

Global scale patterns of fish species richness in rivers

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Explanations of spatial and temporal variation in species richness is a central theme in community ecology. Until recently, most research has focused on small-scale phenomena, often emphasizing on local environmental factors and, thus, poorly reflecting large-scale processes that organize species richness. In this paper, we analyze variations in species richness of indigeneous freshwater fish on a worldwide scale. We show that factors related to species-area and species-energy theories statistically explain most of the variation in freshwater fish species richness across continents. Historical events supposed to influence present distributions of fish are of little assistance in explaining variations in fish species richness at the global scale. Our model, which uses easily measured factors, should also be of practical value to aquatic conservation biology and natural resource management.

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Introduction

Patterns in species richness are strongly influenced by the spatial scale of investigation (Brown and Maurer 1989). Ecologists have focused on local (within a site), regional (among sites in a given region; a region grouping naturally similar ecosystems), or geographical (among regions) explanations of diversity patterns. For freshwater fishes, studies have shown that both biological and physical factors cause differences within and among communities (Schlosser 1987) and that both operate on a range of spatial scales (Tonn 1990). On a local scale, biological factors, e.g. competition (Grossman 1982, Ross et al. 1985) or predation (Moyle and Vondracek 1985), but also physical factors, e.g. habitat diversity (Gorman and Karr 1978), water chemistry traits (Rahel 1986), flow regime, temperature and channel morphology (Horwitz 1978, Matthews 1985, Schlosser 1985), interact to influence species richness patterns. At a local scale, physical factors appear to determine species richness in variable environments (Capone and

Kushlan 1991), biological ones being more important under stable environmental conditions (Ross et al. 1985). On larger spatial scales (regional and geographical), physical factors such as river size (Livingstone et al. 1982, Huguény 1989, Welcomme 1990) and climate (Hughes et al. 1987), along with historical factors such as speciation rates and dispersal (Huguény 1989), are the major determinants of species richness, and regulate the importance of local-scale factors. Thus, patterns and processes observed in local assemblages are determined not only by local mechanisms acting within assemblages but also result from processes operating at larger spatial and temporal scales (Tonn 1990). Until now, little or no attention has been directed towards identifying factors acting on intercontinental scales. In an effort to address this deficiency, we here examine factors that may explain fish species richness in 292 rivers located on an equatorial-polar gradient. We explored the relationship between species diversity and 11 independent variables to address three of the most widely held theories in community ecology: the species-area theory (Preston 1962),

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which implies that species richness increases as a power function of surface area; the species-energy theory (Wright 1983), which predicts that species richness correlates with energy availability; and the historical theory (Whittaker 1977), which explains richness gradients, on a global scale, by patterns of recolonization and maturation of ecosystems after glaciation.

Data

The 292 rivers we studied were distributed as follows (MacNally et al. 1982): 68 rivers in Africa (23%), 95 in Europe (33%), 76 in North and Central America (26%), 16 in South America (5%), 33 in Asia (11%), 4 in Oceania (1%); 72 rivers are between 0-10° of latitude (25%), 18 between 11-20° (6%), 10 between 21-30° (3%), 60 between 31-40° (20%), 103 between 41-50° (35%), 25 between 51-60° (8%), and 4 between 61-70° (1%). We omitted endorheic basins and saharian rivers with temporary water flow. Values for fish species richness from entire drainage basins were obtained from different published sources (see Appendix). These values are subject to several sources of error. First, the number of fish species may be underestimated due to inadequate sampling effort or if extinctions due to human activity occurred before collections were made. Secondly, the number of fish species may be overestimated if some species have been recently introduced in rivers (see Barbour and Brown 1974 for an extended discussion of this). To minimize these potential artifacts, we selected the most recent references and adjusted species number to account for extinctions and introductions wherever possible.

For each river, we determined the following variables: Total surface area of the drainage basin (km²). Values for this variable are compiled from literature or measured with a digital planimeter on 1:1 000 000 scale maps.

Mean annual discharge at river mouth (m³ s⁻¹). Discharge data are compiled from literature but are not available for all rivers. Although this limits the power of some analyses, the missing data are fairly evenly distributed across the globe and are not likely to affect our conclusions.

Mean latitude of river (degree and minutes). The values for mean latitude are for the center of each river basin (weighted by the length of river reaches at various latitude).

