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ORIGINAL ARTICLE

Evidence of history in explaining diversity patterns in tropical riverine fish

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ABSTRACT

Aim Documentation of the ongoing effect of rain forest refuges at the last glacial maximum (LGM) on patterns of tropical freshwater fish diversity.

Location Tropical South and Central America, and West Africa.

Methods LGM rain forest regions and species richness by drainage were compiled from published data. GIS mapping was applied to compile drainage area and contemporary primary productivity. We used multiple regression analyses, applied separately for Tropical South America, Central America and West Africa, to assess differences in species richness between drainages that were connected and disconnected to rain forest refuge zones during the LGM. Spatial autocorrelation of the residuals was tested using Moran's *I* statistic. We added an intercontinental comparison to our analyses to see if a historical signal would persist even when a regional historical effect (climate at the LGM) had already been accounted for.

Results Both area and history (contact with LGM rain forest refuge) explained the greatest proportions of variance in the geographical pattern of riverine species richness. In the three examined regions, we found highest richness in drainages that were connected to the rain forest refuges. No significant residual spatial autocorrelation was detected after considering area, primary productivity and LGM rain forest refuges. These results show that past climatic events still affect West African and Latin American regional and continental freshwater fish richness. At the continental scale, we found South American rivers more species-rich than expected on the basis of their area, productivity and connectedness to rain forest refuge. Conversely, Central American rivers were less species-diverse than expected by the grouped model. African rivers were intermediate. Therefore, a historical signal persists even when a regional historical effect (climate at the LGM) had already been accounted for.

Main conclusions It has been hypothesized that past climatic events have limited impact on species richness because species have tracked environmental changes through range shifts. However, when considering organisms with physically constrained dispersal (such as freshwater fish), past events leave a perceptible imprint on present species diversity. Furthermore, we considered regions that have comparable contemporary climatic and environmental characteristics, explaining the absence of a productivity effect. 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 higher time scales (millions of years).

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Keywords

Central America, freshwater fish, historical factors, last glacial maximum, net primary productivity, rain forest refuge, South America, Species richness, tropics, West Africa.

INTRODUCTION

Many proposals have been made to explain the spatial variability in species richness at broad spatial scales (MacArthur, 1972; Rohde, 1992; Rosenzweig, 1995; Ricklefs, 2004). These proposals can be organized into three main hypotheses: the first hypothesis, the 'area' hypothesis states that species richness increases as a function of surface area through size-dependent extinction/colonization rates (MacArthur & Wilson, 1967) and/or habitat diversity (MacArthur, 1964). The second hypothesis, based on climate, comprises two versions. The 'productivity' hypothesis (Wright, 1983; Wright *et al.*, 1993; Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003a) predicts that species richness will be positively correlated with the total available productivity of the habitat, whereas the 'ambient energy' hypothesis (Turner *et al.*, 1987; Currie, 1991) refers to the physiological tolerance of organisms to low energy environments. The third hypothesis, the 'historical' hypothesis, which includes many variants (Mayr & O'Hara, 1986; Latham & Ricklefs, 1993; Haffer, 1997; Qian & Ricklefs, 2000; Ricklefs, 2004), explains diversity patterns by differential speciation or extinction rates, coupled with dispersal limitation due to historical contingency.

It is clear that area *per se* explains a large portion of richness variability and, due to its universal application, almost serves as a law in community ecology (Rosenzweig, 1995). When area is controlled for (e.g. tests usually performed on equal area grid cells) physical factors such as climate (e.g. temperature, precipitation and seasonality of these variables) and energy supply (e.g. net primary productivity, actual evapotranspiration) are generally strongly correlated with richness gradients of plants and animals (Wright, 1983; Currie & Paquin, 1987; Turner *et al.*, 1987; Adams & Woodward, 1989; Currie, 1991; Guégan *et al.*, 1998; O'Brien *et al.*, 2000; Rahbek & Graves, 2001; Francis & Currie, 2003; Hawkins *et al.*, 2003a,b) and clearly appear to be the most important factors driving the richness of most taxonomic groups (Hawkins *et al.*, 2003b; Ricklefs, 2004). Nevertheless, other factors can be involved. For example, the extent to which the evolutionary history of different regions influences global diversity gradients through differential speciation or extinction rates, coupled with dispersal limitation, remains a contentious issue (see Whittaker & Field, 2000; Jetz *et al.*, 2004; Ricklefs, 2004). Because all species have been generated in the past in specific locations, history must necessarily influence diversity patterns (Haffer, 1969, 1997; Bush, 1994; Hawkins *et al.*, 2003b; Whittaker *et al.*, 2003). However, when specific historical variables (e.g. glacial history) are included in regional analyses, their contribution to explaining species richness variation is generally weak (Latham & Ricklefs, 1993; Schluter & Ricklefs, 1993; Fraser & Currie, 1996; Oberdorff *et al.*, 1997; Kerr & Currie, 1999; Hawkins *et al.*, 2003a; Hawkins & Porter, 2003; Diniz-Filho *et al.*, 2004), although rarely rejected. This lack of evidence could come from: (1) the difficulty of quantifying historical influences (Ricklefs, 2004), (2) the comparatively greater availability of climatic data, and (3) the loss of the historical signal due to species dispersal in response to contemporary factors (Currie, 1991). According to this last hypothesis, we can expect that low dispersal ability increases the likelihood of observing a historical signal. As dispersal in freshwater fishes is restricted by physical barriers (oceans and river divides), this taxonomic group is a good candidate for exploring the relationship between species richness and history.

