Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America

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Abstract. Freshwater fish species richness on 132 West European and North American rivers is analysed using eleven variables related to contemporary ecology (nine) and history (two). This is done in order to examine the relative and joint effects of both historical and ongoing processes on the contemporary richness of these two regional fish faunas. Relationships are quantified by simple and stepwise multiple regression procedures. Species-area curves are presented for the fish faunas within both continents. We show that ecological factors statistically explain most of the variation in freshwater fish species richness for both continents. Effects of historical factors are shown to be statistically significant, but add only a little to the variance already explained by ecological factors. Our analyses further indicate that rivers (which flow directly into the ocean) support fewer species of fish than do similarly sized tributaries. The immigration-extinction hypothesis appears to provide a plausible explanation for this observed pattern. The fact that in our final model, a continental effect is still highly significant, leads us not to exclude the possibility of some other historical influences in generating different overall species richness levels on the two continents.

Key words. Community ecology, pisces, species-area hypothesis, species-energy hypothesis, historical hypothesis.

INTRODUCTION

Why does one area contain more species than another? Many assumptions have been proposed to explain the spatial variability in species richness at several different scales. These may be grouped into three main hypotheses in community ecology: the species-area hypothesis (Preston, 1962), which implies that species richness increases as a power function of surface area; the species-energy hypothesis (Wright, 1983), which predicts that species richness will be positively correlated with available energy; and the historical hypothesis (Whittaker, 1977), which explains diversity gradients by the pattern of recolonization and maturation of ecosystems after glaciation. Determination of the extent to which patterns of species richness are due to historical factors or to contemporary ecological interactions is important to the understanding of these biogeographic phenomena (Lawlor, 1983; Brown, 1987). In a previous study (Oberdorff, Guégan & Hugueny, 1995), we analysed in the light of these hypotheses, global scale patterns in fish species richness in rivers. We showed that three factors,

related to the two first hypotheses (species-area and species-energy hypotheses), statistically explained a major part of the variation in freshwater fish species richness across continents and that the role of historical factors, at this scale of investigation, had a weak effect, if any. We agreed with Currie's (1991) suggestion for this 'oversight' of historical factors which claims that species richness for terrestrial organisms can be affected by historical factors only on short time scales. Nevertheless, this explanation is not evident when concerning the richness of freshwater fish species. The reason for this is that fish, as aquatic animals, cannot disperse across land barriers. Thus, reaching saturated communities (with regard to present conditions) will be harder and will take 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, such as Pleistocene glaciations, may still be discernible in freshwater fish communities of the northern hemisphere.

For example, it is generally accepted that the West European fish fauna is reduced in richness relative to the North American fauna due to historical processes (Mahon, 1984; Moyle & Herbold, 1987; Banarescu, 1989; Tonn, 1990; Wootton, 1991). Two major assumptions have been proposed to explain these different patterns in species

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richness. The first suggests that Western Europe and North America differ considerably topographically and, thus, with regard to the effects of glaciation, the richness of their fish faunas will also differ considerably. A possible factor in generating the pattern of fish distribution observed in North America was the ease with which species driven into the southern parts of the Mississipi basin with the advance of the Pleistocene glaciations were able, as the ice retreated, to recolonize the rivers along the north–south corridors. In Western Europe, 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, and thus, drastic extinctions occurred (Moyle & Herbold, 1987; Wootton, 1991). The second assumption is that the Mississipi Basin provided a much larger total refugial area for freshwater fishes in North America than did the Danube Basin in Europe. On this basis, and considering the absolute overall size, species richness should be greater in North America than in Europe (Mahon, 1984). However, these assumptions are based on comparisons involving a limited number of rivers and/or lakes.

The purpose of the present study is to examine the relative and joint effects of both history and ecology on freshwater fish species richness on an intercontinental scale. Disentangling historical from ecological effects is a difficult task (Endler, 1982). In order to do so, we compared two continents having similar latitudinal ranges and thus, similar ecological and climatic conditions, but with different histories (e.g. North America and Western Europe). We first identify the major ecological factors responsible for variation in species richness across the two continents. In a second step, we introduce factors which presumably reflect historical events, and examine their relative contribution to our ecological model in explaining species richness gradients. We end by discussing predictions suggested by the results of our investigation.