Mean annual temperature (°C), temperature range (°C) and mean annual rainfall in the area (mm). The values are determined for the middle course of river.

Net primary productivity (kg⁻² yr⁻¹). 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. Certainly, it would have been better to consider aquatic primary productivity. However, terrestrial primary productivity and aquatic primary productivity co-vary closely

(Livingstone et al. 1982). This is probably because food webs supporting fish are mainly based on allochthonous (detrital) inputs, and thus are dependent on available terrestrial energy (e.g. terrestrial primary productivity) (Hugueny 1989). Secondly, food webs supporting fish are based on aquatic plant production (e.g. aquatic primary productivity) which depends, in turn, on the same latitudinal factors as terrestrial primary productivity. These two explanations are not mutually exclusive, and it is possible that both may be operating.

Climatic zones were classified into 8 major zones. 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: I the equatorial zone with very high annual precipitation; II the tropical summer-rainfall zone with heavy rains in the summer and an extreme drought during the cooler season; III the subtropical dry-zone of the deserts with low rainfall; IV the transition zone with winter rainfall (typical Mediterranean climate); V the warm-temperate climate with high humidity in the summer; VI the temperate climate as prevailing in continental Europe with moderate humidity; VII the arid temperate climate of continental regions with low rainfall; VIII the cold-temperate or boreal climate with high precipitation. No rivers were located in zone IX corresponding to the arctic zone.

Total surface area of the continent and total fish species richness per continent. The values are compiled from literature.

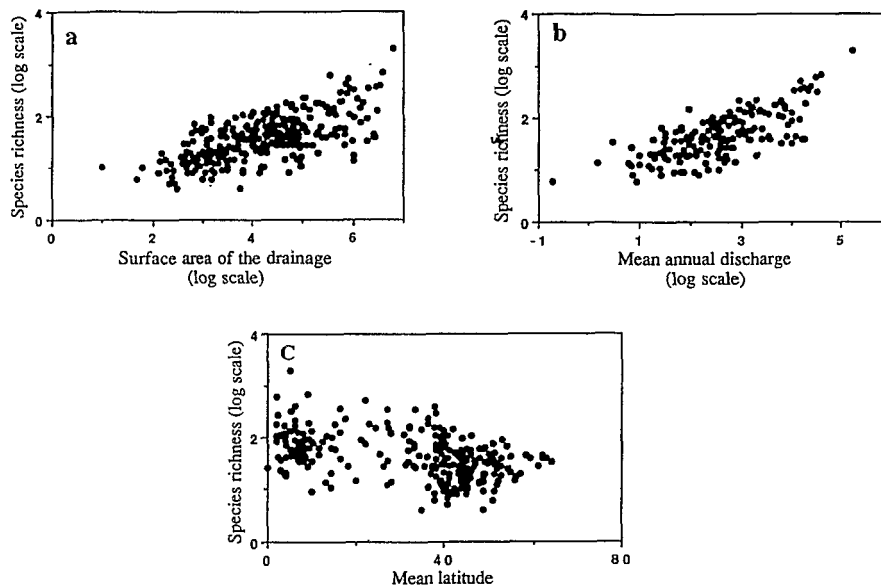
Surface of drainage basin area covered by glaciers during the last Pleistocene glaciation. This variable considers whether or not a river basin has been glaciated or not during the Pleistocene (uncovered = 0; partially covered = 1; totally covered = 2).

The source for data on surface area and river discharge are Pardé (1954), Frécaut (1982), Marsily (1986) and Van der Leeden et al. (1990). Geographical parameters are calculated from MacNally et al. (1982), and climatic variables are from Walter and Lieth (1960), Walter et al. (1975), and Anonymous (1992). The source for data on surface area of continent and fish species richness per continent are Anonymous (1992) and Melvin et al. (1994).

The effect of ecological or historical factors that might be responsible for variation in species richness across continents was investigated using: 1) total surface area of the drainage basin, mean annual discharge, and total surface area of the continent as measures of area, 2) net primary productivity as measure of energy availability, 3) climatic zones; as measures of contemporary climate and/or climatic history, 4) temperature range as a measure of climatic variability, 5) glaciated area as a measure of evolutionary history, 6) total species richness per continent as a measure of regional influence.

