, drainage basin covered by glaciers during the last Pleistocene glaciation; LPI, land mass, peninsula, or island; CLZ, climatic zones; CON, continent (land mass).

explain 86% of the total variability in total species richness. In model B, where endemic species richness is the dependent variable and total species richness one of the independent variables, only total species richness, climatic zones, and drainage basin area covered by glaciers during the last glaciation emerge as significant terms after backward or forward elimination (Table 3). These three independent factors together explain 63% of the total variability in endemic species richness, total species richness explaining the most part of the variation (standart coefficient 0.709, $P < 0.001$). These results demonstrate

Table 2 Summary of stepwise multiple regression analysis of total species richness (log scale) versus the ecological and historical descriptors listed in Table 1. Also given are the slope coefficients, the standard coefficients, and the probability associated with the partial-F of individual terms entered into the model

MODEL A		Variables		
Intercept	Slope coefficient	Standardized regression coefficient	P	
log (SAD)	0.320	0.833	0.0001	
log (NPP)	0.669	0.334	0.0010	
CLZ	-	-	0.0001	
CONT	-	-	0.0300	

Missing entries indicate that the coefficients were not significant ($P > 0.05$). Forward and backward multiple regressions yielded similar results. Final model was highly significant ($R^2 = 0.866$, $P < 0.001$, $N = 118$).

Table 3 Summary of stepwise multiple regression analysis of endemic species richness (log scale) versus the ecological and historical descriptors listed in Table 1 plus total species richness. Also given are the slope coefficients, the standard coefficients, and the probability associated with the partial-F of individual terms entered into the model

MODEL B		Variables		
Intercept	Slope coefficient	Standardized regression coefficient	P	
log (TSR)	1.020	0.709	0.0001	
CLZ	-	-	0.0001	
GLA	-	-	0.0060	

Missing entries indicate that the coefficients were not significant ($P > 0.05$). Forward and backward multiple regressions yielded similar results. Final model was highly significant ($R^2 = 0.633$, $P < 0.001$, $N = 118$).

that much of the variability in endemic species richness seems to be related to changes in total species richness.

To visualize the effect of the eight climatic zones on endemic species richness, we plot residuals of model B (after removing the variable climatic zones) against categories of climatic zones (Fig. 2A). Student's *t*-tests show that the model underestimates endemic species richness for climatic zone III (i.e. the subtropical dry-zone of deserts with very low rainfall) ($P < 0.001$) and overestimates endemic species richness for climatic zone I (i.e. the equatorial zone with very high annual precipitation) ($P < 0.05$).

To visualize the effect of glaciation on endemic species richness, we plot residuals of endemic species richness versus total species richness and climatic zones against categories of drainage basin area covered (or not) by glaciers during the last glaciation (Fig. 2B). Student's *t*-

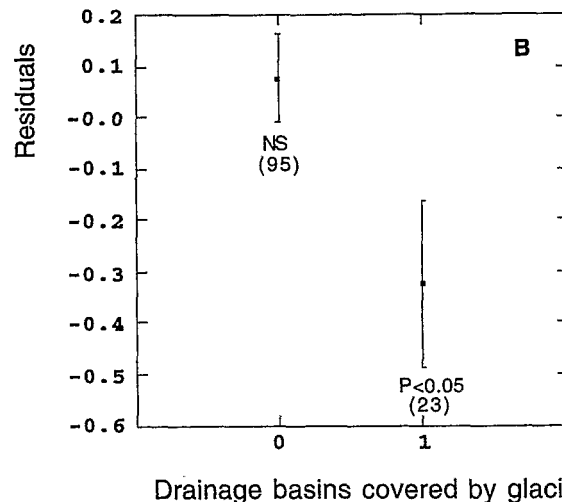
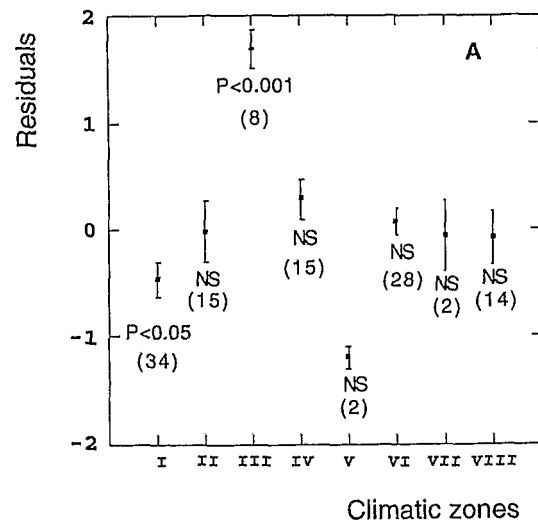