METHODS

The 132 rivers we studied are located as follows (McNally *et al.*, 1982): ninety-one in Europe (69%), forty-one in North America (31%); twenty-three (seventeen in North America, six in Europe) between 30° and 40° (17%), eighty-eight (twenty in North America, sixty-eight in Europe) between 41° and 50° (67%), nineteen (six in North America, thirteen in Europe) between 51° and 60° (14%), and two (one in North America, one in Europe) between 61° and 70° (2%). Values for the freshwater fish species richness in rivers (from the entire drainage basin) are from the following sources: *North America.* Fowler (1945), Hughes & Gammon (1987), Mahon (1984), Mayden (1991), Moyle & Herbold (1987), Sublette, Hatch & Sublette (1990), Warren & Brooks (1994), Watters (1992), World Conservation Monitoring Center (1992). *Europe.* Baglinière (1979), Balon, Crawford & Lelek (1986), Boët, Allardi & Leroy (1991), Busch *et al.* (1988), Cazemier (1988), Changeux (1994), Daget (1968), Daget & Economidis (1975), Dill (1993), Kiener (1985), Lelek (1989), Mahon (1984), Oberdorff, Guilbert & Lucchetta (1993), Pattee (1988), Penczak & Mann (1990), Penczak *et al.* (1991), Philippart (1989), Philippart, Gillet & Micha (1988),

Verneaux (1971), Whitton (1984). Similarly, eleven variables are determined for each river: (1) total surface area of the drainage basin (km²); (2) mean annual discharge at mouth (m³/s); (3) mean latitude of river (degree and minutes); (4) latitude range (degree and minutes); (5) temperature range in the middle course of river (degree Celsius); (6) net terrestrial primary productivity (kg^{-2}y^{-1}); (7) climatic zones split up into four major zones (see Oberdorff *et al.*, 1995 for detail) which are: IV the transition zone with winter rainfall (typical Mediterranean climate); V the warm-temperate climate with a high humidity in the summer; VI the temperate climate with moderate humidity; VIII the cold-temperate or boreal climate with high precipitation; (8) peninsula or island (continental mass, peninsula, island); (9) river or tributary (river, tributary); (10) surface of drainage basin area covered by the ice sheet during the last Pleistocene glaciation (uncovered, partially covered, totally covered); (11) distance of each river from the larger refugial area of the two continents (e.g. Mississippi Basin and Danube Basin) (degree of longitude from the mouth of the two rivers). To test for the predictive power of the previous descriptors in explaining variability in fish species richness across the two continents we introduced the variable continent (Europe, North America).

The source for data on surface area and river discharge are Frécaut (1982), Pardé (1954), Marsily (1986) and Van der Leeden, Troise & Todd (1990). Geographical parameters are calculated from McNally *et al.* (1982), and the climatic variables from Walter & Lieth (1960), Walter, Harnickell & Mueller-Dombois (1975), and World Conservation Monitoring Center (1992). Methods used for the calculation of each variable are given in detail in Oberdorff *et al.* (1995).

The effect of ecological factors that might be responsible for variation in species richness across the two continents was investigated using: (1) total surface area of the drainage basin, and mean annual discharge at mouth; as measures of river size, (2) net terrestrial primary productivity (as net aquatic primary productivity data were not available for the rivers, we used the variables mean annual temperature and mean annual rainfall to estimate average values of terrestrial primary productivity from the Miami models (Lieth, 1975)); as a measure of available energy, (3) mean latitude and climatic zones (entered as dummy variables); as measures of climate, (4) temperature range and latitude range; as measures of climatic variability. Furthermore we considered whether or not a river drainage was on a land mass, a peninsula, or an island (entered as dummy variables). Concerning peninsulas, species richness usually decreases as a function of distance from the mainland base of a peninsula (Simpson, 1964; MacArthur & Wilson, 1963, 1967; Taylor & Regal, 1978). We finally made a distinction between rivers (which flow directly into the ocean) and tributaries (entered as dummy variables).