Mean latitude of river was used to test the predictive power of the previous descriptors in explaining variability in fish species richness across continents.

Fig. 1. Species richness of freshwater fish for each river as a function of total surface area of the drainage basin (a), mean annual discharge at river mouth (b) and mean latitude (c).



Statistical methods

Associations between variables were tested by standard regression, using a set of linear contrasts for each variable (Snedecor and Cochran 1980). The statistic r^2 provides an estimate of the percentage of variance that is accounted for by the regression equation. The contribution of different, independent variables to the among-river variation in species richness was derived by forward, backward and stepwise multiple regression procedures (Draper and Smith 1981). Arithmetic-to-arithmetic and logarithmic-to-logarithmic analyses of X's on Y were made, and those results that best fitted all data points were retained. At each iteration, the variable showing the highest partial correlation with the dependent variable was included in the model if its correlation was significant at the 5% level. When no variable could be added to the model, the procedure was finished. Significant variations of average residual values of fish species richness plotted against climatic zones were analyzed by using Student's t-tests (Scherrer 1984). All statistical analyses were performed using Systat 5 ver. 5.2.1. for the Macintosh (Wilkinson 1990).

Results and discussion

Species richness was significantly correlated with most of the environmental variables we examined (Table 1, Figs 1, 2 and 3). However, the two strongest correlates of species richness were total surface area of the drainage basin and mean annual discharge. Relationships between freshwater fish species richness plots (Y) and total surface area of the drainage basin (X_1), and with mean annual discharge at mouth (X_2) were as follows: $\log Y = 0.478 + 0.266\log X_1$; $r^2 = 0.439$, F-test = 227.01 (df 1, 291), $p=0.0001$ (Fig. 1a), and $\log Y = 0.836 +$

$0.330\log X_2$; $r^2 = 0.520$, F-test = 177.98 (df 1, 165), $p=0.0001$ (Fig. 1b), respectively.

Two distinct models were generated from both forward and stepwise regression procedures. In model A, data from all 292 rivers were modelled following the conventional approach of species-area theory, by using total surface area of the drainage basin (Figs 1a, 4a,b). Model B also incorporated mean annual discharge data, which were available for 166 of the rivers. By using mean annual discharge, we consider a third-dimension

Table 1. Regression coefficients between characteristics of the environment and fish species richness (log scale)

Variables	Theory tested	r^2	p	n
Total surface of the drainage*	S/A	0.439	0.0001	292
Mean annual discharge*	S/A	0.520	0.0001	166
Total surface area of continent*	S/A	0.107	0.0001	292
Net primary productivity*	S/E	0.118	0.0001	292
Mean annual rainfall*	S/E	0.102	0.0001	292
Mean annual temperature	S/E	0.149	0.0001	292
Temperature range*	----	0.074	0.0001	292
Mean latitude	----	0.200	0.0001	292
Climatic zone I	----	0.084	0.0001	292
Climatic zone II	----	0.055	0.0001	292
Climatic zone III	----	0.002	0.4500	292
Climatic zone IV	----	0.080	0.0001	292
Climatic zone V	----	0.021	0.0130	292
Climatic zone VI	----	0.010	0.0970	292
Climatic zone VII	----	0.014	0.0430	292
Climatic zone VIII	----	0.004	0.2870	292
Glaciated area	S/H	0.003	0.3640	292
Continental species richness*	----	0.329	0.0001	292

Legend: S/A Species/Area theory, S/E Species/Energy theory, S/H Species/History theory, * Variables expressed in logarithmic values, r^2 regression-coefficient, p probability associated with F-test, n number of plots.