To evaluate this issue, we studied rivers of the tropical regions of West Africa and Latin America which have comparable contemporary climatic and environmental characteristics, but which have experienced different histories. These criteria allowed us to grossly control for energy and to focus more on potential historical effects. Available evidence suggests that the distribution of lowland tropical rain forests varied greatly in relation to marked climatic changes within the last 40,000 years, sometimes being much more restricted than at present due to glacial aridity (Brown & Lomolino, 1998). At the last glacial maximum (LGM), 18,000 years ago, the African and Latin American climates were considerably drier than that of the present day (Adams & Faure, 1997; Dupont *et al.*, 2000). During this dry period of the Quaternary, lowland tropical rain forests suffered drastic contractions and river basins unconnected to the remaining rain forest areas should have experienced reductions in their drainage area and discharge. By contrast, river basins still in contact with rain forests received comparatively higher precipitation, allowing them to keep their drainage area and discharge more or less constant. We know that drainage area and discharge are two indices of ecological space and habitat heterogeneity and, as such, riverine species richness increases with basin area and discharge, analogous to species–area curves in terrestrial biomes (Livingstone *et al.*, 1982; Hugueny, 1989; Oberdorff *et al.*, 1995; Guégan *et al.*, 1998).

Hence, if past climatic events are still influential on West African and Latin American freshwater fish richness, we should expect, everything else being equal, a significantly lower number of species in river basins which were completely isolated from the rain forest refuges (higher extinction rates during the LGM due to reduced basin area and discharge) compared to river basins having maintained contact with these refuge areas (lower extinction rates during LGM).

Historical influences on species richness can also be addressed at a continental scale. As soon as other contemporary factors (e.g. river size and present energy) have been accounted for, differences in speciation and extinction rates between continents could well reflect historical contingencies (Ricklefs, 2004). We added an intercontinental comparison to our analyses to see if a historical signal would persist even when a regional historical effect (climate at LGM) had already been accounted for. This study thus provides a rather singular assessment of historical effects on species richness on two geographic scales (i.e. within and between regions).

METHODS

Data sources

We used fish species richness data from 141 forested rivers located as follows: 40 in South America, 49 in Central America and 52 in West Africa (see Appendix S1 in Supplementary Material). River or drainage basins are considered here as water bodies, including all tributaries of the main river downstream to its mouth. Species richness (SR) refers to the total number of fish species collected from the entire drainage basin. Only riverine fish species were considered [secondary or migratory euryhaline fishes were systemically withdrawn on the basis of species descriptions provided in *Fishbase* (http://www.fishbase.org)]. Fish species numbers for West African basins were obtained from reviews made by Hugueny (1989), Paugy *et al.* (1994) and Teugels & Guégan (1994). For South and Central American basins, we mainly used Reis *et al.* (2003), supplemented with data provided by several other authors from each of the concerned countries (42 references available on request), producing the most updated *taxa* lists available for the considered drainages.

Area is usually held constant when examining the influence of different contemporary and/or historical factors on species richness patterns for terrestrial organisms (to avoid its confounding effect on the analysis), e.g. by using uniform grid cells. In this study we did not follow this procedure – given that the drainage basin is the only biologically meaningful spatial scale for comparing riverine fish species richness patterns across regions or continents – for three primary reasons: (1) for these organisms, the absence of migration between rivers over large temporal scales implies that extinction and speciation processes are specific to each river basin, (2) within a river basin there is usually a strong longitudinal gradient in local species richness (i.e. an upstream–downstream increase in local species richness) and (3) local species richness is usually related to regional species richness (i.e. basin richness) (Hugueny & Paugy, 1995; Oberdorff *et al.*, 1998). These reasons make the use of equal size quadrats inappropriate as a standardizing method.