The effect of historical factors that might have influenced species richness across the two continents was investigated in light of the last Pleistocene glaciation events (Table 1). We therefore considered the surface area of the drainage basin covered by ice sheet during the last glaciation (entered as dummy variables) and the distance of each river from the larger refugial area of the two continents.

TABLE 1. Correlation between ecological and historical descriptors of the environment and freshwater fish species richness (log scale).

	r	N
Ecological descriptors		
Total surface of the drainage[a]	0.721***	132
Mean annual discharge[a]	0.794***	74
Net primary productivity[a]	NS	132
Temperature range[a]	0.426***	132
Mean latitude	NS	132
Latitude range[a]	0.591***	132
Climatic zones		
Climatic zone IV	NS	132
Climatic zone V	−0.172*	132
Climatic zone VI	0.346***	132
Climatic zone VIII	NS	132
Peninsula	−0.486***	132
Tributaries	0.172*	132
Historical descriptors		
Glaciated area	NS	132
Distance from refugial area	−0.384***	132

[a] Variables expressed in logarithmic values; r, correlation coefficient (Pearson's r); N, Sample size; NS, Not significant; $*P<0.05$; $**P<0.01$; $***P<0.001$.
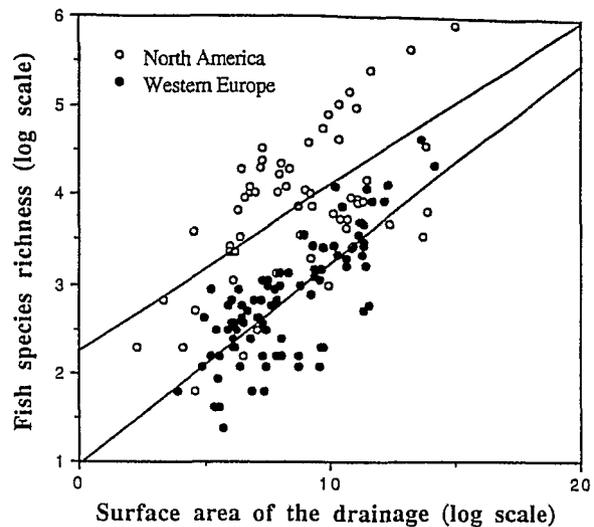

FIG. 1. Plot of fish species richness as a function of total surface area of the drainage basin for West European and North American rivers. Lines represent best fit power functions for each regression.

The existence of association between variables was tested by standard regressions. In all regressions the statistic R^2 provides an estimate of the percentage of variance which is accounted for by the regression equation. Arithmetic-to-arithmetic and logarithmic-to-logarithmic analyses of X's on Y were made, and those results which fitted better all data points were retained. The contribution of different, independent variables to the between-river variation in species richness was derived by forward and stepwise multiple regression procedures (Draper & Smith, 1966). At each iteration, the variable showing the highest partial correlation with the dependent variable was included in 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, 1990).

RESULTS

Species-area relationships for Western Europe and North America

The independent ecological and historical variables used in regression analysis to explain variation in fish species richness across the two continents are presented in Table 1. Species richness is correlated with many of the variables examined. However, species richness is more strongly correlated, first, with mean annual discharge (which accounts for 63% of the variance), and secondly with total surface area of the drainage basin (which accounts for 52% of the variance). Because discharge data were available for only seventy-four rivers, and because these two measures of 'river size' were highly intercorralated ($r=0.975$,

$P<0.001$), we selected total surface area of the drainage basin to illustrate the significant species-area relationships for both West European and North American rivers (Fig. 1). These relationships are :

Western Europe (1) $\ln SR = 0.865 + 0.234 \ln S$; $F = 119.5$, $P<0.001$, $r^2 = 0.573$;

North America (2) $\ln SR = 2.622 + 0.152 \ln S$; $F = 8.526$, $P<0.01$, $r^2 = 0.179$;

where SR is species richness of freshwater fish and S is the total surface area of the drainage basin in km^2. As it has been shown extensively for other biotic groups, freshwater fish species richness for both continents increases as area (river size) increases. However, our data clearly show that even if the species-area curves for both continents are similar in shape (slopes of the two species-area relationships not different; there was no interaction between surface area of the drainage and continent when using all data set; $P>0.05$), species richness for North America is greater than for Western Europe (intercepts of the two regression lines significantly different; continental effect strongly significant; $P<0.001$).