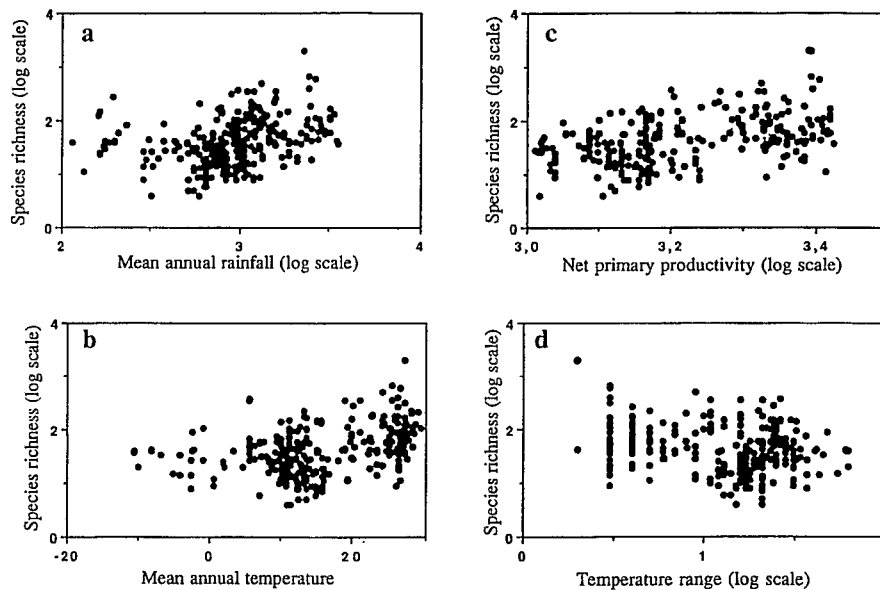


Fig. 2. Species richness of freshwater fish for each river as a function of mean annual rainfall (a), mean annual temperature (b), net primary productivity (c), temperature range (d).

in river size variability (Figs 1b, 4c,d). Multiple regression procedures showed that variation in species richness was most closely related to factors associated with the species-area and species-energy theories (Table 2).

Examination of the results from model A (Table 2) showed that fish species richness was correlated with three independent variables that together explained 68% of the total variability; area explained more of the variation in species richness (e.g. total surface area of the drainage basin, standart coefficient 0.617, $n=292$, $p=0.0001$) than did the supply of usable energy in the environment (e.g. net primary productivity, standart co-

efficient 0.361, $p=0.0001$). A regional effect (e.g. continental species richness) was also highly significant in the model (standart coefficient 0.305, $n=292$, $p=0.0001$). To test the influence of climate on fish species richness, we proceeded by analyzing residual variation in model A versus the 8 classical climatic zones (Fig. 4b). Student's *t*-tests showed that variation of average species richness residuals for zones II ($t=-2.513$; $p<0.05$), IV ($t=-1.995$; $p<0.05$), VI ($t=7.35$; $p<0.001$) and VII ($t=-2.408$; $p<0.05$) differed significantly from a null value. Adding climatic zones as dummy variables (Draper and Smith 1981) in model A confirmed this result ($R^2=0.755$, $n=292$, $p=0.0001$). Thus, model A underestimates species richness for climatic zone VI and overestimates species richness for zones II, IV and VII (Fig. 4b). This suggests that species richness depends upon "something" that co-varies with climatic zones and is not included in model A, thereby giving support, at this step of investigation, to the influence of climatic history and/or contemporary climate on fish species richness.

In fact, climatic zone VI (temperate continental climate) was directly influenced by climatic events during the last Pleistocene ice-age that led, in turn, to the creation of continental refuge areas with higher species richness, notably in eastern North America (Mississippi Basin) and western Europe (Danube Basin) (zone VI: average residual value of species richness underestimated by the model) (Mahon 1984, Moyle and Herbold 1987, Banarescu 1989). For climatic zone VII (average residual value of species richness overestimated by the model) aridity (contemporary climate) has highly reduced fish species richness. In the tropical summer rainfall zone (zone II: average residual value of species richness overestimated by the model), extreme drought during the cooler season (contemporary climate) but also climatic events during the early Quaternary (Hugueny

Table 2. Factors correlated with world freshwater fish species richness

Variables	Slope coefficient	Standart coefficient	P
Model A			
Intercept	-3.218	0.000	0.0001
log (total surface of the drainage)	0.247	0.617	0.0001
log (net primary productivity)	0.908	0.361	0.0001
log continental species richness	0.305	0.259	0.0001
Model B			
Intercept	-3.196	0.000	0.0001
log (mean annual discharge)	0.182	0.399	0.0001
log (total surface of the drainage)	0.134	0.306	0.0010
log (net primary productivity)	0.933	0.377	0.0001
log continental species richness	0.281	0.247	0.0001