We restricted the analysis to the tropical band (18° N, 15° S) where rain forest is currently present in both continents. The total drainage area (DA) of the basins (km^2) was compiled from literature on West African drainages (Hugueny, 1989; Paugy *et al.*, 1994; Teugels & Guégan, 1994) and measured through GIS mapping for South American ones (see Appendix S1). Insufficient discharge data were available for the selected basins but, as river discharge is strongly correlated with the drainage area, we selected only the latter variable as a measure of 'river size'. The mean net primary productivity (NPP) (see Appendix S1) over the surface area of each drainage area (a good indicator of available energy for heterotrophs) was calculated from $0.5° \times 0.5°$ grid cell data (in kg-Carbon m^{-2} year^{-1}) available in the *Atlas of the Biosphere* (http://www.sage.wisc.edu/atlas/).

The past event considered the most likely to have affected species richness across the two continents is the influence of the LGM, 18,000 years ago. In tropical rain forest regions, we therefore considered the contact (or absence of contact) of each basin with late Pleistocene rain forest refuges (contLGM: contact = 1, absence of contact = 0; see Appendix S1) to be a determinant historical factor. A synthesis of the massive shifts in the distribution of rain forest in equatorial Africa was made by Hamilton (1976), who compared the situations of the LGM and the present day. More recently, massive shifts in tropical rain forest in west equatorial Africa were reconstructed over the last 150,000 years, based on a series of marine pollen records from the Atlantic and terrestrial pollen records (Dupont *et al.*, 2000). For West Africa, the extension of rain forest zones at the LGM was thus established from the vegetation maps provided by Dupont *et al.* (2000). The records indicate that, during the LGM, rain forest grew southwest of the Guinean mountains, southwest of the Cameroon Mountains, in Gabon and Congo, and that it had a patchy occurrence along most of the northern coast of the Gulf of Guinea (Fig. 1).

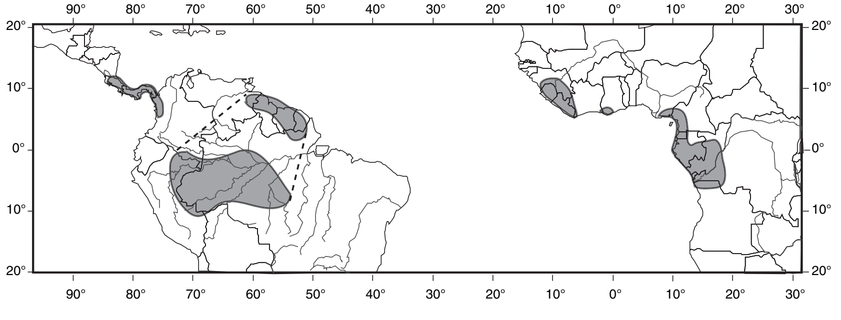

Figure 1 Map of the Neotropics and tropical Africa with grey zones representing the rain forest regions that remained at the LGM (Adams & Faure, 1997; Dupont *et al.*, 2000). Dotted lines represent the rain forest retreat without splitting suggested by some authors (Colinvaux *et al.*, 2000).

Unfortunately, similar studies focusing on rain forest vegetation changes of tropical America are not currently available as they are for West Africa. Therefore, we based our definition of the extension of the rain forest zones at the LGM on a synthesis established from plant fossil, sedimentary and animal fossil evidence (Adams & Faure, 1997). At the LGM, this work is congruent with the previous work of Clapperton (1993) on the positioning of a central Amazonian rain forest refuge zone and a second zone including Guyana, Surinam, French Guyana and part of Venezuela. A third rain forest zone is identified by Adams & Faure (1997) in Central America from the northern Pacific coast of Colombia to Costa Rica (Fig. 1). In contrast with West Africa, the geographical positioning of rain forest refuges in Amazonia at the LGM is still controversial. Some authors suggest that rain forest retreated without splitting into several refuges (Colinvaux *et al.*, 2000). However, even if we assume that there is no gap between the Amazonian and the Guyanese refuges depicted in Fig. 1 (dotted lines), our results should not be affected because drainage connection to refuge remains the same. Other authors propose highly fragmented refuge patches based on endemism patterns (e.g. Haffer, 1969; Prance, 1982). In this case, drainage connection to refuge remains almost the same, excepting the 'Belém refuge' proposed by Haffer (1969) which concerns only one drainage.