Figure 2 (A) Residuals from multiple regression of endemic species richness (ESR) as a function of total species richness (TSR) and drainage basin covered by glaciers during the last Pleistocene glaciation (GLA) plotted against climatic zones (CLZ). The model underestimates endemic species richness for climatic zone III (deserts) and overestimates endemic species richness for climatic zone I (equatorial zone). (B) Residuals from multiple regression of endemic species richness as a function of total species richness and climatic zones plotted against drainage basin covered (or not) by glaciers during the last Pleistocene glaciation. The model overestimates endemic species richness for partially or totally glaciated zones.

tests show that the model overestimates ESR for partially or totally glaciated area ($P < 0.05$).

DISCUSSION

As shown by Fig. 3, diversity *per se* and endemism are influenced by somewhat different factors, such that the

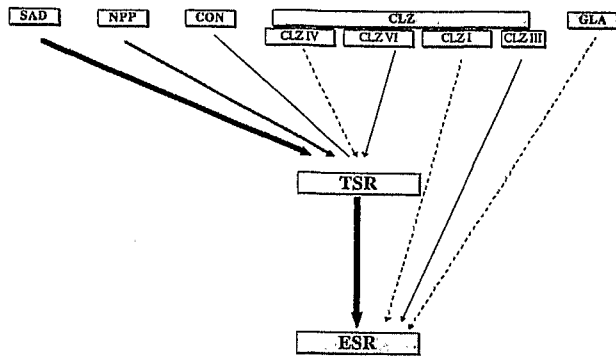


Figure 3 Diagram of the determinants of variation in total species richness (TSR) and in endemic species richness (ESR). Solid lines indicate positive effects and dashed lines indicate negative effects. The width of the line represents the magnitude of the effect. TSR, total species richness; ESR, endemic species richness; SAD, total surface area of the drainage basin; NPP, net primary productivity; LAT, mean latitude of river; GLA, drainage basin covered by glaciers during the last Pleistocene glaciation; LPI, land mass, peninsula, or island; CLZ I, equatorial zone with very high annual precipitation; CLZ III, the subtropical dry-zone of deserts with very low rainfall; CLZ IV, the Mediterranean transition zone with winter rainfall; CLZ VI, the temperate climate zone with moderate humidity; CON, continent (land mass).

correspondence between hot-spots (centres) of diversity and endemism will not always be expected. This result is not surprising because while endemic species richness in rivers is a pure product of isolation, increasing total species richness requires isolation to allow genetic differentiation between populations, as well as removal of isolation to bring new allopatrically formed species back into sympatry. Here, species diversity (e.g. total species richness) is influenced by factors related to components of river size (i.e. surface area of the drainage basin), energy availability (i.e. net primary productivity), and history and/or contemporary climate (i.e. climatic zones IV and VI, continent), as previously reported in other studies (Oberdorff *et al.* 1995, 1997; Guégan *et al.* 1998). Endemic species richness is directly dependent on total species richness, but is also influenced by climatic and/or historical factors such as glaciation and climatic zones I (the equatorial zone) and III (the subtropical dry-zone of deserts).

Do hot-spots (centres) of diversity correspond to areas of endemism?

Total species richness (TSR) statistically explains most of the variation in endemic species richness. Species-rich basins are generally rich in endemic species, all other things being equal. This relationship is partly dependent on the contribution that endemic species make to the total

species count (the high number of endemic species found in the richest basins is a probabilistic function of high species numbers). Nevertheless, given the shape of the relationship between ESR and TSR (Fig. 1), it is clear that endemic species are grossly under-represented in species-poor rivers and over-represented in species-rich rivers, though there are obvious exceptions. Huguéy (1990), working on 20 West African rivers, found an inverse relationship between the total fish species richness of a river and the average range size of species living in it; then, species with small geographical range (e.g. endemic species) should be rare in species-poor rivers and more numerous in species-rich rivers. Another explanation for the under-representation of endemic species in species-poor rivers and their over-representation in species-rich rivers could be related to the "endemic-area relationship" (Harte & Kinzig 1997). The argument is that however many species there are in a small area, none of them can be endemic, and yet at the largest scale, all of them must be. So endemics should increase faster than the number of species with increasing area (and with increasing number of species).