Slope and standart coefficients of predictable variables against log(species richness), after controlling for the effect of other variables. Analyses used stepwise procedure in multiple regression analyses to retain only variables with significant partial correlations ($p<0.05$). Examination of residual values were performed at each step of the procedure. Final multiple regressions were highly significant: Model A ($F = 206.251$, $n = 292$, $R^2 = 0.682$, $p=0.0001$); Model B ($F = 144.243$, $n = 166$, $R^2 = 0.782$, $p=0.0001$). Forward and backward multiple regressions yielded similar results in both cases

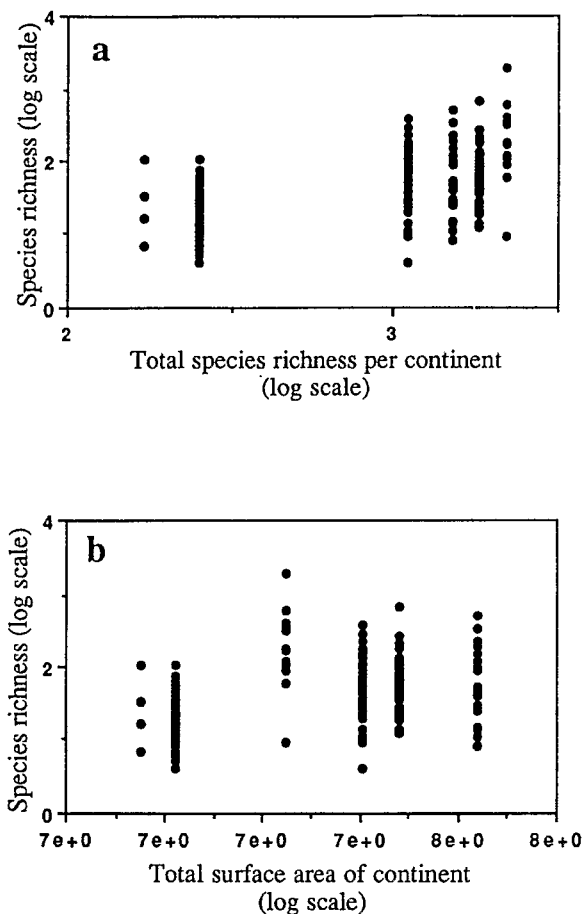


Fig. 3. Species diversity of freshwater fish for each river as a function of total freshwater fish species richness per continent (a), and total surface area of continent (b).

and Lévêque 1994) could be responsible for the reduction in fish species richness.

A problem arises in explaining species richness patterns by climatic events for the mediterranean area (zone IV: average residual value of species richness overestimated by the model), an area which is often considered as a refuge zone with a high number of endemic species (Banarescu 1989). In such areas, species richness should be underestimated by the model. The results from model A indicate that factors other than climatic events might be implicated. Two possible explanations for this can be advanced. Firstly, most of these circum-mediterranean regions are peninsulas. As species extinction rate is area-dependent (it increases as the size of the area decreases), peninsulas, by the absence of land around most of their boundaries, should have fewer species than comparable continental areas (MacArthur and Wilson 1967). Secondly, arid climates prevailing in circum-mediterranean regions (contemporary climate) can lead to a drastic intermittent decrease in flow regime, which generates, in turn, a low fish species richness in rivers.

For model B, which integrates a third dimension to

river size, i.e. mean annual discharge, only one climatic zone is still significantly related to the residual values of the model (zone VI; $t=4.412$, $p<0.001$) (Fig. 4d). This was confirmed by multiple regression analysis and could indicate the influence of historical factors on contemporary distributions of fish in this zone, e.g. the post-glacial recolonization of western Europe and North America. In North America species were driven into the southern parts of the Mississippi basin with the advance of the Pleistocene glaciations, and, as the ice retreated, recolonized the rivers along north-south corridors. In western Europe, where the freshwater fish fauna of Europe is impoverished than in eastern North America, the drainage divides generally run east-west. As a result, fish could not easily retreat southwards to seek refuge from the effects of Pleistocene glaciations (Moyle and Herbold 1987, Wootton 1991).