Statistical analysis

The association between contemporary and historical variables on one hand and species richness on the other was tested by standard regression. Species richness, drainage area and NPP were ln transformed before analysis to minimize effects of non-normality and heteroscedasticity. In all regressions, the R^2 provided an estimate of the percentage of variance which is accounted for by the regression equation. We tested the observed relationships using multiple regression analysis in two nested ways: (1) first, West Africa, South America and Central America [South and Central American drainages were considered separately on distinct analyses because of the recent origin of the isthmus of Panama (3 Ma), (CAM:isthmus effect)] and (2) then, all the data were combined in one global analysis. By analysing the entire data set, we also tested the potential continental (CON) effect (binary variable: Central and South America = 1, West Africa = 0) after all other factors had been controlled for, including CAM (binary variable: Central America = 1, South America and West Africa = 0).

Spatial autocorrelation may be present in these geographic data leading to non-independence of residuals and thus violating one of the assumptions of standard regression analysis. We tested for spatial autocorrelation of residuals using Moran's *I* (Sokal & Oden, 1978). For this purpose we constructed a neighbourhood graph. The vertices are rivers and the edges contiguity between rivers. Geographical distance between rivers was defined as the minimum number of divides separating basins along the neighbourhood graph. A value of 1 corresponds to river basins that are contiguous. These distances have been computed for each region and used as a discrete geographical distance for autocorrelation analyses. Distance values higher than 5 were aggregated into the sixth class because we expected spatial correlation for short and medium distances. For instance, in West Africa, fish faunal dissimilarity between basins increased with geographical distance (as defined here) up to a value of 6 (Hugueny & Lévêque, 1994). For each region and geographical distance, standardized Moran's *I* coefficients have been computed for model residuals. Expected mean and variance for the *I* statistic computed from OLS residuals are given in Cliff & Ord (1981). A Bonferonni-corrected significance level (0.05/6) has been used to assess the probability of observing at least one significant autocorrelation coefficient per region. Statistical analysis was performed using the S-plus software package (Mathsoft, Inc.).

RESULTS

As expected, SR is strongly correlated with drainage basin area, which accounts for 52%, 46% and 80% of the variance of the SR in South America, Central America and Africa, respectively (Table 1). In the three cases, the NPP does not explain a significant part of the variance (Table 1). The contact of basins with the LGM refuges (contLGM) shows a positive effect on the species richness in all three cases, explaining a highly

Table 1 Summary of the multiple regression analyses of fish species richness vs. the current and past variables for South America, Central America and West Africa (significant values are in bold). Maximal absolute Moran's *I* coefficients and *P*-values of the residuals are also given, with the corresponding geographical distance values in brackets. After applying the Bonferonni-corrected significance level, none of the Moran's *I* coefficients are significant

Variable	Coefficients	*P*-values
South America (n = 40)		
ln(DA)	0.349	< **0.0001**
ln(NPP)	−0.361	0.208
contLGM	1.212	< **0.0001**
Moran's *I*	2.05 (1)	0.050
Central America (n = 49)		
ln(DA)	0.290	< **0.0001**
ln(NPP)	0.140	0.678
contLGM	0.508	< **0.0001**
Moran's *I*	2.72 (1)	0.010
West Africa (n = 52)		
ln(DA)	0.297	< **0.0001**
ln(NPP)	−0.047	0.758
contLGM	0.290	**0.0015**
Moran's *I*	−1.70 (5)	0.250

ln(DA): ln-transformed drainage area
ln(NPP): ln-transformed net primary productivity
contLGM: contact to refuge zones.