Relationships between endemic species richness and glaciated areas

The fact that the model overestimates endemic species richness for partially and totally glaciated zones corroborates the assumption that the lowest levels of endemism should be recorded at high latitudes in Northern Hemisphere areas that were glaciated during the pleistocene (Hawksworth & Kalin-Arroyo 1995). Fish taxa existing in these areas today are present by virtue of postglacial colonization from refugial zones to the south (Banareescu 1989; Matthews 1998). Thus, there is no reason to expect the presence of endemic species in such areas.

Relationship between endemic species richness and climatic zones

Of particular interest are the outlying basins that have a larger or a lower number of endemics than expected on the basis of total richness (i.e. basins situated in climatic zone III and climatic zone I, respectively). The limited dispersal power of freshwater fishes (either by crossing ocean margins or by colonizing new areas via physical connections between basins) stipulates that the degree of endemism in a river basin depends on three main nonexclusive factors: (i) the degree of isolation of the basin, (ii) the degree of climatic stability of the basin over history, and (iii) the rate of speciation within the basin.

If we first consider the outlying basins that have a larger number of endemics than expected on the basis of

total richness, we find that they are all situated in arid or semiarid areas (latitudes corresponding to climatic zone III) and share the traits of a long history of isolation. The climate in these areas has been quite stable since the Holocene (Roberts & Wright 1993; Thompson *et al.* 1993), thereby favouring speciation, and their endemics are perforce narrowly distributed (i.e. exclusive to each basin) by virtue of this strong isolation of these desert rivers for which there has been no interbasins colonization since the Holocene. Furthermore, aridity itself may have increased the rates of speciation in these basins. In fact, in arid climates, aquatic habitats are dramatically altered through extremes in magnitude and variance of discharge, and through pronounced patterns of river expansion, contraction, and fragmentation throughout the basin (Stanley *et al.* 1997). Repeated cycles of isolation and sympatry may have promoted hybridization to produce the existing high endemism. This hypothesis is corroborated by two studies highlighting the predominant role played by interspecific hybridization in promoting existing endemism in the Colorado river basin in south-western United States (DeMarais *et al.* 1992; Dowling & DeMarais 1993).

If we now consider those outlying basins that have a lower number of endemics than expected on the basis of total richness (exclusively African basins situated in the equatorial zone), a possible explanation could refer to the climatic history of this region.

Through the Quaternary, the African climate has undergone considerable change, with alternating wet periods and severe droughts (Hugueny & Lévêque 1994). Therefore, species originally endemic to a basin (narrow endemics) had time and opportunity to expand their range into other areas by means of temporary physical connections between basins.

CONCLUSION

We performed in this paper an exploratory analysis of a unique global level dataset related to riverine fish endemism. By using simple exploratory variables to model the abiotic and biotic correlates of endemic fishes of the Northern Hemisphere, we can reasonably predict the location of narrow endemic-rich basins. We found that endemism correlates strongly with total species richness, is negatively influenced by history of glaciation, and is unusually high in arid drainages. These specific areas (arid drainages) should be important for conservation strategies as habitat destruction in such areas is a critical issue, because unlike more widespread species, endemic taxa are not replaceable from elsewhere. In addition, these arid regions, at least for aquatic ecosystems, could have a strong role in favourizing speciation rates and thus are important for biodiversity.

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APPENDIX

Data on endemic fish richness in this paper are from the following sources: Hugueny (1989); Krupp & Schneider (1989); Lelek (1989); Burr & Mayden (1992); WCMC (1992); Warren & Burr (1994); Almaça (1995); Bianco (1995); Changeux & Pont (1995); Revenga *et al.* (1998).

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BIOSKETCH

Thierry Oberdorff works in community ecology. His research focuses more specifically on the role of the different spatial scales in the regulation of riverine fish communities. He is also interested in examining the consequences of anthropogenic effects (e.g. habitat alteration, water quality alteration) on fish community structure and function.

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