In model B, river size (i.e. total surface area of the drainage basin and mean annual discharge), energy availability (i.e. net primary productivity), and to a lesser extent regional richness (i.e. continental species richness) together, explain 78% of the total variability in fish richness. This result emphasizes the predominant role played by mean annual river discharge as a synthetic descriptor of species richness integrating, among other things, regional climatic variability (contemporary climate), e.g. volume availability for fish. Moreover, with respect to circum-mediterranean regions, this result is consistent with the second assumption proposed above, that drastic intermittent flow regimes generate low fish species richness. Nevertheless, a new study (Oberdorff et al. unpubl.) shows that the first assumption (the peninsular structure acts on fish species richness patterns) is equally true. In model B, as in model A, continental species richness is the best predictor of river species richness when river size (i.e. total surface area of the drainage basin and mean annual discharge) and energy availability (i.e. net primary productivity) are factored out. However, this result is difficult to discuss further as a formal statistical approach is not capable of separating effects of environmental differences from evolutionary histories.

Model B, as in model A, shows a weaker relationship between species richness and energy availability (net primary productivity, standard coefficient 0.377, $n=166$, $p=0.0001$) than between species richness and river size (mean annual discharge, standard coefficient 0.399, $n=166$, $p=0.0001$, total surface area of the drainage basin, standard coefficient 0.306, $n=166$, $p=0.0001$). This result contrasts with those of previous studies dealing with angiosperm (Wright 1983), bird (Wright 1983), and mammal (Wylie and Currie 1993) species richness, for which available energy explained more of the variation in species richness than did area. What accounts for this difference? Energy can act on species richness in two distinct ways: indirectly, through overall productivity; or, directly due to the lethal effect of extreme temperatures (Turner et al. 1988, Currie 1991). The lower effect

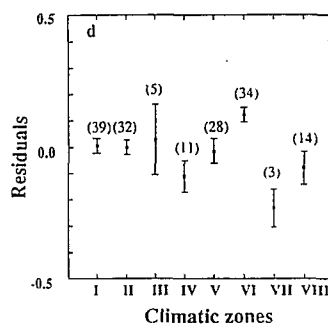
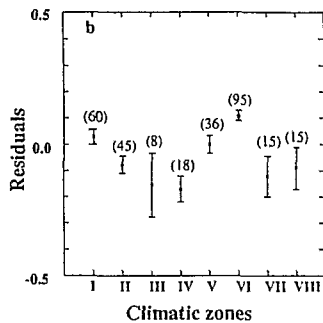
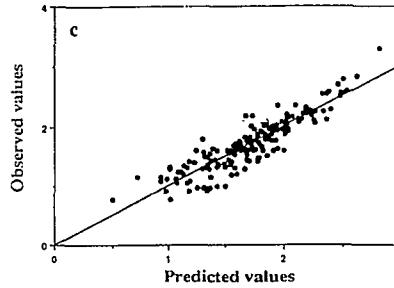
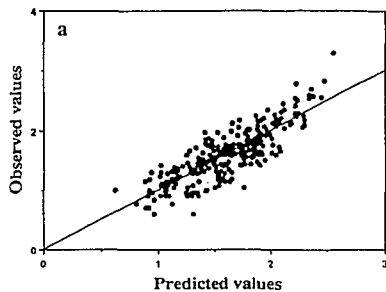


Fig. 4. (a, c) Relationships between the number of freshwater fish species observed and the number predicted by multiple regression for model A (Fig. 4a), and for model B (Fig. 4c). Straight lines represent points at which the predicted value equals the observed value. Conformity was tested with the χ^2 -test (model A, $\chi^2=34.4354$, $\nu=292$, $p=0.0001$; model B, $\chi^2=23.815$, $\nu=166$, $p=0.0001$). As can be seen by examining the relationship between observed values and those expected based on the multiple regressions, the combination of variables used in model A and B achieved a good fit of the data with no obvious signs of nonlinearities (b, d). Residuals from multiple regressions of species richness as a function of listed variables in model A (Fig. 4b) and as a function of listed variables in model B (Fig. 4d) plotted against categories of climatic zones. Mean, standard error and number of plots are indicated for each climatic zone.

of energy on fish richness is probably related to the higher specific heat and greater density of water over air, thus acting as a heat sink. Thus, the risk of exposure to extreme temperatures is minimized by the fact that water has a narrower range of temperature variation than air. In addition, changes in water temperature occur less abruptly, allowing fish (as opposed to terrestrial organisms) to move into more favorable conditions, thus avoiding the potentially lethal effects of temperature variation. Consequently, energy-related variables have less influence on the species richness of riverine fish, than on that of terrestrial organisms.