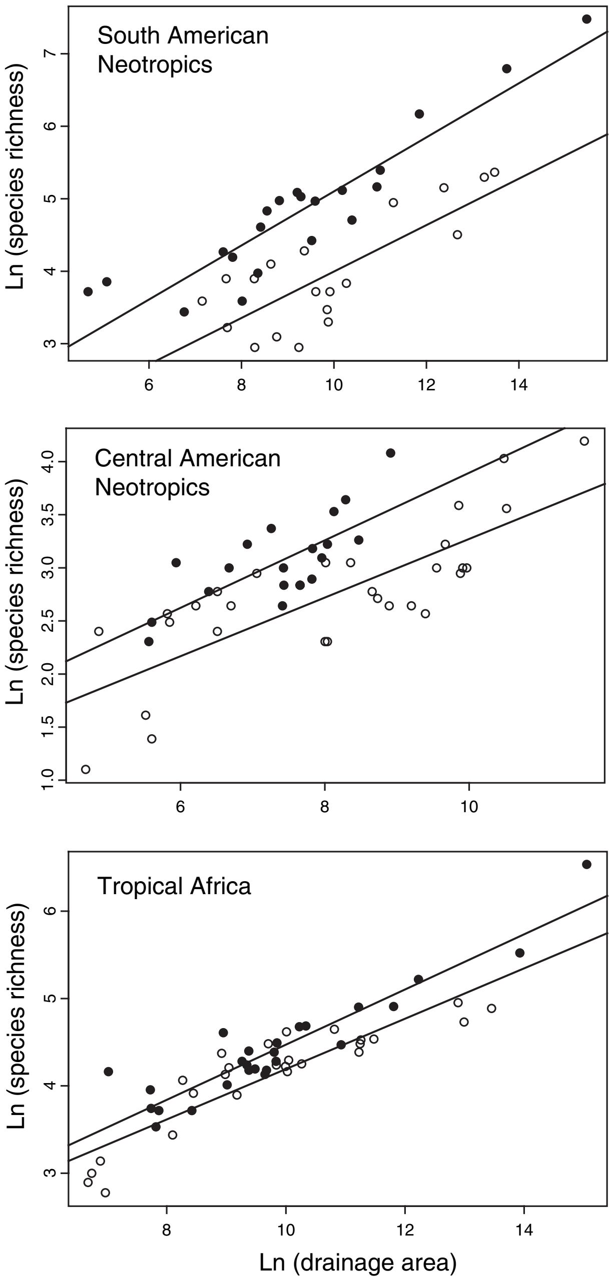

Figure 2 Plot of species richness as a function of total surface area of the drainage for South American Neotropics, Central American Neotropics and tropical Africa river basins. Black circles represent the basins that were in contact with a rain forest refuge zone during the LGM; white circles represent basins completely isolated from rain forest refuges. Lines correspond to simple linear regressions for each group.

significant part of the variance (Table 1). The non-significant Moran's *I* values found in the three cases (Table 1) show that no residual spatial autocorrelation is detectable after considering the current and past variables. No significant differences between the regression slopes (interaction between contLGM and DA) were found in any of the three analyses (*t*-test, $\alpha = 0.05$).

Table 2 Summary of the multiple regression analysis of fish species richness vs. the current and past variables for the global data set (significant values are in bold), and considering the continental (CON) and isthmus effects (CAM) ($n = 141$). Other abbreviation as for Table 1

Variable	Coefficients	*P*-values
ln(DA)	0.311	< **0.0001**
ln(NPP)	−0.040	0.776
contLGM	0.598	< **0.0001**
CAM	−0.917	< **0.0001**
CON	0.207	**0.014**

Figure 2 illustrates the significantly higher SR of the basins connected to the LGM refuge zones in the tropical basins of South America, Central America and Africa, compared to disconnected basins. After the DA has been factored out, the SR of rivers connected with rain forest refuge areas during the LGM is on average 3.0, 1.7 and 1.3 times greater than rivers unconnected to rain forest refuge zones during the LGM, for South America, Central America and Tropical Africa respectively (Fig. 2).

When all the data were mixed into one global analysis, the nature of the relationships did not change (Table 2). The global model reveals SR to be positively correlated with DA (62.7% of the variance), no significant relationship with NPP (1% of the variance), a highly significant effect of contLGM (10.3% of the variance), a highly significant effect of CAM (11.2% of the variance) and a significant effect of CON (0.7% of the variance). South American rivers are more species-rich than expected on the basis of their area, productivity and connectedness to forest refuge. On the other hand, Central American rivers are less species-diverse than expected by the grouped model. African rivers are intermediate.

DISCUSSION

Regional historical effect

Without exception, works focusing on the relative influence of historical and current factors on species diversity gradients consistently find that, once the area effect has been factored out, present energy inputs explain the greatest part of the remaining variance in the geographical pattern of SR (Currie & Paquin, 1987; Fraser & Currie, 1996; Oberdorff *et al.*, 1997; Kerr & Currie, 1999; Hawkins *et al.*, 2003a,b; Hawkins & Porter, 2003; Hawkins, 2004). In contrast, the influence of historical factors is generally found to be marginal. For freshwater fish SR in the Neotropics and tropical Africa, our results lead to a different conclusion: after controlling for area, historical influence [measured here by the connection (or absence of connection) of river basins with rain forest refuge zones during the LGM] explains the most variance in the basin SR pattern, whereas present energy inputs (NPP) do not contribute significantly to the explanation. Two reasons may explain this finding: (1) the spatial scale analysed here, where the gradient of current climate energy variables (mainly driven by latitude) is reduced and (2) the limited dispersal possibilities of riverine fishes.