Therefore, the question to address is: what are the main sources of variation in intercept of these two species area relationships? Or, in other words, why species richness is greater in North America than in Western Europe?

In order to answer the previous question, we used stepwise multiple regressions to distinguish the relative effects of ecological and historical factors on species richness of the two continents. First we determined which ecological factors were the best predictors of species richness on the inter-continental scale (model A) (Table 2). Then, using model A, we analysed the capability of historical factors in contributing to the prediction of species richness (model B) (Table 3).

TABLE 2. Summary of multiple regression analysis (stepwise procedure) of fish species richness (log scale) versus the ecological 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 of the model. Missing entries indicate that the coefficients were not significant ($P>0.05$). Forward and backward multiple regressions yielded similar result. Final model was highly significant ($F=81.412$, $R^2=0.796$, $P<0.001$, $N=132$).

Model A

Ecological descriptors	Slope coefficient	Standardized regression coefficient	P (2 Tail)
Intercept	−3.595	0.000	0.1080
log (Total surface area of the drainage)	0.180	0.449	0.0001
log (Latitude range)	0.306	0.201	0.0001
Log (Net primary productivity)	0.617	0.093	0.0410
Tributaries	0.308	0.165	0.0001
Climatic zone VI	0.406	0.216	0.0001
log (Mean annual discharge)	—	—	—
log (Temperature range)	—	—	—
Mean latitude	—	—	—
Climatic zone IV	—	—	—
Climatic zone V	—	—	—
Climatic zone VIII	—	—	—
Peninsula	—	—	—
Continent	0.744	0.372	0.0001

TABLE 3. Summary of multiple regression analysis (stepwise procedure) of fish species richness (log scale) versus the ecological descriptors retained by model A plus the 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 of the model. Missing entries indicate that the coefficients were not significant. Forward and backward multiple regressions yielded similar result. Final model was highly significant ($F=75.765$, $R^2=0.810$, $P<0.001$, $N=132$).

Model B

Ecological and historical descriptors	Slope coefficient	Standardized regression coefficients	P (2 Tail)
Intercept	−3.809	0.000	0.0790
log (Total surface area of the drainage)	0.189	0.470	0.0001
log (Latitude range)	0.274	0.180	0.0030
Climatic zone VI	0.263	0.140	0.0050
Tributaries	0.259	0.138	0.0010
log (Net primary productivity)	0.689	0.104	0.0190
Distance from refugial area	−0.054	−0.149	0.0030
Glaciated area	—	—	—
Continent	0.759	0.379	0.0001

Influence of ecological factors on fish species richness for both continents

Examination of the results from model A (Table 2) shows that fish species richness is higher in tributaries compared to rivers and varies positively as a function of surface area of the drainage basin, net primary productivity, climatic zones (zone VI), and latitude range; area (e.g. surface area of the drainage) making the most important contribution to the model. It is notable that after accounting for these variables, no significant variation was related to the fact that the river basin is on a peninsula (or an island). It is also interesting to note that the continental effect on species richness is highly significant in the model (standardized regression coefficient = 0.372; $P<0.001$). One might conclude that species richness for both continents depends on something more than the ecological descriptors introduced in the model.

Influence of historical factors on fish species richness for both continents

To test the hypothesis that glacial history could have an effect on contemporary species richness, we entered in the former model two historical descriptors related to Pleistocene glaciation events, and supposed to have influenced species richness across the two continents (i.e. the surface area of the drainage basin covered by ice sheet, and the distance of each river from the larger refugial area of the two continents) (Table 3). In considering the model B (Table 3), effect of the distance of each river from the larger refugial area of the two continents is shown to be statistically significant ($P<0.05$), but adds only 1% to the variance already explained by model A. The surface area of the drainage basin covered by ice sheet does not contribute a significant proportion of the sums of squares and is rejected by the model. The continental effect on species richness is still highly significant in the model (standardized regression coefficient = 0.350; $P<0.001$). As can be seen by examining the relationship between observed values and those expected based on the multiple regression, the combination of variables used in the model B achieved a good fit of the data with no obvious signs of nonlinearity (Fig. 2).