The energy-species richness relationship may also be scale dependent (Wright et al. 1993). On a local scale, species richness is frequently a peak function of energy (Wright et al. 1993, Tilman and Pacala 1993, Rosenzweig and Abramsky 1993), whereas on a regional or a global scale species richness increases linearly with energy (Wright et al. 1993). Our study supports the latter view, that a linear relationship between species richness and primary productivity is more appropriate for designing models on a global scale.

Conclusion

The aim of this study was to identify predictors of freshwater fish species richness (associated with area, energy and history processes) on a global scale. The data and analyses presented here lead to the conclusion that river size (surface area of the drainage basin and mean annual river discharge), and to a lesser extent, energy availability (net primary productivity) are the most important fac-

tors influencing fish species richness patterns on a global scale. Considering only these three descriptors, without explicit information concerning history, climate, and topography, one can statistically explain most of the natural variability of freshwater fish species richness. The fact that latitude (i.e. mean latitude of the river) is invariably rejected from both models reinforces the satisfactory predictive power of the models we propose. The role of historical factors in contemporary fish distribution patterns generally tend to be overshadowed at this scale of investigation. Currie (1991) suggested that species richness for terrestrial organisms can be affected by historical factors only on short time scales (e.g. richness can reach a plateau in something less than the time since the end of the last glaciation). Our study on riverine fish richness only partially agrees with this hypothesis. Naturally, fish, as aquatic animals, cannot easily disperse across terrestrial barriers. Thus, achieving saturated communities will be harder and longer for fish than for terrestrial organisms (the ease of colonization depending primarily on the number and suitability of river connections). Consequently, some traces of past historical events on a global scale may be still discernible in freshwater fish communities, as indicated in this study for rivers located in climatic zone VI. Thus, the possibility that some other historical variables not accounted for in our analyses could have an influence on species richness gradients cannot be unequivocally excluded, all the more since we are not capable in this study of eliminating the possibility that richness differences between continents are due to an effect of evolutionary history.

Much of the recent discussion of biodiversity focuses

on concern for species-rich terrestrial ecosystems. Aquatic ecosystems, because they are accessible below the surface, go comparatively unnoticed. With freshwater fishes concentrated as they are, into the lakes and rivers of the earth, freshwater fish faunas, are often as diverse and endemic as are terrestrial island populations, and as vulnerable. The aim of this paper was to analyze variations in freshwater fish species richness in aquatic systems with a macroecological approach. It seemed to us that the development of such models was a task of major importance, in view of current predictions of massive global environmental change and for water resource management in general.

According to the patterns and explanations presented here, the various effects of human activity on natural aquatic ecosystems, in particular, the flow modification of river (mainly due to widespread reservoir construction and use of water for agricultural practices), and the global net primary productivity directly used by humans (almost 40% of all NPP generated on land; Brown and Maurer 1989) may have a profound effect on aquatic species richness at a global scale.

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Appendix.

Data on freshwater fish richness used in this paper are from the following sources. Africa. Welcomme (1972), Bruton and Cooper (1980), Bernacsek (1981), Paugy et al. (1988), Huguény (1989), Anonymous (1992), Teugels and Guégan (1994). North America. Mahon (1984), Hughes and Gammon (1987), Moyle and Herbold (1987), Sublette et al. (1990), Anonymous (1992), Watters (1992), Warren and Brooks (1994). South and Central America. Welcomme (1990), Anonymous (1992), Orstom (1993). Europe. Daget (1968), Verneaux (1971), Daget and Economidis (1975), Baglinière (1979), Mahon (1984), Whitton (1984), Kiener (1985), Balon et al. (1986), Busch et al. (1988), Cazemier (1988), Pattee (1988), Philippart et al. (1988), Lelek (1989), Philippart (1989), Penczak and Mann (1990), Boët et al. (1991), Penczak et al. (1991), Oberdorff et al. (1993), Changeux (1994). Asia. Andreev and Reshetnikov (1978), Kottelat (1989), Pethiyagoda (1991), Anonymous (1992), Edds (1993), Reshetnikov and Shakirova (1993), Mina (pers. comm.). Oceania. Walker (1979), Sagar and Eldon (1983), Parenti and Allen (1991), Anonymous (1992), Coates (1993).

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