Regarding spatial scale, the rivers analysed are all located in the tropical band between 18° N and 15° S. At these latitudes, the annual photon flux, mean annual temperature and correlated energetic variables typically attain high and quite homogeneous values (Rosenzweig, 2003). In our study, the coefficient of variation of NPP values for the entire data set is 0.244 ($n = 141$), indicating that the amount of available energy within these tropical latitudes varies too little to significantly influence richness patterns in the chosen areas. Furthermore, energy is usually considered a strong predictor of animal diversity gradients in parts of the planet where cold terrestrial climates are found, i.e. a restrained part of the world in which energy inputs are particularly low (Currie, 1991; Kerr & Packer, 1997; Hawkins *et al.*, 2003a). Hence the absence of a relationship in this study between NPP and SR is not surprising. However, this finding strongly suggests that the factors contributing to richness gradients are scale-dependent. Scale is certainly a parameter that should be taken into account when studying species diversity patterns (Willis & Whittaker, 2002), namely in relation to species attributes, such as dispersal ability (Kerr & Currie, 1999), body size, trophic level or geographic range (Jetz & Rahbek, 2002), as all these attributes are thought to be related to probability of extinction.

Regarding the dispersal possibilities of riverine fishes, river basins are separated from one another by barriers (oceans or land) that are insurmountable for freshwater fish, and thus form kinds of well-delimited biogeographical islands. Matching geographic distribution to present climatic conditions should therefore be difficult for fishes, as their colonization potential requires physical connections between river basins, which are extremely rare events. In contrast, the dispersal ability of mammals enables the expansion and contraction of their terrestrial geographic range (tracking consistent climatic profiles; Martinez-Meyer *et al.*, 2004), which may explain why little evidence of historical influence on mammalian species diversity has been reported at the continental scale (Hawkins & Porter, 2003). The few studies supporting the historical hypothesis are intercontinental comparisons (Latham & Ricklefs, 1993; Qian & Ricklefs, 1999; Ricklefs *et al.*, 2004) in which migrations are unlikely for any group. This assumption can easily be extrapolated from mammals to any other highly mobile group such as birds (Hawkins *et al.*, 2003a; Hawkins & Porter, 2003).

Having little ability to easily track the climatic optimum of freshwater fish, we logically expected that the influence of historical events would still be detectable in fish communities. At the end of the most recent glacial period, 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 (Brown & Lomolino, 1998). Following this scenario, reduced precipitation in the tropical zone of the Southern Hemisphere may have led to extensive fish extinction in river basins affected by drier climates (through a decrease in river basin discharge and surface area) (i.e. rivers disconnected to rain forest refuge zones during LGM). Besides, fewer or no extinctions occurred in river basins having kept their characteristic nature (e.g. precipitation patterns and vegetation conditions) (i.e. rivers connected to rain forest refuge zones during LGM). For the three regions analysed, our results are consistent with this scenario: the factor used to quantify history is the major factor contributing significantly to the richness pattern, after controlling for river size (i.e. DA) and productivity. It must be noted that our approach focuses on extinction processes related to the harsh climatic conditions of the late Pleistocene. In addition, an enormous body of literature, not discussed here, deals with speciation processes in forest refuges during dry periods (Haffer, 1969, 1997; Prance, 1982; Mayr & O'Hara, 1986; Bush, 1994).

Intercontinental comparison

Once the DA was factored out, the SR of basins connected with rain forest refuge areas during the LGM was found to be around 3, 1.7 and 1.3 times greater than their counterparts (i.e. basins not connected with rain forest refuge areas during the LGM), for South America, Central America and West Africa, respectively. This result also suggests that rain forest refuge areas were more efficient in preserving (or generating) SR in South America than in Africa. Furthermore, the fact that a 'continental' effect is significant in the global model suggests that other historical factors, unmeasured in the study, are perhaps also involved in differences between river SR on the two continents, as they separated *c.* 120 Myr BP. As an example, Farias *et al.* (1999) showed that Neotropical cichlid fishes, a monophyletic assemblage, have experienced accelerated rates of molecular evolution compared to African cichlids, its sister group. This may reflect higher speciation rates in the Neotropics, leading to differences in riverine species richness (*c.* 400 for South America and *c.* 200 for Africa, excluding the Great Lakes).