DISCUSSION

Species-area hypothesis

Aquatic organisms such as fish, cannot disperse across terrestrial barriers. Thus, for these organisms, rivers (which flow directly into the ocean) can be considered as islands since there are no aquatic connections between most of them. The equilibrium theory of island biogeography, proposed by MacArthur & Wilson (1963, 1967), considers that the number of species found on an island is the result of a dynamic equilibrium between immigration and extinction rates determined by island isolation and island size. The authors reasoned that immigration rates should decrease with increasing distance from colonizing source areas and that more species should survive on larger islands because populations on large islands are large enough to make extinction less likely.

We found a significant and positive relationship between species richness and river size (e.g. surface area of the
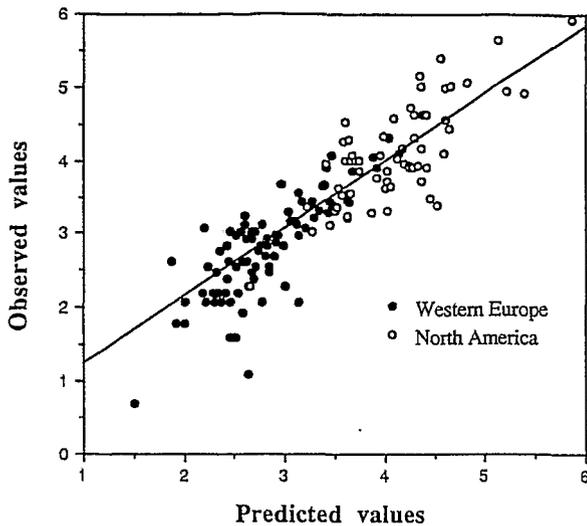
FIG. 2. Relationships between the number of freshwater fish species observed and the number predicted by multiple regression for model B. Straight lines represent points at which the predicted value equals the observed value. As can be seen by examining the relationship between observed values and those expected based on the multiple regression, the combination of variables used in the model B achieved a good fit of the data with no obvious signs of nonlinearity.

drainage basin). This finding is consistent with the results of several other studies on freshwater fish communities (Daget, 1968; Hugueny, 1989; Watters, 1992; Oberdorff *et al.*, 1995) and represents a basic tenet of island biogeography theory (MacArthur & Wilson, 1963, 1967).

Of greater interest is the highest fish species richness found in tributaries compared to rivers. For rivers (which flow directly into the ocean), which are usually completely surrounded by terrestrial barriers, the rate of contemporary colonization is zero or nearly so. For tributaries, local extinction can be quickly compensated by the immigration of new individuals from neighbouring populations of the main channel. Thus, considering a river and a tributary of similar drainage areas, species richness must be higher in the tributary. The data analysed during this study corroborate this hypothesis and confirm the assumption made by Hugueny (1989) in a previous study dealing with West African rivers. Furthermore, this result is coherent with recent studies on freshwater fish assemblages which emphasized the importance of inter-drainage immigration processes in shaping community structure, and particularly the relationship between distance to colonization source and local species richness (Detenbeck *et al.*, 1992; Osborne & Wiley, 1992). Differences in species richness among similarly sized rivers and tributaries have significant implications from a resource managment perspective. For instance, as there is a positive relationship between local species richness (within a sample site) and regional species richness (species richness from the entire drainage basin) (Hugueny & Paugy, 1995) fish communities inhabiting rivers (which flow directly into the ocean) can be mistakenly classified if evaluation criteria are based upon information gathered from tributaries of similar size.