Once the effect of basin area and productivity have been factored out, Central American rivers harbour fewer species than rivers located in South America, regardless of their connection to LGM refuge areas. This result may reflect the complex history of extinctions and invasions from northwestern South America, as suggested by phylogeographical studies of Neotropical freshwater fishes (Bermingham & Martin, 1998). The extreme high sea-level stand at the start of the Pliocene inundated southern Central America and caused wide scale extinction of freshwater faunas while preventing the colonization of northern Central America from South America. The terrestrial isthmus was again completed around 3 Ma, enabling more recent colonization events. A combination of extinction and recent colonization events may explain why Central America is poorer in fish fauna.

CONCLUDING REMARKS

From our results, we can conclude that history does matter in this case and gives a strong signal that is independent of contemporary factors. Our interpretations are based on the considered spatial scale (reducing the influence of contemporary factors) and the limited dispersal possibilities of riverine fishes, both of which increase the likelihood of observing a historical signal. However, the historical signals related to the regional and continental spatial scales are attributable to mechanisms acting at different time scales. From the LGM to the present day (a time scale of 18,000 years), primarily extinction processes should have shaped the diversity pattern currently observable. In contrast, the intercontinental comparison revealed an older historical signal (a time scale of millions of years), where mechanisms such as speciation and colonization by river connections have also contributed to the present diversity pattern.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from http://www.Blackwell-Synergy.com:

Appendix S1 List of the studied river systems and data.

REFERENCES

Adams, J.M. & Faure, H. (1997) Preliminary vegetation maps of the world since the Last Glacial Maximum: an aid to archeological understanding. *Journal of Archaeological Sciences*, **24,** 623–647.

Adams, J.M. & Woodward, F.I. (1989) Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature*, **339,** 699–701.

Bermingham, E. & Martin, A.P. (1998) Comparative mtDNA phylogeography of neotropical freshwater fishes: testing shared history to infer the evolutionary landscape of lower Central America. *Molecular Ecology*, **7,** 499–517.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer Associates, Inc., Sunderlands, MA.

Bush, M.B. (1994) Amazon speciation: a necessarily complex model. *Journal of Biogeography*, **21,** 5–17.

Clapperton, C.M. (1993) Nature of environmental changes in South America at the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **101,** 189–208.

Cliff, A.D. & Ord, J.K. (1981) *Spatial processes: models and applications*. Pion Limited, London.

Colinvaux, P.A., de Oliveira, P.E. & Bush, M.B. (2000) Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypothesis. *Quaternary Science Reviews*, **19,** 141–169.

Currie, D.J. (1991) Energy and large-scale patterns of animal and plant species richness. *The American Naturalist*, **137,** 27–49.

Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature*, **329,** 326–327.

Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Hawkins, B.A. (2004) A test of multiple hypotheses for the species richness gradient of South American owls. *Oecologia*, **140,** 633–638.

Dupont, L.M., Jahns, S., Marret, F. & Ning, S. (2000) Vegetation change in equatorial West Africa: time-slices for the last 150 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **155,** 95–122.

Farias, I.P., Orti, G., Sampaio, I., Schneider, H. & Meyer, A. (1999) Mitochondrial DNA Phylogeny of the family Cichlidae: monophyly and fast molecular evolution of the Neotropical Assemblage. *Journal of Molecular Evolution*, **48,** 703–711.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, **161,** 523–536.

Fraser, R.H. & Currie, D.J. (1996) The species richness-energy hypothesis in a system where historical factors are thought to prevail: Coral reefs. *The American Naturalist*, **148,** 138–159.

Guégan, J.F., Lek, S. & Oberdorff, T. (1998) Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, **391,** 382–384.

Haffer, J. (1969) Speciation in Amazonian forest birds. *Science*, **165,** 131–137.

Haffer, J. (1997) Alternative models of vertebrate speciation in Amazonia: an overview. *Biodiversity and Conservation*, **6,** 451–476.

Hamilton, A. (1976) The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of Upper Pleistocene palaeoenvironments: a review. *Palaeoecology of Africa*, **9,** 63–97.

Hawkins, B.A. (2004) Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. *Global Ecology and Biogeography*, **13,** 321–325.

Hawkins, B.A. & Porter, E.E. (2003) Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography*, **12,** 475–481.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003a) Energy, water and broad-scale geographic patterns of species richness. *Ecology*, **84,** 3105–3117.

Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003b) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84,** 1608–1623.

Hugueny, B. (1989) West African rivers as biogeographic islands: species richness of fish communities. *Oecologia*, **79,** 236–243.

Hugueny, B. & Lévêque, C. (1994) Freshwater fish zoogeography in west Africa: faunal similarities between river basins. *Environmental biology of fishes*, **39,** 365–380.

Hugueny, B. & Paugy, D. (1995) Unsaturated fish communities in African rivers. *The American Naturalist*, **146,** 162–169.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297,** 1548–1551.

Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centers of endemism. *Ecology Letters*, **7,** 1180–1191.

Kerr, J.T. & Currie, D.J. (1999) The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience*, **6,** 329–337.

Kerr, J.T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385,** 252–254.

Latham, R.E. & Ricklefs, R.E. (1993) Continental comparisons of temperate-zone tree species diversity. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 294–314. The University of Chicago Press, Chicago, IL.

Livingstone, D.A., Rowland, M. & Bailey, P.E. (1982) On the size of African riverine fish faunas. *American Zoologist*, **22,** 361–369.

MacArthur, R.H. (1964) Environmental factors affecting bird species diversity. *American Naturalist*, **98,** 387–397.

MacArthur, R.H. (1972) *Geographical ecology. Patterns in the distribution of species*. Princeton University Press, Princeton, NJ.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Martinez-Meyer, E., Townsend Peterson, A. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, **13,** 305–314.

Mayr, E. & O'Hara, R.J. (1986) The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution*, **40,** 55–67.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82,** 2381–2396.

O'Brien, E.M., Field, R. & Whittaker, R.J. (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residuals variation, and topography. *Oikos*, **89,** 588–600.

Oberdorff, T., Guégan, J.F. & Hugueny, B. (1995) Global scale patterns of fish species richness in rivers. *Ecography*, **18,** 345–352.

Oberdorff, T., Hugueny, B. & Guégan, J.F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography*, **24,** 461–467.

Oberdorff, T., Hugueny, B., Compin, A. & Belkessam, D. (1998) Non-interactive fish communities in coastal streams of the North-Western France. *Journal of Animal Ecology*, **3,** 472–484.

Paugy, D., Traoré, K. & Diouf, P.S. (1994) Faune ichtyologique des eaux douces d'Afrique de l'Ouest. Annales du Musée royal d'Afrique Centrale. *Zoologie*, **275,** 35–66.

Prance, G.T. (1982) Forest refuges: evidence from woody angiosperms. *Biological diversification in the tropics* (ed. by G.T. Prance), pp. 137–158. Columbia University Press, New York.

Qian, H. & Ricklefs, R.E. (1999) A comparison of the taxonomic richness of vascular plants in China and the United States. *The American Naturalist*, **154,** 160–181.

Qian, H. & Ricklefs, R.E. (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, **407,** 180–182.

Rahbek, C. & Graves, G. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Science USA*, **98,** 4534–4539.

Reis, R.O., Kullander, S.O. & Ferraris, C.J. (2003) *Check list of the freshwater fishes of South and Central America*. EDIPUCRS, Porto Alegre.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7,** 1–15.

Ricklefs, R.E., Qian, H. & White, P.S. (2004) The region effect on mesoscale plant species richness between eastern Asia and eastern North America. *Ecography*, **27,** 129–136.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65,** 514–527.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

Rosenzweig, M.L. (2003) How to reject the area hypothesis of latitudinal gradients. *Macroecology – concept and consequences* (ed. by T.M. Blackburn and K.J. Gaston), pp. 87–106. Blackwell Publishing, Oxford.

Schluter, D. & Ricklefs, R.E. (1993) Species diversity: an introduction to the problem. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 1–10. The University of Chicago Press, Chicago.

Sokal, R.R. & Oden, N.L. (1978) Spatial autocorrelation in biology. 1. Methodology. *Biological Journal of the Linnean Society*, **10,** 199–228.

Teugels, G.G. & Guégan, J.F. (1994) Diversité biologique des poissons d'eaux douces de la Basse-Guinée et de l'Afrique Centrale. Annales du Musée royal d'Afrique Centrale. *Zoologie*, **275,** 67–85.

Turner, J.R.G., Gatehouse, C.M. & Corey, C.A. (1987) Does solar energy control organic diversity? Butterflies, moths and British climate. *Oikos*, **48,** 195–205.

Whittaker, R.J. & Field, R. (2000) Tree species richness modelling: an approach of global applicability? *Oikos*, **89,** 399–402.

Whittaker, R.J., Willis, K.J. & Field, R. (2003) Climatic-energetic explanations of diversity: a macroscopic perspective. *Macroecology – concepts and consequences* (ed. by T.M. Blackburn and K.J. Gaston), pp. 107–129. Blackwell Publishing, Oxford.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity – scale matters. *Science*, **295,** 1245–1248.

Wright, D.H. (1983) Species-energy theory: an extension of the species-area theory. *Oikos*, **41,** 496–506.

Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 66–74. The University of Chicago Press, Chicago.

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