Historical hypothesis

Oberdorff *et al.* (1995), in an attempt to explain fish species richness patterns on a global scale, showed that the major part of the variability can be statistically explained as a function of area and energy suggesting that historical factors (glaciation and dispersal) had probably a limited impact. They hypothezized that this minor role played by history, at this scale of investigation, was probably due to the dilution of data concerning northern hemisphere (where glaciated area caused drastic extinction during Pleistocene events) with that from the southern hemisphere. However, studies on terrestrial vertebrates in northern hemisphere (Turner, Gatehouse & Corey, 1987; Currie, 1991) suggest that factors related to present ecological conditions, such as available energy, have a better explanatory power than the time elapsed since the retreat of glaciers. This pattern can be explained by a fast and efficient recolonization of formerly depauperate areas from refugial zones. In the present study a similar pattern is observed (when ecological factors are integrated in the model, the variable related to glaciation intensity is invariably rejected). This result is quite surprising with regards to the poor dispersal ability generally attributed for freshwater fish. However, nordic areas in Western Europe as well as in North America (areas being directly subjected to glaciations during the Pleistocene) are principally inhabited by euryhalin species which probably recolonized rivers along the sea coast. In this case, detrimental effect of glaciation on fish community richness can be balanced by fast immigration processes. Past immigration events are more likely to affect contemporary fish community richness if dispersal through land mass is involved (where fish species depend on intermittent inter-drainage connections to disperse). Previous studies lead to identify the Danube and Mississippi drainage basins as major Pleistocene refuges respectively for West European and North American fish faunas (Mahon, 1984; Moyle & Herbold, 1987; Banarescu, 1989; Tonn, 1990; Wootton, 1991). In our study, a negative relationship between distance from these refugial areas and rivers species richness is observed for both continents. This suggests that past immigration events affect contemporary fish species richness, as expected since dispersal through land masses is a slow process. Furthermore, the fact that there is a positive effect of climatic zone VI (where refugial areas of both continents are located) on fish species richness corroborates this hypothesis (Oberdorff *et al.*, 1995).

If we assume that, during the Pleistocene, fish moved along a north-south axis in order to seek refuge from glaciations, we can expect that less climatically driven extinctions occurred in rivers having a north–south orientation (North American rivers) than in rivers having an east–west orientation (European rivers) (Moyle & Herbold, 1987; Matthews & Zimmermann, 1990). The positive relationship observed during this study between latitudinal range of rivers and species richness is in good agreement with this hypothesis.

Nevertheless, the influence of past dispersal processes (e.g. distance of each river from the refugial area and river basin orientation) accounts, here, for only a few proportions

of the variability in contemporary species richness, and thus, it is tempting to argue that current ecological factors are largely responsible for present-day distribution of fish species richness, and that historical factors play a little role. In the meantime, the fact that in our final model (model B), a continental effect is still highly significant, leads us to consider a possible influence of other past events (not included during this study) in generating different overall species richness levels on the two continents. One of these events could be a difference in speciation processes between the two continents. For example, some North American genus such as *Notropis* and *Etheostoma* have radiated with a rate not encountered in any of the European genus (Mahon, 1984). If speciation rate is assumed to be inversely related to body size (Marzluff & Dial, 1991), a low speciation rate is also suggested by body size distribution of European fish (dominance of medium and large species), conversely to North America where small fish predominate (Mahon, 1984, Moyle & Herbold, 1987; McDowall, 1994). 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 (Mahon, 1984).

Species-energy hypothesis

Recent studies have stressed the importance of energy-related factors in explaining species richness within regions or continents (Turner *et al.*, 1988; Currie, 1991). The great explanatory power of these models can lead to two conclusions: (1) level of community saturation is determined by the partitioning of energy among species, and (2) historical factors have a reduced role in the shaping of community diversity. Our study suggests that these conclusions are likely to be invalid when spatial scale is broadened in order to allow intercontinental comparisons. As we observed both ecological and historical effects on species richness, we cannot conclude that factors such as available energy set the species saturation level in river communities. Our observations are more consistent with a stochastic view of the species-energy hypothesis postulating that the probability of population extinctions is higher in area with low available energy (Turner, 1992). Given this assumption, and controlling for effect of available energy, areas located in regions (or continents) with large species pool size must harbour more species than areas located in regions with smaller species pool size.

CONCLUSION

In this study, 'continent' is the best predictor of river species richness when river size is factored out. Despite the fact that processes underlying this pattern are not precisely known, history is undoubtly involved, and our results stress the need for intercontinental comparisons to assess the relative importance of ecological and historical processes in shaping fish communities.

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